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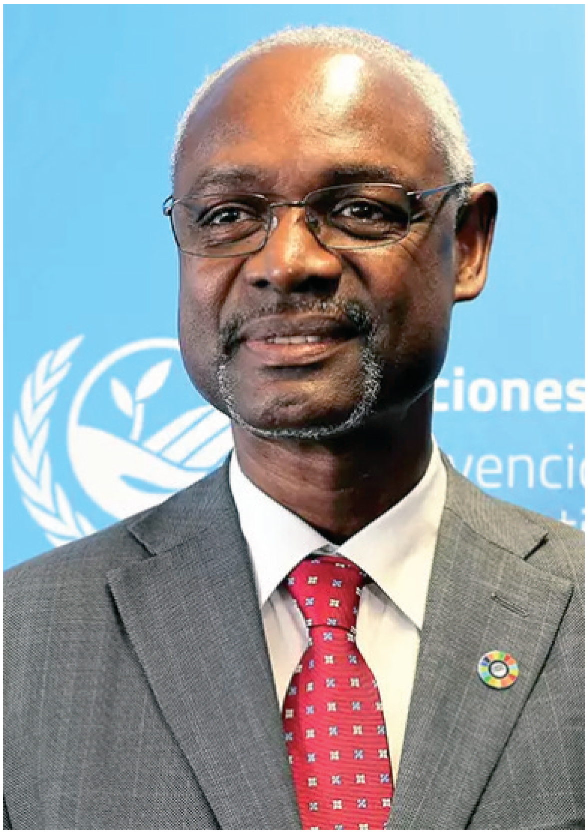
Foreword

Ibrahim Thiaw



Ibrahim Thiaw is the Under-Secretary-General and Executive Secretary of the United Nations Convention to Combat Desertification (UNCCD). With an advanced degree in forestry and forest product techniques and ten years in the Ministry of Rural Development in Mauritania, Ibrahim Thiaw previously was Special Adviser to the Secretary-General for the Sahel, in this capacity supporting the development of a UN Support Plan for the Sahel. He also served as Assistant Secretary General and Deputy Executive Director of the United Nations Environment Programme (UNEP), Director of UNEP's Division for Environmental Policy Implementation, and Acting Director General of the International Union for Conservation of Nature (IUCN).

This foreword is written under personal title.

I was born and raised in the Sahel and, over the course of my life, I have seen this region undergo many changes. Climate change has affected these lands causing extreme weather events, such as the great drought of the 1970s, as well as contributing to less dramatic, yet profound deteriorations, like the advancing of land degradation and desertification. The resulting ecological effects can be seen in the structural changes of the local biodiversity, the decline of plant and animal species, and the compromised ecosystem resilience.

The Sahel is home to millions of people. A fast-growing society that has greatly suffered from a lack of stability, primarily caused by unpredictable and changing climate and the loss of land productivity. As a consequence, Sahelian people have been facing enormous social challenges, such as food security and cross-border displacement, with major impacts on local communities dependent on agriculture and livestock.

Growing up in arguably one of the most vulnerable zones of the Sahel – the south of Mauritania – during the great drought of the 1970s, left indelible memories of how nature could suddenly shift from healthy – full of trees and birds – into barren landscapes, empty of life and full of dust! I have seen how fragile the ecosystem of the Sahel is and how changes in vegetation cover could have devastating effects on both domestic and wild animals, as well as the livelihoods of people who depend on them. Historically, the south of Mauritania was the food basket of the people living north of the Senegal river all the way up to southern Morocco, but this suddenly changed.

The drought of the 1970s led to soil degradation and resulted in turmoil and socio-economic disaster still affecting those living in the area today, explaining why many young Sahelians try to make a living elsewhere. Herd keepers lost their animals, perhaps the only source of income and protein they had, and the farmers could no longer support their way of life or even put enough food on the table. The forests that contained so many tree species and sustained neighbouring communities turned into open, lifeless landscapes. The rich wildlife that I used to see and hear around our village as a child also disappeared, leaving a big gap in our culture and tradition as sources of inspiration and cultural identity.

Yet, over the last decade, rainfall has increased close to the levels known before the great drought. Still, this did not bring a return to the old days, nor to the landscapes and biodiversity that I recalled from my childhood. The changes in people's livelihoods and lifestyles were so drastic that the return of the Sahel into this pre-drought state is still something to cherish as a memory and dream about. I have seen all these socio-ecological changes with my own eyes, and so have many others. As the local proverb says: “an eye witness is better than hearsay”.

The lack of capacity to monitor and document all the socio-ecological changes occurring in the region has left Sahelian people with many unanswered questions on the causes and nature of these changes. In addition, lack of data makes it challenging for future land-use planning in the region to be efficiently implemented. This is of particular importance if we consider the Sahel to also be a land of hope, with major efforts underway in the region to combat such adverse ecological changes. The Great Green Wall, for instance, is an African-led initiative that aims to reverse land degradation by creating a mosaic of restored and sustainably managed lands.

In this special issue of Ardea we are offered a priceless gift that captures the nature of these changes in the landscape and biodiversity across the Sahel. In the various papers, the authors try to identify the causes of observed habitat changes and how they are interlinked with changes in land use and human activities.

In particular, this study is the result of the laborious work of a small team of dedicated ecologists, mostly self-funded ornithologists, who managed to document the ecological state of the Sahel, focusing on the status of migratory birds and their interaction with plant species. The present series of papers provides, in a comprehensive way and comprising observations across the entire Sahel, from the Mauritanian and Senegalese Atlantic coast in the west to the Red Sea shores in the east, not only up to date summaries on rainfall patterns, vegetation, human densities and farming intensities, but also explanations on the distributions of both migrant and resident birds, their habitat selection and how all these factors may affect their numbers.

Increasing desertification and extreme weather events in the Sahel represent ecological barriers to bird migration in the African-European Flyway, as the overall distance that birds must cross between the northernmost limit of the forests and the southern limit of the Sahara continues to increase, ending up requiring more energy than a bird can store to cope with migration. It is documented that birds are highly selective in their use of plants: changes in land use, agricultural or breeding practices, as well as restoration intervention, can influence their distribution, occurrence and survival.

If desertification is a threat to migration, restoration measures, on the contrary, can encourage resting and feeding breaks, thus helping to restore the ecological connectivity necessary for birds to migrate between north and south. However, this does not happen regardless, it is more a potential for restoration measures, depending on how they are carried out.

Providing data on the status of migratory birds, their interactions with local plants and how they have changed over time, can therefore be a first indicator of the ecological effects of interventions shaping the landscape in the Sahel and can inform how to better implement future actions. Indeed, the findings of this study intend to inform future land-use planning and support future generations of Sahelians in implementing restoration efforts in the region. Their significance is most easily appreciated when looking back at the challenges that the Sahel ecosystems experienced over the last few decades.

The authors, in carrying out all this diligent fieldwork, have also analysed their hard-won data and synthesized them in a series of topical papers. I was particularly impressed by the extent to which the team embraced the measurement of trees and other woody plant species which include around 100 tree and bush species, in addition to the many bird species. This illustrates the staggering biodiversity in the region.

In reading this study, you will be fascinated to discover that the trees which we know are so vital for the survival of human communities across the Sahel, mostly *Acacias* and *Faidherbia* on floodplains and desert dates *Balanites* in the more arid zones, are also the 'refuge trees' for birds! These species are used widely in traditional medicines, bee keeping, feeding livestock in dry seasons, and their wood is used in cooking, handcraft, furniture and building. It was surprising to discover that the shrubs of the northern Sahel with the highest bird densities (*Salvadora persica*, *Capparis decidua* and *Maerua crassifolia*) are those also favoured by livestock, and that granivore birds love the seeds of *Panicum* grasses, again preferred by livestock grazers.

This work in the special issue embeds a valuable diagnosis of the urgent issues facing the terrestrial ecosystems in the Sahel, increasing livestock and overgrazing in some parts, and conversion of the savannah into relatively intense farmlands in other parts. The work is full of material on what would be the most sustainable and beneficial strategies to managing our fragile dry and semi-dry ecosystems. It can help guide the creation of Africa's Great Green Wall, as well as other national and regional agroforestry plans.

I thank the team for their magnificent and significant work. Their endeavours provide a founding resource for the next generations to build on. I sincerely hope that this large-scale monitoring work will serve as an example and inspiration for better understanding and investing in restoring the Sahel landscape, as an intergovernmental and intergenerational effort that involves all Sahel countries. I hope that today's young Sahelians will get to experience the beauty and bounty of this harsh yet hopeful land, and will ensure its future stewardship.

To see, hear and speak: how counts of birds in individual trees help address the environmental causes of the Sahel

Theunis Piersma & El-Hacen M. El-Hacen

Rudi Drent Chair in Global Flyway Ecology at 'BirdEyes - Centre for Global Ecological Change'
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Remember Mizaru, Kikazaru and Iwazaru? These were the three 'wise monkeys' originating in Japanese and Chinese philosophical traditions going back at least 1000 years. Mizaru was the monkey that covered its eyes, Kikazaru plugged both ears with fingers, and Iwazaru held its mouth shut with a clasping hand. Together they "saw no evil, heard no evil and spoke no evil", a wonderful ambiguity, because is it really a virtue to withdraw? Or is it a virtue to see and hear attentively, and thus sense the state of the world around us; and then speak about it?

This special issue of ARDEA is filled with papers painstakingly reporting the work of a small and dedicated team who set out to map the birds across the entire Sahel (an area the size of the USA!). Although mapping is inherently biased by the knowledge and cognitive facilities, as well as the interests, of the mappers (Malavasi 2020), within the limits of their sensibilities, and negotiating serious political and safety realities, the team tried to do this in temporally and spatially unbiased and methodologically robust and repeatable ways. The way that single trees and bushes disperse across the landscape of the Sahel, rather than connect-up into a dense forest, inspired a mapping approach that is both brilliant and unique. Rather than taking 'an area' as the spatial unit to measure bird abundance, the team began with 'individual trees' (Figure 1), with the plots in which these trees occurred being carefully pre-selected along trajectories that could be travelled "easily" (i.e. within the reach of a 4×4 vehicle). In their ensemble, the effort would give unbiased measurements of birds ánd trees across the entire Sahel, from Senegal in the west to Ethiopia in the east. This design also enabled assessments of the consequences of the steep latitudinal gradients in rainfall as one moves south from the Sahara sands towards the Sudan forests across 1000 km, and sometimes less.

Figure 1. The realities of daily field work, in this case in Sikasso in southern Mali in January 2012, by the Dutch team researching the trees and the birds of the Sahel. Top: Leo Zwarts (at left), Jan van der Kamp (centre) and Marten Sikkema (at right) screen the canopies of Shea Trees for birds; middle: Leo Zwarts making notes as Marten Sikkema checks his bird IDs with camera shots; bottom: only 10 min before nightfall, with bedding arranged, Leo Zwarts carries out more book-keeping, whilst Jan van der Kamp rests in contemplation. (Photos by Eddy Wymenga).

Figure 2. A hemispheric view centred on the Sahel region of Africa showing (in green) the extent of the Great Green Wall proposed by African leaders, and (in black) the plots visited by the Dutch team who mapped trees, birds and indicators of human activity (e.g. human presence, dung left by livestock, fires).

In this way, the team opened the eyes, unplugged the ears and, in this volume, opened their mouths, to tell us what the Sahel was like during the northern hemisphere winters in the second decade of the 21th century. In their endeavour, Zwarts, van der Kamp, Bijlsma and Sikkema documented virtue, and perhaps they also documented evil. In any case, they produced a monumental synoptic assessment of the environmental conditions in the thinly wooded environments of the Sahel from the viewpoint of birds.

We tend to think about the Sahel as a region with particularly serious human, political and ecological challenges, and surely this is the case. At the same time we may also see it as a region of hope. As documented in this special issue of ARDEA, widespread declines of birds are associated with declines in rainfall, but the increases in rainfall in recent decades were also associated with increases in bird numbers, at least in some species. We see that transitions from savannah to farmland may favour the very tree species that have a lot to offer to birds (and farmers), amongst them the Winter Thorn *Faidherbia albida* (Morrison 2016). Interestingly, at the start of the rainy season, just when other trees grow their foliage, the Winter Thorns drop their leaves. The fallen leaves contribute to the fertilizing effect on soils contributed most strongly to by the nitrogen-fixing nodules in the root systems of these same Winter Thorns. Another virtue, obviously, is that leave-less trees will not shade the crops during the growing season! And during the subsequent dry season, when other trees lose their foliage, the leaves of *Faidherbia* appear especially attractive for the caterpillars of the moths that are good food (both in their larval and mature stages) for insectivorous birds that then start to fuel up for northward migration (Zwarts *et al.* 2023a, 2023b).

The Sahel is also home to one of the most ambitious exercises in resilience thinking and acting, the dream of creating a Great Green Wall (Figure 2). This is an effort to halt land degradation and reduce the severity of local climate change by restoring forests across the width of the African continent (Goffner *et al.* 2019). Initially the Great Green Wall was envisaged as the building of a biotic barrier between an encroaching Sahara and everything south of it. It evolved to provide a measured large-scale response to land degradation and the poverty of people relying almost fully on agriculture and/or livestock production in a region where global climate change is predicted to lead to air temperature increases by 3–6°C over the next century (Diffenbaugh & Giorgi 2012), with rain predicted to become more extreme and falling over shorter periods (Salack *et al.* 2016). Aiming to unite forces across national governments, international organizations, businesses and civil society, the "Great Green Wall is designed to enable these actors to collectively manage natural resources in the Sahel region from Senegal to Djibouti" (Goffner *et al.* 2019).

On the basis of an atmospheric modelling exercise, Saley *et al.* (2019) suggested that the complete Great Green Wall would induce changes in atmospheric circulation. An increase of moisture convergence and evapotranspiration would increase the number and intensity of rainy days, while extreme dry spells would decrease. There would also be a decrease in the likelihood of extreme temperatures. In practice, rather than establishing a 'wall of trees', local implementation plans now strive for more mosaic, landscape scale actions that include the strategic planting of trees, along with the creation of communal vegetable gardens and even protected wildlife reserves (Goffner *et al.* 2019). In the extensive regions of Zinder and Maradi in southern Niger (Figure 2), re-greening has already occurred (Sendzimir *et al.* 2011). In this case, forest declines were reversed when "critical interventions helped to shift the direction of reinforcing feedbacks, i.e. vicious cycles changed to virtuous ones. Reversals toward deforestation or reforestation were preceded by institutional changes in governance, then livelihoods and eventually in the biophysical environment." Still, Sendzimir *et al.* (2011) acknowledge that "the resilience of society and nature in the Maradi/Zinder region to global sources of uncertainty remains a pressing question in a society with one of the highest population growth rates on Earth."

Indeed, the tenfold increase of the human population of the Sahel over the last century, beyond dramatic variations in rainfall, has had strong effects on land use, the enormously increased densities of livestock modifying landscapes and the variety of resources used by birds. On the basis of the mapping of trees and birds across the width of Africa, the smart, targeted, comparative analyses in this special issue of ARDEA lay bare a wealth of significant ecological relationships, mutual relationships that shape the form, and indeed the fate, of the Sahel. For example, on the basis of estimates of ground cover vegetation in the plots, supplemented by landscape photos to infer livestock presence and counts of cowpats and of droppings of sheep and goats to estimate grazing pressure, Zwarts *et al.* (2023d) showed that livestock negatively impacted bird numbers, especially in the western Sahel. To increase the fertility of the land, each year bush fires are ignited by livestock holders across several millions of square kilometers of mostly humid savannah. The comparison of bird numbers in burnt and non-burnt plots showed that insectivores temporarily profited from the insects escaping fire and smoke, whereas the disappearance of grass and herbs facilitated the food finding of some ground-foraging bird species. However, especially in the more humid zones of the savannah (annual rainfall > 800 mm), bush fires led to immediate reductions of the densities of seed-eating birds by an average 72%, although insectivorous birds were unaffected (Zwarts *et al.* 2023e).

Meanwhile the Sahel, by nature a huge savannah, has been converted into farmland for about half its extent. This conversion has affected the composition of the trees, with downstream repercussions for birds (Zwarts *et al.* 2023c). For example, in the (semi) arid zone, farmers removed bird-rich trees such as the Umbrella Thorn *Acacia tortilis* and the Desert Date *Balanites aegyptiaca*. It is not all bad though. As shown by Brandt *et al.* (2018), in the semi-arid Sahel farmland management actually led to an increase in woody cover to a level (12%) higher than found in neighbouring savannas (6%). Although farmlands in sub-humid zones show reduced woody cover (20%) compared with adjacent savannas (30%; Brandt *et al.* 2018), farming may actually have created a richer bird habitat as the original trees were replaced by Winter Thorns. Further south still, two bird-poor trees, the Shea Tree *Vitellaria paradoxa* and the African Locust Bean Tree *Parkia biglobosa*, now dominate the farmland. The farmers' efforts thus made it worse for birds in the south of the Sahel zone, but often better in the drier parts of the rainfall gradient.

Clearly, these findings have immediate relevance to how the genesis of the Great Green Wall might facilitate avian migratory connectedness between north and south. For example, efforts should not enable the spread of an invasive acacia look-alike like *Prosopis juliflora*, an exotic tree species from Latin America which is not only avoided by birds, but also by Dromedaries *Camelus dromedarius*, who instead love munching on the leaves of Umbrella Thorns (Figure 3). Instead, efforts to increase the extent of trees should bring more of the latter, and more Winter Thorns and Desert Dates to the land.

The fact that this 'bird work', carried out by a team of ornithologists who trained themselves to be competent dendrologists as well, has resulted in what may

Figure 3. Dromedaries nipping away the fine leaves from between the hefty thorns of Umbrella Thorns *Acacia tortilis* (Photo by Leo Zwarts).

now be the most complete description of the changing biota in the Sahel, begs the question why such a piece of work should be so fortuitous, be such an 'accident' in time? Why did the world need this small team of friends with complementary skills devoting their lives to it (and also bear the majority of the costs)? Why was this not the product of a mapping and monitoring plan on the part of the national governments, international organizations and business partners that dreamed up that incredible ecological restoration plan for the Sahel, the Great Green Wall? Why was this left to 'luck', rather than strategy?

We probably need to turn this question on its head and argue that what the Zwarts team has achieved, is a veritable, ground-truthed, baseline to eventually document the ecological effects of the Great Green Wall. If we accept that, then we also accept that the spatial monitoring of trees and birds belongs to the responsibilities of civil society, just as the monitoring of rainfall and other aspects of the weather are taken care of. The development of such an international portfolio of mapping and monitoring of the biota of the Sahel would leverage all kinds of initiatives, empowering local biologists and environmentalists to develop their skills, and put them to good use to try and develop environmentally resilient societies during rather challenging times.

It is time to reconsider the wisdom of Mizaru, Kikazaru and Iwazaru, and instead to open-up to all that wonderful life in the Sahel, to all the wonderful, puzzling and important interactions between soils, weather & water, people, trees and birds. Perhaps then, ornithology should not be left to the ornithologists alone. Now that birds have proven to open integrative windows on our changing environments, ornithology, along with dendrology, should begin to be considered a core part of the agendas of the national governments in the region, as well as of the international bodies of concern.

We thank Eddy Wymenga, Leo Zwarts and Mohamed Henriques for critical reflection and feedback.

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Distribution and numbers of ground-foraging birds between the hyper-arid Sahara and the hyper-humid Guinea forests

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This paper quantifies the density and the total number of granivorous and insectivorous ground-foraging birds, whether Afro-Palearctic migrants or Afro-tropical residents, in the transition zone between the arid Sahara and the humid Guinea zone. Situated between 17°W and 42°E and between 7°N and 22°N, this is an area covering 10 million km^2. The study took place during the northern winter, between 20 November and 10 March (thus covering much of the long dry season) from 2011 up to and including 2019. Using a stratified random sampling regime, we counted birds at 1901 sites of 4.5 ha in area. We present background information about the study region, with maps showing variation in elevation, rainfall, woody cover, land use and human population density. The bird counts were converted into average densities for 43 bird species in 150 grid cells of 1° latitude × 1° longitude. The distribution of the various bird species was predominantly related to annual rainfall, but because woody cover increases with rainfall, species' preferences for arid or more humid zones were partly influenced by an overall preference for open or more wooded landscapes. Bird species such as larks and Tawny Pipit *Anthus campestris*, even when rainfall was accounted for, selected comparatively open landscapes, whereas species feeding on the ground near trees or using them as perches (e.g. sparrows, finches, shrikes, Tree Pipit *Anthus trivialis*) preferred relatively more enclosed environments. To estimate total population size, the 150 grid cells were assembled into eleven rainfall categories (per 100 mm rainfall) and six longitudinal bands. To assess the reliability of these estimations, population sizes were calculated separately on the 1901 study sites split in two halves. The estimated population sizes were precise for migrants, especially for insectivores (7% deviation for the split-half estimates), but less precise for residents (22–28% deviation). Most ground-foraging birds were granivorous (at least in the dry season), their total number being estimated at 4000 million residents and 133 million migrants, residents being 30 times as abundant as migrants. Ground-foraging insectivores were less numerous, the total estimated being 920 million birds, of which 694 million were residents and 221 million migrants, the ratio residents/migrants being an order of magnitude smaller than in granivores. The three most abundant granivorous residents were Red-cheeked Cordon-bleu *Uraeginthus bengalus* (467 million), Sudan Golden Sparrow *Passer luteus* (375 million birds) and Red-billed Quelea *Quelea quelea* (311 million). The Greater Short-toed Lark *Calandrella brachydactyla* (126 million) was the only common granivorous migrant. The most common insectivorous ground-foraging bird was a resident (Greater Blue-eared Starling *Lamprotornis chalybaeus*; 100 million), and more commonly encountered than all the ground-foraging insectivorous migrants such as Isabelline Wheatear *Oenanthe isabellina* (32 million), Northern Wheatear *Oenanthe oenanthe* (27 million) and Western Yellow Wagtail *Motacilla flava* (24 million) together.

Key words: Sahel, ground-foraging birds, bird distribution, bird population estimates

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Millions of birds from Europe, Asia and North America spend the northern winter in Africa. While some Afro-Palearctic migrant species are found in the rainforest in central Africa (Congo Basin and along the Gulf of Guinea) and the deserts (Sahara, Danakil, Ogaden and Kalahari), the majority concentrate in the transition zones between deserts and tropical rainforests, with most birds remaining north of the equator (Elgood *et al.* 1966, Moreau 1972, Newton 1995, Jones *et al.* 1998, Wisz *et al.* 2007). The transition zone between the Sahara and the humid forests farther south stretches 6000 km from the Atlantic Ocean in the west to the Red Sea in the east, and 1600 km from north to south between 7°N and 22°N (Figure 1). With a total surface area of 10 million km^2, the region is as large as the European continent or the United States of America.

Of the migratory bird species spending the northern winter in one or more of these transition zones, many are in decline (e.g. Zwarts *et al.* 2009, Atkinson *et al.* 2014, Vickery *et al.* 2014). This region has seen huge changes in annual rainfall and land use since the 1970s, which coincide with changing fortunes of Palearctic long-distance migrants (e.g. Winstanley *et al.* 1974 for Common Whitethroat *Sylvia communis* and Den Held 1981 for Purple Heron *Ardea purpurea*). In addition, an accumulation of other factors is also taking its toll, such as overhunting (Thiollay 2006, Buij *et al.* 2015, Whytock *et al.* 2016), poisoning (Ogada *et al.* 2016), overexploitation of waterbirds by local people and shrinkage of seasonal floodplains due to dams and irrigation (Zwarts *et al.* 2009). Furthermore, many Palearctic bird species suffering from adverse conditions in the non-breeding areas, also experience stressors in their breeding areas and on route (e.g. Morrison *et al.* 2013, Caruana-Galizia & Fenech 2016). Explanations for long-term declines of migratory landbirds often focus on desertification, habitat degradation, overgrazing and rainfall data. Such explanations are not sufficiently specific to understand the detail of complicated processes. Moreover, most studies carried out by European researchers focus on Eurasian bird species wintering in Africa, disregarding any changes in fortunes of African bird species (notable exceptions being e.g. Morel 1968, Cresswell 2018, Freeman & Peterson 2019). The relative impact of habitat variables on birds needs substantiation in the field, as for example demonstrated for NW Senegal where a steep decline in tree-dwelling and ground-foraging birds, Afro-Palearctic migrants as well as Afro-tropical residents, has been recorded (Zwarts *et al.* 2018). Had that estimate been representative for the entire Sahel, the region would have lost 1.5–2.0 billion birds by the 2010s compared to the 1960s, mainly granivorous, Afro-tropical residents. At this point we realised that we lack basic information about distribution, abundance and habitat choice of the bird species concerned.

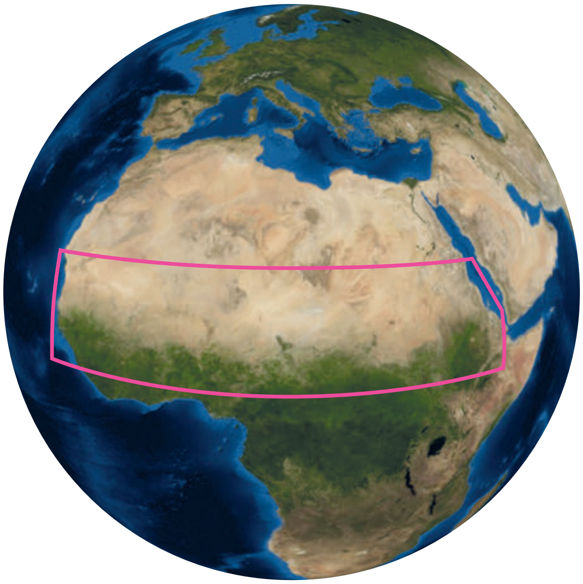

Figure 1. The study area in Africa, outlined in red, measures 10 million km^2 and lies between 7°N and 22°N and between 17°W and 42°E.

In the past half century great strides have been made in our knowledge of the distribution of birds in Africa. The pioneering work of Grote (1930), Moreau (1966), Hall & Moreau (1970), Moreau (1972), Snow (1978) and Curry-Lindahl (1981) paved the way to a better understanding of distributional patterns of African birds and the millions of migrants from Eurasia and North America. In the wake of accumulating knowledge derived from birders and researchers active in the region, many field guides and avifaunas have been published, each one more detailed than its predecessor. Some of the latest avifaunas even used a systematic atlas-approach, including the use of pre-determined visits to squares for which little or no avifaunal information was available. In Africa, the latter approach was first applied in Somalia (Ash & Miskell 1983), Sudan (Nikolaus 1987), Egypt (Goodman & Meininger 1989) and Kenya (Lewis & Pomeroy 1989) and has been used in several countries since, including – for the region under consideration here – Ethiopia and Eritrea (Ash & Atkins 2009), Ghana (Dowsett-Lemaire & Dowsett 2014), Benin and Togo (Dowsett-Lemaire & Dowsett

2019), Cameroon (Languy 2019), Mauritania (Browne 2020) and Burkina Faso, Niger and Chad (West African Bird DataBase www.wabdab.org/db).

However, ecological summaries of birds in the Sahel often lack sufficient detail. For example, where exactly do Palearctic migratory birds spend the northern winter and in which habitats? Avifaunas, except the ones based on a systematic survey, are usually largely based on birders' reports. Birders selectively visit areas with large numbers and high diversity, resulting in a skewed view of overall distribution and abundance of birds (Freeman & Peterson 2019). Reliable data can be obtained only through systematic density counts. These data are not yet available for the region except for the studies of Morel (1968) and Morel & Morel (1974, 1978) in N Senegal, Browne (1982) in SW Mauritania, Brouwer & Mullié (2001) for wetlands in Niger, Petersen *et al.* (2007) in Senegal and Niger, Jones *et al.* (1996) and Wilson & Cresswell (2006, 2010) in northern Nigeria and Zwarts *et al.* (2009, 2014) for mangroves, floodplains and rice fields in West Africa. However, these density counts were not performed at randomly chosen sites, a failing that prevents reliable and rigorous assessment of the overall densities (and, by default, of population size) of common bird species.

Since 2010, tracking individuals via geolocators and stable isotopes has much improved our knowledge of distribution and within- and between-season variations therein, not just for common but also for scarce or patchily distributed bird species. For example, Swedish Ortolan Buntings *Emberiza hortulana* were found to spend the winter in the Guinean Highlands (Selstam *et al.* 2015), Cyprus Wheatears *Oenanthe cypriaca* in southern Sudan (Xenophontos *et al.* 2017). As spectacular and probably unbiased as these data may be, in the sense that the data were collected by the birds themselves, proper assessments of distributions and population sizes require data collection in the field.

Based on systematic bird counts in random plots, we present maps with the distribution and regional variation in density of ground-foraging Afro-Palearctic migrants and Afro-tropical species in the sub-Saharan zone north of 7°N. These data are used to provide estimates of the total number of birds present in the region. Tree-dwelling bird species will be described separately (Zwarts *et al.* 2023a). Other papers in this special issue of *Ardea* use these data to explain the distribution patterns and analyse the impact of changes in the region which might explain numerical changes in migratory bird species.

METHODS

Study sites and grid cells

When we started the study in 2007, counting sites were delineated during field work using a GPS and high-resolution satellite images. The sites were selected to cover specific habitats, such as flooded forests. From 2011 onwards, however, the counts were done follow-

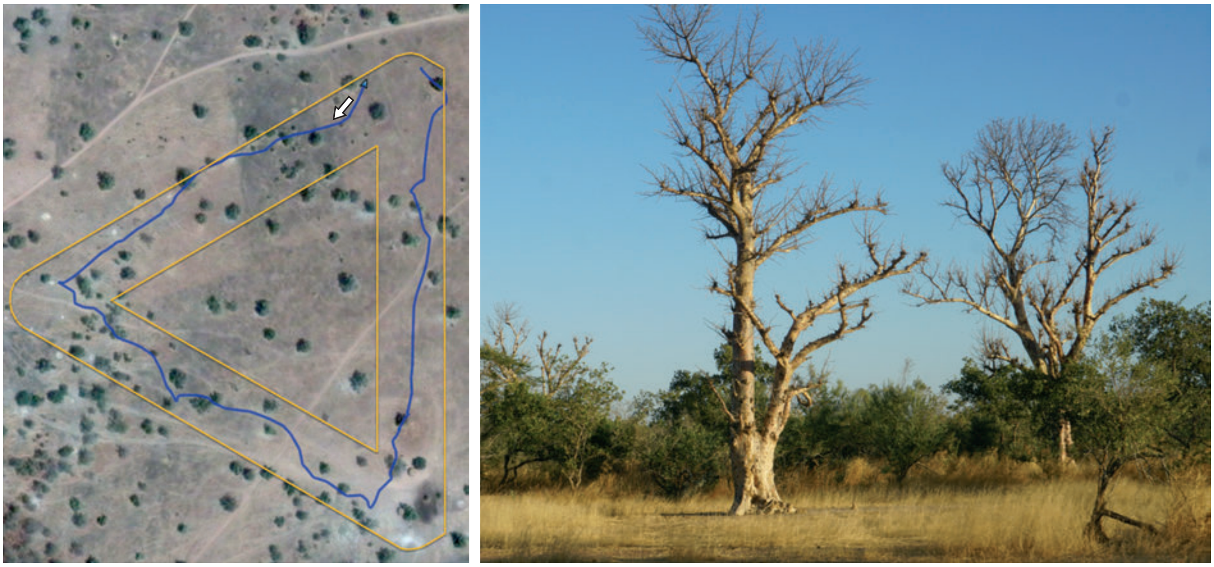

Figure 2. All trees and shrubs are clearly visible on a satellite image (Google Earth, 5 February 2013) of site N27 (14.65°N, 14.68°W). The yellow lines delimit the three transects of 300 × 50 m. The blue line shows the track walked by one of the three observers on 12 January 2017. Location of the photo taken during the visit to the site indicated with an arrow.

ing a systematic random sampling regime. Along tracks heading north-south, study sites were located at latitudes intersecting the track exactly at x.000°N, x.050°N, x.0100°N and so on (between-site distance min. 5.5 km) or at x.000°N, x.100°N, x.200°N and so on (between-site distance min. 11 km), alternately to the left or right side of the track. In a similar way, sites were selected intersecting longitudes along tracks with an east-west-direction. All sites had the same shape: three transects of 300 × 50 m in a triangular configuration (Figure 2) and a total surface of 4.5 ha. The woody plants and birds were usually counted in all three transects, but when it was too time-consuming (e.g. in dense scrub or woodland), we did only one or two transects (16% of the sites). The high-resolution satellite images (with individual trees being visible) and the boundary of the study sites (Figure 2) were downloaded beforehand on our field laptop and GPS. This enabled us to check in the field precisely which trees and birds were still within or beyond the boundaries of the transect, thus preventing a serious, and often overlooked, sampling error in this type of (ornithological) field work.

For a number of reasons, it was not always possible to visit all preselected sites. If not, we selected a neighbouring site and used our GPS and high-resolution satellite image to delimit three transects of 300 × 50 m. If this were not feasible either, we skipped the site. Indeed, despite our best efforts, the coverage of the entire region remained incomplete, mostly because local authorities refused to issue permits or danger of terrorism and acts of war prevented safe fieldwork. As a consequence, the southern Sahara remained largely beyond our intended study area except in the far west (Mauritania) and far east (Sudan).

Between 2007 and 2019 systematic counts were performed at 2144 sites in 14 countries (Figure 3A, Table S4). All counts took place between September and March, but data collected in September – 20 November were omitted because many migrants wintering farther south were then still present in the Sahel. Non-random sites (and therefore all sites from 2007–2010) were also disregarded. Counts in the Central African Republic (2017) and Ivory Coast (2018) were, however, included because random sites could not be determined beforehand, and instead sites were randomly selected on the spot during field work. In Ivory Coast, all data were collected within Comoé National Park (11,500 km^2), which is clearly not representative of the humid zone in West Africa at large.

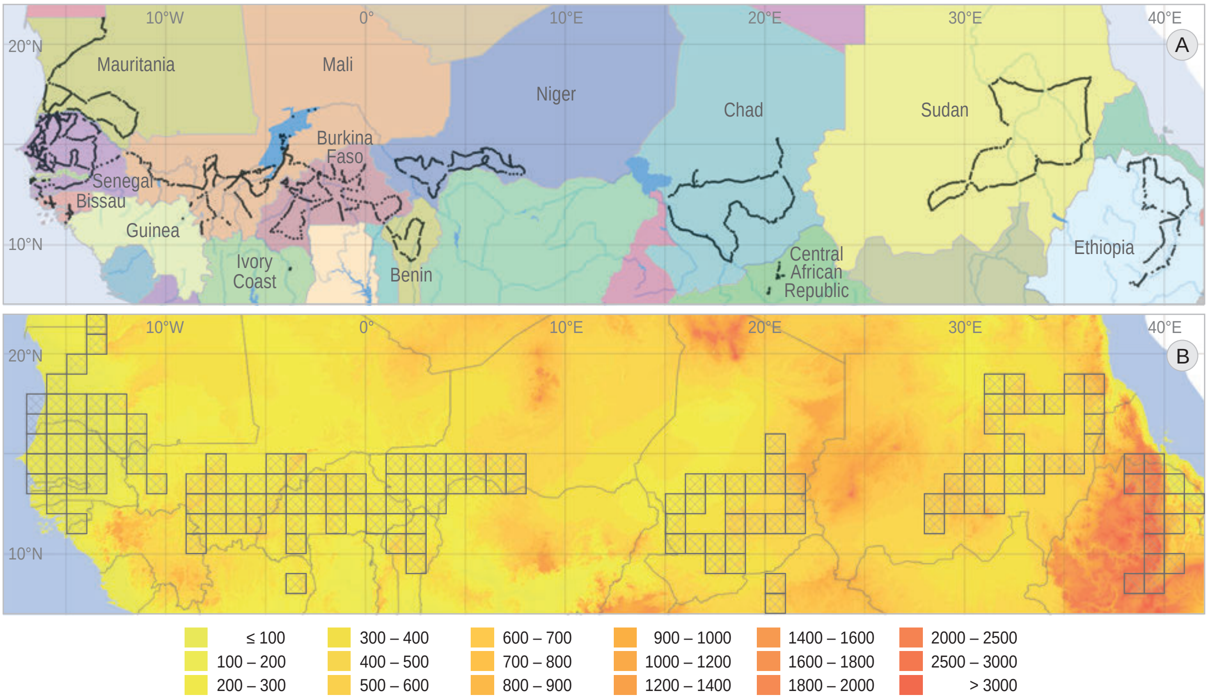

Figure 3. (A) Location of all study sites (•) in the 14 countries that constitute the Sahel as defined in this study, and (B) elevation in m relative to sea level (source: ASTER Global Digital Elevation Map V3) with 150 squares representing grid cells of 1° latitude × 1° longitude where the field work was performed.

The final analysis is based on a total of 1901 random winter sites, with a total surface of 8022 ha. The 1901 sites are situated in 178 1° latitude × 1° longitude grid cells, but since data from cells with fewer than ten sites were combined with data from adjacent grid cells, bird densities are presented for 150 1 × 1° grid cells (Figure 3B). These grid cells measure 111 × 109 km at 7°N, but are narrower farther north, being 111 × 98 km at 22°N. The altitude of the sites varies between 100 m below (Danakil Desert) and 3500 m above sea level, both in Ethiopia, but elsewhere most sites are situated between 100 and 500 m above sea level (Figure 3B).

Birds

This paper deals with ground-foraging birds only (see Zwarts *et al.* 2023a for arboreal birds). Doves, sparrows and starlings are included, because they feed on the ground and use trees only for roosting or seeking shade. Shrikes, which use trees as a perch to pounce at prey on the ground, are also included in this paper, as well as species which feed more often on the ground than in the woody vegetation (two scrub robins and Cricket Warbler *Spiloptila clamans*; Figure 1 in Zwarts *et al.* 2023a).

The bird species included were categorised as granivores or insectivores, based on Morel (1968), Morel & Morel (1978), Keith *et al.* (1992), Fry & Keith (2000, 2004) and own observations. Shrikes were assigned to the insectivorous guild, notwithstanding their occasional predation of larger prey such as lizards and small birds. Species with mixed insectivorous-granivorous diets were categorised as granivorous, because of their consumption of seeds in the dry season. Bird species were also classified as Afro-Palearctic migrants (breeding north of the Sahara), from now on called migrants, or Afro-tropical residents (breeding south of the Sahara, including intra-tropical migrants), from now on called residents. Eurasian Hoopoe *Upupa epops*, Desert Wheatear *Oenanthe deserti* and Rufous-tailed Scrub Robin *Cercotrichas galactotes* are partly migrant, partly resident, depending on whether they breed north or south of the Sahara. They are treated here as migrants. Recently, Black-eared Wheatear has been split into Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*. We assume that all birds west of 8°E and east of 15°E were Western or Eastern Black-eared Wheatears, respectively.

Between 2007 and 2012 we restricted our counts to migrants and a few insectivorous resident species. From 2013 onwards all insectivorous residents were included, and from 2014 through 2019 also all granivorous residents. Consequently, the densities for migrants are based on counts in 1901 sites with a total surface area of 8022 ha situated in 150 grid cells. Insectivorous residents were counted in 1623 sites, 6542 ha and 138 grid cells and granivorous residents in 1153 sites, 5250 ha and 111 grid cells.

During the counts three persons slowly traversed the 50 m wide transects on foot to detect, identify, and count birds. Birds were usually easy to approach. Flight distances (measured in a horizontal plane) in most species were less than 25 m; flight distances were larger in ground-foraging birds than in arboreal birds (Figure 14 in Zwarts & Bijlsma 2015). The rarely spotted European Turtle Doves *Streptopelia turtur* were difficult to count due to their relatively large flight distance (52 m on average; $n = 15$; R.G. Bijlsma unpubl. data). Birds feeding on the ground were easy to count since the soil was largely bare during the dry season. Soon after the last rains in September or October the vegetation was eaten by livestock, and if not, became withered or was burned. In the humid zone, however, a dense vegetation of high grass was locally still present after October. The few skulking bird species located in this dense vegetation, such as quails, may have been partly overlooked. Ground-foraging birds present in trees were less conspicuous, but easily detected and flushed because most trees were small and isolated; they also held little foliage in the dry season. Extensive testing proved that our absolute counts of birds in trees were accurate for all species (Zwarts & Bijlsma 2015).

Rainfall and woody cover

For each study site, using Hijmans *et al.* (2005), we determined the average annual rainfall over the period 1950–2000; for background information, see Supplementary Material 4. Average annual rainfall in the sites varied between 27 and 2285 mm and, averaged for the grid cells, between 32 and 1802 mm (Figure 4). Rainfall increased going from north to south, but this shift is much larger in western Africa than farther east (Figure 4). From Mauritania southwards, the annual rainfall (mm) showed a negative exponential relationship with latitude (L):

$$\text{rain} = 163411e^{-0.393L} \ (r^2 = 0.971), \qquad (1)$$

in other words, rainfall doubles every 167 km southwards, gradually to more than 2000 mm per annum in Guinea and Guinea-Bissau. In Mali and Niger, the degree of change was less steep, with rainfall doubling

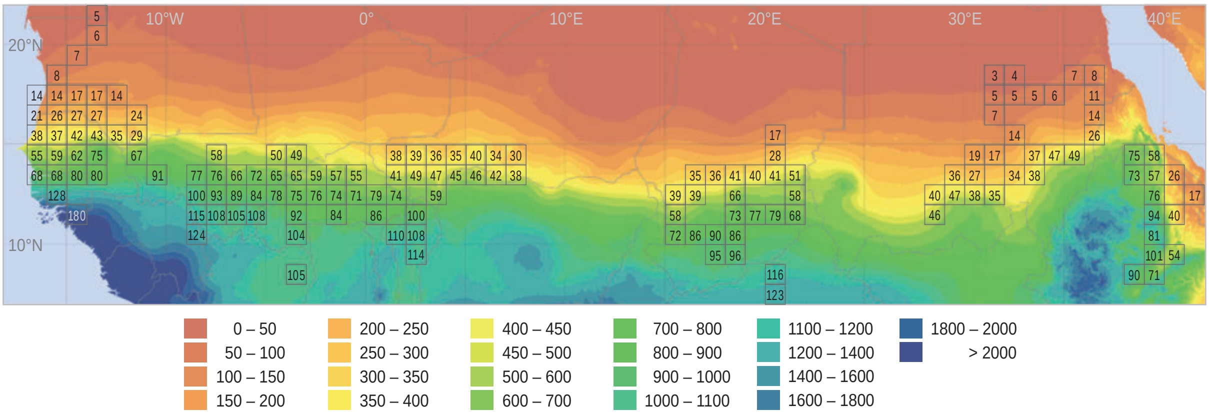

Figure 4. Average annual rainfall based on rain gauge measurements from the period 1950–2000 given for the 150 1 × 1° grid cells where field work was performed (to save space expressed as cm/year in the grid cells, and not, as usual, mm/year) plotted on a map with rainfall contour lines (source: Hijmans *et al.* 2005).

every 194 km south, on average, up to 1100–1200 mm farther south. This is much less than that recorded at the same latitude further west in the coastal zone along the Guinean Gulf. Rainfall from north to south again increased somewhat farther east in Chad, doubling every 177 km. In fact, the 500 mm rain isoline in the Central Sahel extends about 400 km farther to the south than in the western Sahel. Therefore, we provide bird densities for 100 mm rainfall classes and not per latitude. The rainfall in Ethiopia is related to altitude, with arid lowlands in the northeastern part of the country (Danakil Desert) and (extremely) humid highlands in the central part of the country (Figure 3B and 4).

The region is usually subdivided into a number of zones from north to south (Figure 5), each characterised by rainfall, and, by default, vegetation (White 1983, Le Houérou 1989):

- Sahara (hyper-arid zone with <100 mm rainfall/year),
- Sahel (arid and semi-arid savannah zone with 100–600 mm rainfall per year, subdivided in three subzones: Sahel proper (200–400 mm rainfall) and two transition zones: Saharo-Sahelian (100–200 mm) and Sahelo-Sudanian (400–600 mm),
- Sudan zone (woody savannah; 600–900 mm rainfall per year), and
- Guinean zone (woody savannah and forest; > 900 mm rainfall per year).

The Congo-Guinean rain forest farther south, is beyond our region.

26% of our data were collected in the Sahel proper (200–400 mm rainfall/year) and 56% in the Sahel including transient zones to the Sahara and the Sudan zone (i.e. 100–600 mm rainfall/year; Figure 5). Although the Sahel is strictly defined as the ecoclimatic and biogeographic region bordering the Sahara and Sudan ecological zone (between 100- and 600-mm isohyets; Le Houérou 1989), the term Sahel is loosely used in practice, especially in the ornithological literature, to indicate the entire transition zone between Sahara and humid forests. In this paper we will use it in a broad sense and will state specific rainfall or aridity zones if necessary.

Annual rainfall in the Sahel typically shows large between-year variations (Supplementary Material 4). This may have had an impact on the distribution of the bird species during the dry season (Zwarts *et al.*

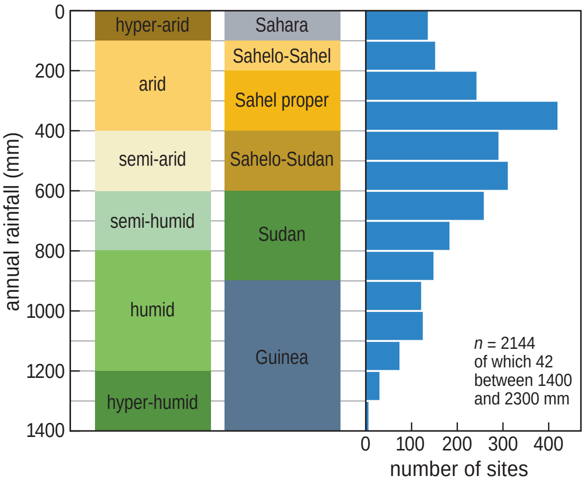

Figure 5. Division of the region between 7 and 22°N in six aridity and climate classes, with frequency distribution of the study sites (shown in Figure 3A) over the 14 rainfall classes in the right panel.

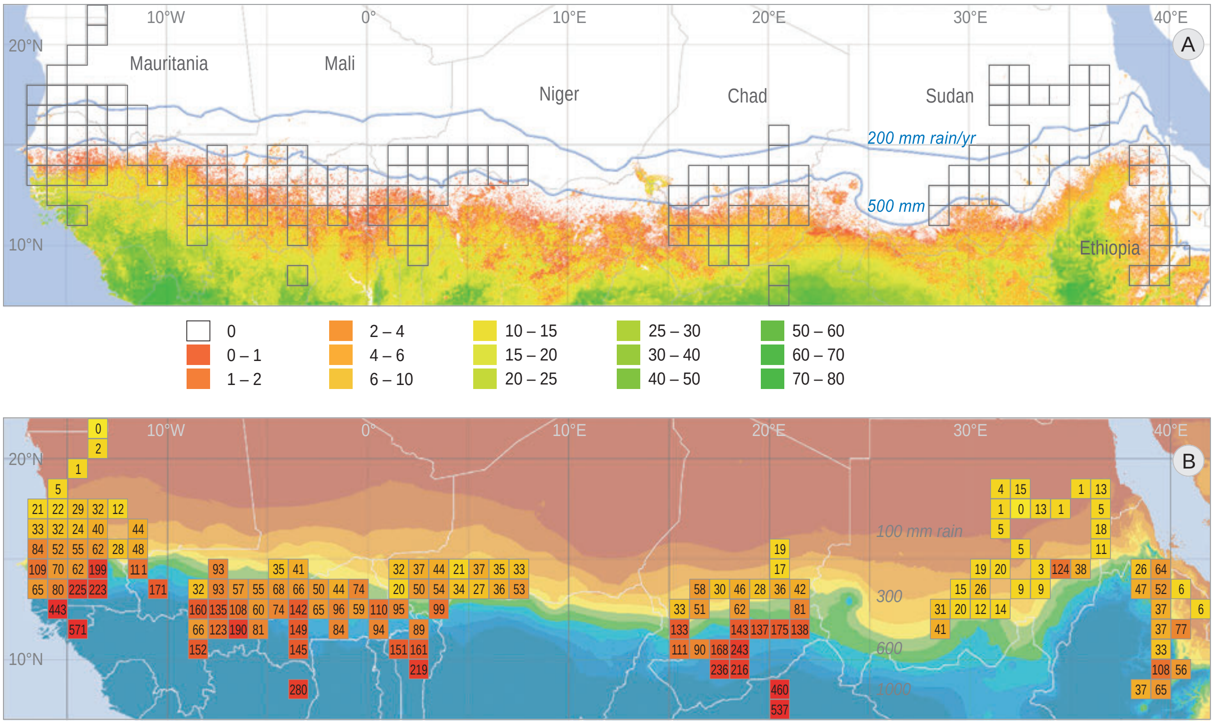

Figure 6. (A) Forest cover (%) in 2000–2012, according to Hansen *et al.* (2013), based on Landsat satellite imagery. The blue lines show the 200- and 500-mm isohyets (from Figure 4). (B) Woody cover (‰) of all tree species based on our field work (2007–2019) in 150 grid cells. Mean ± SD: 75‰ ± 92; trees or shrubs were present in 148 of the 150 cells; background: rainfall (as Figure 4; simplified).

2023c). In our years of observation rainfall did not deviate much from the average for the 20th century (–2%) The rainfall map (Figure 4) is based on data collected in 1950–2000, i.e. when rainfall was 2% less than in our years of observation (Supplementary Material 4).

The increase in rainfall from north to south is reflected in a gradual increase of the woody cover. Hansen *et al.* (2013), using satellite imagery, found an absence of woody vegetation in regions with <500 mm rainfall/year and a forest cover of 50 to 80% in the most humid regions (Figure 6A). These figures are inflated, however, as our ground-truthing showed that aquatic vegetation in lakes, floodplains and irrigated areas was incorrectly identified as woodland. Furthermore, our field data showed that sparse woody vegetation emerged as soon as rainfall was >100 mm/year, further increasing to woody cover of about 10% in the rainfall zone of 500–800 mm/year and 30–50% in the most humid zone (Figure 6B; see Zwarts *et al.* 2023a on how woody cover was measured). The woody cover extent as accurately determined in the field was twice as large as satellite imagery indicated for regions with >1000 mm rainfall/year, and even ten times as large for regions with rainfall of 500–700 mm/year (Figure 7). This discrepancy can be explained by the fact that woody cover, based on satellite imagery, is defined as

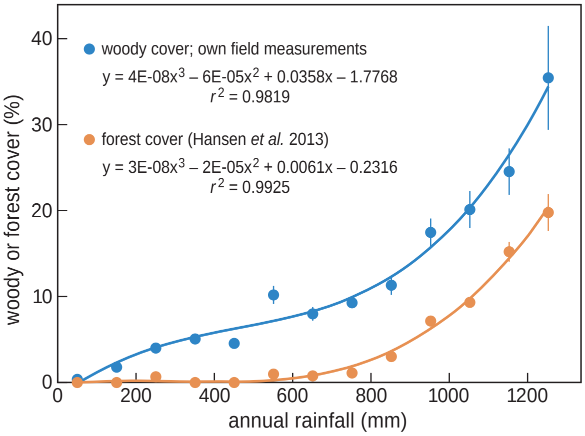

Figure 7. The percent cover of woody vegetation ± SE in 2144 study plots (Figure 6) as a function of annual rainfall (Figure 4). 'Woody cover' was measured in the field (Figure 6B). 'Forest cover' is based on the pixel values for the same study plots as derived from Landsat imagery by Hansen *et al.* (2013; Figure 6A).

"25% or greater canopy closure at the Landsat pixel scale (30-m × 30-m spatial resolution) for trees >5 m in height" (Hansen *et al.* 2010). In other words, isolated trees and shrubs were systematically discarded in their study. The interval between the blue and green line in Figure 7 may therefore be interpreted as woody cover of shrubs and isolated trees which indeed dominate the woody vegetation where annual rainfall is less than 800 mm.

Human population

The human population in Africa between 7 and 22°N was estimated at 300 million in 2019 (https://data.worldbank.org/country). The average population density amounts to 30 inhabitants/km^2 but the variation is large, from 197/km^2 in Nigeria to 7.9/km^2 in the Central African Republic (averages for both countries as a whole, thus extending south of 7°N). The impact of people on land use, and by implication on bird populations, is likely to show equally large regional variations. However, it is the presence of people, rather than density per se, that counts when distribution and density of birds are considered. As a measure of the presence of people we use the percent surface area covered by buildings. This percentage varied per grid cell between 0% in the Sahara and 8.6% in the suburban zone around Khartoum in Sudan (Figure 8). Rainfall explained much of the variation. In regions with <100 mm rainfall/year, buildings covered only 0.04% of the surface area, increasing to – and remaining more or less stable at – 1% in regions with >400 mm/year. Within each rainfall zone large longitudinal differences were found, with far fewer buildings between 19 and 30°E and >500 mm rainfall. In the hyper-arid zone (<100 mm rain) the presence of buildings was relatively high between 11 and 19°W (Mauritania) and 30 and 38°E (Sudan; Figure 8).

Vegetation and land use

White (1983) distinguished 80 vegetation types in Africa, of which 21 occur between 7°N and 22°N (simplified to nine zones in Figure 9). The vegetation zones are closely related to the annual rainfall with, for instance, 'Acacia woodland + scrubland' between the 200- and 500-mm isohyets.

During field work, we classified sites either as 'woodland' (n = 78), 'farmland' including land in fallow (n = 971) or 'savannah', a broad category of uncultivated land, from tree-less desert to wooded savannah, but also rock, scrub and grassland (n = 1095). The tripartite division was not always unambiguous. Farmland in fallow for a long time looked like savannah. Also, the distinction between woodland (more or less closed canopy) and woody savannah

Photo 1. The Sourou valley in eastern Mali near Bandiagara (January 2016) is intensively used as farmland; the scattered trees on the photo are mainly Umbrella Acacia *Acacia tortilis* and Winter Thorn *Faidherbia albida*. This agroforestry parkland, common in the rainfall zone of 300–700 mm/year, is hard to distinguish from savannah in remote sensing studies using satellite imagery (Table 1).

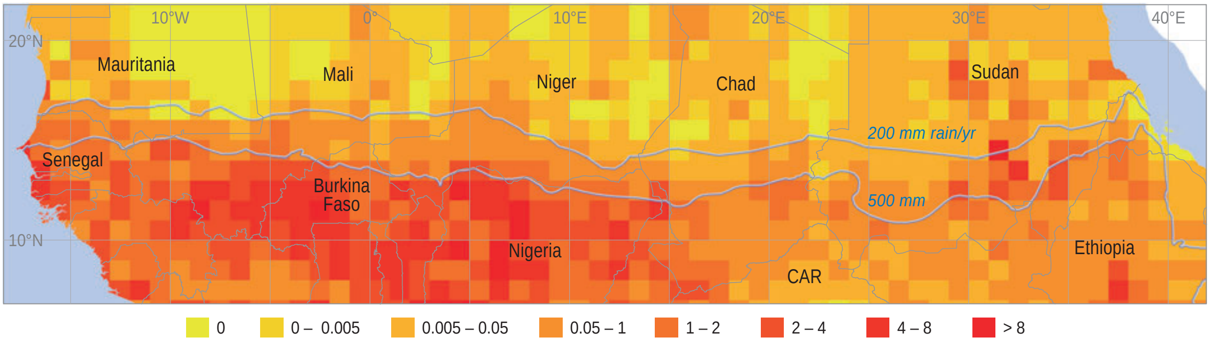

Figure 8. Percent cover in 2016 of cities, villages and single houses and huts combined, averaged per grid cell, based on data provided by ESRI at a resolution of 150 × 150 m. The 200- and 500-mm isohyets are shown as blue lines. CAR is Central African Republic.

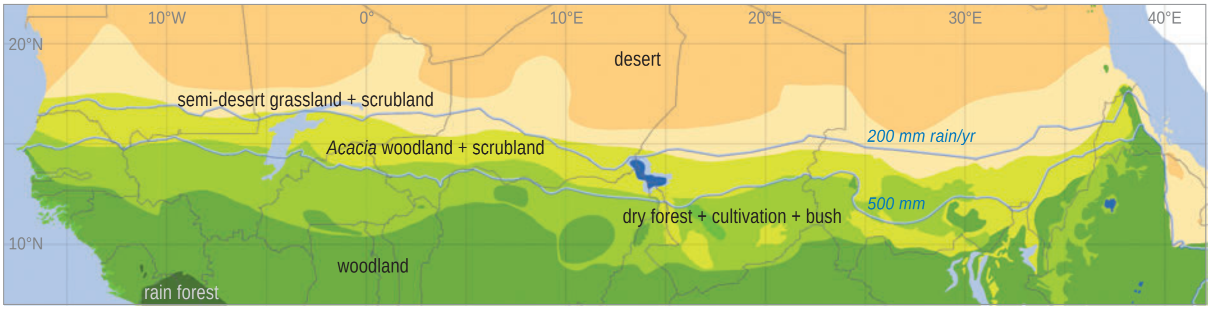

Figure 9. Six main vegetation zones between Sahara and the tropical forest; also indicated: floodplains and swamps (Inner Niger Delta, zone around Lake Chad, Sudd; light blue), open water (Lake Chad and Lake Tana; dark blue) and mangrove along the Atlantic coast (light green). The 200- and 500-mm isohyets are shown as blue lines. Source: White (1983).

(scattered trees) seems arbitrary, but the measurements of woody cover showed a rather clear dichotomy at a woody cover between 20% (with 95% of savannah sites below this level) and 26% (with 95% of the woodland sites above this level).

Table 1. Land use in our 2144 study sites (see Figure 3) was categorised as woodland, agriculture ("farm", including land in fallow) or savannah (sav.). The percentage of classifications which agreed with our field data varied between 63.5% (Mayeux *et al.* 2004) and 72.7% (Buchhorn *et al.* 2020).

	Agreement		No agreement	
Field measurements	farm	sav.	sav.	farm
Remote-sense data	farm	sav.	farm	sav.
Mayeux *et al.* 2004	29.9	33.6	20.4	16.0
Arino *et al.* 2007	25.6	45.2	9.3	20.0
Buchhorn *et al.* 2017	33.7	33.1	20.4	12.7
Buchhorn *et al.* 2020	38.7	34.0	19.6	7.6

On the first land cover map of Africa, using low resolution satellite imagery from 1992–1993, savannah and farmland had been lumped (Loveland *et al.* 2000). Later land cover maps of Africa distinguished farmland from savannah. A comparison of four such studies with our classification of three habitat types in 2144 sites (Table 1) revealed a difference in accuracy, but also that farmland as percentage of open landscape (excluding woodland, covering 10–13% of the region) varied considerably. In total, 41% of our sites had been categorised in the field as farmland. Based on remote sensing data, Arino *et al.* (2007) arrived at 30% for our sites, Mayeux *et al.* (2004) at 46%, Buchhorn *et al.* (2017) at 48% and Buchhorn *et al.* (2020) at 51%. The most recent land-use map (Figure 10) is, in our experience, the best land cover map presently available for Africa. We use this map in further analyses, even though the extent of farmland is overestimated at the expense of savannah (Table 1).

The land use and land cover map (Figure 10) shows that when rainfall is less than 100 mm per year, hardly any vegetation is recorded. Further south regional differences in land use become more prominent, also across the same latitudes. For example, between 16 and 7°W and between 18 and 32°E the woody cover of ‘trees’ and ‘scrub’ is high when rainfall exceeds 500 mm/year, but ‘scrub’ and ‘trees’ are replaced in the same zone by ‘cropland’ between 7°W and 18°E and between 32 and 40°E. ‘Trees’ is the dominant category in the most humid zone, but it varies from 34% in Ethiopia to 75% in Sudan (Figure 10). ‘Scrub’ is mostly found in the zone with 400 to 800 mm rain per year, ‘cropland’ is associated with 300–800 mm of rain (but see the more humid areas in Ethiopia), and ‘grassland’ with 200–500 mm of rain. Longitudinal differences in the cover of ‘trees’ are smallest for the arid zone and largest for the humid zone with relatively much ‘cropland’ instead of ‘trees’ between 9°W and 10°E and in Ethiopia (Figure 10).

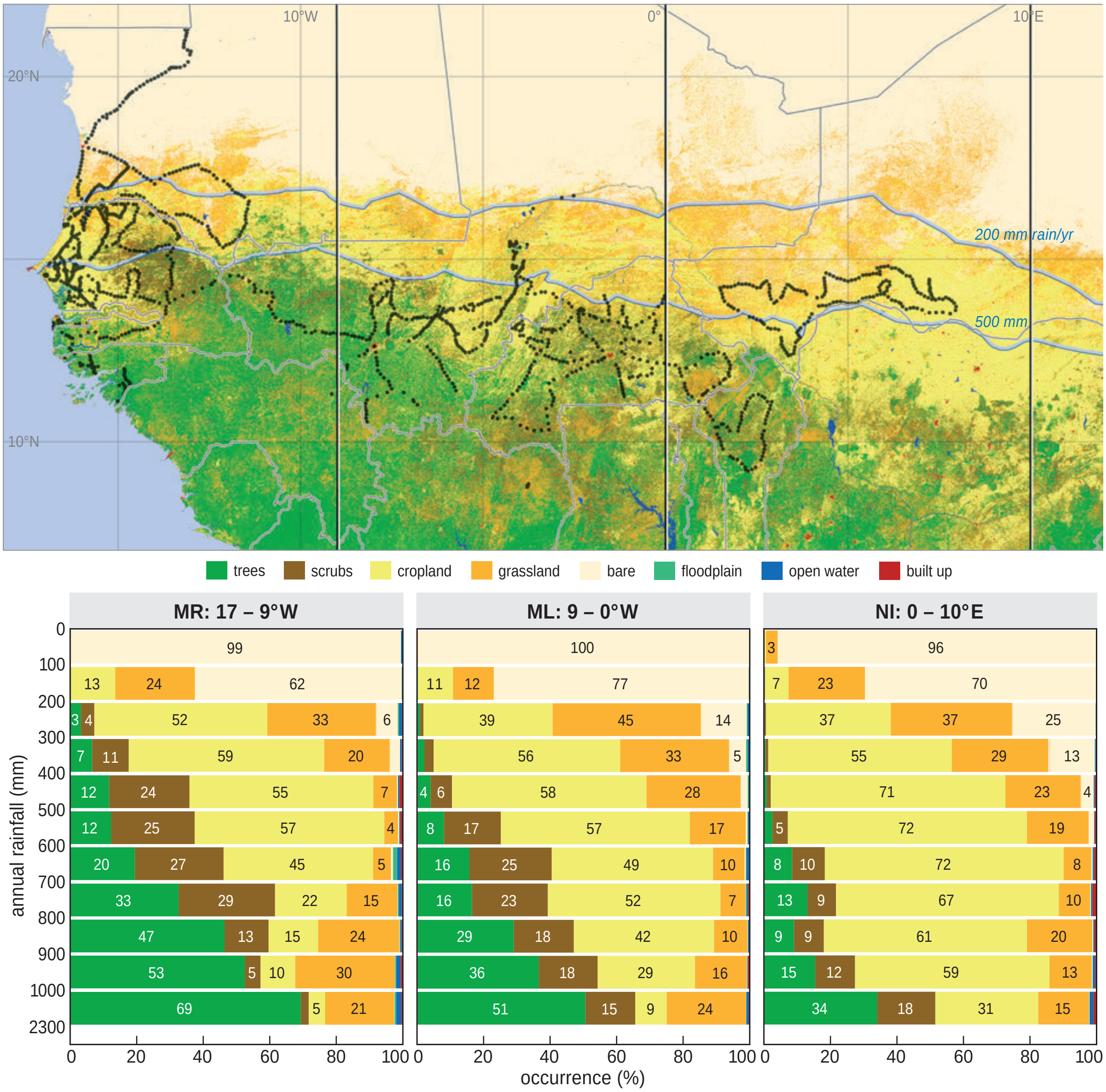

Figure 10A. Land use and land cover in the western half of the Sahel in 2015; trees, scrub, cropland, grassland and bare are by far the most common types of land cover. Source: Buchhorn *et al.* 2020; resolution: 100 m. The blue lines show the 200- and 500-mm isohyets. The study sites are indicated with black dots. The graphs show the occurrence (%) of the categories for 11 rainfall zones (see Figure 6) in three longitudinal bands as indicated on the map; two-letter code in the heading refers to the country at 10–15°N; MR=Mauritania, ML=Mali, NI=Niger.

Analysis

Maps show the density for 43 bird species for 150 grid cells across the Sahel. For the analysis of the distribution of bird species in relation to rainfall and woody cover, data collected in the Ethiopian highlands (700–3500 m above sea level) are excluded. Many bird species that are widespread in the region are replaced by other species in the Ethiopian highlands. Moreover, rainfall in Ethiopia is related to altitude, with the wettest areas high up in the mountains. We therefore selected sites of <700 m relative to sea level to exclude altitude as a confounding variable.

Desert and humid woodlands were under-recorded in the 150 grid cells, as is the eastern half of the region (details in Supplementary Material 2). Unequal distribution of grid cells is solved by calculating the average bird density for 11 rainfall zones in six longitudinal bands, in total 65 subregions (Figure S1). Bird densities

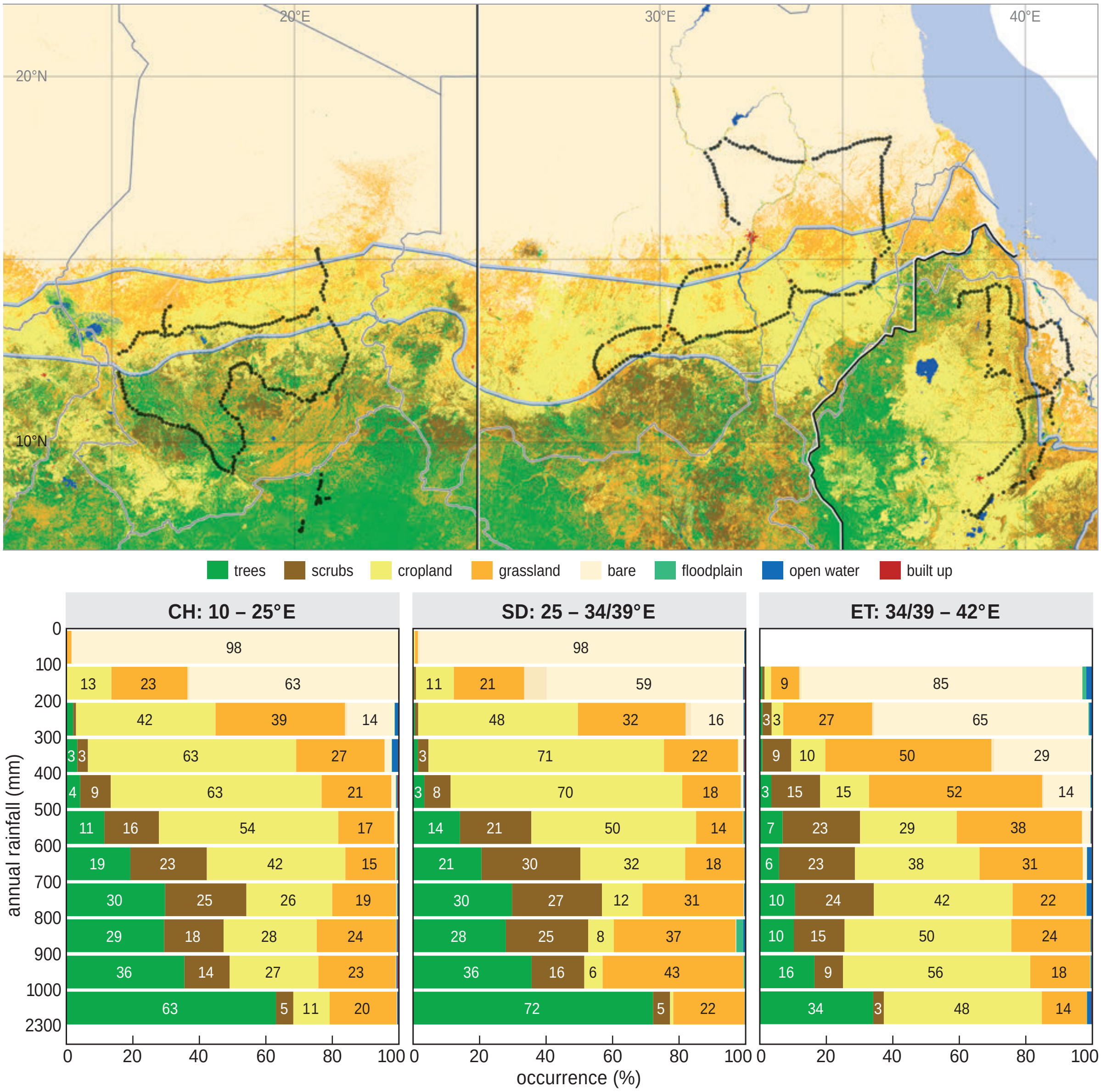

Figure 10B. As Figure 10A but for the eastern half of the Sahel; CH=Chad, SD=Sudan, ET=Ethiopia.

of migrants are available for 53 of the 65 subregions. To estimate bird densities in the 12 missing subcategories, we averaged the densities in two adjacent cells with a similar rainfall. Since the grid cells of South Sudan differ substantially from those in the nearby Ethiopian Highlands, we substituted the adjacent values of Chad and the Central African Republic for missing South Sudan cells. No bird counts are available for the ground-foraging residents in Guinea-Bissau, Mali and Benin, necessitating interpolation of bird densities in another 10 subcategories. The total number of birds present between 7 and 22°N is calculated from the measured or interpolated bird density in 65 subregions multiplied by the surface area of 65 subregions (Figure S1).

To estimate the average bird density in the entire region, it is necessary to correct for the unequal distribution of grid cells within the region (see Supple-

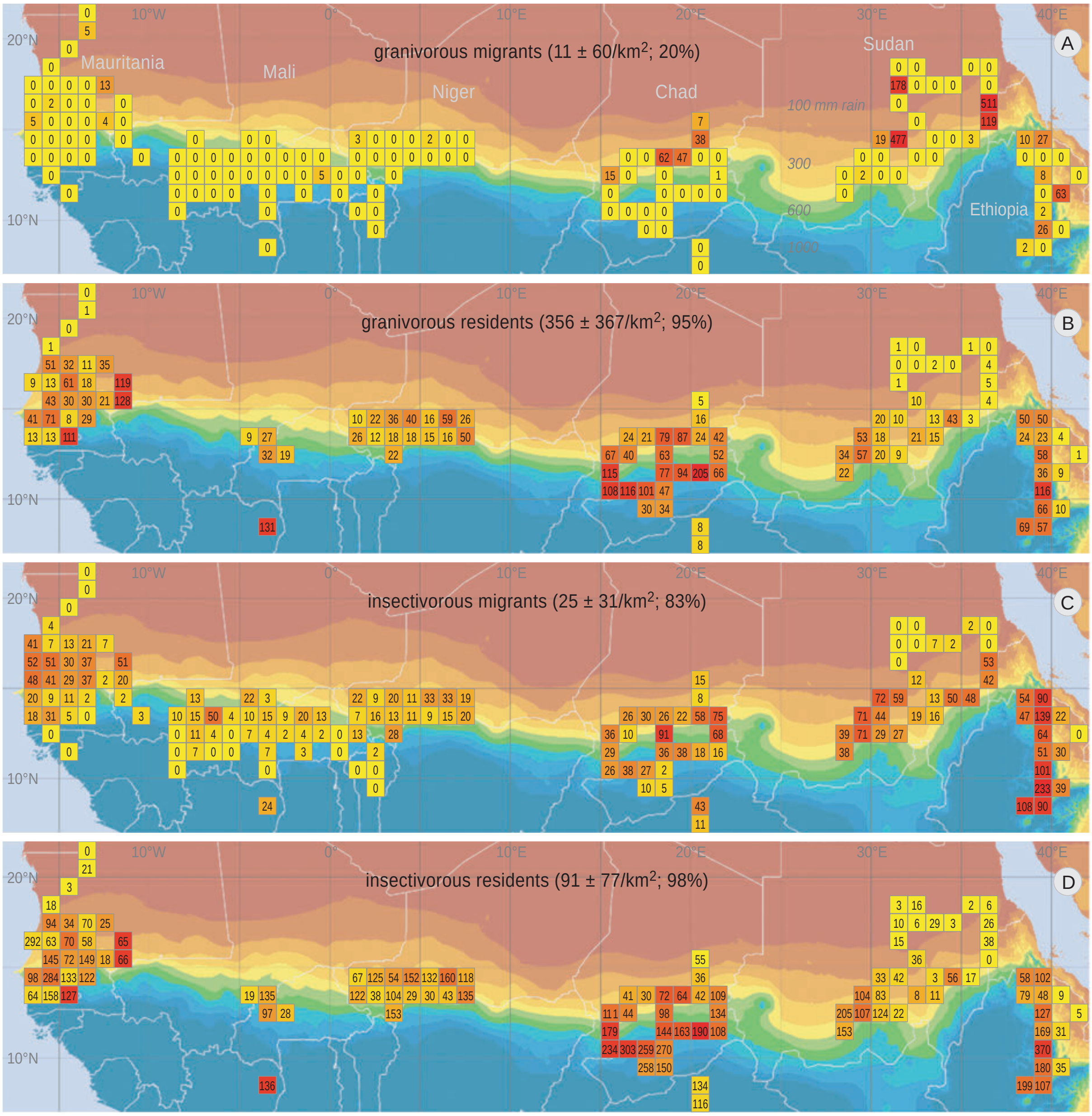

Figure 11. Density of ground-foraging birds (n/km^2) in 111 (residents) or 150 (migrants) grid cells; average density (mean ± SD) and presence in the grid cells (%) given between brackets; background colours refer to rainfall (as Figure 4; simplified). N.B. Densities of granivorous residents in grid cells are – for practical reasons – depicted per 10 km^2.

mentary Material 2). The average density and the estimated total number of birds in the region for 43 bird species, as provided in the legends of Figures S2–S44, are used to assess the reliability of the estimated total population size, by repeating the calculations for the same data split in two halves, i.e. for sites with even and odd rank numbers. For instance, using all data, we arrived at 126 million Greater Short-toed Larks (Figure S18), but using the split-half method, estimated totals arrived at 100 and 151 million birds, i.e. deviating 20% from the estimated 126 million. The deviation is much smaller in, for example, Northern Wheatear (range 25.5–28.4 million, deviating 5.4% from the estimated 27.1 million based on all data). The average deviation for 43 species amounts to 16%, varying between 1.7% (Western Yellow Wagtail) and 53.8% (Greater Blue-eared Starling). The deviation does not decline, as expected, in bird species with a larger population ($r = -0.02$). The deviation is smaller, however, in bird species with a wider distribution: $r = -0.31$ ($P = 0.02$; distribution defined as frequency of occurrence (%) in sites; see Table S1). The correlation between both split-half averages in 43 bird species is very high, $r = 0.90$ ($P < 0.001$), which shows that the estimates of the population size are accurate, albeit varying per species.

RESULTS

Density and distribution

All the common ground-foraging birds in the region were granivorous (Figure 11A and 11B). The average density of granivorous species amounted to 367 birds/km^2 (average of the grid cell means), among which were only three migrants: Greater Short-toed Lark *Calandrella brachydactyla* (10/km^2; Figure S18), European Turtle Dove (0.35/km^2) and Common Quail *Coturnix coturnix* (0.32/km^2). A fourth migratory granivore, Ortolan Bunting, had a patchy distribution within the region, i.e. confined to the Ethiopian Highlands (annual rainfall 700 mm) with 10–30 birds per km^2 in our study and in two areas not visited by us: to the Guinean Highlands (Selstam *et al.* 2015) and the Jos Plateau in Nigeria (Elgood *et al.* 1994). The density of insectivorous ground-foraging species was 126 birds/km^2, of which 32 birds/km^2 were migrants (Figure 11C) and 93 birds/km^2 residents (Figure 11D). Overall, granivorous birds were nearly three times more common than insectivorous birds, and residents were ten times more common than migrants.

Three species among the granivorous residents were more common than all ground-foraging migrants together:

- Red-billed Quelea *Quelea quelea* (40/km^2; Figure S35),
- Red-cheeked Cordon-bleu *Uraeginthus bengalus* (40/km^2; Figure S39),
- Sudan Golden Sparrow *Passer luteus* (90/km^2; Figure S32).

Other abundant granivorous residents were:

- Laughing Dove *Spilopelia senegalensis* (18/km^2; Figure S5),
- Northern Grey-headed Sparrow *Passer griseus* (18/km^2; Figure S31),
- Speckle-fronted Weaver *Sporopipes frontalis* (16/km^2; Figure S33),
- Namaqua Dove *Oena capensis* (12/km^2; Figure S7),
- Chestnut-backed Sparrow-Lark *Eremopterix leucotis* (11/km^2, Figure S16),
- Black-crowned Sparrow-Lark *Eremopterix nigriceps* (11/km^2; Figure S15),
- African Silverbill *Euodice cantans* (10/km^2; Figure S31).

The two most common ground-foraging insectivorous birds were residents:

- Chestnut-bellied Starling *Lamprotornis pulcher* (13/km^2; Figure S24),
- Greater Blue-eared Starling *Lamprotornis chalybaeus* (7/km^2; Figure S21).

Ground-foraging insectivorous migrants were much less common:

- Northern Wheatear *Oenanthe oenanthe* (3.9/km^2; Figure S27),
- Isabelline Wheatear *Oenanthe isabellina* (4.2/km^2; Figure S28),
- Western Yellow Wagtail *Motacilla flava* (3.2/km^2; Figure S41).

The most widely distributed bird species in the area were granivorous residents: the Sudan Golden Sparrow was present in 24.3 % of the study sites, followed by Laughing Dove (20.9%), Namaqua Dove (18.3%) and Northern Grey-headed Sparrow (17.0%). Insectivorous species were recorded in far fewer sites, of which only the Northern Wheatear (15.1%), a migrant, was common. The 43 most common ground-foraging bird species were found in 8.0% of the sites, on average, and in 33.7% of the grid cells (see last three columns in Table S1).

Other bird species had a much patchier distribution, but reached high densities where present. Red-billed Queleas, for example, were observed in 7.3% of the sites, but reached a density, on average, of 28.2 birds per occupied 4.5 ha-site. Greater Short-toed Larks were observed in just 3.5% of the sites, but then with 29.4 birds per site, on average. In contrast, Abyssinian Rollers *Coracias abyssinicus* rarely exceeded one bird per 4.5-ha site when present.

In general, granivores reached higher numbers per occupied site than insectivores (Figure 12), and among granivores, sparrows occurred in larger flocks than doves. Among insectivores, starlings were often encountered in flocks whereas wheatears and shrikes were typically solitary.

Distribution, rainfall and woody cover

The many climatic zones within the region produce a wide range of habitat types, each inhabited by specific bird species. Desert Wheatear and Greater Short-toed Lark were the only two migrants found in the arid zone among several residents such as Desert Sparrow *Passer simplex*, Crested Lark *Galerida cristata*, Desert Lark *Ammomanes deserti* and Greater Hoopoe-Lark *Alaemon alaudipes* (Figures 13A and 14A). At the other end of the climatic extreme within the region, in the most humid zone, all birds feeding on the ground were residents except Tree Pipit *Anthus trivialis* and Whinchat *Saxicola rubetra*. The other ground-foraging migrants were mainly confined to the zone with 200–700 mm rain per year.

The increase of rainfall between the Sahara and Guinean zones (Figure 4) is reflected in a gradual increase of woody cover, from <1% in the most arid environment to 40–60% in the most humid zone (Figure 6B). The preference of birds for dry or humid habitat, as shown in Figure 13A and 14A, is concomitant with open or closed landscapes. Even so, the variation in habitat choice within the same rainfall zone is considerable, as evident for example in Black-headed Lapwing *Vanellus tectus* (open habitat) and Masked Shrike *Lanius nubicus* (wooded habitat; Figure 14B). The same variation is apparent among birds using the

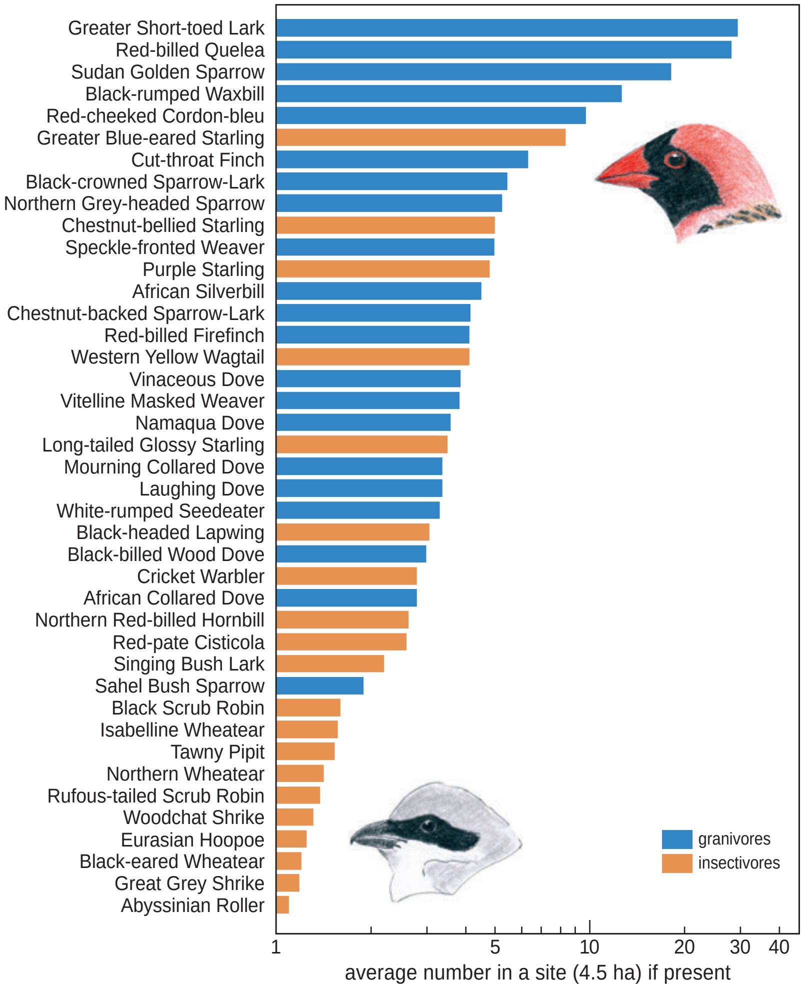

Figure 12. Average number of birds in 4.5 ha-sites if present; note log scale.

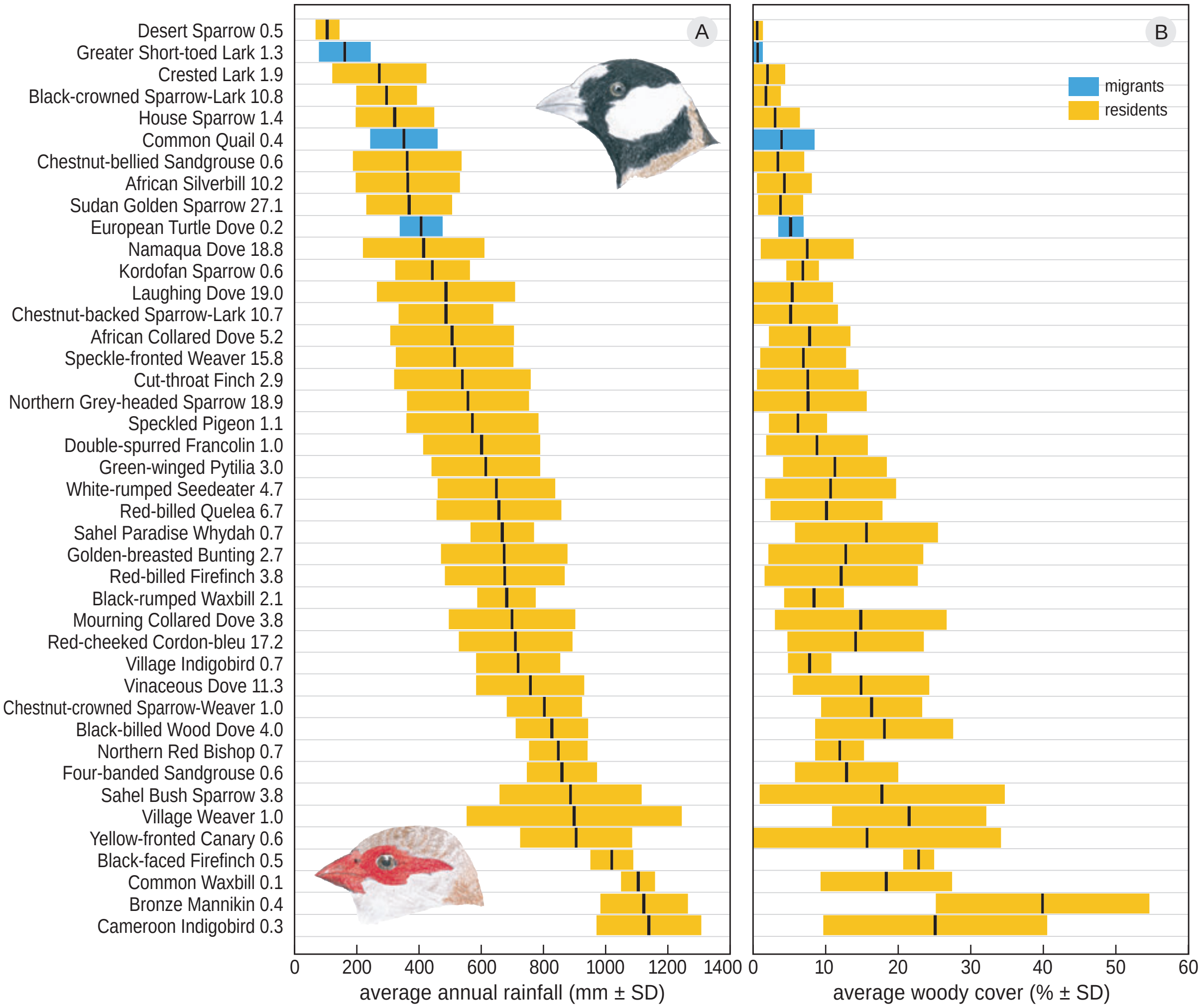

Figure 13. (A) Average rainfall and (B) average woody cover (±SD) as measured in study sites where granivorous birds were present, shown for 3 migrants and 38 residents. The species were ranked according to average rainfall. The number after the bird names indicates in how many sites a species was present (%); sites from the Ethiopian Highlands (>700 m above sea level) were excluded.

other vegetation zones. In nearly all species, the SD was larger for woody cover (Figure 13B and 14B) than for rainfall (Figure 13A and 14A). The SD of the rainfall as % relative to the average (RSD) amounted to 28% for the granivores in Figure 12A, but it was 74% when plotted against woody cover (Figure 13B). The same differences existed for insectivorous ground-feeding birds: RSD is 35% when plotted against rainfall (Figure 14A), but 101% for woody cover (Figure 14B). This implies that birds were more specific in their selection of rainfall zones, than they were for habitats with less or more woody cover.

The relationships between the average values of presence of 87 bird species relative to rainfall and woody cover are not linear but exponential (Figure 15). The ratio between observed and expected (derived from the exponential function given in Figure 15) woody cover per bird species and expected woody cover were calculated for all bird species as a mean. This quantified to what degree bird species differed in their preference for areas with a higher or lower than expected woody cover. Among the granivores, two weavers, five sparrows and three finches were recorded in relatively woodier habitat within the rainfall zone of occurrence than three (sparrow)-larks and Four-banded Sandgrouse *Pterocles quadricinctus*, with a preference for a more open landscape (Figure 16). Among the insectivores, three lark species, Tawny Pipit *Anthus campestris*, Whinchat and Black-headed Lapwing preferred a more open landscape than expected. Other

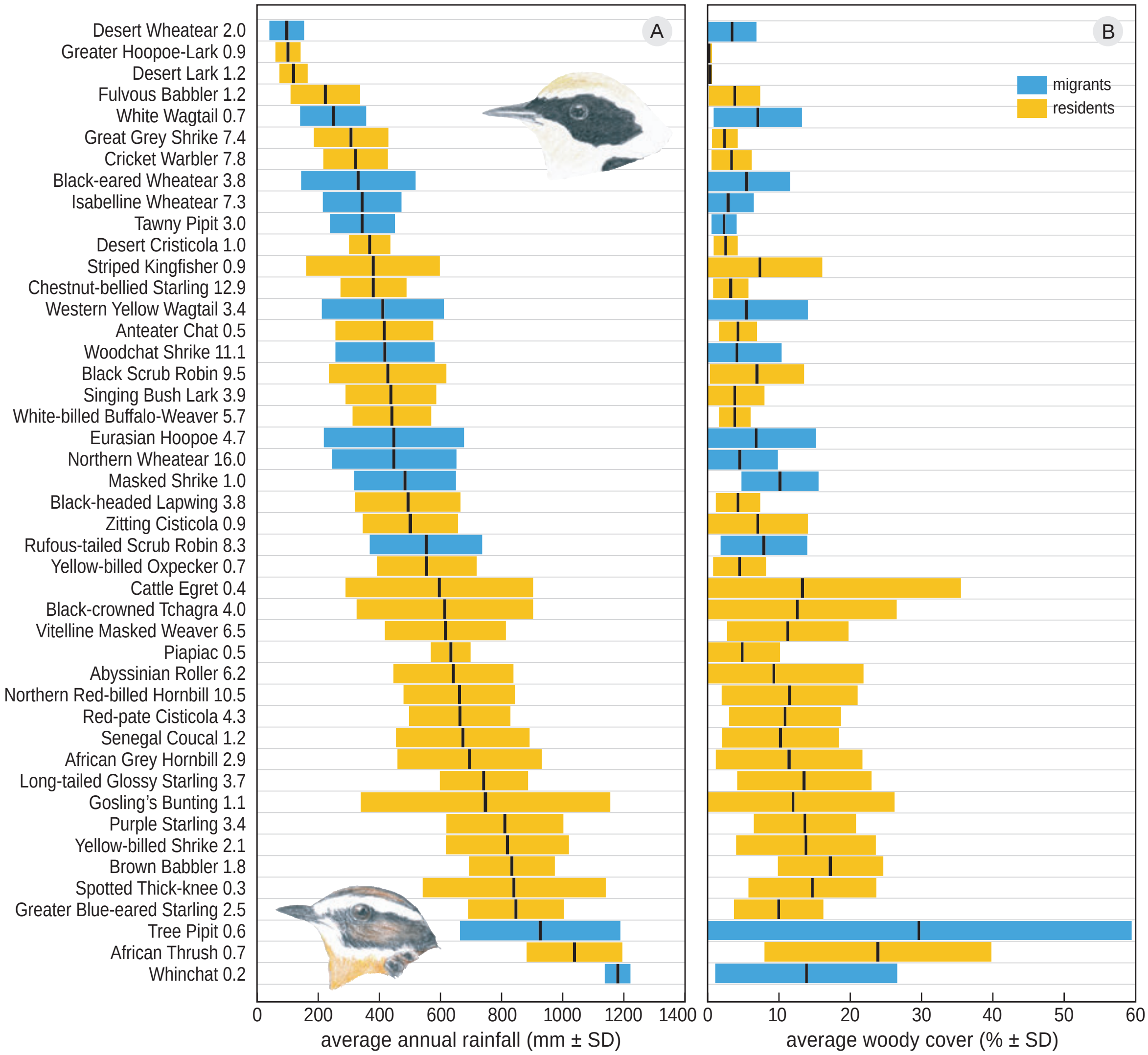

Figure 14. (A) Average rainfall and (B) average woody cover (±SD) in the study sites where a species was present for 46 most common insectivorous bird species, 13 migrants (including Eurasian Hoopoe and Rufous-tailed Scrub Robin, although partly resident) and 33 residents. The numbers after the bird names indicate in how many sites a bird species was present (%); excluding sites from the Ethiopian Highlands (>700 m above sea level).

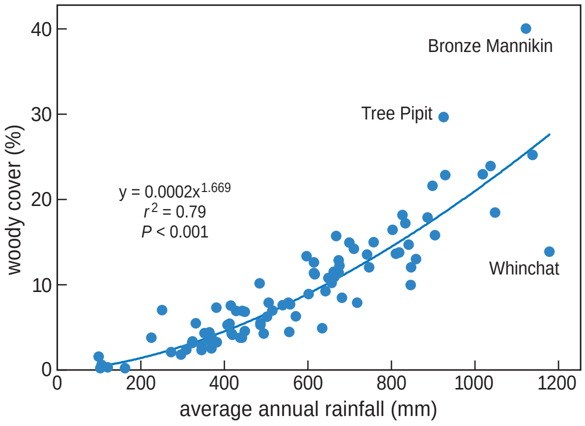

Figure 15. The relationship between woody cover (%) and average annual rainfall (mm) averaged for study sites where 41 granivorous (same data as Figure 13) and 46 insectivorous (same data as Figure 14) bird species were present. Bronze Mannikins and Tree Pipits are bound to relatively woody areas, whereas Whinchats select relatively open areas.

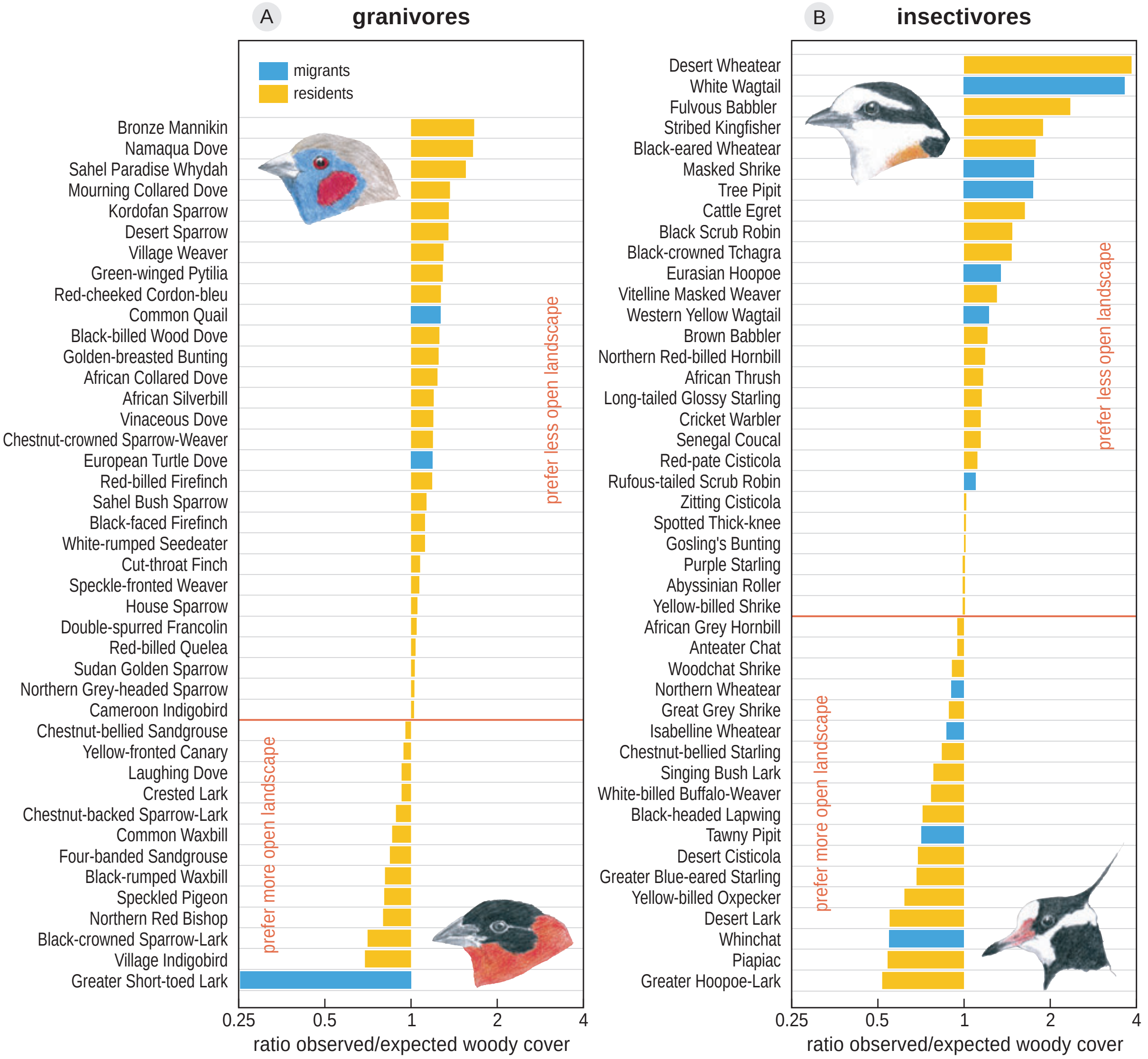

Figure 16. The preference of (A) 41 granivorous and (B) 46 insectivorous ground-foraging birds for open landscape, independent of rainfall, expressed as the ratio between observed and expected woody cover (as derived from Figure 15) in the study sites where the different bird species were recorded (Figure 12B and 13B). Note log scale on horizontal axis.

insectivores were recorded more in woodier habitat than expected, e.g. two babblers, Tree Pipit, Black Scrub Robin *Cercotrichas podobe*, Masked Shrike, Eurasian Hoopoe and Cricket Warbler. Wheatears did not show a clear preference for more open or closed landscapes. The Desert Wheatear inhabited extremely dry and bare landscapes but they were mainly found in the few sites with some vegetation.

The distribution of bird species was determined mainly by rainfall and less by longitude, but the relationship between bird density and rainfall differed per longitude, i.e. the interaction term is significant in 22 of the 43 bird species (Table S1). Consequently, bird densities were investigated separately per rainfall class and per longitude (Figure S2–S44).

Numbers

We used a split-half method to assess the reliability of the estimated total number. The deviations of the split-half estimates were relatively large in species feeding in flocks (Figure 12), e.g. in Red-billed Quelea (deviation 43%) and four starling species (34%). In contrast, the deviation was remarkably small in solitary foraging species, e.g. the three wheatear species (11%) and three shrike species (9%). The estimate for insectivores was reliable for migrants but less so for residents (Table 2).

The total number of ground-foraging birds within the region is estimated at 5118 million birds, of which 7% (354 million) were migrants and 93% (4764 million) residents. Granivores (4203 million, 82%) were more common than insectivores (915 million, 18%). The seven most common ground-foraging birds were granivores, of which three were particularly abundant: Red-cheeked Cordon-bleu (467 million birds; Figure S39), Sudan Golden Sparrow (375 million; Figure S32) and Red-billed Quelea (311 million; Figure S35). The Bronze Mannikin *Spermestes cucullata* is another common seedeater, but it was recorded only in the humid zone (>1000 mm/year): our estimate (208 million birds) seems accurate (range: 198–218 million), but more than half of the bird numbers were interpolated (113 million) and the total estimate is therefore less reliable.

The most common migrant was the Greater Short-toed Lark, occurring in the arid zone (<500 mm rain) from Senegal to Ethiopia. This species foraged in small flocks in the Western Sahel, but it was more abundant in larger flocks in Sudan and Ethiopia. For an accurate density estimate more counts are necessary to validate whether the 245 birds/km^2 in Sudan at 100–200 mm rainfall and 116/km^2 in Ethiopia at 400–500 mm rainfall were outliers or not, due to the presence of several large flocks in our sites (Figure S18). On the other hand, in between sites we observed the species in even larger flocks, suggesting that the calculated densities might be accurate. Nonetheless, the estimate of the total number of the Greater Short-toed Lark should be regarded as preliminary: 2.7 million in Ethiopia (where less common than Thekla's Lark *Galerida theklae*, but more common than Blanford's Lark *Calandrella blanfordi*), 21.4 million along the southern edge of the Sahara in Chad and 10.2 million further west. The largest numbers, an estimated 91.3 million, were recorded in Sudan where sandy and rocky grassland and extensive treeless croplands were inhabited. Out of a total of 126 million birds, 25 million were interpolated.

Table 2. Population estimates (millions) of granivorous and insectivorous migrants and residents. Minimum and maximum refer to two estimates based on half of the data. Deviation is a measure of reliability and defined as the average deviation of both split half estimates from the estimate based on all data. See Supplementary Material 1 how the population size of bird species was estimated and partly interpolated. Migratory insectivores include the partly residents Eurasian Hoopoe (10.4 million) and Rufous-tailed Scrub Robin (19.3 million).

Status	migrants		residents	
Food	gran.	ins.	gran.	ins.
Population	133	221	4070	694
Interpolated	26	40	1829	262
Minimum	114	213	3639	596
Maximum	152	229	4528	789
Deviation (%)	14.3	7.2	21.8	27.8

Twenty-four migratory ground-foraging species, either rare or with a limited distribution area, are not included in Supplementary Material 1. Twelve out of these 24 were so rarely encountered that an estimate of the total number present was impossible. Eurasian Stone-curlew *Burhinus oedicnemus* (Senegal), European Nightjar *Caprimulgus europaeus* (Burkina Faso), Blue Rock Thrush *Monticola solitarius* (Ethiopia) and Meadow Pipit *Anthus pratensis* (Senegal) were each recorded but once. Rufous-tailed Rock Thrush *Monticola saxatilis* (one in Burkina Faso, one in Chad, three in Ethiopia), Black Redstart *Phoenicurus ochruros* (four in Ethiopia), White-crowned Wheatear *Oenanthe leucopyga* (two in Ethiopia), and Grey Wagtail *Motacilla cinerea* (five in Ethiopia) were recorded in very small numbers. Two wetland birds were incidentally seen in our dryland plots, although they were common on floodplains (Sedge Warbler *Acrocephalus schoenobaenus*) and in mangroves (Eurasian Reed Warbler *Acrocephalus scirpaceus*). Two other wetland species wintering south of our region were seen once in the winter months: Common Grasshopper Warbler *Locustella naevia* and Great Reed Warbler *Acrocephalus arundinaceus*. Common Quail was recorded occasionally in Senegal (4), Niger (1), Sudan (3) and Ethiopia (1).

Small flocks of European Turtle Doves were seen flying between roost and feeding ground in early morning and late evening in Senegal, Mali and Chad, but altogether we encountered just 46 birds in our fixed study sites, of which 31 birds in three sites in Chad. The total number is estimated at 4.2 million birds, of which 0.9 million were interpolated; range (split half method): 0.2–8.2 million. The clustered presence of this species prevents an accurate estimate of the numbers in the region.

Cream-coloured Coursers *Cursorius cursor* were seen only in the arid regions where annual rainfall was <200 mm (10 in Mauritania, 3 in Sudan, 7 in Ethiopia). Total estimate: 1.8 million birds, of which 1.0 million were interpolated; range (split half method): 0.9–2.6

million. Most of the birds spend the northern winter north of 22°N, i.e. beyond the region covered in this study.

The Isabelline Shrike *Lanius isabellinus* was observed only in Sudan (0.5 million birds at 100–300 mm rain) and Ethiopia (5.2 million at 200–1000+ mm rain). Total estimate: 5.7 million; none were interpolated; range (split half) 2.4–8.9 million. Most of the birds spend the northern winter south of 7°N, i.e. beyond the region covered in this study.

The Whinchat was confined to regions in the rainfall zone >1000 mm, with a maximal density in the Central African Republic (8.1/km^2). Total estimate: 4.0 million birds, of which 0.7 million were interpolated; range (split half) 0.5–7.4 million. Most of the birds winter south of the region covered in this study.

The Siberian Stonechat *Saxicola maurus* was recorded only in Ethiopia in the rainfall zone 500–1000 mm and in Sudan in the rainfall zone 100–500 mm. The population estimate: 1.7 million birds; range (split half) 0.6–2.7 million. Most of the birds winter south of the region covered in this study.

The Desert Wheatear was more common in the eastern than in the western part of the Sahel, but always restricted to the driest zones, i.e. <200 mm rain in Chad and further west and <300 mm in Sudan and

Photo 2. The diversity of landscape types in Ethiopia is very large. (A) The bare plains in the highlands (3180 m above sea level; 11.800°N, 39.010°E; 6 February 2019) look Sahel-like, but the average, annual rainfall amounts to 1080 mm. (B) Highlands are converted into cropland whenever possible, with scattered trees providing food and shelter for birds (2470 m above sea level; 620 mm rainfall/year; 14.273°N, 39.651°E; 12 February 2019). Ground-feeding birds are common nearly everywhere (Figure 11), profiting from the high food supply on the clayish, fertile ground. This habitat is the main wintering ground of Red-throated Pipit *Anthus cervinus*.

Ethiopia. The total population is estimated at 18.5 million, of which 10.0 million were interpolated; range (split half): 18.2–18.9 million. Most of the birds winter north of the region covered in this study.

Mourning Wheatears *Oenanthe lugens* were recorded exclusively in Ethiopia in regions where annual rainfall amounts to 600–1000 mm. The total population is estimated at 0.8 million birds, of which none were interpolated; range (split half): 0.8–0.9 million. Most of the birds winter north of the region covered in this study.

Pied Wheatear *Oenanthe pleschanka* recordings were restricted to Ethiopia and produced a density of 8 to 14 birds/ha in the zone with an annual rainfall >600 mm; the total population is estimated at 8.3 million birds; none were interpolated; range (split half): 8.5–10.4 million. Most of the birds winter south of the region covered in this study.

All but one Red-throated Pipit *Anthus cervinus* were recorded in Ethiopia, where it was common in regions where annual rainfall exceeded 500 mm (on average 12.3 birds/km^2). The total population is estimated at 8.5 million birds, of which none were interpolated; range (split half): 5.3–11.9 million. Most of the birds winter south of the region covered in this study.

White Wagtail *Motacilla alba* occurred in the most western (Mauritania, Senegal; 0.5 million) and most eastern part of the region (Sudan, Ethiopia; 2.5 million), mostly at about 300 mm rainfall/year, but with a wide range (65–608 mm rainfall/year). The total population is estimated at 3.0 million birds, of which 0.2 million were interpolated; range (split half): 2.5–3.6 million. Most of the birds winter north of the region covered in this study.

Ortolan Bunting was restricted to, and rather common in, Ethiopia in the zone with 500 to 900 mm rain (7 birds/km^2). The total population estimate: 2.5 million birds; range (split half) 0.5–7.4 million). The total wintering population is probably slightly larger given the fact that the Guinean Highlands and Jos Plateau in Nigeria, where the species is known to winter (Elgood *et al.* 1994, Selstam *et al.* 2015), were beyond the scope of our study.

DISCUSSION

Among the ground-foraging birds in the broader Sahel, granivorous species were more common than insectivorous species, and residents more common than migrants. Variations in the ratio granivorous-insectivorous were related to climate zones (Figure 17A). In the desert, insectivores were more common than granivores, but in the more humid zone, ground-foraging birds were mostly granivorous. The distribution of species (Supplementary Material 1) largely followed rainfall zones (see Figure 12A and 13A) and woody cover (Figure 13B, 14B and 16). Even so, not all species-specific distributions were related to rainfall zones, as can be illustrated with the distribution of dove species (Figure 17B based on Figure S2–S5). The Namaqua Dove is ubiquitous across the entire Sahel except eastern Ethiopia. The Laughing Dove is widely distributed and common throughout the Western Sahel and in Ethiopia, but Ring-necked Doves *Streptopelia capicola* are confined to Eastern Ethiopia. Similarly, the distribution of eight species of wheatears shows a complicated biogeographic variation (Figure 17C based on Figure S27–S29 for the three most common wheatears): Western and Eastern Black-eared Wheatears in the western and eastern Sahel, respectively, Pied Wheatear only in Ethiopia and Isabelline Wheatear in the eastern Sahel. Northern Wheatear was mostly found in the western and central parts of the Sahel (even extending into the more humid zone) but less so in the eastern Sahel where Isabelline Wheatear was by far the most common wheatear. The latter species in general occupied drier habitats further north than Northern Wheatear.

Despite distinct species-specific longitudinal variations in distribution, as shown for doves and wheatears, rainfall is the overriding factor explaining the distribution of birds in the 1600 km wide transition zone between Sahara and Guinean woodland. Not surprisingly, typical desert species were found exclusively in the most arid zone. Other bird species in the semi-arid and more humid zones were also distributed along rainfall zones (Figure 13A and 14A). Wheatears and larks were confined to the Sahara and Sahel, but it is not immediately obvious whether this is due to a preference for dry or open habitat per se since woody cover is highly related to rainfall. However, within the arid zone larks appeared to prefer a more open landscape (Figure 16). In contrast, other species from the arid zone, such as Cricket Warbler and Fulvous Babbler *Argya fulva*, inhabited dry habitats only when some vegetation was available. A functional explanation might be found in the way that different species cope with predation risk: larks prefer to forage in the open to minimise the risk of a surprise attack by a raptor, while most other ground-foraging species, such as the babblers, feed below and close to the woody vegetation which is used as a refuge when predation risk increases (Schneider 1984, Lima & Valone 1991, Schluter & Repasky 1991, Robinson & Sutherland 1999). Other ground-foraging species that were found more often in woody habitat than expected, given their preference for a specific rainfall zone, used trees as perches (e.g. Masked Shrike) or foraged also in the woody vegetation (e.g. Black Scrub Robin, Cricket Warbler). Shrubs and trees were also used as thermal refugium to avoid heat stress during the hottest hours of the day, when the temperature of the ground surface may exceed 50 or even 60°C (Zwarts *et al.* 2023f). The need to avoid such heat is evident given the widespread habit among birds of the (semi-)arid zone to search for shade, or when there is no shade from trees to search for a termite mound, stick or branch to escape the heat of the ground surface (Williams & Tieleman 2001, Dean & Williams 2004, Manu & Cresswell 2013, Martin *et al.* 2015).

Rainfall and woody cover are the overriding factors explaining the distribution of birds in the region, but small-scale variations on this general theme abounded. These were usually associated with specific conditions related to feeding, drinking and roosting. Gosling's Bunting *Emberiza goslingi* was confined to stony habitats and Yellow-billed Oxpecker *Buphagus africanus* occurred only where there were cattle. Western Yellow Wagtails were almost completely absent throughout the Sahel unless cattle were grazing in humid grasslands and riverbeds (offering plenty of opportunity for foraging on insects) or within flying reach of large wetlands (providing roosts, e.g. Inner Niger Delta, Senegal Delta; Figure S41). The large herds in the drylands of the Sahel were typically ignored by Western Yellow Wagtails. For granivorous birds the presence of water within 10 to 20 km of foraging spots is of crucial importance; a diet of seeds necessitates a drinking schedule with regular flights between foraging and drinking sites (e.g. Ward 1972, Molokwu *et al.* 2010).

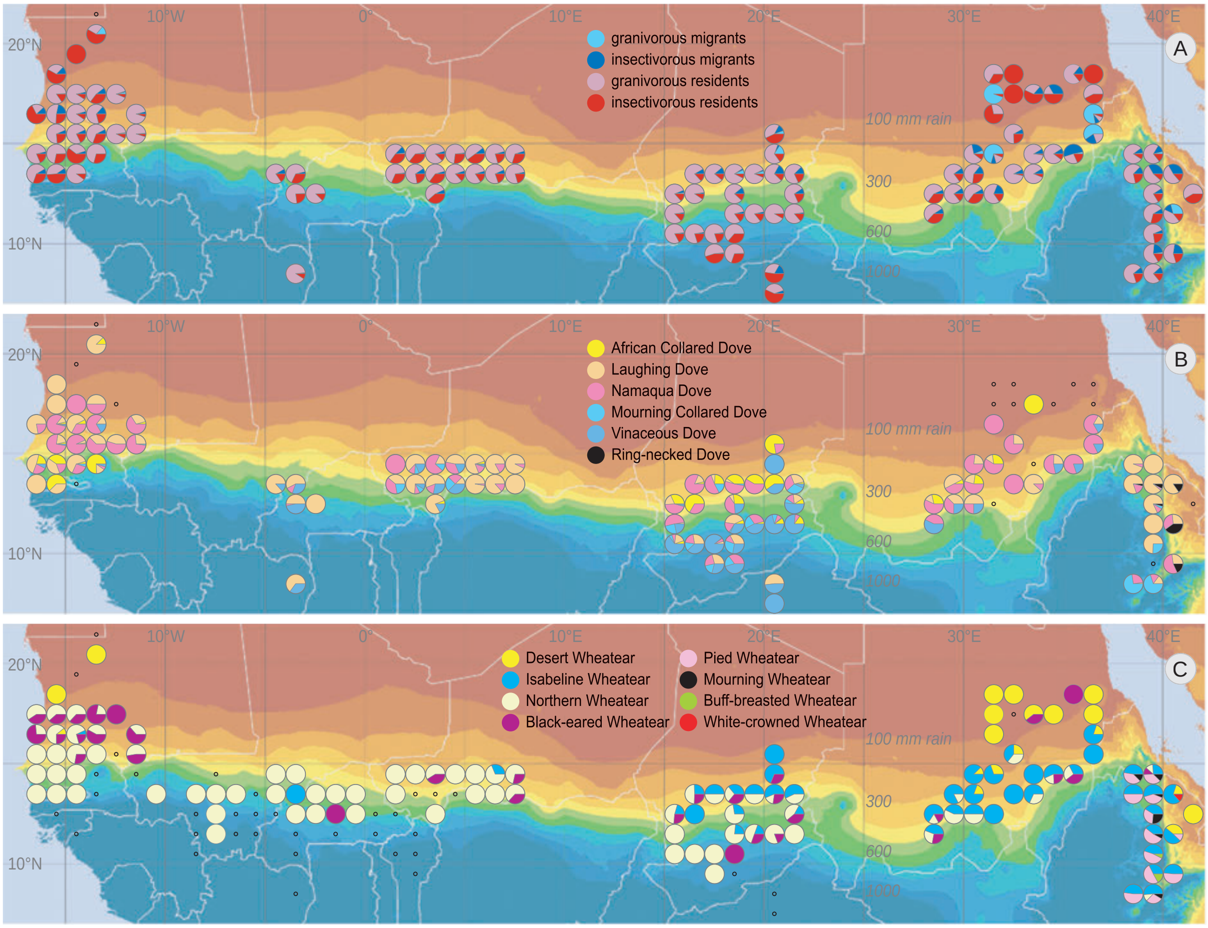

Figure 17. The relative occurrence of ground-foraging birds. (A) granivorous residents and insectivorous residents/migrants (no birds in 1 of 111 grid cells) , (B) six dove species (no doves in 16 of 111 grid cells), (C) eight wheatear species; same symbol used for Western and Eastern Black-Eared Wheatears (no wheatears in 35 of the 150 grid cells).

The dependence on water means that, particularly in dry years, large parts of the arid zone become unsuitable as feeding areas during the course of the dry season when water becomes scarcer (Morel & Morel 1978). As much as water can attract birds, so do bushfires during the dry season when they are widespread in the woody savannahs (Rano *et al.* 2021; see also Zwarts *et al.* 2023g). Purple Starling *Lamprotornis purpureus*, Chestnut-backed and Black-crowned Sparrow-Larks readily forage on burned ground, but Singing Bush Lark *Mirafra cantillans*, Cricket Warbler, Green-winged Pytilia *Pytilia melba* refrain from doing so (Morel & Morel 1978). Temporary and local conditions are evidently shaping the distribution of ground-foraging birds, but such subtle niceties fail to materialise on large-scale distribution maps (Figure S2–S44).

Within the overall impact of rainfall and woody cover on bird densities, some large variations in regional densities within the same rainfall zone could not be attributed to either rainfall or woody cover. This is particularly evident from the high density found for most ground-foraging bird species in Chad, granivores (Figure 11A) as well as insectivores (Figure 11C and 11D), compared to those found in the same climatic zone in the western Sahel (see Zwarts *et al.* 2023e for a detailed analysis). Variations in grazing pressure are likely involved, being higher in the western Sahel than in the central Sahel. Some bird species prefer bare foraging and may profit from a higher grazing pressure. This applies for sit-and-wait predators (Woodchat Shrike *Lanius senator*, Masked Shrike and Great Grey Shrike *Lanius excubitor*, Abyssinian Roller, Anteater Chat *Myrmecocichla aethiops*) and to a lesser degree also for wheatears and Tawny Pipit. Heavy grazing by livestock, on the other hand, negatively impacts ground-foraging species which prefer to forage in grassy vegetation (e.g. Desert Cisticola *Cisticola aridulu*s, Red-pate Cisticola *Cisticola ruficeps* and Zitting Cisticola *Cisticola juncidis*, Yellow-fronted Canary *Crithagra mozambica*, Black-rumped Waxbill *Estrilda troglodytes* and Common Waxbill *Estrilda astrild*). A high grazing pressure also reduces seed supply, with dire consequences for granivorous birds.

Our data collection covered the period between 2007 and 2019, in a Sahel that in many aspects had changed considerably from the region where our illustrious predecessors, like Gérard & Marie-Yvonne Morel (and many others), had paved the way. What would the maps have looked like if a similar study had been carried out 50 years earlier? The snippets of historical information suggest that the losses in the intervening period have been great. Densities of Common Quail in N Senegal declined from 2.6/km^2 in the 1960s (Morel 1968; 11 Quails on 425 ha) to 0.1/km^2 half a century later (own data; 3 Quails on 2709 ha). In Mali in the 1970s Lamarche (1980) recorded flocks of dozens of Quails, assessing the species as wintering "in large numbers" in the Sahel and near the Inner Niger Delta where, according to Curry & Sayer (1979), they were "found throughout the drier areas". In Chad the species was described as "a common migrant (..), occurring wherever suitable vegetation was available, mainly south of 15°N" (Newby 1979). In neither country did we observe Quails in our study sites in 2012–2018 (1091 ha surveyed in Mali and 1048 ha in Chad). Or take Greater Short-toed Larks, for which Salvan (1967) mentioned flocks of 100 to 1000 in Chad between 14 and 17°N. In Mali they were in the early 1970s still "locally common, occurring in large flocks" (Curry & Sayer 1979) of five to ten thousand birds, and even more (Lamarche 1981). Flocks of similar size were still seen in Mauritania until 1997 (Browne 1982, Isenmann *et al.* 2010). In the same regions we noted only a few groups of some individuals in the 2010s, and larger groups (i.e. hundreds) only in Sudan (Figure S20). During our survey, Tawny Pipits were rare in West Africa (Figure S42), but they were still common in central Mali in 1960, even occurring in flocks (Duhart & Descamps 1963), and in the early 1970s still frequenting "a wide variety of habitats (..) found in most situations" (Curry & Sayer (1979). The few European Turtle Doves we recorded in the western Sahel, exclusively in the vicinity of the Senegal River in NW Senegal and the Inner Niger Delta in Mali, were a pitiful reminder of the millions that spent the winter in these regions only half a century ago (Curry & Sayer 1979, Morel & Morel 1987).

In NW Senegal, systematic bird counts have been carried out in 1960/1962 (Morel 1968), 1969/82 (Morel & Morel 1992) and in 1993/94 (Tréca *et al.* 1996). A comparison with our more recent counts in the same area revealed a tremendous decline of all ground-foraging bird species (Zwarts *et al.* 2018), but whether these declining trends in NW Senegal are representative for the entire Sahel is still the question, as further discussed in Zwarts *et al.* 2023e. We will use the data presented here to separately investigate the impact of the large-scale conversion of savannah into farmland on ground-foraging birds (Zwarts *et al.* 2023d) and to compare the wintering totals in the wider Sahelian region with the size of breeding populations of the respective bird species (Zwarts *et al.* 2023b).

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SAMENVATTING

Dit artikel beschrijft het voorkomen en de dichtheid van op de grond foeragerende vogelsoorten in de noordelijke helft van Afrika, in de brede overgangszone tussen de aride Sahara in het noorden en de natte tropische bossen in het zuiden. Gelegen tussen 17°W en 42°O en tussen 7° en 22°N gaat het om een gebied van 6000 bij 1600 km, in totaal bijna 10 miljoen km^2. Dat betreft een areaal zo groot als het hele Europese continent. Het gebied beslaat 833 cellen van één lengtegraad bij één breedtegraad (ruwweg 100 × 100 km, enigszins variërend afhankelijk van de breedtegraad), waarvan in 150 (18%) cellen vogeltellingen werden uitgevoerd. We deden dat tussen 2011 en 2019 in 1901 telvakjes van 4,5 ha. De telvakjes waren willekeurig gekozen, en zijn als zodanig representatief voor de omgeving en geschikt om een schatting te maken van het totale aantal vogels dat in het gebied verblijft. Door logistieke en veiligheidsproblemen was de dekking van het gebied in het westen beter dan in het oosten (meer gradencellen bemonsterd). Vergeleken met het aanbod van de verschillende habitattypes waren de woestijn en de natte bossen ondervertegenwoordigd in de tellingen (wat een correctie noodzakelijk maakte, zie hieronder). De tellingen werden uitgevoerd tussen 20 november en 10 maart, overeenkomend met het droge seizoen (vrijwel alle regen valt tussen juli en september). Vogels die op de grond foerageren, eten zaden of insecten. In het hier beschreven gebied gaat het vooral om 'lokale' vogels, dat wil zeggen soorten die ten zuiden van de Sahara broeden. In de winterperiode komen hier nog trekvogels uit Noord-Afrika, Europa, Azië en zelfs Noord-Amerika bij. Het artikel geeft eerst achtergrondinformatie over het studiegebied, met kaarten die variaties in hoogteligging, regenval, boombedekking, landgebruik en menselijke bevolkingsdichtheid laten zien. Voor 43 vogelsoorten worden verspreidingskaartjes gegeven met de gemiddelde dichtheid in de 150 gradencellen. De verspreiding van de verschillende vogelsoorten was voornamelijk gerelateerd aan de jaarlijkse regenval. Aangezien de boombedekking toeneemt met de regenval, was de voorkeur voor meer droge of meer natte zones voor een deel toe te schrijven aan een voorkeur voor een open of een meer gesloten landschapstype. Vogelsoorten zoals leeuweriken en Duinpieper *Anthus campestris* selecteerden binnen de zone waar ze voorkwamen een relatief meer open landschap, terwijl soorten die op de grond bij bomen foerageerden of deze als rustplek gebruikten (bijv. mussen, vinken, klauwieren, Boompieper *Anthus trivialis*) de voorkeur gaven aan een relatief meer besloten omgeving. Gezien de ondervertegenwoordiging van woestijn en nat bos was een correctie nodig om de totale populatieomvang goed te kunnen schatten. Daartoe werden de 150 gradencellen samengevoegd in elf categorieën van droog (minder dan 100 mm regenval per jaar, 100–200 mm, enz.) tot heel nat (meer dan 1000 mm regen) en in zes lengtegraadzones, met Mauritanië, Senegal en Guinee-Bissau als meest westelijke en Ethiopië als meest oostelijke zone. De gemiddelde vogeldichtheid werd voor al deze deelzones berekend en vermenigvuldigd met hun oppervlaktes om tot een totaalschatting te komen. De betrouwbaarheid van deze schattingen werd getoetst door de 1901 telvakjes in tweeën te splitsen en alle populatieschattingen te herhalen voor de even en de oneven genummerde vakjes. De geschatte populatiegroottes bleken nauwkeurig te zijn voor trekvogels, vooral voor insecteneters (7% afwijking voor de gesplitste schattingen), maar minder nauwkeurig voor Afrikaanse vogelsoorten (22–28% afwijking). De meeste vogels die op de grond foerageerden, waren zaadeters (of alleseters, hier als zaadeter beschouwd omdat de tellingen plaatsvonden in het droge seizoen wanneer deze vogels vrijwel uitsluitend zaden eten). Het totale aantal zaadeters werd geschat op vier miljard lokale vogels en 133 miljoen trekvogels. Op de grond foeragerende insecteneters waren minder talrijk, met in totaal 915 miljoen vogels, waarvan 694 miljoen lokale vogels en 221 miljoen trekvogels. De drie meest voorkomende lokale zaadeters waren Blauwfazantje *Uraeginthus bengalus* (467 miljoen), Bruinruggoudmus *Passer luteus* (375 miljoen vogels) en Roodbekwever *Quelea quelea* (311 miljoen). De Kortteenleeuwerik *Calandrella brachydactyla* (126 miljoen) was onder de trekvogels de enige talrijke zaadeter. Van de op de grond foeragerende insecteneters was een lokale soort het meest algemeen Groenstaartglansspreeuw *Lamprotornis chalybaeus*: 100 miljoen). Alle op de grond foeragerende insectenetende trekvogels waren veel minder algemeen, zoals Izabeltapuit *Oenanthe isabellina* (32 miljoen), Tapuit *Oenanthe oenanthe* (27 miljoen) en Gele Kwikstaart *Motacilla flava* (24 miljoen).

RÉSUMÉ

Cet article fournit des densités et estimations de population d’espèces d’oiseaux granivores et insectivores se nourrissant au sol dans la zone de transition entre le Sahara aride au Nord et les forêts humides de la zone Soudano-Guinéenne au Sud. Située entre les longitudes 17°O et 42°E et entre les latitudes 7°N et 22°N, cette vaste étendue couvre une superficie 10 millions de km^2, équivalente à celle du continent européen. Entre 2011 et 2019, 150 des 833 cellules d’un degré de longitude par un degré de latitude que couvre cette zone ont fait l’objet d’inventaires lors de la saison sèche, qui correspond à l’hiver boréal (20 novembre au 10 mars). Les comptages ont été réalisés au sein de 1901 carrés de 4,5 ha sélectionnés aléatoirement selon une méthode d’échantillonnage stratifié. Les difficultés logistiques et sécuritaires rencontrées ont conduit à une moindre couverture de la partie orientale de la zone. Tous les habitats ont été parcourus, mais avec une sous-représentation du désert et des forêts humides. Les espèces concernées sont principalement afro-tropicales et sédentaires, mais elles sont rejointes en hiver par des migrateurs venus d’Afrique du Nord, d’Europe, d’Asie et même d’Amérique du Nord. L’article décrit le contexte physique et biologique de la zone d’étude grâce à des cartes du relief, des précipitations, du couvert arboré, de l’utilisation des sols et de la densité de population humaine. Il présente ensuite des cartes des densités moyennes pour 43 espèces d’oiseaux. La répartition de ces espèces est avant tout corrélée aux hauteurs de précipitations annuelles, dont dépend également le taux de couverture arborée. Les espèces montrant une préférence pour les paysages ouverts fréquentent donc des zones en moyenne plus sèches que celles liées aux paysages plus boisés. Les alouettes et le Pipit rousseline *Anthus campestris* sélectionnent les habitats les plus ouverts disponibles, tandis que les espèces qui se nourrissent au pied des arbres ou les utilisent comme perchoirs, telles que les moineaux, pinsons, piesgrièches et le Pipit des arbres *Anthus trivialis* préfèrent des habitats plus arborés. La sous-représentation des forêts sèches et humides dans l’échantillon inventorié a nécessité une correction. Les 150 cellules ont été regroupées en onze classes de pluviométrie, de sec (moins de 100 mm de pluie par an, 100–200 mm, etc.) à très humide (plus de 1000 mm de pluie) et en six bandes de longitude. Les densités moyennes ont été calculées pour chacune de ces entités et multipliées par leurs superficies pour obtenir les estimations de populations. La fiabilité de ces estimations a été testée en divisant par deux les 1901 carrés de comptage et en calculant séparément les populations pour les carrés pairs et impairs. Les estimations se sont avérées précises pour les migrateurs, en particulier pour les espèces insectivores (écart de 7 % entre les populations calculées), mais moins pour les espèces sédentaires (écart de 22 à 28 %). La plupart des oiseaux se nourrissant au sol sont granivores, bien que certaines, en réalité omnivores, ne le soient que lors de la saison sèche au cours de laquelle les ressources alimentaires sont essentiellement constituées de graines. Le nombre total de granivores a été estimé à quatre milliards d'oiseaux sédentaires et 133 millions de migrateurs. Les insectivores se nourrissant au sol, moins abondants, totalisent 915 millions d’individus, dont 694 millions d'oiseaux sédentaires et 221 millions de migrateurs. Les trois granivores locaux les plus abondants sont le Cordonbleu à joues rouges *Uraeginthus bengalus* (467 millions), le Moineau doré *Passer luteus* (375 millions d’oiseaux) et le Travailleur à bec rouge *Quelea quelea* (311 millions). L’Alouette calandrelle *Calandrella brachydactyla* (126 millions) est la seule espèce migratrice granivore abondante. Parmi les insectivores, l’espèce la plus abondante est le Choucador à oreillons bleus *Lamprotornis chalybaeus*, qui est sédentaire (100 millions). Les migrateurs insectivores terrestres, tels le Traquet isabelle *Oenanthe isabellina* (32 millions), le Traquet motteux *Oenanthe oenanthe* (27 millions) et la Bergeronnette printanière *Motacilla flava* (24 millions), sont bien moins abondants.

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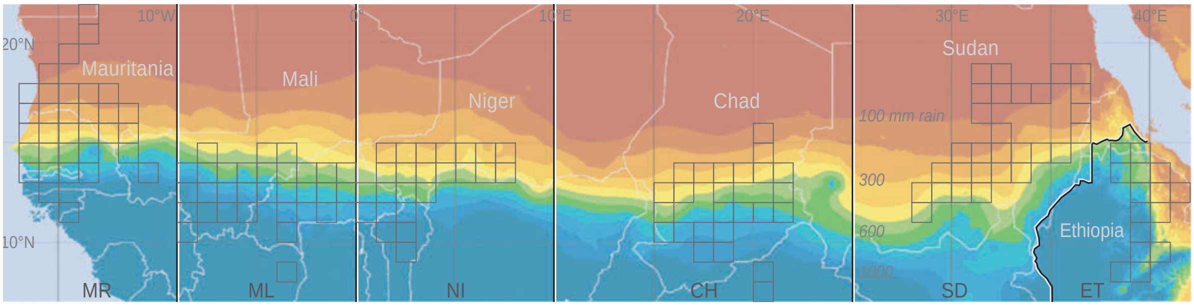
SUPPLEMENTARY MATERIAL 1: Distribution maps for 43 ground-foraging bird species

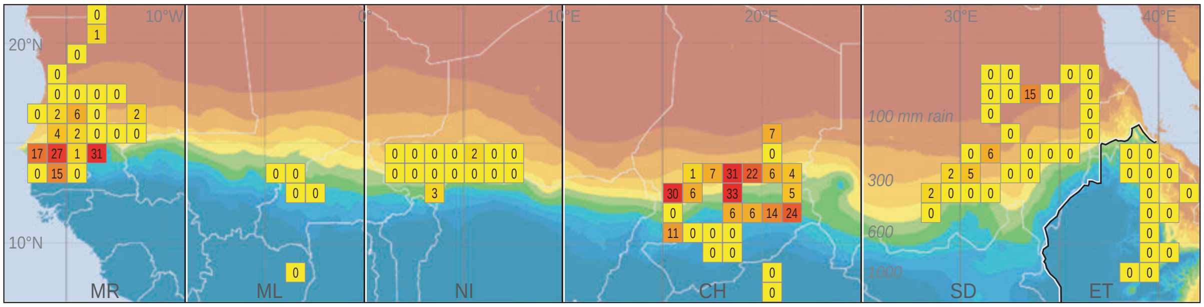
Table S1. Explained variance (r^2) in covariance analyses with bird density as a function of four variables: woody cover (covariate), longitude (6 classes), rainfall (11 classes), land use (3 classes: farmland, savannah, woodland) as main effects and 4 interaction terms; 'all' is the explained variance of variables together, including interaction terms. Also given number of sites, % presence in sites, % presence and average density/km^2 in the grid cells (see Figures S2–S44 above).
Level of significance: $P <$ 0.05, $P <$ 0.01, $P <$ 0.001.

Fig.	Bird species	w.cover	longit.	rainfall	land use	long×rain	long×use	rain×use	l×r×u	all	sites	%cells	%sites	n/km^2
S2	African Collared Dove	0.005	0.005	0.020	0.001	0.017	0.001	0.019	0.008	0.112	1173	31	4.7	3.2
S3	Mourning Collared Dove	0.000	0.022	0.038	0.000	0.021	0.022	0.036	0.008	0.172	1173	25	4.4	3.3
S4	Vinaceous Dove	0.008	0.022	0.061	0.003	0.064	0.010	0.127	0.022	0.360	1173	38	10.1	9.9
S5	Laughing Dove	0.000	0.003	0.010	0.001	0.024	0.004	0.007	0.006	0.115	1173	70	20.9	17.7
S6	Black-billed Wood Dove	0.008	0.014	0.011	0.004	0.029	0.007	0.027	0.010	0.179	1173	14	3.7	2.6
S7	Namaqua Dove	0.012	0.005	0.004	0.003	0.009	0.003	0.003	0.003	0.080	1173	68	18.3	12.4
S8	Black-headed Lapwing	0.003	0.005	0.020	0.002	0.023	0.013	0.006	0.007	0.089	1173	25	3.4	2.2
S9	Eurasian Hoopoe	0.000	0.002	0.010	0.000	0.023	0.005	0.013	0.017	0.095	1901	35	4.9	1.3
S10	Northern Red-billed Hornbill	0.024	0.032	0.019	0.015	0.027	0.011	0.020	0.016	0.219	1173	14	9.7	6.3
S11	Abyssinian Roller	0.006	0.058	0.052	0.004	0.064	0.059	0.059	0.087	0.305	1613	37	5.8	1.9
S12	Great Grey Shrike	0.001	0.001	0.006	0.000	0.020	0.005	0.006	0.008	0.121	1901	34	6.9	1.5
S13	Woodchat Shrike	0.000	0.011	0.010	0.003	0.033	0.006	0.011	0.008	0.164	1901	39	10.6	2.0
S14	Masked Shrike	0.002	0.050	0.021	0.007	0.064	0.026	0.028	0.069	0.152	1901	13	1.2	0.6
S15	Black-crowned Sparrow-Lark	0.003	0.000	0.004	0.001	0.011	0.001	0.001	0.001	0.055	1173	42	9.9	11.1
S16	Chestnut-backed Sparrow-Lark	0.000	0.009	0.008	0.000	0.054	0.005	0.006	0.027	0.137	1173	50	10.6	11.0
S17	Singing Bush Lark	0.001	0.005	0.007	0.003	0.039	0.006	0.019	0.037	0.105	1613	20	3.6	1.8
S18	Greater Short-toed Lark	0.000	0.002	0.001	0.001	0.047	0.000	0.011	0.001	0.084	1901	11	1.3	10.0
S19	Red-pate Cisticola	0.000	0.033	0.006	0.005	0.058	0.030	0.012	0.041	0.305	1613	13	4.0	2.7
S20	Cricket Warbler	0.000	0.002	0.009	0.001	0.018	0.001	0.005	0.010	0.101	1613	36	7.2	4.4
S21	Greater Blue-eared Starling	0.001	0.000	0.008	0.002	0.011	0.001	0.014	0.002	0.123	1173	21	3.5	7.1
S22	Purple Starling	0.000	0.006	0.007	0.005	0.020	0.010	0.030	0.021	0.144	1173	14	3.1	3.6
S23	Long-tailed Glossy Starling	0.005	0.004	0.019	0.002	0.017	0.004	0.015	0.018	0.154	1173	22	3.3	3.3
S24	Chestnut-bellied Starling	0.000	0.002	0.004	0.000	0.011	0.001	0.001	0.001	0.059	1173	41	11.7	12.6
S25	Black Scrub Robin	0.002	0.006	0.014	0.003	0.038	0.004	0.012	0.022	0.147	1613	39	8.8	2.8
S26	Rufous-tailed Scrub Robin	0.004	0.008	0.014	0.008	0.060	0.021	0.045	0.078	0.212	1901	48	8.2	2.7
S27	Northern Wheatear	0.000	0.006	0.010	0.001	0.044	0.002	0.009	0.024	0.168	1901	51	15.1	3.9
S28	Isabelline Wheatear	0.001	0.045	0.046	0.000	0.095	0.005	0.007	0.024	0.340	1901	31	9.4	4.2
S29	W.+E. Black-eared Wheatear	0.001	0.023	0.012	0.001	0.040	0.017	0.012	0.008	0.127	1901	21	3.6	1.1
S30	Sahel Bush Sparrow	0.006	0.007	0.047	0.006	0.036	0.003	0.005	0.007	0.182	1173	21	4.0	2.6
S31	Northern Grey-headed Sparrow	0.002	0.012	0.009	0.004	0.052	0.011	0.025	0.053	0.143	1173	53	17.0	18.3
S32	Sudan Golden Sparrow	0.000	0.001	0.007	0.000	0.017	0.002	0.001	0.005	0.071	1173	59	24.3	90.0
S33	Speckle-fronted Weaver	0.001	0.016	0.019	0.001	0.045	0.011	0.009	0.022	0.199	1173	45	15.3	15.8
S34	Vitelline Masked Weaver	0.019	0.020	0.008	0.011	0.042	0.006	0.016	0.021	0.143	1173	28	5.9	6.0
S35	Red-billed Quelea	0.004	0.000	0.007	0.002	0.008	0.003	0.003	0.011	0.087	1173	36	7.3	39.6
S36	African Silverbill	0.006	0.009	0.007	0.011	0.052	0.015	0.016	0.045	0.117	1173	49	9.1	10.2
S37	Black-rumped Waxbill	0.001	0.007	0.004	0.000	0.067	0.010	0.017	0.054	0.188	1173	10	1.9	6.0
S38	Cut-throat Finch	0.001	0.001	0.008	0.001	0.018	0.003	0.007	0.017	0.069	1173	23	3.2	5.1
S39	Red-cheeked Cordon-bleu	0.029	0.036	0.033	0.016	0.057	0.021	0.023	0.037	0.414	1173	49	17.6	40.0
S40	Red-billed Firefinch	0.011	0.001	0.005	0.006	0.005	0.002	0.004	0.006	0.091	1173	30	4.2	6.8
S41	Western Yellow Wagtail	0.000	0.004	0.006	0.004	0.034	0.011	0.009	0.026	0.117	1901	16	4.4	3.2
S42	Tawny Pipit	0.000	0.003	0.017	0.001	0.022	0.005	0.012	0.009	0.078	1901	21	2.9	0.9
S43	Tree Pipit	0.008	0.001	0.007	0.002	0.025	0.005	0.007	0.018	0.085	1901	10	1.3	0.9
S44	White-rumped Seedeater	0.000	0.012	0.019	0.001	0.042	0.013	0.019	0.022	0.164	1173	30	4.3	3.2



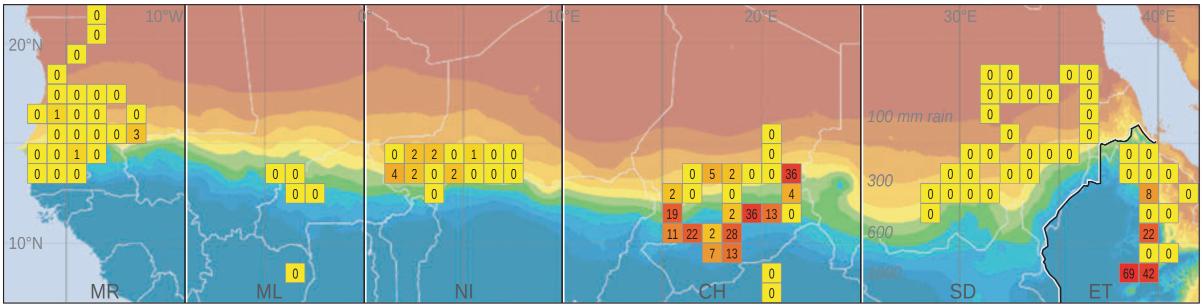
rain (mm)	MR	ML	NI	CH	SD	ET	total
<100	294	435	473	1101	778	0	3081
100–200	148	144	210	194	252	40	989
200–300	82	91	169	144	175	34	694
300–400	45	69	105	113	131	17	480
400–500	40	70	66	101	100	23	399
500–600	35	68	53	102	89	41	388
600–700	40	53	50	121	109	57	429
700–800	54	63	44	119	146	40	466
800–900	33	66	58	136	141	64	498
900–1000	23	72	56	152	53	71	427
>1000	300	473	500	398	84	279	2121
total	1183	1604	1783	2681	2058	665	9974

Figure S1. The delineation of 11 rainfall zones and six longitudinal bands used in the calculation of bird density. Bird density was measured in 150 grid cells (grey squares). The table gives land surface (x 1000 km²) per rainfall zone (mm rain/year) for six longitudinal bands between 7 and 22 °N in Africa. Two-letter codes refer to the main countries within the longitudinal band (MR=Mauritania, ML=Mali, NI=Niger, CH=Chad, SD=Sudan, ET=Ethiopia).
The measured or interpolated bird densities given in the tables are multiplied by the calculated land surface to arrive at an estimate of the total bird population present in the entire region.



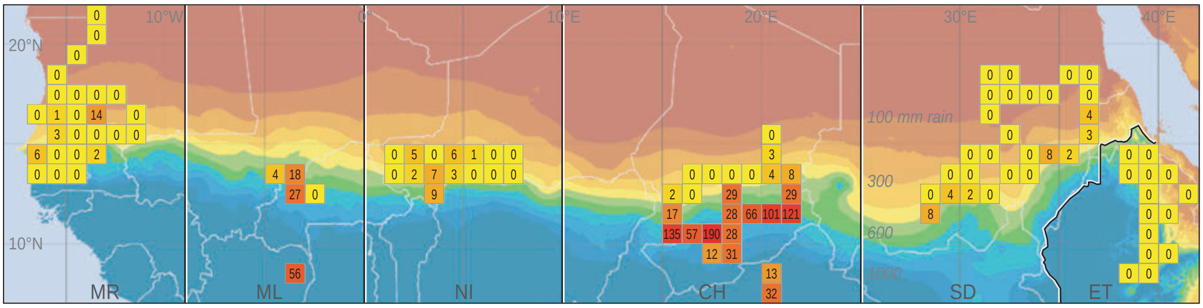
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.4	0.8	1.1	1.5	1.9	
100–200	0.0	2.2	4.5	6.7	1.2	0.0
200–300	2.9	1.4	0.0	0.0	3.7	0.0
300–400	2.0	1.3	0.5	11.1	0.8	0.0
400–500	1.6	0.8	0.0	19.4	0.0	0.0
500–600	0.0	0.0	0.0	4.1	0.0	0.0
600–700	9.8	0.0	4.0	17.2	17.2	0.0
700–800	22.2	0.0	5.1	10.1	10.1	0.0
800–900	3.4	3.4	3.4	3.4	3.4	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S2. African Collared Dove *Streptopelia roseogrisea* (n/km²).
Granivorous resident.
Present in 31% of the 111 cells.
Average density (n/km², ±SD) in grid cells: 3.2 ± 7.4.
Estimated overall density: 2.2/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 22.2 million, of which 8.6 million birds interpolated; range: 21.1–23.0 million (split-half).



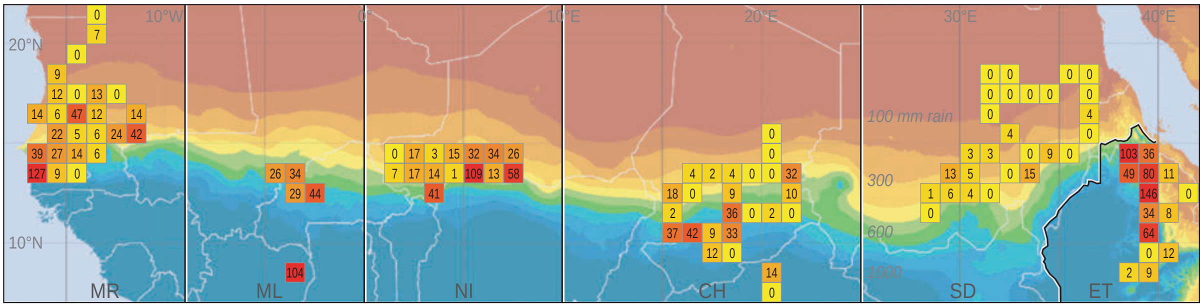
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	1.5	0.7	0.0	0.0	0.0	0.0
300–400	0.0	0.5	1.0	1.3	0.0	0.0
400–500	0.0	0.2	0.3	0.9	0.0	0.0
500–600	1.2	0.0	2.2	25.7	0.0	0.0
600–700	0.7	0.0	0.0	2.0	2.0	0.0
700–800	0.0	0.0	6.4	12.8	12.8	0.0
800–900	22.6	22.6	22.6	22.6	22.6	50.6
900–1000	8.5	8.5	8.5	8.5	8.5	14.0
>1000	0.0	0.0	0.0	0.0	0.0	12.7

Figure S3. Mourning Collared Dove *Streptopelia decipiens* (*n*/km²).
Granivorous resident.
Present in 25% of 111 cells.
Average density (*n*/km², ±SD) in grid cells: 3.3 ± 9.9.
Estimated overall density: 2.8/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR >800 mm and ML 800–1000 mm set to 0 (beyond distribution area).
Estimated total number: 28.1 million, of which 11.0 million birds interpolated; range: 20.0–35.9 million (split-half).



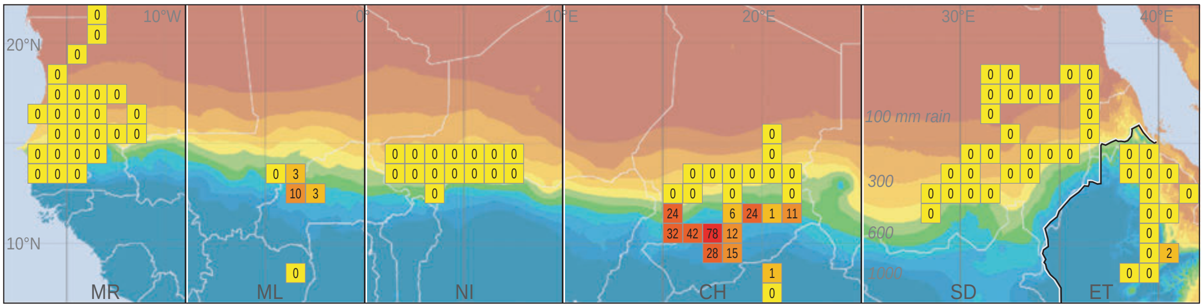
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	1.8	0.0
200–300	2.1	1.1	0.0	3.6	0.0	0.0
300–400	1.2	1.5	1.7	0.4	0.3	0.0
400–500	0.0	0.7	1.4	1.7	4.2	0.0
500–600	3.5	133.3	6.7	4.0	4.4	0.0
600–700	0.7	17.1	9.1	50.1	50.1	0.0
700–800	1.3	8.6	43.3	77.9	77.9	0.0
800–900	73.8	73.8	73.8	73.8	73.8	0.0
900–1000	66.6	66.6	66.6	66.6	66.6	0.0
>1000	55.9	55.9	39.0	22.1	22.1	0.0

Figure S4. Vinaceous Dove *Streptopelia vinacea* (*n*/km²).
Granivorous resident.
Present in 38% of the 111 cells.
Average density (*n*/km², ±SD) in grid cells: 9.9 ± 28.
Estimated overall density: 18.3/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 182.7 million, of which 97.5 million birds interpolated; range: 176.2–188.8 million (split-half).



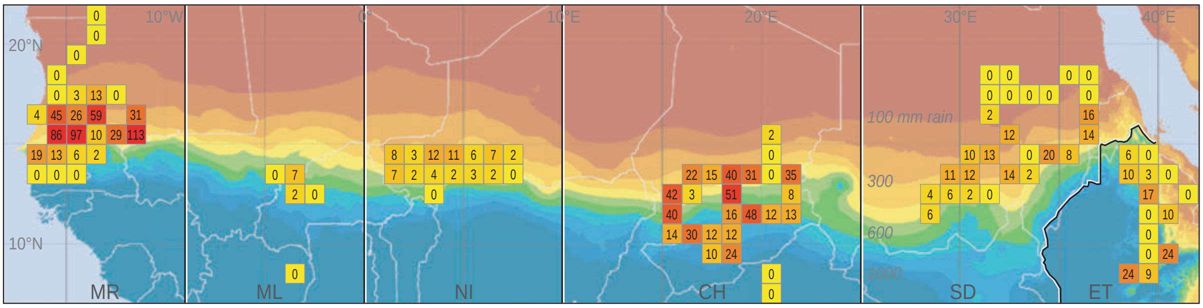
rain (mm)	MR	ML	NI	CH	SD	ET
<100	4.4	0.0	0.0	0.0	0.3	
100–200	4.7	3.1	1.5	0.0	2.4	0.0
200–300	22.4	49.5	76.6	2.5	3.7	0.0
300–400	19.8	21.3	22.9	5.4	4.6	0.0
400–500	12.7	19.8	26.8	1.7	4.4	19.8
500–600	10.1	0.0	0.0	12.0	0.0	40.6
600–700	47.4	44.9	59.0	11.3	11.3	99.2
700–800	5.2	28.0	23.5	19.0	19.0	33.3
800–900	25.0	25.0	25.0	25.0	25.0	38.2
900–1000	4.2	4.2	4.2	4.2	4.2	52.3
>1000	103.8	103.8	55.3	6.9	6.9	23.2

Figure S5. Laughing Dove *Spilopelia senegalensis* (n/km^2).
Granivorous resident.
Present in 70% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 17.7 ± 27.3.
Estimated overall density: 21.3/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 212.5 million, of which 94.2 million birds interpolated; range: 193.4–237.5 million (split-half).



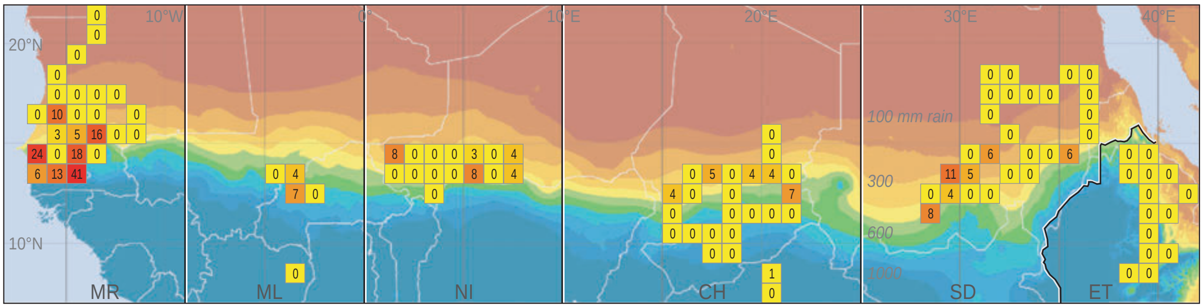
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	1.1	0.0	0.6
600–700	0.0	6.0	0.0	10.7	10.7	0.0
700–800	0.0	4.6	11.8	18.9	18.9	0.0
800–900	32.1	32.1	32.1	32.1	32.1	0.0
900–1000	23.9	23.9	23.9	23.9	23.9	0.0
>1000	0.0	0.0	0.2	6.9	6.9	0.0

Figure S6. Black-billed Wood Dove *Turtur abyssinicus* (n/km^2).
Granivorous resident.
Present in 14% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 2.6 ± 9.8.
Estimated overall density: 3.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR >800 mm set to 0 (beyond distribution area).
Estimated total number: 31.5 million, of which 19.0 million birds interpolated; range: 25.6–37.3 million (split-half).



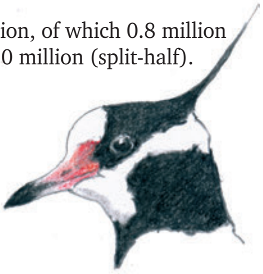
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.3	
100–200	2.9	2.7	2.4	2.2	11.6	0.0
200–300	50.7	27.0	3.4	14.8	14.8	0.0
300–400	57.1	31.6	6.2	23.8	3.6	16.2
400–500	80.2	42.0	3.8	14.5	8.9	0.0
500–600	13.8	0.0	2.2	24.4	15.6	0.6
600–700	4.4	7.3	0.0	30.0	30.0	10.0
700–800	1.3	0.0	10.3	20.6	20.6	0.0
800–900	24.5	24.5	24.5	24.5	24.5	13.0
900–1000	17.2	17.2	17.2	17.2	17.2	7.4
>1000	0.0	0.0	0.0	0.0	0.0	0.0

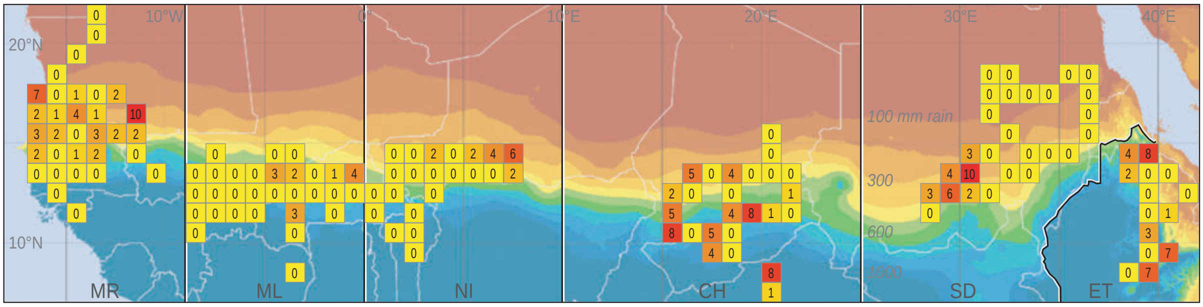
Figure S7. Namaqua Dove *Oena capensis* (n/km^2).
Granivorous resident.
Present in 68% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 12.4 ± 19.4.
Estimated overall density: 7.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 71.6 million, of which 26.3 million birds interpolated; range: 60.7–82.7 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	1.4	0.0
200–300	4.9	2.5	0.0	0.0	0.0	0.0
300–400	1.9	2.0	2.0	3.5	2.3	0.0
400–500	3.6	2.7	1.8	0.0	2.8	0.0
500–600	15.6	0.0	0.0	4.4	8.9	0.0
600–700	17.0	0.0	0.0	0.0	0.0	0.0
700–800	13.1	5.8	2.9	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.3	0.3	0.0

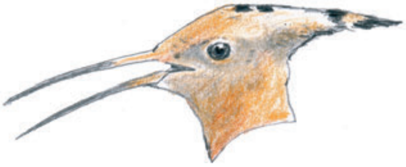
Figure S8. Black-headed Lapwing *Vanellus tectus* (n/km^2).
Insectivorous resident.
Present in 25% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 2.2 ± 5.5.
Estimated overall density: 0.7/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 6.7 million, of which 0.8 million birds interpolated; range: 5.4–8.0 million (split-half).

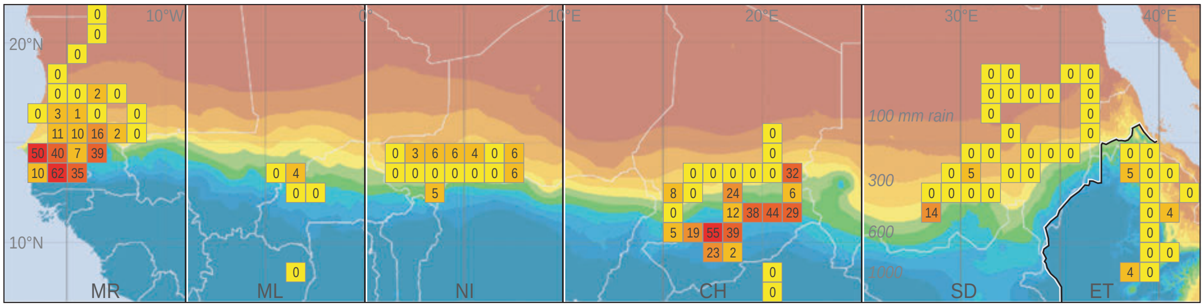




rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	2.2	1.5	0.7	0.0	0.6	0.0
200–300	2.2	2.7	3.2	0.0	7.4	0.0
300–400	2.1	2.0	2.0	3.0	1.3	2.0
400–500	3.3	0.0	0.7	0.0	2.2	2.5
500–600	2.2	1.4	0.0	3.0	0.0	3.5
600–700	0.4	0.5	0.0	1.4	1.4	2.2
700–800	0.7	0.5	0.0	5.2	5.2	0.0
800–900	0.0	1.3	0.0	0.6	0.6	5.0
900–1000	0.0	0.0	0.0	3.0	3.0	1.2
>1000	0.0	0.0	0.0	4.2	4.2	0.0

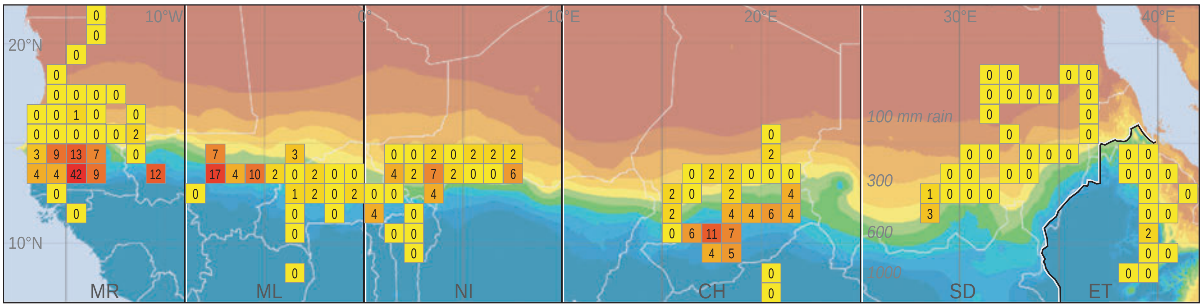
Figure S9. Eurasian Hoopoe *Upupa epops* (n/km^2).
Insectivorous migrant / resident.
Present in 35% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 1.3 ± 2.3.
Estimated overall density: 1.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 10.4 million, of which 2.3 million birds interpolated; range: 8.4–12.3 million (split-half).





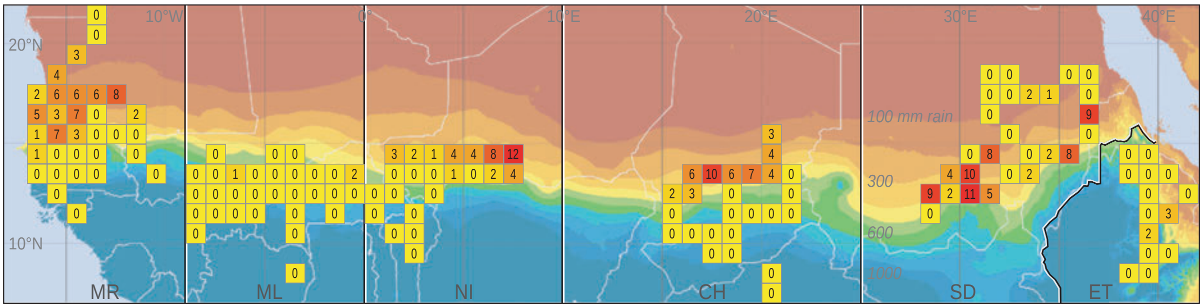
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.3	0.2	0.1	0.0	0.0	0.0
200–300	0.5	0.2	0.0	0.0	3.7	0.0
300–400	7.7	6.3	4.9	0.9	0.0	0.0
400–500	16.7	8.3	0.0	1.7	2.8	0.0
500–600	27.4	0.0	0.0	12.7	0.0	2.0
600–700	34.7	3.4	7.6	14.6	14.6	2.2
700–800	32.7	0.0	13.8	27.5	27.5	0.0
800–900	39.1	39.1	39.1	39.1	39.1	1.8
900–1000	14.7	14.7	14.7	14.7	14.7	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S10. Northern Red-billed Hornbill *Tockus erythrorhynchus* (n/km^2).
Insectivorous resident.
Present in 37% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 6.3 ± 13.1.
Estimated overall density: 4.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 43.7 million, of which 22.0 million birds interpolated; range: 39.7–47.6 million (split-half).



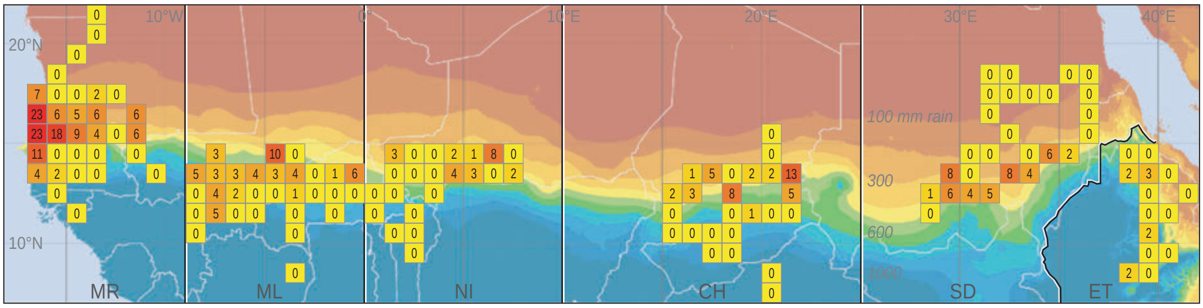
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.5	0.3	0.0	1.8	0.0	0.0
300–400	0.0	1.3	2.5	0.9	0.3	0.0
400–500	0.0	4.2	2.0	0.9	0.6	0.0
500–600	4.2	2.4	0.0	3.0	0.0	0.0
600–700	5.8	2.4	6.1	1.4	1.4	0.0
700–800	5.9	2.8	0.0	4.2	4.2	0.0
800–900	25.0	0.0	3.7	6.8	6.8	0.0
900–1000	28.2	0.0	0.0	6.3	6.3	0.0
>1000	0.0	0.0	0.0	0.0	0.0	9.6

Figure S11. Abyssinian Roller *Coracias abyssinicus* (*n*/km²).
Insectivorous resident.
Present in 37% of the 138 cells.
Average density (*n*/km², ±SD) in grid cells: 1.9 ± 4.5.
Estimated overall density: 1.0/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 9.9 million, of which 2.2 million birds interpolated; range: 8.8–11.0 million (split-half).



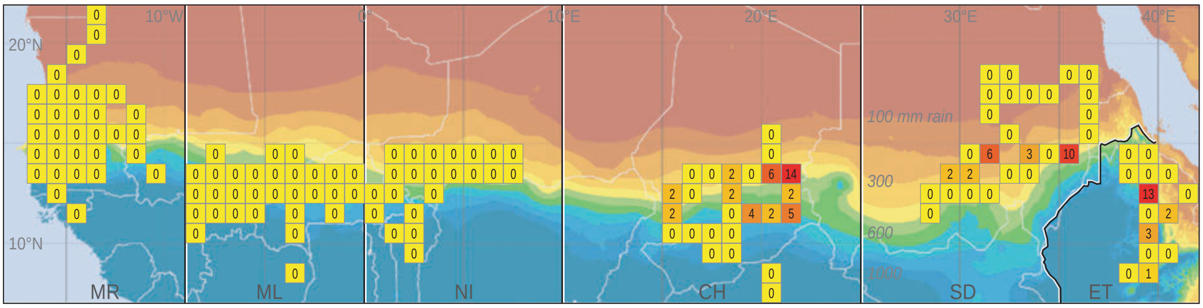
rain (mm)	MR	ML	NI	CH	SD	ET
<100	1.5	1.2	0.9	0.6	0.3	
100–200	7.2	6.0	4.7	3.4	4.2	0.0
200–300	2.1	5.9	9.7	1.8	7.4	0.0
300–400	2.4	3.4	4.4	5.3	4.6	6.1
400–500	2.7	0.0	1.9	5.9	2.8	0.0
500–600	0.6	0.4	0.0	0.0	8.9	0.0
600–700	0.4	0.3	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S12. Great Grey Shrike *Lanius excubitor* (*n*/km²).
Insectivorous resident.
Present in 34% of the 150 cells.
Average density (*n*/km², ±SD) in grid cells: 1.5 ± 2.7.
Estimated overall density: 1.5/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 15.0 million, of which 4.3 million birds interpolated; range: 14.0–15.9 million (split-half).



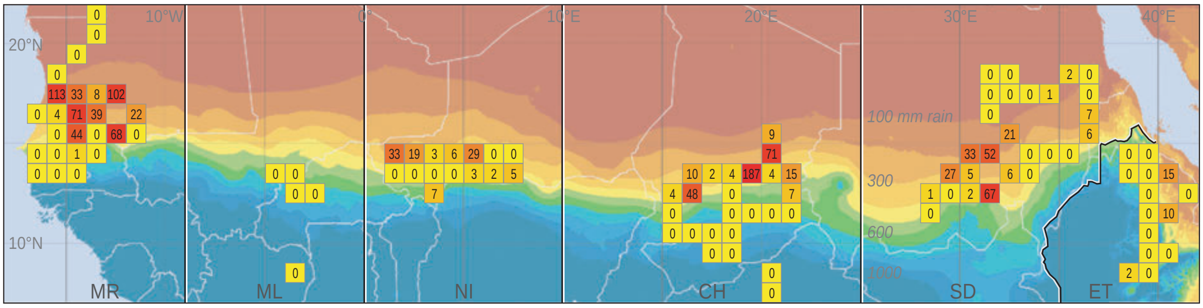
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	2.6	1.7	0.9	0.0	0.0	0.0
200–300	7.9	4.0	0.0	0.0	0.0	0.0
300–400	12.5	7.5	2.5	2.2	4.0	0.0
400–500	16.2	4.2	1.6	2.5	3.1	0.0
500–600	9.6	3.8	0.0	4.2	4.4	0.3
600–700	2.1	1.6	0.0	3.9	3.9	1.1
700–800	0.7	1.5	0.0	0.5	0.5	0.0
800–900	0.0	1.2	0.0	0.0	0.0	1.8
900–1000	0.0	1.9	0.0	0.0	0.0	0.0
>1000	0.0	0.9	0.0	0.0	0.0	1.5

Figure S13. Woodchat Shrike *Lanius senator* (*n*/km^2).
Insectivorous migrant.
Present in 39% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 2.0 ± 3.8.
Estimated overall density: 0.9/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 9.5 million, of which 1.8 million birds interpolated; range: 8.8–10.4 million (split-half).



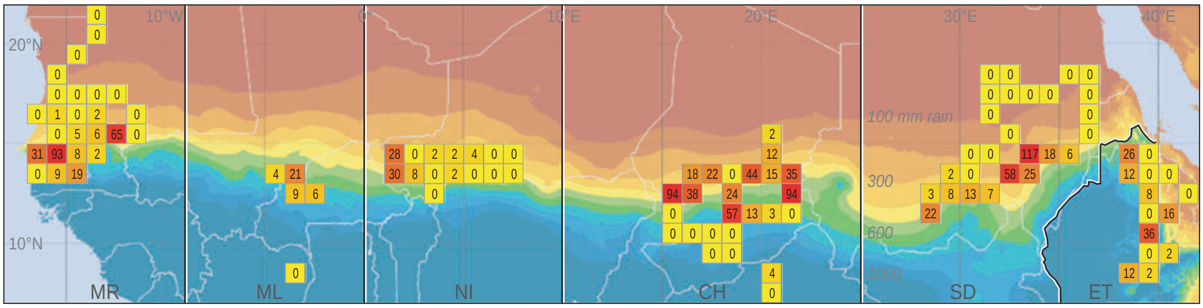
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	1.2	0.0
200–300	0.0	0.0	0.0	0.0	1.9	0.0
300–400	0.0	0.0	0.0	0.9	0.7	0.0
400–500	0.0	0.0	0.0	2.6	1.1	0.0
500–600	0.0	0.0	0.0	7.3	8.9	1.3
600–700	0.0	0.0	0.0	2.0	2.0	5.0
700–800	0.0	0.0	0.0	1.4	1.4	0.0
800–900	0.0	0.0	0.0	0.7	0.7	0.6
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	3.2

Figure S14. Masked Shrike *Lanius nubicus* (*n*/km^2).
Insectivorous migrant.
Present in 13% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 0.6 ± 2.0.
Estimated overall density: 0.5/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 5.0 million, of which 0.5 million birds interpolated; range: 3.4–6.4 million (split-half).



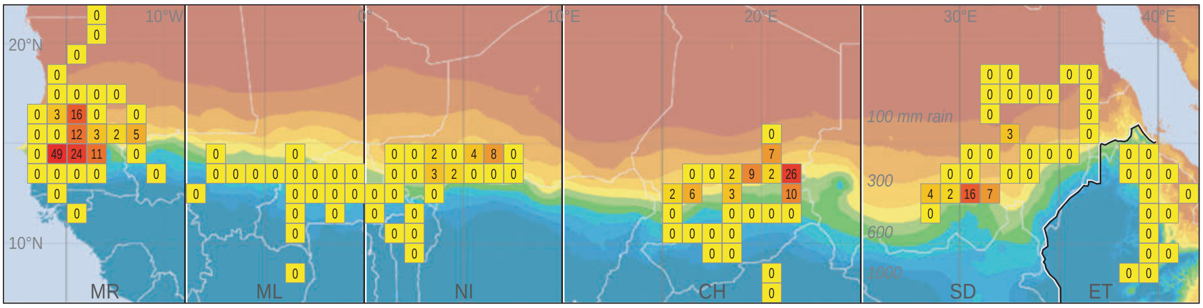
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.1	0.2	0.2	0.3	
100–200	41.1	30.6	19.8	9.4	17.4	0.0
200–300	28.6	14.3	0.0	0.0	20.4	0.0
300–400	30.2	20.8	11.4	60.4	13.9	28.3
400–500	0.0	3.3	6.5	8.5	1.1	4.9
500–600	0.0	0.0	0.0	8.0	0.0	0.0
600–700	0.7	0.0	4.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	1.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S15. Black-crowned Sparrow-Lark *Eremopterix nigriceps* (*n*/km^2).
Granivorous resident.
Present in 42% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 11.1 ± 26.9.
Estimated overall density: 4.5/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 44.7 million, of which 11.9 million birds interpolated; range: 31.5–57.8 million (split-half).



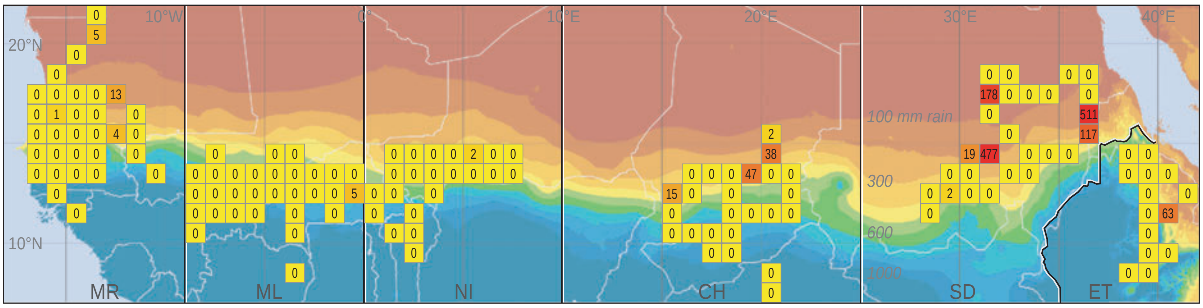
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.4	1.0	1.6	2.2	0.0	0.0
200–300	0.5	0.3	0.0	13.1	0.0	0.0
300–400	15.6	10.2	4.8	28.2	26.5	0.0
400–500	3.2	2.6	2.0	40.2	11.1	85.2
500–600	30.4	0.0	8.9	19.6	8.9	0.7
600–700	11.9	17.5	0.0	46.5	46.5	15.2
700–800	1.3	6.8	10.5	14.3	14.3	2.5
800–900	2.1	2.1	2.1	2.1	2.1	13.1
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	1.8	1.8	0.0

Figure S16. Chestnut-backed Sparrow-Lark *Eremopterix leucotis* (*n*/km^2).
Granivorous resident.
Present in 50% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 11.0 ± 21.8.
Estimated overall density: 4.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 44.2 million, of which 10.2 million birds interpolated; range: 36.2–52.4 million (split-half).



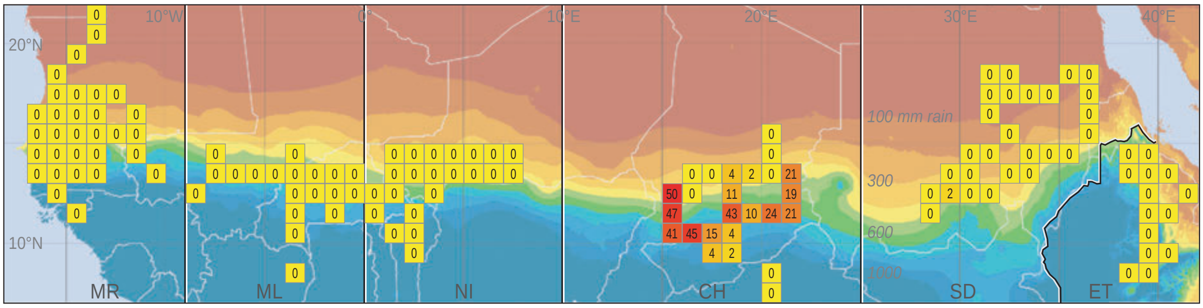
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.4	0.0
200–300	2.8	1.4	0.0	0.0	0.0	0.0
300–400	9.7	5.9	2.2	3.5	2.7	0.0
400–500	0.0	0.0	1.6	7.7	3.3	0.0
500–600	4.5	0.0	0.0	5.8	0.0	0.0
600–700	9.5	0.0	0.0	1.8	1.8	0.0
700–800	3.7	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S17. Singing Bush Lark *Mirafra cantillans* (n/km^2).
Insectivorous resident.
Present in 20% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 1.8 ± 5.7.
Estimated overall density: 0.5/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 5.3 million, of which 0.7 million birds interpolated; range: 4.4–6.1 million (split-half).



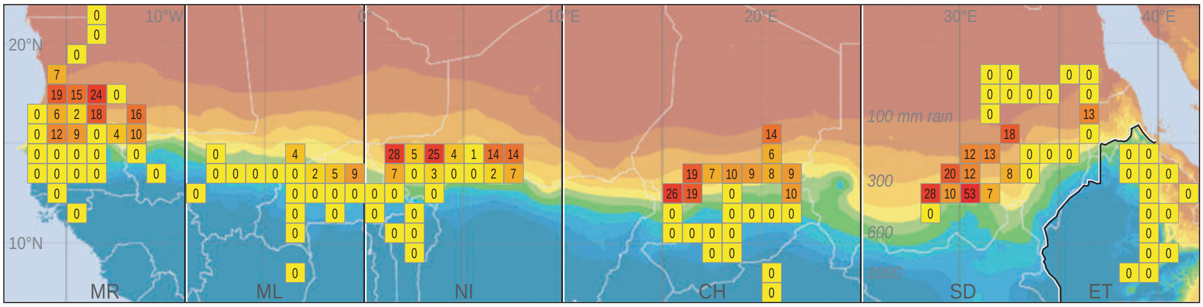
rain (mm)	MR	ML	NI	CH	SD	ET
<100	1.5	6.2	11.0	15.8	20.5	
100–200	1.8	2.0	2.2	2.5	244.9	0.0
200–300	0.6	0.3	0.0	24.7	77.8	0.0
300–400	0.5	0.5	0.5	15.6	0.0	2.0
400–500	0.0	0.0	0.0	0.0	0.6	116.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.0	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S18. Greater Short-toed Lark *Calandrella brachydactyla* (n/km^2).
Granivorous migrant.
Present in 11% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 10.0 ± 59.5.
Estimated overall density: 12.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 126.7 million, of which 26.1 million birds interpolated; range: 100.0–153.0 million (split-half).



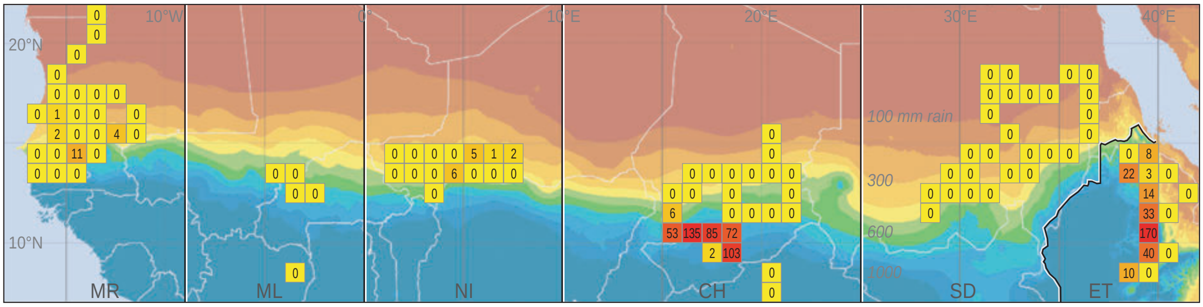
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	9.6	0.0	0.0
400–500	0.0	0.0	0.0	5.1	0.6	0.0
500–600	0.0	0.0	0.0	31.8	0.0	0.0
600–700	0.0	0.0	0.0	25.2	25.2	0.0
700–800	0.0	0.0	0.0	30.1	30.1	0.0
800–900	0.0	0.0	0.0	19.2	19.2	0.0
900–1000	0.0	0.0	0.0	6.3	6.3	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S19. Red-pate Cisticola *Cisticola ruficeps* (*n*/km²).
Insectivorous resident.
Present in 13% of the 138 cells.
Average density (*n*/km², ±SD) in grid cells: 2.7 ± 9.2.
Estimated overall density: 2.5/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; NI 800–1000 mm set to 0.
Estimated total number: 25.3 million, of which 10.2 million birds interpolated; range: 24.4–26.3 million (split-half).



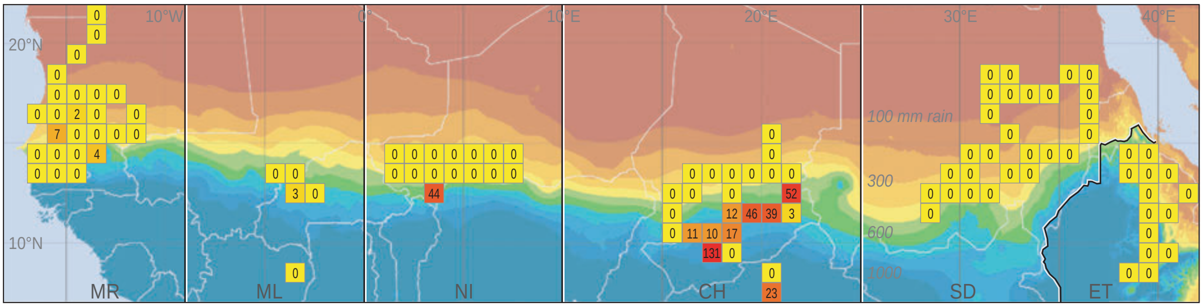
rain (mm)	MR	ML	NI	CH	SD	ET
<100	1.7	1.3	0.8	0.4	0.0	
100–200	13.2	13.3	13.5	13.6	9.3	0.0
200–300	7.5	15.0	22.6	6.7	14.8	0.0
300–400	7.8	9.3	10.9	15.0	14.8	0.0
400–500	0.0	13.9	2.2	12.6	10.0	0.0
500–600	0.0	3.5	0.0	4.4	0.0	0.0
600–700	0.0	0.0	0.0	2.7	2.7	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.6
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S20. Cricket Warbler *Spiloptila clamans* (*n*/km²).
Insectivorous resident.
Present in 36% of 138 the cells.
Average density (*n*/km², ±SD) in grid cells: 4.4 ± 8.1.
Estimated overall density: 3.4/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 33.4 million, of which 8.4 million birds interpolated; range: 31.8–34.4 million (split-half).



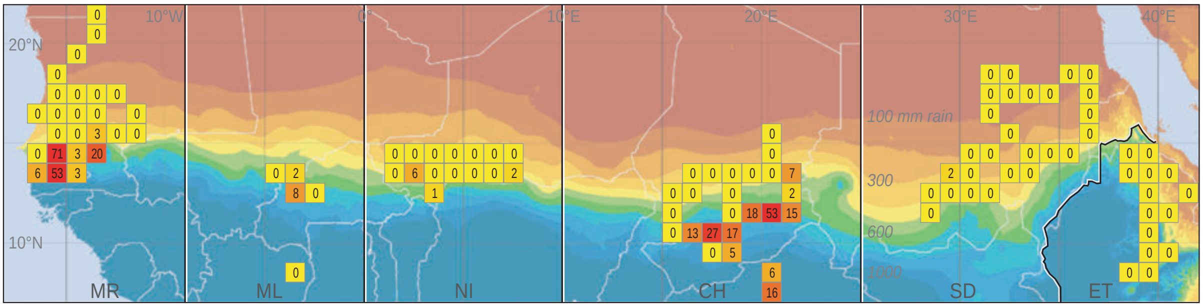
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.2	1.8	3.4	0.0	0.0	0.0
300–400	1.0	1.2	1.4	0.0	0.0	0.0
400–500	2.4	1.7	1.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	3.3	0.0	3.6
600–700	5.9	0.0	0.0	16.9	16.9	10.0
700–800	0.0	0.0	0.0	0.0	0.0	7.4
800–900	85.6	85.6	85.6	85.6	85.6	3.8
900–1000	49.0	49.0	49.0	49.0	49.0	87.2
>1000	0.0	0.0	0.0	0.0	0.0	114.9

Figure S21. Greater Blue-eared Starling *Lamprotornis chalybaeus* (*n*/km^2). Insectivorous resident. Present in 21% of the 111 cells. Average density (*n*/km^2, ±SD) in grid cells: 7.1 ± 25.4. Estimated overall density: 10.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 99.9 million, of which 37.7 million birds interpolated; range: 45.6–153.0 million (split-half).



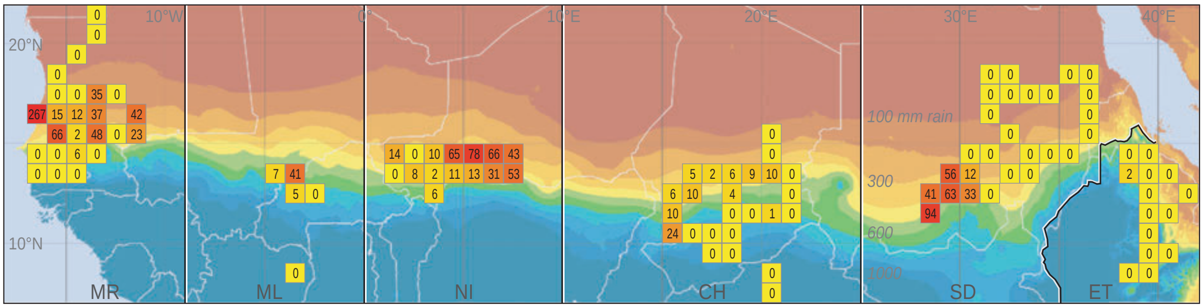
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.5	0.2	0.0	0.0	0.0	0.0
300–400	3.4	1.7	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	20.0	0.0	0.0	0.0
600–700	0.0	0.0	45.5	18.8	18.8	0.0
700–800	2.6	1.9	15.7	29.5	29.5	0.0
800–900	16.7	16.7	16.7	16.7	16.7	0.0
900–1000	49.0	49.0	49.0	49.0	49.0	0.0
>1000	0.0	0.0	5.8	11.6	11.6	0.0

Figure S22. Purple Starling *Lamprotornis purpureus* (*n*/km^2). Insectivorous resident. Present in 14% of the 111 cells. Average density (*n*/km^2, ±SD) in grid cells: 3.6 ± 15.1. Estimated overall density: 5.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 50.0 million, of which 26.0 million birds interpolated; range: 47.5–52.6 million (split-half).



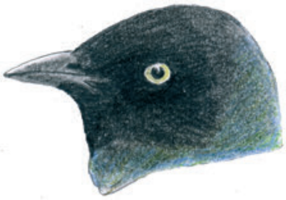
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.4	0.7	0.0	0.3	0.0
400–500	1.6	1.1	0.7	0.0	0.0	0.0
500–600	0.0	0.0	0.0	3.8	0.0	0.0
600–700	23.7	1.7	2.0	3.6	3.6	0.0
700–800	15.7	4.7	12.8	20.8	20.8	0.0
800–900	24.1	24.1	24.1	24.1	24.1	0.0
900–1000	4.0	4.0	4.0	4.0	4.0	0.0
>1000	0.0	0.0	0.0	11.2	11.2	0.0

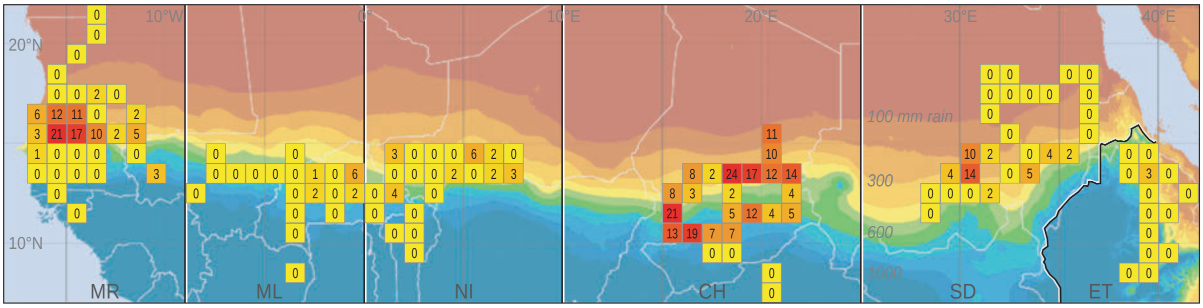
Figure S23. Long-tailed Glossy Starling *Lamprotornis caudatus* (*n*/km^2).
Insectivorous resident.
Present in 22% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 3.3 ± 10.6.
Estimated overall density: 3.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 30.5 million, of which 16.3 million birds interpolated; range: 15.9–44.2 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	28.2	18.9	9.3	0.0	0.0	0.0
200–300	20.7	29.9	39.0	0.0	7.4	0.0
300–400	36.6	41.3	46.1	5.7	22.9	0.0
400–500	19.4	22.3	25.1	8.4	36.1	0.0
500–600	7.1	0.0	2.2	5.9	0.0	0.0
600–700	5.9	34.6	5.9	8.4	8.4	1.1
700–800	0.0	2.9	2.0	1.2	1.2	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

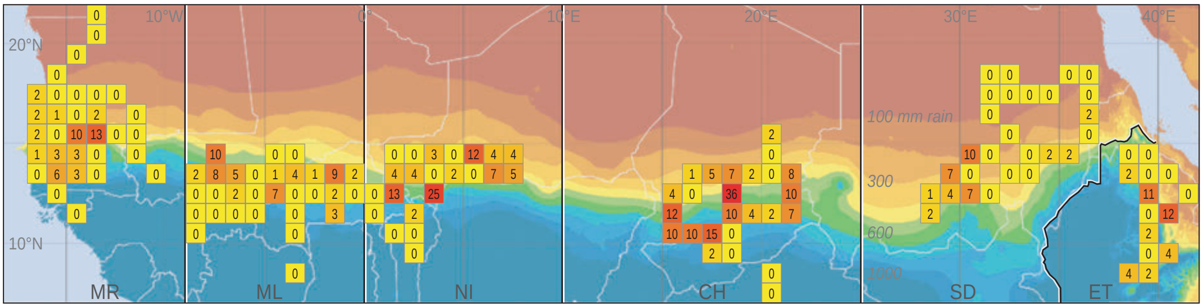
Figure S24. Chestnut-bellied Starling *Lamprotornis pulcher* (*n*/km^2).
Insectivorous resident.
Present in 41% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 12.6 ± 31.4.
Estimated overall density: 4.9/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 48.5 million, of which 13.0 million birds interpolated; range: 33.9–63.4 million (split-half).





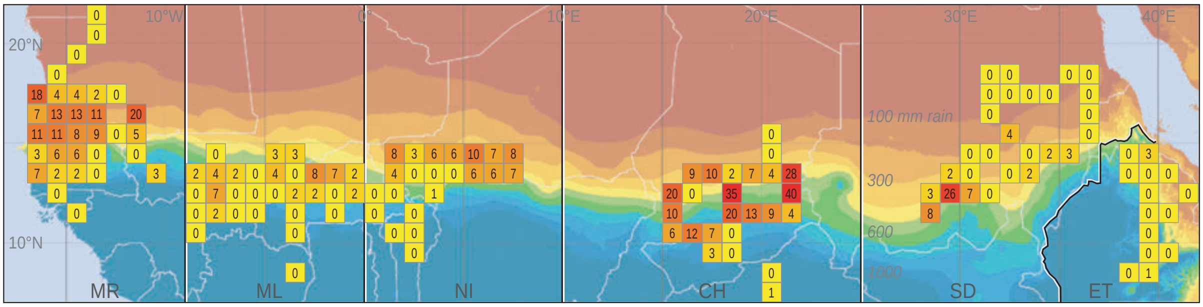
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.9	4.9	8.1	11.1	0.5	0.0
200–300	9.1	4.5	0.0	9.2	13.0	0.0
300–400	11.3	6.4	1.5	8.2	2.3	0.0
400–500	9.2	0.0	2.4	16.0	1.1	0.0
500–600	2.1	1.8	0.0	9.1	2.2	1.1
600–700	0.0	0.8	0.0	9.2	9.2	0.0
700–800	0.0	0.0	3.0	9.7	9.7	0.0
800–900	0.0	0.0	0.0	10.8	10.8	0.0
900–1000	3.2	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S25. Black Scrub Robin *Cercotrichas podobe* (n/km^2).
Insectivorous resident.
Present in 39% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 2.8 ± 5.1.
Estimated overall density: 2.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 23.6 million, of which 7.2 million birds interpolated; range: 18.3–28.8 million (split-half).



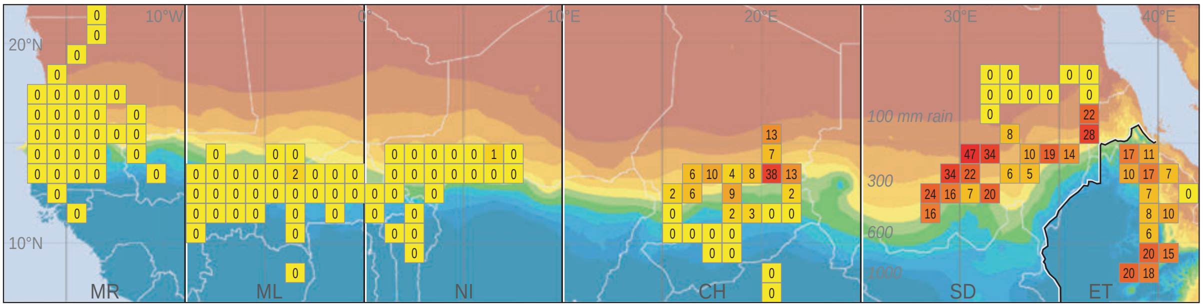
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.2	0.9	1.6	2.2	0.6	0.0
200–300	1.1	2.1	3.0	0.0	5.6	2.8
300–400	1.2	2.1	3.1	3.1	2.0	10.1
400–500	6.0	2.1	4.6	1.7	2.6	2.5
500–600	2.1	2.5	6.7	8.5	2.2	4.2
600–700	3.5	4.7	34.9	17.1	17.1	4.4
700–800	0.0	2.6	9.1	8.1	8.1	0.0
800–900	0.0	1.1	0.0	6.6	6.6	1.1
900–1000	0.0	0.0	0.0	3.2	3.2	2.2
>1000	0.0	0.0	0.5	0.0	0.0	0.0

Figure S26. Rufous-tailed Scrub Robin *Cercotrichas galactotes* (n/km^2).
Insectivorous migrant/resident.
Present in 48% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 2.7 ± 4.8.
Estimated overall density: 1.9/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 19.3 million, of which 4.9 million birds interpolated; range: 17.2–21.2 million (split-half).



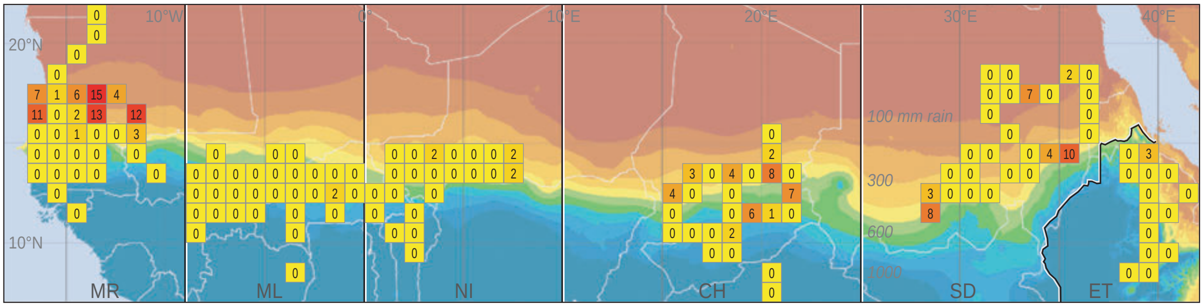
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	7.5	5.0	2.5	0.0	0.6	0.0
200–300	11.0	10.3	9.5	0.0	0.0	0.0
300–400	11.0	8.3	5.6	9.1	2.7	0.0
400–500	8.8	2.1	5.3	6.8	8.3	0.0
500–600	4.2	5.4	0.0	27.0	6.7	0.0
600–700	2.7	2.1	2.0	20.7	20.7	1.1
700–800	0.0	2.0	0.0	13.4	13.4	0.0
800–900	0.0	1.7	0.0	6.4	6.4	0.6
900–1000	3.2	0.0	0.0	2.8	2.8	0.0
>1000	0.0	0.4	0.0	0.6	0.6	0.0

Figure S27. Northern Wheatear *Oenanthe oenanthe* (n/km^2).
Insectivorous migrant.
Present in 51% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 3.9 ± 6.5.
Estimated overall density: 2.7/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 27.1 million, of which 8.1 million birds interpolated; range: 25.5–28.4 million (split-half).



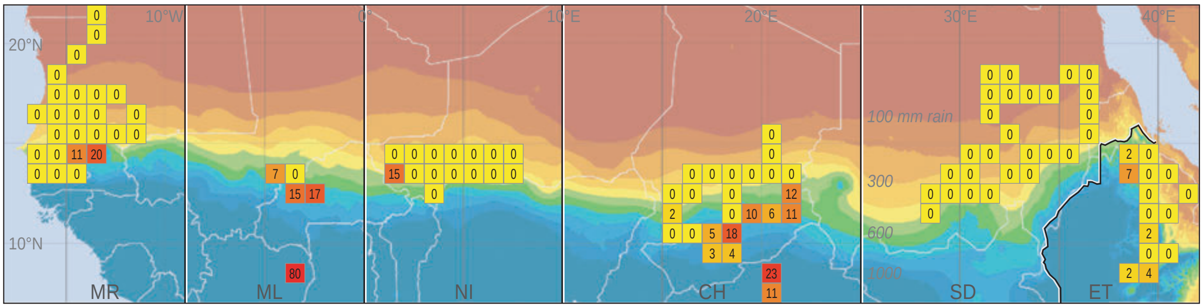
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	13.0	20.2	0.0
200–300	0.0	0.0	0.0	4.9	37.0	13.9
300–400	0.0	0.1	0.2	7.1	17.8	10.1
400–500	0.0	0.0	0.0	17.5	13.6	0.0
500–600	0.0	0.0	0.0	5.7	15.6	13.4
600–700	0.0	0.2	0.0	4.2	4.2	10.1
700–800	0.0	0.0	0.0	0.9	0.9	9.0
800–900	0.0	0.0	0.0	0.0	0.0	21.8
900–1000	0.0	0.0	0.0	0.0	0.0	17.3
>1000	0.0	0.0	0.0	0.0	0.0	8.8

Figure S28. Isabelline Wheatear *Oenanthe isabellina* (n/km^2).
Insectivorous migrant.
Present in 31% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 4.2 ± 8.5.
Estimated overall density: 3.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 31.6 million, of which 0.6 million birds interpolated; range: 28.7–34.3 million (split-half).



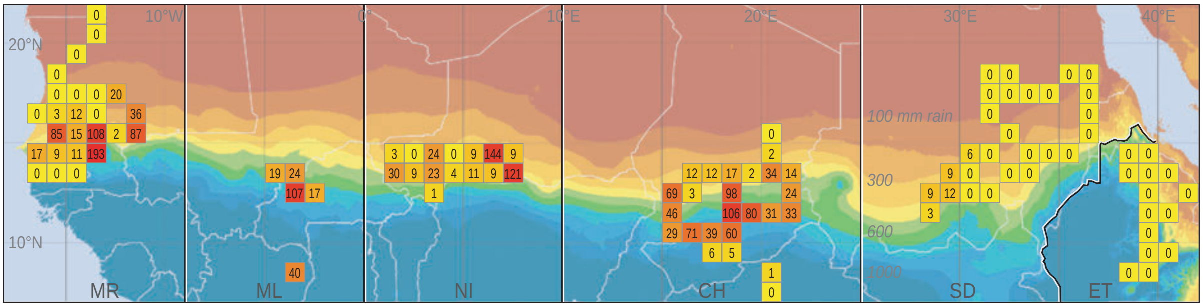
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.3	0.6	0.9	1.2	
100–200	6.6	4.4	2.2	0.0	0.0	0.0
200–300	3.6	1.8	0.0	1.8	0.0	0.0
300–400	0.0	0.5	1.0	2.4	0.7	0.0
400–500	0.4	0.0	0.0	4.2	2.8	0.0
500–600	0.0	0.0	0.0	4.4	13.3	0.0
600–700	0.0	0.0	0.0	0.0	0.0	1.1
700–800	0.0	0.2	0.0	2.0	2.0	0.0
800–900	0.0	0.0	0.0	1.3	1.3	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S29. Western Black-eared Wheatear *Oenanthe hispanica* (MR+ML+NI) / Eastern Black-eared Wheatear *Oenanthe melanoleuca* (CH+SD+ET) (*n*/km²).
Insectivorous migrant.
Present in 11 / 11% of the 150 cells.
Average density (*n*/km², ±SD) in grid cells: 0.6 ± 2.3 / 0.5 ± 1.7.
Estimated overall density: 0.3 / 0.6/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 3.1 / 5.9 million, of which 1.7 / 0.9 million birds interpolated; range: 3.0–3.2 / 3.9–7.0 million (split-half).



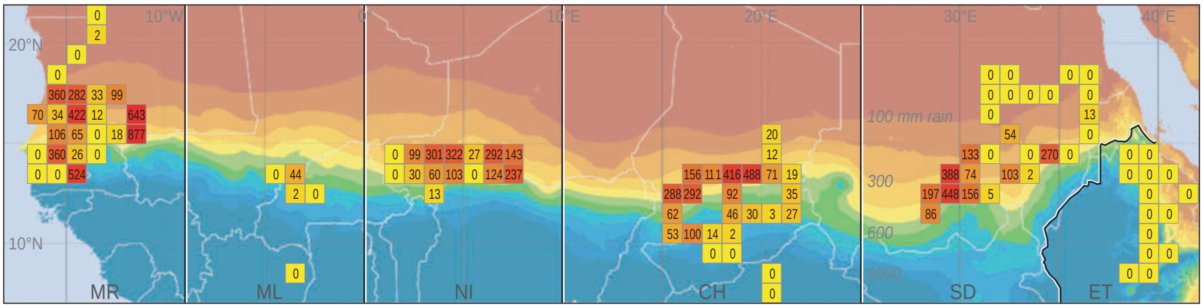
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.7	1.3	0.0	0.0	0.0
500–600	1.2	0.0	0.0	1.5	0.0	0.0
600–700	5.9	5.1	0.0	7.1	7.1	0.0
700–800	13.1	13.5	8.8	4.1	4.1	0.0
800–900	7.0	7.0	7.0	7.0	7.0	0.0
900–1000	4.5	4.5	4.5	4.5	4.5	0.0
>1000	79.8	79.8	48.3	16.8	16.8	3.0

Figure S30. Sahel Bush Sparrow *Gymnoris dentata* (*n*/km²).
Insectivorous resident.
Present in 21% of the 138 cells.
Average density (*n*/km², ±SD) in grid cells: 2.6 ± 8.8.
Estimated overall density: 11.3/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 112.3 million, of which 61.4 million birds interpolated; range: 106.0–118.8 million (split-half).



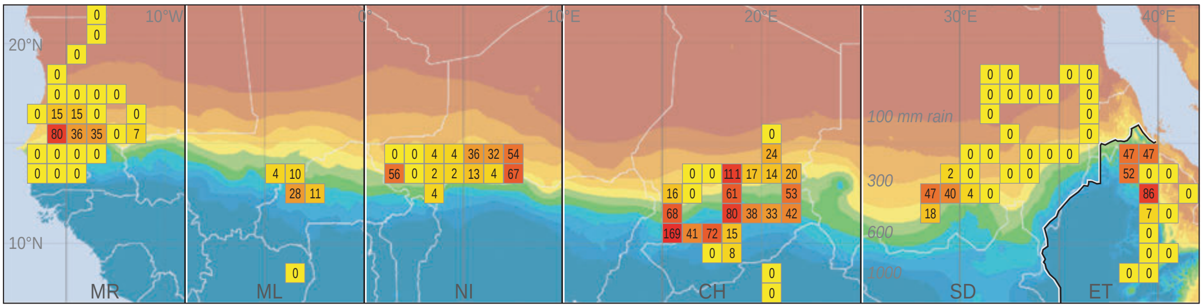
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	6.8	4.5	2.2	0.0	0.0	0.0
200–300	14.3	23.0	31.7	2.5	3.7	0.0
300–400	36.8	33.2	29.5	12.9	3.0	0.0
400–500	38.9	44.4	49.9	39.1	4.4	0.0
500–600	52.0	0.0	0.0	27.6	0.0	0.0
600–700	10.4	68.4	2.0	55.3	55.3	0.0
700–800	135.9	43.1	62.1	81.1	81.1	0.0
800–900	50.2	50.2	50.2	50.2	50.2	0.0
900–1000	7.4	7.4	7.4	7.4	7.4	0.0
>1000	39.9	39.9	20.1	0.3	0.3	0.0

Figure S31. Northern Grey-headed Sparrow *Passer griseus* (*n*/km^2).
Granivorous resident.
Present in 53% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 18.3 ± 34.5.
Estimated overall density: 15.8/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 157.7 million, of which 71.2 million birds interpolated; range: 153.7–165.0 million (split-half).



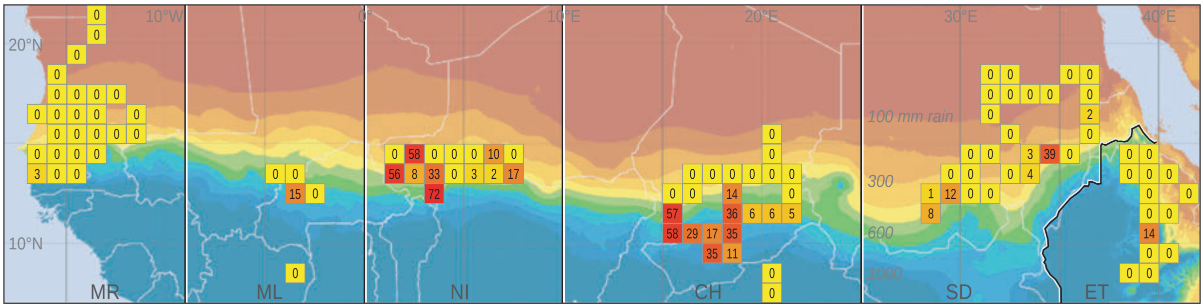
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.7	1.4	2.1	2.8	3.5	
100–200	194.4	136.8	77.6	20.0	20.4	0.0
200–300	214.0	203.5	193.0	58.3	61.1	0.0
300–400	168.3	181.1	193.9	265.4	94.0	0.0
400–500	157.3	115.1	74.0	186.8	285.8	0.0
500–600	0.0	0.0	17.8	47.0	11.1	0.0
600–700	196.3	34.2	18.2	60.9	60.9	0.0
700–800	0.0	1.0	16.2	31.5	31.5	0.0
800–900	35.7	35.7	35.7	35.7	35.7	0.0
900–1000	0.8	0.8	0.8	0.8	0.8	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S32. Sudan Golden Sparrow *Passer luteus* (*n*/km^2).
Granivorous resident.
Present in 59% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 90.0 ± 156.4.
Estimated overall density: 37.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 374.6 million, of which 102.3 million birds interpolated; range: 366.4–382.3 million (split-half).



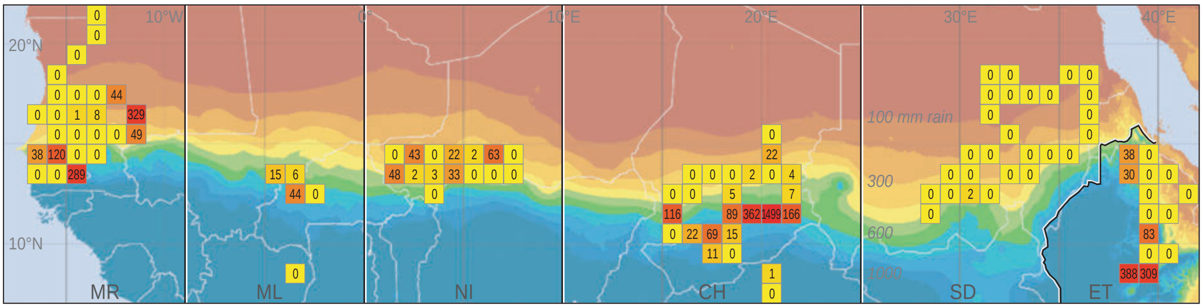
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	11.4	12.1	12.9	22.2	0.0	0.0
300–400	41.2	34.6	28.0	15.5	7.3	0.0
400–500	53.8	36.0	18.2	34.0	22.0	0.0
500–600	8.6	0.0	0.0	64.9	0.0	0.0
600–700	0.0	9.4	6.1	82.1	82.1	83.9
700–800	0.0	19.7	35.0	50.2	50.2	0.0
800–900	0.0	0.0	22.8	45.5	45.5	17.3
900–1000	0.0	0.0	5.4	10.9	10.9	4.9
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S33. Speckle-fronted Weaver *Sporopipes frontalis* (n/km^2).
Granivorous resident.
Present in 45% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 15.8 ± 28.
Estimated overall density: 9.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density MR >800 and ML >800 set to 0.
Estimated total number: 94.1 million, of which 32.4 million birds interpolated; range: 77.3–110.6 million (split-half).



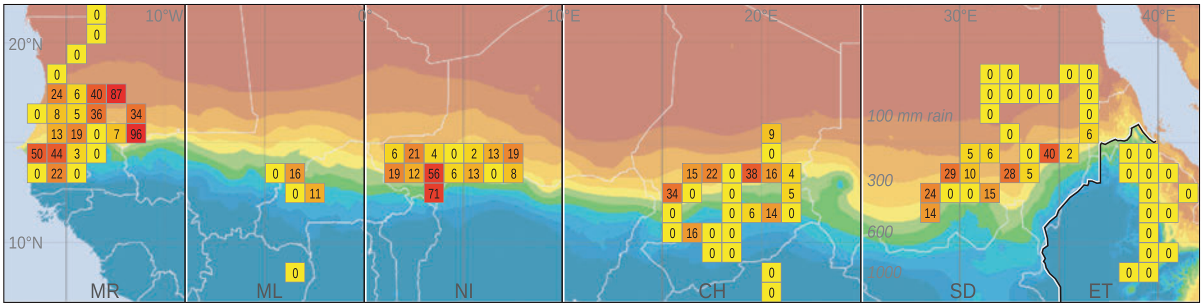
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.6	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	6.6	13.2	0.0	1.2	0.0
400–500	0.0	5.4	10.7	0.0	12.5	0.0
500–600	0.0	0.0	8.9	4.4	8.9	0.0
600–700	0.7	15.4	105.1	28.1	28.1	0.0
700–800	0.0	0.0	15.0	29.9	29.9	0.0
800–900	0.0	0.0	10.0	20.1	20.1	0.0
900–1000	0.0	0.0	10.0	20.0	20.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	12.7

Figure S34. Vitelline Masked Weaver *Ploceus vitellinus* (n/km^2).
Granivorous resident.
Present in 28% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 6.0 ± 14.5.
Estimated overall density: 4.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density in MR = MR, ML >800 mm set to 0.
Estimated total number: 41.7 million, of which 13.9 million birds interpolated; range: 33.1–50.5 million (split-half).



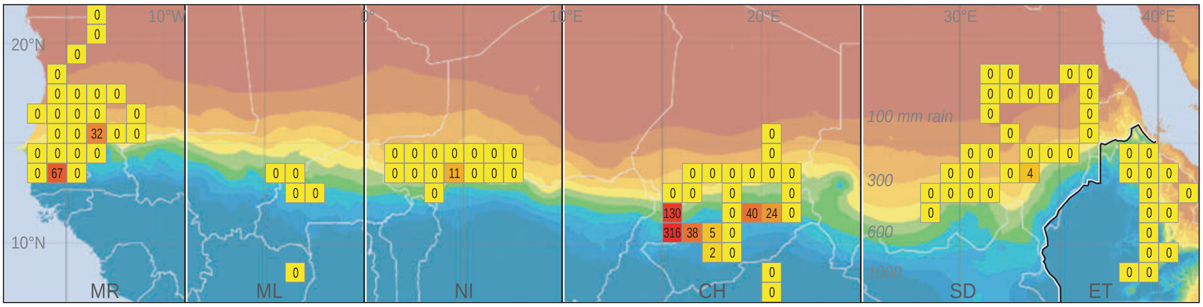
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	47.3	31.7	15.6	0.0	0.0	0.0
200–300	18.2	15.5	12.7	24.9	0.0	0.0
300–400	0.0	12.8	25.6	0.0	0.3	0.0
400–500	0.0	3.1	6.3	0.9	0.0	0.0
500–600	8.3	0.0	0.0	54.7	0.0	0.0
600–700	87.4	48.7	0.0	31.8	31.8	0.0
700–800	0.0	3.9	251.8	499.7	499.7	85.2
800–900	0.0	0.0	173.9	347.8	347.8	307.6
900–1000	0.0	0.0	8.4	16.7	16.7	92.6
>1000	0.0	0.0	0.2	0.4	0.4	0.0

Figure S35. Red-billed Quelea *Quelea quelea* (*n*/km²).
Granivorous resident.
Present in 36% of the 111 cells.
Average density (*n*/km², ±SD) in grid cells: 39.6 ± 157.8.
Estimated overall density: 32.2/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density in MR = MR, ML >800 mm set to 0.
Estimated total number: 330.9 million, of which 158.2 million birds interpolated; range: 182.9–477.9 million (split-half).



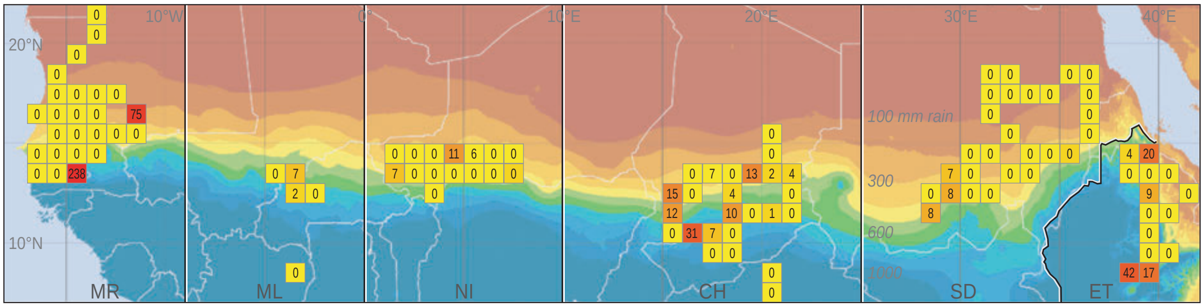
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	31.4	23.9	16.3	8.9	3.3	0.0
200–300	18.1	9.1	0.0	0.0	7.4	0.0
300–400	9.7	11.2	12.7	16.2	15.6	0.0
400–500	17.5	13.8	10.1	21.4	12.8	0.0
500–600	22.2	0.0	4.4	4.1	2.2	0.0
600–700	6.7	12.4	103.0	0.0	0.0	0.0
700–800	0.0	3.9	6.1	8.3	8.3	0.0
800–900	0.0	0.0	2.4	4.9	4.9	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S36. African Silverbill *Euodice cantans* (*n*/km²).
Granivorous resident.
Present in 49% of the 111 cells.
Average density (*n*/km², ±SD) in grid cells: 10.2 ± 17.7.
Estimated overall density: 4.2/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR 800 mm and ML 800 mm set to 0.
Estimated total number: 41.8 million, of which 11.7 million birds interpolated; range: 37.0–47.5 million (split-half).



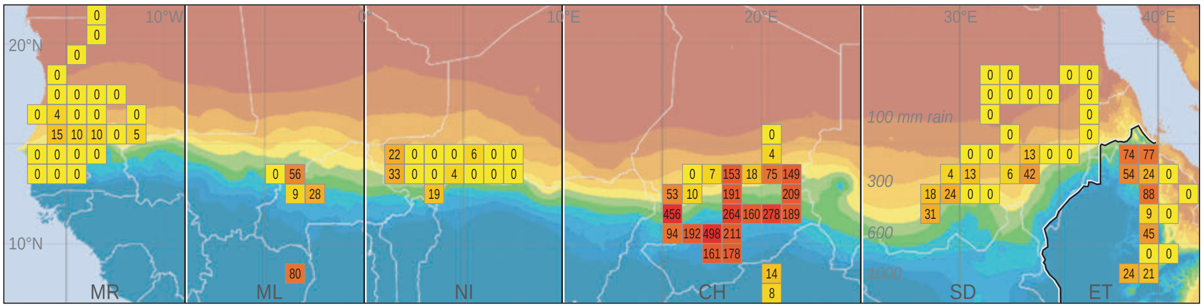
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	1.0	2.0	0.0	0.0	0.0
500–600	12.3	0.0	0.0	48.2	0.0	0.0
600–700	11.1	0.0	0.0	44.4	44.4	0.0
700–800	0.0	0.0	42.3	84.6	84.6	0.0
800–900	9.8	9.8	9.8	9.8	9.8	0.0
900–1000	2.4	2.4	2.4	2.4	2.4	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S37. Black-rumped Waxbill *Estrilda troglodytes* (*n*/km^2).
Granivorous resident.
Present in 10% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 6.0 ± 33.3.
Estimated overall density: 4.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 45.6 million, of which 22.5 million birds interpolated; range: 44.3–46.4 million (split-half).



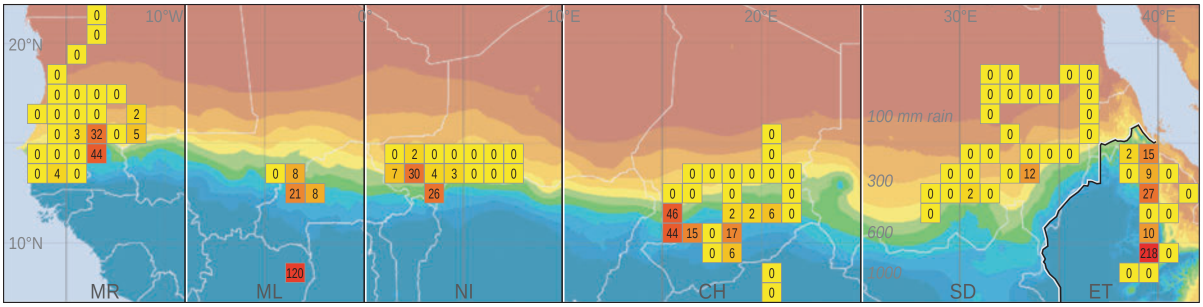
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	11.5	7.7	3.8	0.0	0.0	0.0
200–300	1.2	0.6	0.0	0.0	0.0	0.0
300–400	0.0	0.5	1.0	5.1	1.0	0.0
400–500	0.0	1.0	2.0	2.6	3.9	0.0
500–600	0.0	0.0	0.0	8.6	2.2	0.0
600–700	55.6	6.8	0.0	2.5	2.5	10.3
700–800	0.0	0.0	1.4	2.8	2.8	0.0
800–900	10.3	10.3	10.3	10.3	10.3	26.4
900–1000	2.4	2.4	2.4	2.4	2.4	7.4
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S38. Cut-throat Finch *Amadina fasciata* (*n*/km^2).
Granivorous resident.
Present in 23% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 5.1 ± 24.2.
Estimated overall density: 1.9/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 18.6 million, of which 6.4 million birds interpolated; range: 11.6–25.7 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	2.8	1.4	0.0	4.9	0.0	0.0
300–400	0.5	2.4	4.2	29.3	10.1	0.0
400–500	31.3	17.0	2.7	68.3	19.5	0.0
500–600	28.7	0.0	13.3	316.1	0.0	17.3
600–700	0.0	42.7	15.2	200.6	200.6	45.8
700–800	0.0	14.5	111.2	208.0	208.0	7.4
800–900	255.7	255.7	255.7	255.7	255.7	73.8
900–1000	233.0	233.0	233.0	233.0	233.0	47.2
>1000	79.8	79.8	45.6	11.3	11.3	10.4

Figure S39. Red-cheeked Cordon-bleu *Uraeginthus bengalus* (*n*/km^2).
Granivorous resident.
Present in 49% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 40.0 ± 85.9.
Estimated overall density: 46.8/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 467.2 million, of which 237.0 million birds interpolated; range: 447.0–488.6 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.7	0.4	0.0	0.0	0.0	0.0
300–400	0.0	2.4	4.9	0.0	2.0	0.0
400–500	3.2	1.8	0.5	0.0	0.0	0.0
500–600	12.3	0.0	0.0	14.3	0.0	6.0
600–700	0.7	21.8	37.4	8.0	8.0	2.7
700–800	31.4	5.8	10.5	15.1	15.1	2.5
800–900	9.6	9.6	9.6	9.6	9.6	9.7
900–1000	3.0	3.0	3.0	3.0	3.0	0.0
>1000	119.8	119.8	59.9	0.1	0.1	169.5

Figure S40. Red-billed Firefinch *Lagonosticta senegala* (*n*/km^2).
Granivorous resident.
Present in 30% of the 111 cells.
Average density (*n*/km^2, ±SD) in grid cells: 6.8 ± 24.9.
Estimated overall density: 20.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 201.3 million, of which 83.8 million birds interpolated; range: 153.2–255.6 million (split-half).

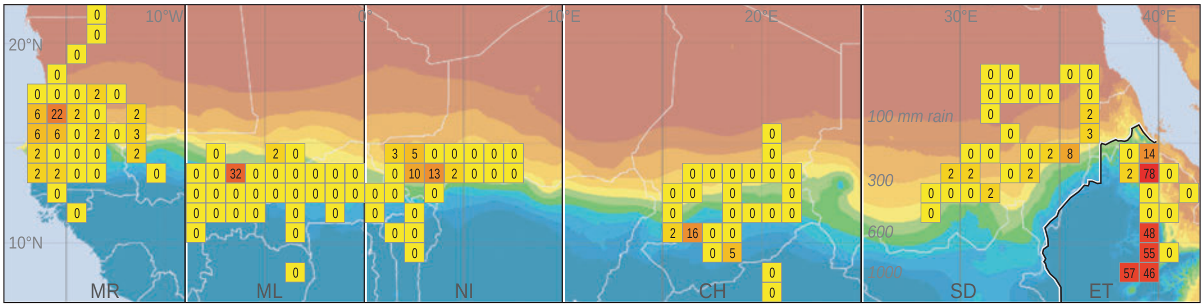


Figure S41. Western Yellow Wagtail *Motacilla flava* (*n*/km²).
Insectivorous migrant.
Present in 26% of the 150 cells.
Average density (*n*/km², ±SD) in grid cells: 3.2 ± 10.9.
Estimated overall density: 2.4/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 24.0 million, of which 1.9 million birds interpolated; range: 23.6–24.4 million (split-half).

rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.5	0.4	0.2	0.0	0.6	0.0
200–300	14.2	7.1	0.0	0.0	3.7	0.0
300–400	5.4	3.8	2.2	0.0	1.0	0.0
400–500	0.0	1.1	0.3	0.0	1.1	0.0
500–600	2.2	0.0	11.1	0.0	8.9	33.3
600–700	1.3	9.9	0.0	0.0	0.0	6.7
700–800	0.0	0.0	0.0	0.6	0.6	0.0
800–900	0.0	0.0	0.0	4.9	4.9	48.5
900–1000	0.0	0.0	0.0	2.4	2.4	47.4
>1000	0.0	0.0	0.0	0.2	0.2	28.1

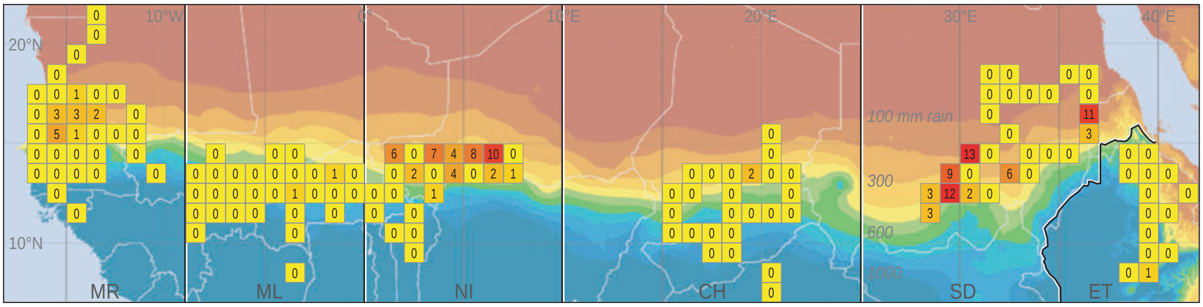
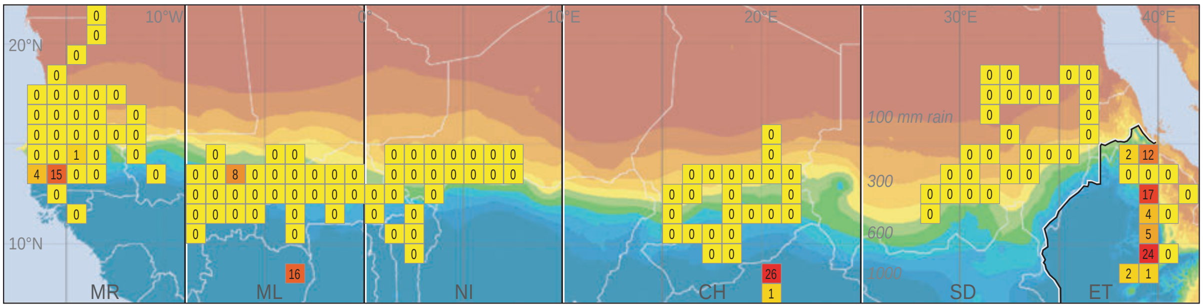


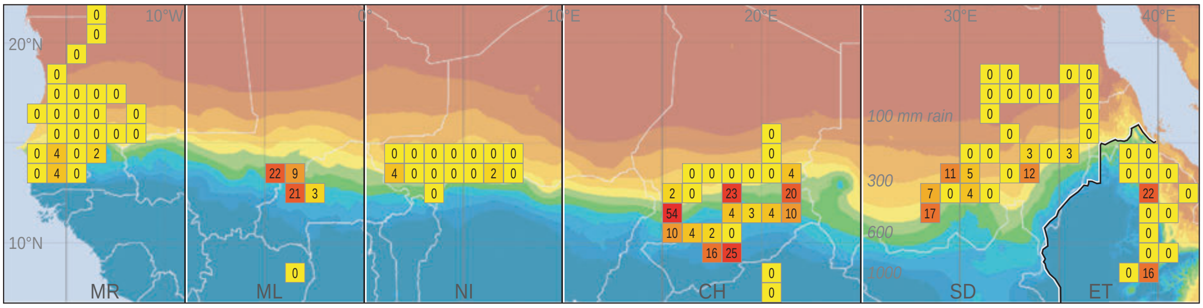
Figure S42. Tawny Pipit *Anthus campestris* (*n*/km²).
Insectivorous migrant.
Present in 21% of the 150 cells.
Average density (*n*/km², ±SD) in grid cells: 0.9 ± 2.3.
Estimated overall density: 0.7/km² based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 7.0 million, of which 0.8 million birds interpolated; range: 5.0–8.4 million (split-half).

rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.5	0.3	0.2	0.0	3.0	0.0
200–300	1.8	5.7	9.5	0.0	9.3	0.0
300–400	2.8	3.2	3.6	0.4	3.0	0.0
400–500	0.4	0.0	3.9	0.0	3.9	0.0
500–600	0.0	0.4	2.2	0.0	0.0	0.0
600–700	0.0	0.0	0.0	0.0	0.0	0.0
700–800	0.0	0.2	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.7	2.6
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	4.4	1.6	0.0	0.0	0.0	10.9
700–800	0.0	0.7	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	2.1
900–1000	0.0	0.0	0.0	0.0	0.0	5.1
>1000	0.0	0.3	0.0	13.1	13.1	20.7

Figure S43. Tree Pipit *Anthus trivialis* (n/km^2). Insectivorous migrant.
Present in 10% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 0.9 ± 3.8.
Estimated overall density: 1.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 13.7 million, of which 1.1 million birds interpolated; range: 11.5–15.3 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	3.7	0.0
300–400	0.0	0.1	0.2	0.0	4.3	0.0
400–500	0.0	0.2	0.3	0.9	5.9	0.0
500–600	0.0	0.0	0.0	36.6	4.4	0.0
600–700	1.5	20.9	0.0	11.7	11.7	0.0
700–800	1.3	10.6	10.4	10.1	10.1	0.0
800–900	1.3	1.3	1.3	1.3	1.3	15.3
900–1000	18.2	18.2	18.2	18.2	18.2	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S44. White-rumped Seedeater *Crithagra leucopygia* (n/km^2).
Granivorous resident.
Present in 30% of the 111 cells.
Average density (n/km^2, ±SD) in grid cells: 3.2 ± 7.6.
Estimated overall density: 2.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 21.8 million, of which 7.3 million birds interpolated; range: 20.5–23.6 million (split-half).

SUPPLEMENTARY MATERIAL 2: Are our sites representative?

The aim of our stratified sampling regime was to obtain reliable average bird densities across the entire study zone. Very remote areas could often not be reached with a 4×4 car and are for that reason underrepresented, with dire consequences for estimates of the rarer bird species typical of remote terrain, such as bustards. Our aim was, however, focused on common bird species for which our dependency of dirt tracks is presumably of no consequence for occurrence or density of the bird species under consideration.

Of all habitats available, wetlands were clearly under-represented in our random sites. We had no sites in the mangroves along the West African coast between Mauritania and Sierra-Leone (Figure 8); bird numbers present in this zone (total surface 8400 km^2) have been estimated by Zwarts *et al.* (2014). We had random sites in several small seasonal floodplains, but not in the seven larger ones: Senegal Delta (1700 km^2), Senegal Valley (7500 km^2), Inner Niger Delta (35,000 km^2), Hadejia-Nguru (2000 km^2), Lake Chad (3500 km^2), Waza-Lagone (8000 km^2), and the Sudd (15,000 km^2) (surface areas given in Zwarts *et al.* 2009 and Mettrop *et al.* 2019). The total surface of these wetlands is large, 73,000 km^2, but relative to the 10 million km^2 of the study area, represents only 0.7%. Non-random bird counts performed during the present study in the Senegal Delta and Inner Niger Delta, and systematic bird counts in both wetlands carried out earlier (Zwarts *et al.* 2009), had shown that some bird species reach much higher densities in these habitats than in the dry surroundings, as in Western Yellow Wagtail and Crested Lark. For species associated with wetlands our total estimates are definitely too low.

For the many dryland species, however, coverage is much better and the chance of underestimating population size much less likely. The possible bias in our dryland sampling sites was quantified at two levels: (1) are the grid cells a representative sample of the entire region, and (2) are the sites within each grid cell an accurate sample of the grid cell itself regarding the presence of human habitation and the various land cover categories?

Grid cells

The 150 grid cells covered in the present study are not entirely representative of the region, the cells containing a relatively higher proportion of human habitation. This applies for all rainfall zones (Figure S45, based on the same GIS data provided by ESRI shown in Figure 8). For some 1000 sites of 1 km^2 we checked the accuracy of the GIS data by comparing the percent built-up with data from high resolution satellite images in which houses and huts were clearly visible. The percent built-up was slightly overestimated in sparsely populated areas (partly because bridges, stone walls, and similar constructions are recognised as buildings), but slightly underestimated in densely populated areas (since not all buildings are detected). Despite this slight bias, the conclusion is that the 150 grid cells have more built-up habitat in each rainfall zone than in the entire region (Figure S45). This bias hinges on the fact that we sampled comparatively many grid cells in the densely populated western Sahel and in the Sahara of Mauritania and Sudan where the density of the human population is higher than elsewhere along the southern fringe of the Sahara (Figure 7).

In the entire region, 39.53% of the total surface area is bare (mostly desert), compared to 14.35% in the 150 grid cells (Figure S46). Woodland is also under-represented in our sites. However, when the data are subdivided per rainfall zone, the frequency distribution of habitat categories is quite similar to that of the entire region and the 150 cells with one notable exception: more cropland in the 150 cells than found overall (Figure S46).

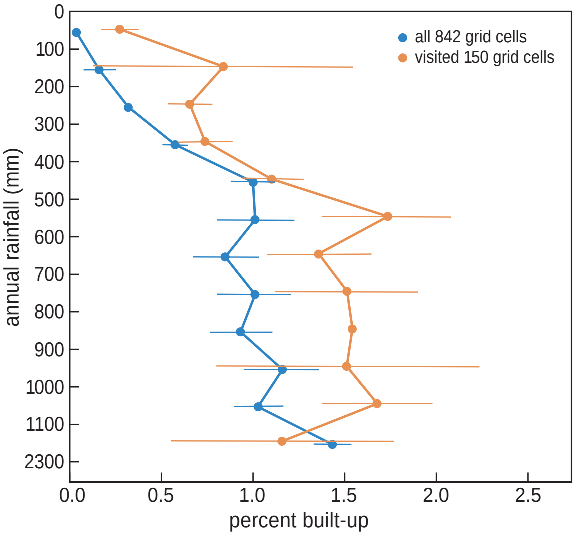
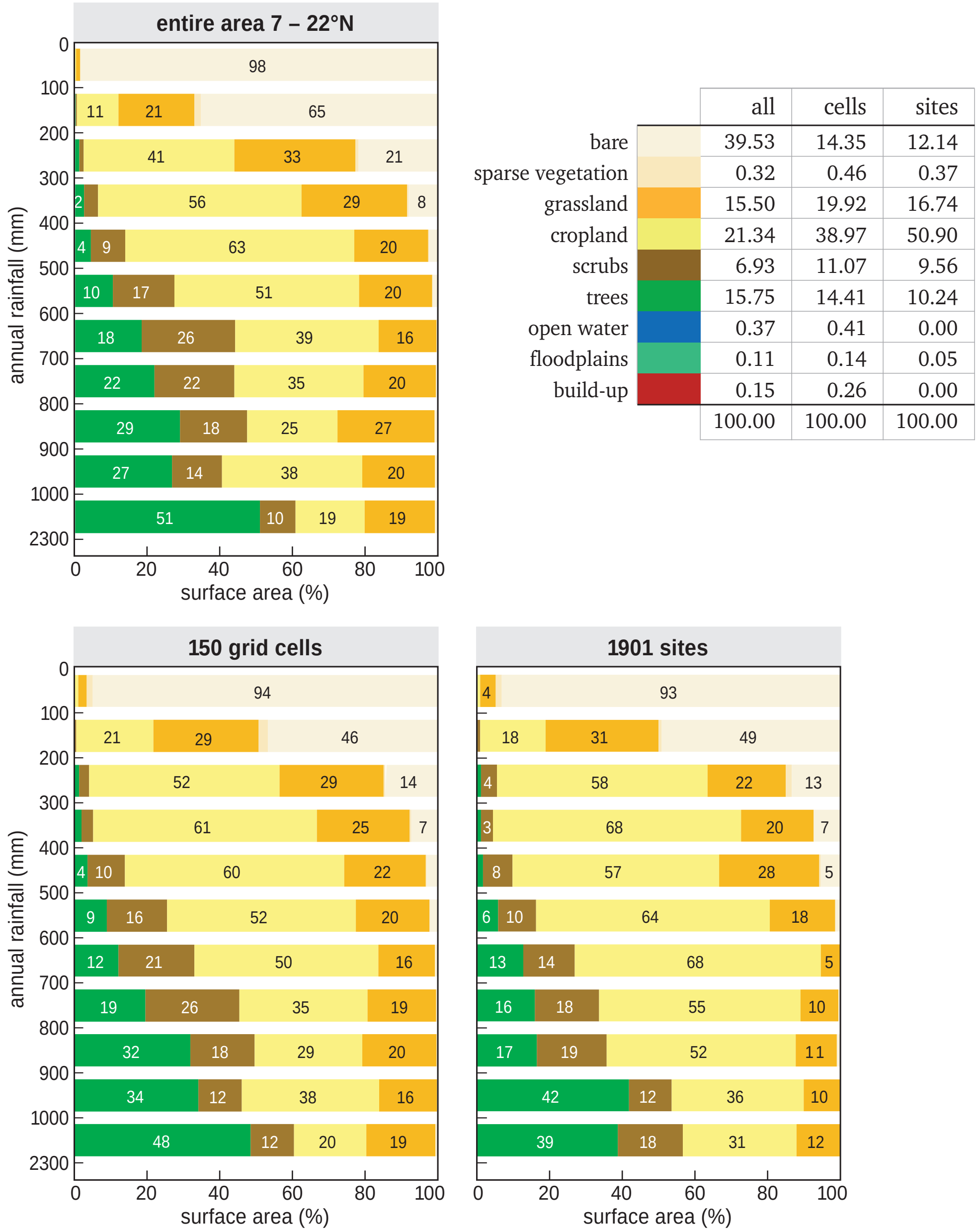


Figure S45. Percent built-up ± SE per rainfall zone in the 150 grid cells visited and for all 842 grid cells in the region (see Figures 3 and 4 and Figure 8 in the main text, respectively). Data for areas with >1100 mm rainfall are combined.



		all	cells	sites
bare	⬜	39.53	14.35	12.14
sparse vegetation	⬜	0.32	0.46	0.37
grassland	🟧	15.50	19.92	16.74
cropland	🟨	21.34	38.97	50.90
scrubs	🟫	6.93	11.07	9.56
trees	🟩	15.75	14.41	10.24
open water	🟦	0.37	0.41	0.00
floodplains	🟩	0.11	0.14	0.05
build-up	🟥	0.15	0.26	0.00
		100.00	100.00	100.00

Figure S46. Relative surface area of different land cover categories (based on Figure 10 in the main text; numbers in the bars indicate %) as a function of annual rainfall, given separately for the entire region (top), for the 150 grid cells where we performed field work (left below) and for 1901 random winter sites (right below). The table gives the average percentages of the nine land cover categories combined for the eleven rainfall zones.

Sites

Our sites were largely representative for the land cover categories in grid cells, except for cropland. We had more sites with cropland (50.9%) than expected from their occurrence in grid cells (39.0%), especially in the humid zone (Figure S46). This discrepancy was validated with high resolution satellite images (made available by Google Earth and ESRI). The images showed that 92% of the 971 sites identified in the field as cropland coincided with our assessment from satellite imagery. The 8% difference can be explained with the presence of fallow land, an arbitrary category that might be identified as savannah or cropland. The satellite images also revealed that croplands were almost exclusively found within 3.5 km of villages except for two large-scale irrigation schemes (Senegal Delta, Sudan between Blue and White Nile) where the distance to the nearest village increased to an average of 7 km. Since our field sites were slightly closer to human settlements than for randomly generated points (Figure S47A), more sites with cropland were to be expected from the fact that cropland is usually restricted to within 3.5 km of villages. However, when tested, this was not the case: within the zone with an annual rainfall of 300– 1200 mm, 56% of the field sites is cropland against 53% in the random-generated sites (Figure S47B).

We conclude that the grid cells sampled for this study are representative for the entire region when considering rainfall zones and longitude (Figure 9) and that the stratified sites are representative for the grid cells.

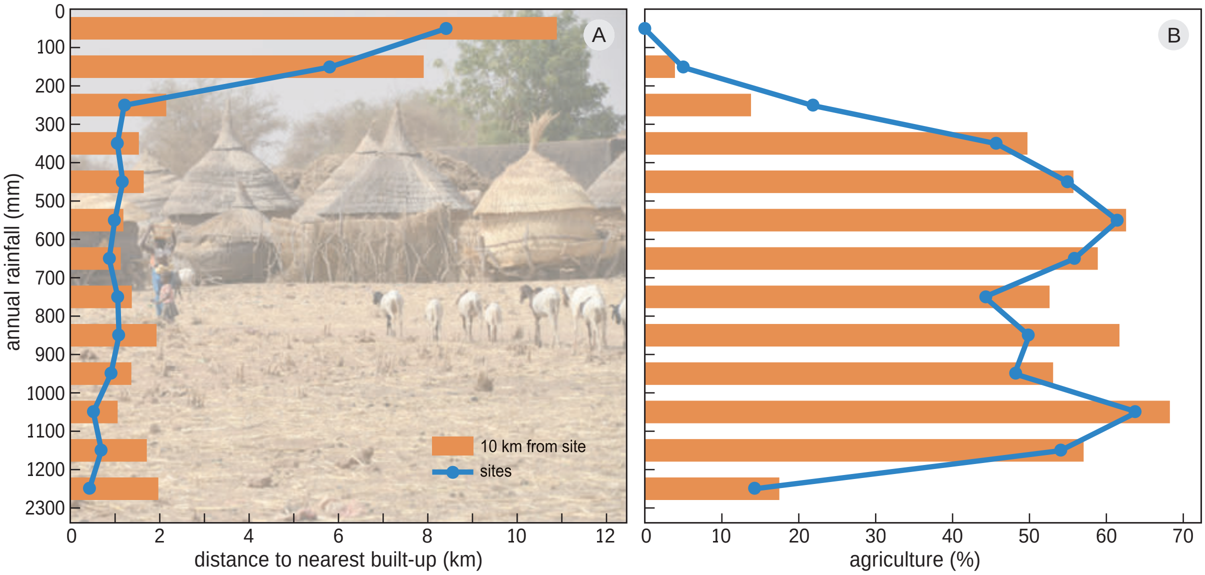


Figure S47. (A) Average distance from sites (Figure 3 in the main text) or from randomly generated spots at 10 km of the sites (direction and distance randomised) to the nearest human settlement (including remote houses and huts, visible on satellite images of Google Earth or ESRI) separately shown per rainfall zone; data >1200 mm rain taken together. (B) Percent of the sites being cropland using the same data as in (A). Rainfall has a significant impact on distance and land use ($P < 0.001$), but neither differed between the visited and randomly generated sites; the interaction is also non-significant (two-way ANOVA; $r^2 = 0.13$, $n = 2054$ for (A) distance and $r^2 = 0.03$ for (B) % agriculture).

SUPPLEMENTARY MATERIAL 3: Additional data NE Nigeria

Thanks to the field work done by Wilson & Cresswell (2006) bird density data are available for 16 sites in NE Nigeria situated between 12 and 14°N and 10 and 13°E. The counts from 2002 were repeated in 2007 by Stevens *et al.* (2010). Since we have no data for the region between 8 and 14°E, the study in NE Nigeria would be a valuable addition to our distribution maps. The average bird densities in Nigeria were two to three times as high as we found in the surrounding countries, even when we disregard the extremely high density of Red-billed Quelea in the 2007-count in Nigeria. This species forms large, mobile and temporary flocks and so it was not realistically possible to produce reliable densities from their small plots (Table S2). Figure S48 compares the average bird density in Niger and Chad with the average of both counts in Nigeria (except Red-billed Quelea). Rare and common bird species in Nigeria were also recorded as respectively rare and common in the surrounding countries, but only 5 of the 35 bird species were more common in the same latitudinal belt in Chad+Niger than in Nigeria. There are three possible explanations for this large difference:

The discrepancy might be due to the different methods used. We have no indication that our tested, time-consuming census method underestimated the birds present in the precisely delineated counting sites (Zwarts & Bijlsma 2015). Wilson & Cresswell (2006) and Stevens *et al.* (2010) used a more complex method to estimate bird density, including a correction factor, but we have no indication that their bird densities are overestimated.

It is possible that bird density has declined in the past 20 years, but in Nigeria no decline was apparent between 2002 and 2007. Whether a decline had commenced after 2007 is unknown but is not very likely given the above average rainfall between 2004 and 2020.

We used strict rules in the selection of random counting sites, resulting in the inclusion of sites where it was obvious at arrival that there would be no birds (the sites were, of course, counted nevertheless). As the 16 sites in Nigeria were selected to have "relatively high densities of birds (…) and in no way represent a random sample" (Stevens *et al.* 2010), it is to be expected that the measured average bird density in Nigeria is higher than in Niger and Chad. The 114 random sites in Niger and Chad were situated on farmland (46%) or savannah (54%), and none in woodland or wetland. The woody cover varied between 1 and

Table S2. Average bird density (n/ha) for 16 sites in NE Nigeria measured in 2002 (Wilson & Cresswell (2006) and in 2007 (Stevens *et al.* 2010) compared to our measurements in Niger and Chad between 12 and 14°N and between 3 and 18°E. All counts were from January–February.

Country	Nigeria	Nigeria	Niger	Chad
Year	2002	2007	2016	2018
Number of sites	16	16	71	43
African Collared Dove	0.251	0.497	0.006	0.109
Mourning Collared Dove	0.000	0.088	0.003	0.016
Vinaceous Dove	0.000	0.059	0.034	0.005
Laughing Dove	0.068	0.118	0.382	0.067
Namaqua Dove	0.156	0.316	0.014	0.226
Black-headed Lapwing	0.023	0.074	0.017	0.020
Blue-naped Mousebird	0.343	0.083	0.000	0.109
Northern Red-billed Hornbill	0.078	0.058	0.027	0.021
African Grey Hornbill	0.015	0.005	0.003	0.010
Eurasian Hoopoe	0.045	0.032	0.006	0.025
Vieillot's Barbet	0.022	0.004	0.016	0.010
Great Grey Shrike	0.108	0.071	0.016	0.026
Woodchat Shrike	0.023	0.020	0.017	0.052
Chestnut-backed Sparrow-Lark	0.316	0.196	0.003	0.416
Crested Lark	0.045	0.054	0.000	0.010
Western Bonelli's Warbler	0.087	0.004	0.185	0.000
Eastern Olivaceous Warbler	0.497	0.528	0.046	0.026
Cricket Warbler	0.287	0.170	0.024	0.185
Yellow-bellied Eremomela	0.023	0.094	0.006	0.057
Lesser Whitethroat	0.347	0.131	0.000	0.161
Subalpine Warbler	0.557	0.247	0.215	0.345
Common Whitethroat	0.318	0.559	0.221	0.310
Greater Blue-eared Starling	0.028	0.019	0.009	0.000
Chestnut-bellied Starling	0.212	0.137	0.225	0.056
Black Scrub Robin	0.188	0.062	0.015	0.059
Rufous-tailed Scrub Robin	0.015	0.005	0.082	0.025
Northern Wheatear	0.226	0.124	0.006	0.023
Pygmy Sunbird	0.147	0.083	0.146	0.228
Northern Grey-headed Sparrow	0.189	0.533	0.366	0.253
Sudan Golden Sparrow	2.210	5.500	1.046	2.027
White-billed Buffalo Weaver	0.277	0.239	0.043	0.010
Speckle-fronted Weaver	0.092	0.250	0.205	0.040
Little Weaver	0.085	0.221	0.060	0.083
Red-billed Quelea	1.370	16.100	0.059	0.000
Red-cheeked Cordon-bleu	0.588	0.494	0.049	0.165
Western Yellow Wagtail	1.420	0.364	0.018	0.000
SUM	**10.656**	**27.539**	**3.570**	**5.175**

17% and amounted to, on average, 4.6%. High-resolution satellite images revealed that the woody cover in the 16 Nigerian sites was higher (in one site even much higher). The bird density of migrants as well as residents in Nigeria was in woodland 2–4 times higher than in farmland and savannah (Figure 4 in Wilson & Cresswell 2006). The same high-resolution images also showed that several of the 16 Nigerian sites were situated at or near seasonally flooded areas along the fringe of the Hadejia, Jama'are and Yobe Rivers, which also explains why the density of two species common in emerged seasonal floodplains, i.e. Western Yellow Wagtail and Crested Lark (Zwarts *et al.* 2009), was relatively very high (Figure S48). Floodplains are extremely rich in birds (Zwarts *et al.* 2009) and the bird density in flooded forests is much higher than in dry forests (Zwarts *et al.* 2015; Zwarts *et al.* 2023c).

We conclude that the bird density in NE Nigeria was relatively high due to the presence of seasonal floodplains and as such a valuable addition to our distribution maps, but that the non-random surveys in Nigeria resulted in inflated densities which prevented inclusion in our dataset generated via stratified random sampling.

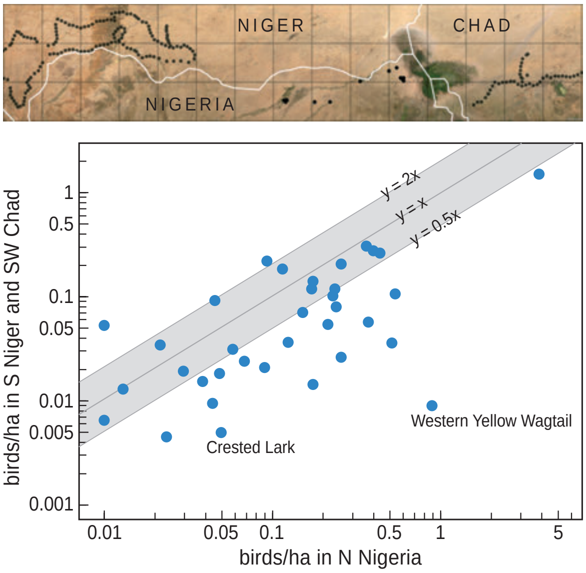


Figure S48. Average density of 35 bird species in S Niger and W Chad compared to the average bird density in NE Nigeria. Note log scales. Raw data in Table S2. The map shows the position of the sites in the three countries between 12 and 14°N and between 3 and 18°E.

SUPPLEMENTARY MATERIAL 4: Annual rainfall

Sahel rainfall index

The longest available series of rainfall measurements in the Sahel are from stations along the Atlantic coast (Saint Louis since 1848, Dakar since 1853) but in later years also from further inland, for example in Timbuktu from 1897 onwards. It was not until 1920 that rainfall was measured across the entire Sahel. The number of stations in the Sahel gradually increased during the 20th century up to 860 in 1961, after which there was a decline to 103 in 2020. We could not obtain access to all these data sources, but many referred to a short span of years. From the available data, we selected 215 stations where rainfall had been measured for at least 24 years. In 2022, the longest series covered 174 years, the average for the selected stations being 93 years. Most of these stations were operational between 1950 and 1975, after which there was a decline in their number, from 180 in the 1960s to 80 in the 2020s. If we select only those weather stations where the annual rainfall was based on full sets of daily measurements (blue bars in Figure S49), then the decline in number from the 1960s to the 2020s was even greater, down to just 20.

In the Sahel, it rains in only a few months, most of it falling during a limited number of tropical storms. That is why the annual rainfall varies from site to site (Taupin 2003) and why data from many weather stations are needed to arrive at reliable estimates of the average annual rainfall in the Sahel (Ali & Lebel 2008). To quantify the year-to-year variation in rainfall, several authors calculated a Sahel rainfall index, in which the annual rainfall is given as percent deviation from the long-term average, which thereafter was often standardised by dividing the percentage deviation by the standard deviation. Table 3 lists a selection of recent papers where the rainfall index has been calculated, sometimes separately for different longitudinal or latitudinal zones, to determine whether it is justified to use one single rainfall index for the entire Sahel. The published Sahel rainfall indices are highly correlated (L'Hôte *et al.* 2002, Dai *et al.* 2004), which is unsurprising because all are based on a comparable selection

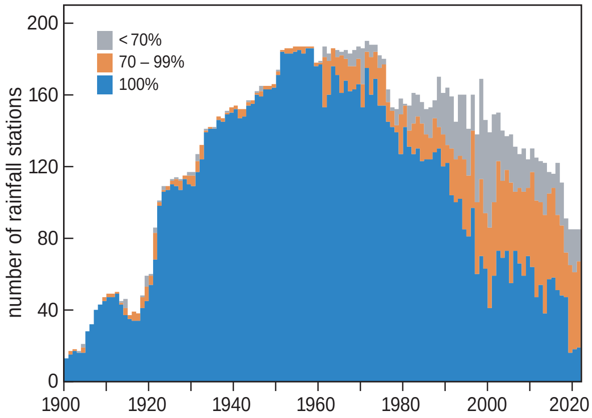


Figure S49. Number of operational rainfall stations in the Sahel between 1900 and 2021 used in this paper to calculate the Sahel rainfall index. We selected stations where rainfall had been measured in at least 24 years, separating stations where annual rainfall was measured every day of the year (blue bars) from stations where rainfall measurements were irregular (>70% of the annual total was measured (red bars) or <70% (grey bars)).

Table S3. Ten studies in which a Sahel rainfall index is produced; period = years over which the index is given and *n* = number of rainfall stations. JISAO = http://research.jisao.washington.edu/data/sahel/.

Source	**Period**	***n***	**latitude**	**longitude**
Ali & Lebel 2008	1905–2006	4–725	10–17°N	17°W–17°E
Dai *et al.* 2004	1920–2004	27–190	10–20°N	17°W–20°E
Descroix *et al.* 2009	1951–2013	12,12	12–17°N	17–12°W; 1°W–4°E
Frappart *et al.* 2009	1950–2007	60	14–20°N	4°W–2°E
Hulme 2002	1891–1992	?	13–21°N	17°W–38°E
JISAO	1900–2017	4–14	10–20°N	17°W–10°E
Lebel & Ali 2009	1950–2007	33,22,14	11–16°N	17–10–0°W–10°E
L'Hôte *et al.* 2002	1896–2000	21	9–17°N	17°W–18°E
Nicholson 2005	1931–2003	37,34,20,8	12–14–16–18–20°N	17°W–15°E
Nicholson 2005	1931–2003	16,4,3,3	12–14–16–18–20°N	15°E–35°E
Zwarts *et al.* 2009	1901–2005	4–38	8–22°N	17°W–6°E

of rainfall stations with the longest and more or less complete series of measurements.

The declining number of rainfall stations increases the difficulty of calculating the Sahel rainfall index for recent years. The rainfall index of http://research.jisao.washington.edu/data/sahel/, for instance, was based on 14 stations, of which only a few were operating after 2004. From 2015 onwards, the JISAO index was based on the average rainfall such as calculated by the Global Precipitation Climatology Centre (GPCC) which gives worldwide the daily and monthly rainfall per grid cell of one degree of longitude by one degree of latitude using neighbouring grid cells to interpolate values if these were lacking from the cell initially selected (see https://opendata.dwd.de/climate_environment/GPCC/). However, the GPCC is also faced by the same problem of declining number of Sahel rain gauges. For instance, in 1961, measurements were available for 49% of the grid cells in the Sahel, but the availability rate has declined to less than 10% in 2020. Indeed, there is no current measurement of rainfall in the rain-rich zone along the coast of the Gulf of Guinea, nor in the entire eastern Sahel (https://opendata.dwd.de/).

There is no Sahel rainfall index available after 2017 (Table 3), making it worthwhile to update the series. To compensate for the large decline of the number of stations where rainfall was continuously measured (blue bars in Figure S49), we calculated for all stations

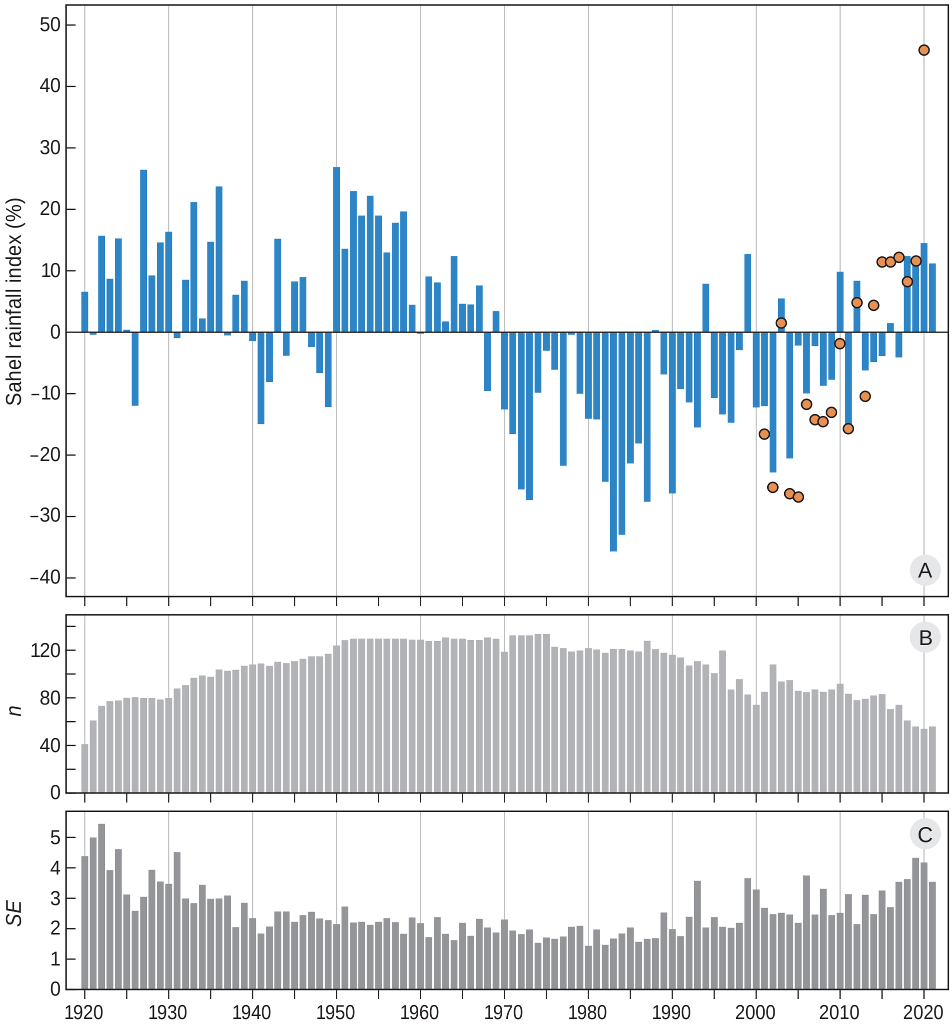


Figure S50. (A) The Sahel rainfall index, given as percent deviation from the average determined for the 20th century, based on measured rainfall on 148 ground stations (bars) between 1920 and 2021 or estimated using satellite measurements (RFE2) between 2001 and 2020 (red dots); detailed explanation is in the text. (B) Number of ground stations used to calculate the index shown in (A). (C) The standard error of the Sahel index (same data as both other panels).

the percentage rainfall per month and used these average figures to estimate per year what the rainfall would have been in months with missing data. For instance, when rainfall was known in a year for all months, except for September (accounting for x % of the annual rainfall, on average), we used this percentage to arrive at a corrected annual total for that year. Years in which the actual measured estimated rainfall was greater than 70%, relative to the annual total (red bars in Figure S49), were included in the calculation of the Sahel rainfall index. In this way, an additional error was introduced, but the number of stations that could be used in the calculations became twice as large since 2000 and more than three times as large in the most recent years (Figure S49).

The next step was to convert annual rainfall for each of the selected stations into percent deviation from its average over the period 1950–1975, then to calculate the average percent deviation for all stations combined and use this data set to determine the item-total correlations between the individual stations and the average for all stations together. The correlation between the stations and the overall mean amounted to $r = +0.54$, on average, but there was a large variation. Some stations, mostly in the north (desert) or south (hyper-humid zone) were weakly correlated or uncorrelated with the average index, but most stations in the Sahel, especially in the western part, showed a high correlation, up to $r = +0.77$. That is why we omitted not only all stations situated in the desert (>22°N) and in the hyper-humid south (<8°N), but also those poorly correlated with the average for all stations together (i.e. $r < 0.23$); this left us 148 rainfall stations from whose data we finally determined the Sahel rainfall index (Figure S50). The average rainfall in the 20th century was 4.7% higher than in the period 1950–1975, so this percentage was included to show the variation of annual rainfall relative to the average of the 20th century.

The decline of the number of operational rainfall stations is a worldwide phenomenon (Sun *et al.* 2018), but this loss of data can to some extent be compensated for by substituting satellite-derived estimates of rainfall. The great advantage of satellite measurements is that the rainfall can be assessed not only at a high resolution anywhere, but also continuously. Such rainfall estimates are indirect; for instance, a satellite infrared sensor measures the temperature of clouds (the colder the high clouds usually means a greater amount of rain). There are at least 9 different satellite-related rain estimates available, varying in frequency, in resolution (from 0.1° to 2.5°) and also in the time span over which measurements are available: the longest series (GPCP) runs from 1979 to the present, but most others run from around 2000 (see Sun *et al.* 2018 for an overview). We used Rainfall Estimates 2.0 (RFE2), developed by the (US) Climate Prediction Centre (CPC) https://www.cpc.ncep.noaa.gov/products/international/africa/africa.shtml. RFE2 has been available since January 2001 and since then has been providing daily rainfall maps (usually with a one-day delay). These daily rainfall estimates were added per year. As shown below, the annual estimates are less reliable in the arid zone (annual rainfall <400 mm) and the humid zone (rainfall >900 mm). Hence the average estimated rainfall (excluding Ethiopia) was calculated for the 400 to 900 mm rainfall zones and plotted against the ground measurements. The result is shown as red dots in Figure S50. The correlation with the Sahel rainfall index is significant ($r = +0.75$, $n = 20$, $P < 0.001$), but RFE2 is clearly not accurate enough to be used as alternative for ground measurements. As might be expected, given the decline of the number of stations (Figure S50B) and the loss of quality (Figure S49) in recent years, the most recent Sahel rainfall indices are less accurate: the standard error, being about 2.5% before 2018, was in subsequent years a bit higher (Figure S50C). It is obvious, however, that the rainfall in the Sahel, after the disastrous drought in 1983 and 1984, has gradually increased over the last 40 years.

Rainfall maps

The rainfall map used in this paper (see Figure S51A) is based on Hijmans *et al.* (2005) who averaged the annual rainfall measured on ground stations between 1950 and 2000. This period started with 18 relatively wet years in the Sahel (1950–1968; rainfall, on average, 13% above the average for the 20th century) and was followed by a long, dry period (1969–1992; annual rainfall 16% below the long-term average) and 7 years (1993–2000) with annual rainfall 5% below average (Figure S50). The average rainfall during those 50 years was 4% below the average for the 20th century. During our surveys in the Sahel in 2010/11–2018/19 we recorded no drought years equivalent to those in the 1970s and 1980s, although 2011/12 was very dry. The average rainfall in 2010–2019 was 2% below the average rainfall in the 20th century and thus 2% higher than in 1950–2000 (therefore in practice not different from that shown on the rainfall maps used in our paper). The scarcity of recent rainfall data prevented us from constructing a meaningful rainfall map.

It was dry everywhere in the Sahel during the drought years of 1972, 1973, 1983, 1984, 1987 and

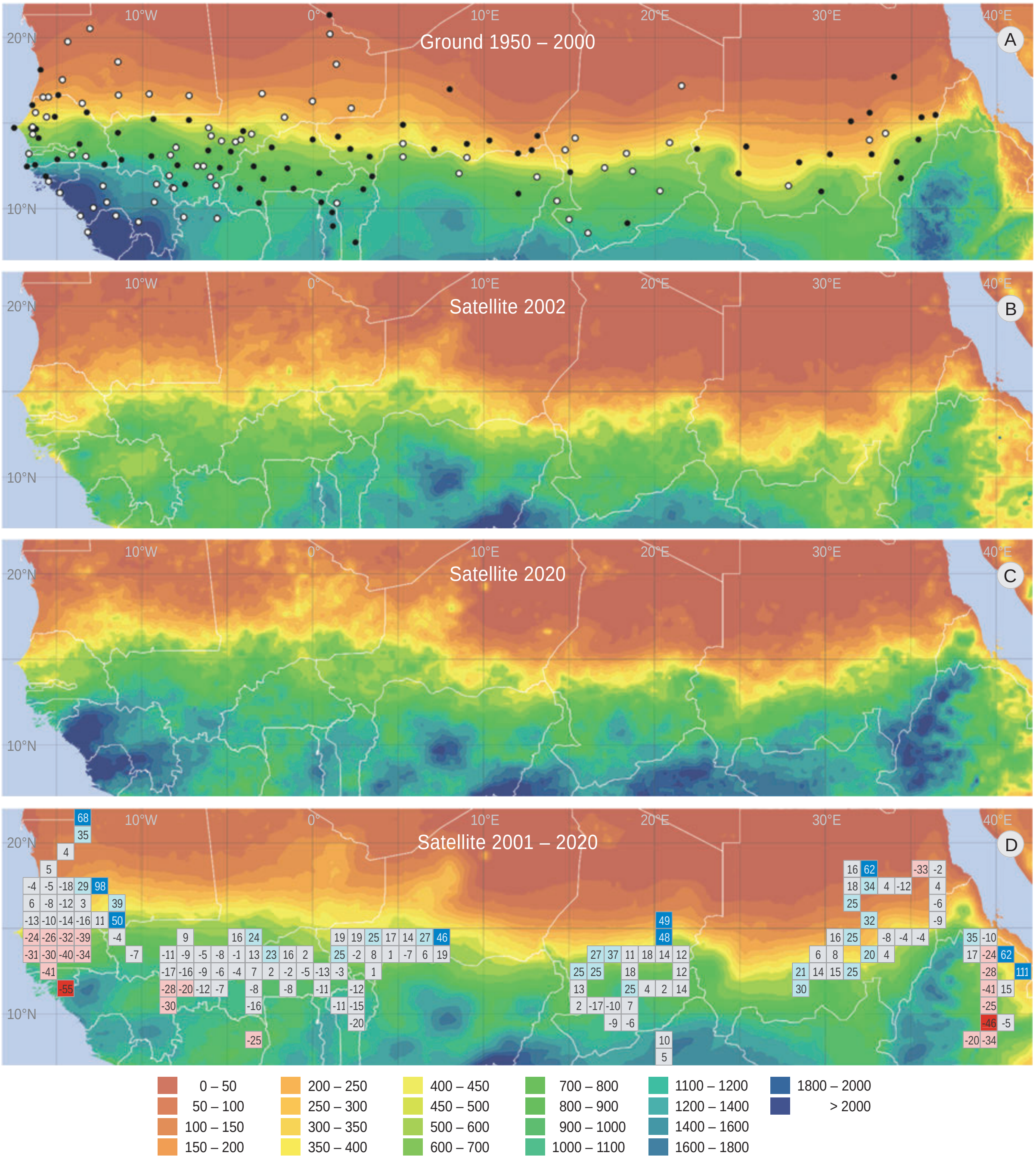


Figure S51. Annual rainfall (mm/year) based on (A) ground measurements (1950–2000; Hijmans *et al.* 2005) or daily satellite-derived rainfall estimates (RFE2) in (B) 2002, (C) 2020 and (D) averaged for 20 years, 2001–2020. Panel A also shows the 148 rainfall stations used to construct the Sahel rainfall index, of which the stations still operational since 2020 are indicated separately (●). Panel D also shows for 150 grid cells the average annual rainfall in the years during which the study sites in the grid cells were visited, given as percent deviation from the average satellite-derived rainfall estimates in the same sites calculated over the observation period (2010–2019). The estimated rainfall in the years of field work did not deviate more than 20% from the 2010–2019-average in 97 of the 150 grid cells (marked grey).

1990, and wet everywhere in the 1950s, but this does not imply that the annual rainfall in the Sahel shows no large spatial variations. In 2010, for instance, a relatively wet year with rainfall being 10% above average, the east (≥18°E) experienced rainfall some 3% below average (22 stations). In the western Sahel, there was exceptional rainfall in the (semi)-arid zone, 85% above average in Mauritania and N Senegal (9 stations), but only 5% above average in mid and south Senegal (7 stations). Even more exceptional was 2020, a wet year (rainfall +22% above average) everywhere in the Sahel, but nowhere so extreme as in Sudan where record amounts of rainfall (not recorded before in the 20th century) caused devasting flash floods.

To establish local rainfall per site and per year, we could not rely on nearby meteorological sites, most situated hundreds of km distant. We therefore used rainfall maps based on satellite measurements, although these data are obviously not sufficiently accurate to replace rain gauge data (Figure S50A). Figure S51 gives, as an example, the annual estimated rainfall for two years and an average over a period of 20 years, 2001–2020. To calibrate the satellite estimates, the rainfall measured at 163 ground stations was plotted against the estimated rainfall for the same locations, in both cases summed per month. The correlations varied between $r = 0.15$ and $r = 0.99$, and averaged $r = 0.897$. A high correlation was to be expected given the pronounced difference in rainfall between dry and wet seasons, but is meaningless as a validation of RFE2, because ground station measurements, if available, are used to improve RFE2 when estimating the daily RFE. Unfortunately, it is not possible to gauge the dominance of ground station measurements in determining the RFE2, nor to determine the periods of use for the ground stations they used.

A second problem is that satellite-derived rainfall estimates may systematically deviate from actual measurements of rainfall. This was apparent from the 163 linear regression equations just mentioned (also evident from a comparison of panels A and D in Figure S51). Rainfall estimates for the desert are systematically too high. Although the absolute deviation in mm is small, the relative error (percent deviation) is large. In contrast, the rainfall along the Gulf of Guinea is often strongly underestimated because the rain in this region not only derives from thunderclouds (with low temperatures at 10 km and higher, used as indirect measure of the estimated rainfall), but also from 'warm' clouds that are missed by the sensor of the satellite. RFE2 also systematically produces too low rainfall estimates for mountainous areas, such as the Ethiopian highlands. This – for our purposes – is a lesser problem because we are mostly concerned with the estimated rainfall in the Sahel; for this region rainfall calculated via satellites does not deviate systematically from the rainfall measured on the ground.

The distribution of some, but not all, bird species in Senegal and Mauritania differed in conjunction with annual rainfall (Zwarts *et al.* 2023c). The distribution maps of the bird species given in this paper are based on density counts, averaged for different years: multiple years in Senegal, Mali, Mauritania and Burkina Faso, and single years in the other countries (Table S4). It would complicate the analysis had the rainfall differed much between years, especially for countries visited only once. Consequently, we determined for all study sites the average RFE for 2010–2019 and for the year(s) when the sites were visited (Figure S51D). RFE2 turned out to be unreliable for the humid zone along the Gulf of Guinea and for the Ethiopian highlands. We cannot conclude from Figure S51 that less rain than average had fallen during our field work in southern Senegal, Guinea-Bissau and Ethiopia. The arid zone in Niger, Chad and Sudan, and in northern Senegal and Mauritania was visited in years with relatively high rainfall. Apart from the arid and most humid zones, the deviation from the average rainfall did not differ much from average for the period 2000–2019. We conclude that we had relatively slightly more rainfall preceding our field work in Niger and further east than we had in the western Sahel.

SUPPLEMENTARY MATERIAL 5: Field periods

Table S4. Year and start/finish of fieldwork in the countries visited between 2007 and 2019, with total number of sites (*n* = 2484; in 2144 sites surface areas were measured) and number of random sites, with known surface area, visited between 20 November and 10 March (w-sites; *n* = 1901). Region/country: BF = Burkina Faso, BN = Benin, IND = Inner Niger Delta, ML = Mali, MR = Mauritania, SN = Senegal. Most sites had a surface of 4.5 ha, but were smaller in the Central African Republic (CAR; *n* = 51) and Ivory Coast (*n* = 12); these were condensed into 2 and 1 site(s), respectively.

year	start	end	sites	w-sites	region/country
2007	5–2	26–2	5		IND
2008	14–2	28–2	3		IND
2009	26–1	13–2	4		IND
2009	3–3	7–3	3		IND
2010	18–2	27–2	5		IND
2011	21–1	16–2	147	111	SN+MR
2011	21–2	21–2	3	3	Mali
2012	5–1	10–2	180	170	Mali
2012	13–2	23–2	4		IND
2012	5–10	11–10	12		Senegal
2013	13–1	22–1	7	4	Senegal
2013	7–11	29–11	56		Mali
2013	29–11	30–11	8		Senegal
2013	24–12	30–12	8		Senegal
2014	4–1	11–2	110	67	SN+G-Bissau
2014	14–11	22–11	11		SN+G-Bissau
2014	9–12	15–12	16		Gambia
2014	9–12	23–12	86	75	Senegal
2015	7–2	16–2	59	55	Burkina Faso
2015	23–2	10–3	106	80	Senegal
2015	3–3	12–3	17		Gambia
2015	18–10	3–11	97		Senegal
2016	6–1	13–2	307	280	SN+ML+BF+BN
2016	28–11	22–12	184	184	Niger
2017	8–1	4–2	223	202	SN+MR+ML
2017	23–2	28–2	8		Gambia
2017	28–11	15–12	2	2	CAR
2018	15–1	20–2	233	227	Chad
2018	1–2	1–2	3		G-Conakry
2018	9–12	16–12	39	37	Burkina Faso
2018	7–12	21–12	1	1	Ivory Coast
2019	9–1	30–1	247	244	Sudan
2019	1–2	24–2	160	159	Ethiopia
2019	27–9	17–10	130		Senegal

Distribution and numbers of arboreal birds between the hyper-arid Sahara and the hyper-humid Guinea forests

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This study quantifies the spatial variation in the density of 50 arboreal bird species (17 insectivorous Afro-Palearctic migrants and 33 Afro-tropical residents: 20 insectivores, 7 frugivores and 6 sunbirds) in the transition zone between the arid Sahara and the humid Guinea zone, measured during the dry season in 2011–2019. The distribution of bird species was related to annual rainfall, with Afro-Palearctic migrants found mainly in the relatively dry zone and Afro-tropical residents in the more humid zone. As woody cover increases with rainfall, bird species from the dry zone are by default found in more open habitats than species from the humid zone. This effect of woody cover largely dissolves when corrected for rainfall. The data – pertaining to absolute bird counts in stratified random sites – were used to estimate the total number of birds in this region. To assess the reliability of these estimations, population sizes were calculated separately per species on half-split data. The two estimates deviated about 10% from the averages calculated for the full data set. Among arboreal birds (1322 million), insectivorous residents were most abundant (547 million), followed by insectivorous migrants (326 million), nectarivorous residents (272 million) and frugivorous residents (177 million). The two most numerous arboreal bird species were insectivorous residents: Tawny-flanked Prinia *Prinia subflava* (128 million) and Green-backed Camaroptera *Camaroptera brachyura* (103 million). Among the migrants, the three most abundant were Subalpine Warbler *Curruca iberiae* + *subalpina* + *cantillans* (62 million), Lesser Whitethroat *Curruca curruca* (48 million) and Western Bonelli's Warbler *Phylloscopus bonelli* (30 million).

Key words: Sahel, arboreal birds, bird distribution, bird population size

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The Sahel shows a tremendous change in landscape as one travels from north to south, from the bare Sahara with scattered scrub and small, spiny trees to dense Guinea forests. The aim of the present paper is to show the distribution of arboreal bird species south of the Sahara and to estimate their total number between the Atlantic Ocean and the Red Sea (a distance of 6000 km) in a 1600 km wide band. The paper is complementary to the one describing the distribution of ground-foraging birds (Zwarts *et al.* 2023a). Together they form the descriptive basis for attempts to explain the observed bird distributions and why so many migratory – and African – bird species are in decline.

METHODS

Study sites

The data for this particular study were collected between 2011 and 2019 during the dry season (20 November – 10 March), in sites (usually 4.5 ha; a triangle with three sides of 300 × 50 m) situated between 7°N and 22°N and between 17°W and 42°E (see Figure 3A and 3B in Zwarts *et al.* 2023a). As described in that paper, we used a stratified random sampling regime in order to generate data that are representative for the region. For each study site, we determined the average annual rainfall in the period 1950–2000 on the basis of Hijmans *et al.* (2005). The present analysis is based on a total of 1901 random sites with a combined surface of 8022 ha. The 1901 sites are situated in 178 1° latitude × 1° longitude grid cells (111 × c. 104 km). Since data from grid cells with less than 10 sites were combined with adjacent grid cells, bird densities are given for 150 grid cells (see Figure 3B in Zwarts *et al.* 2023a).

In a strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a). We use the term in a wider sense as the transition zone between the arid Sahara in the north (>30 mm rainfall/year) and the humid forests in the south (<1200 mm rainfall/year).

Birds

This paper deals with birds feeding in woody vegetation. Ground-feeding birds which use trees for roosting (such as doves) are excluded. Some species, usually found in lower woody vegetation, may also forage on the ground or in herbs. Three species of which more than half of the recorded birds foraged on the ground or in the herbaceous layer (Cricket Warbler *Spiloptila clamans*, Black Scrub Robin *Cercotrichas podobe* and Rufous-tailed Scrub Robin *C. galactotes*; Figure 1) are excluded (but have been included in Zwarts *et al.* 2023a), as well as Woodchat Shrike *Lanius senator* and Great Grey Shrike *Lanius excubitor*, which use trees as perches and take food from the ground. The arboreal bird species are categorised as Afro-Palearctic (termed migrants) and Afro-tropical (residents), and as insectivorous, frugivorous or nectarivorous, based on Morel (1968), Morel & Morel (1978), Urban *et al.* (1997), Fry & Keith (2000, 2004) and own observations.

In order to generate reliable density estimates, comparable within and between species, we developed a system of counting absolute numbers of birds inhabiting landscapes with scattered trees and shrubs. This method bypasses the problems associated with relative census methods (Zwarts & Bijlsma 2015). First, we counted arboreal birds per individual woody plant and recorded for each bird in which tree or shrub it was detected. Second, each tree was watched with three, and sometimes two or four, observers for as long as necessary to detect all birds present. The time spent to count all birds in a single tree varied between a few seconds for a small bare tree to 50 minutes for a tall tree with a dense canopy in which several birds resided. For the same reason, the time spent in counting birds in a 4.5-ha site varied between 5 to 10 minutes in treeless desert to 573 minutes in dense forest, but amounted to, on average, 47 minutes since most sites were situated

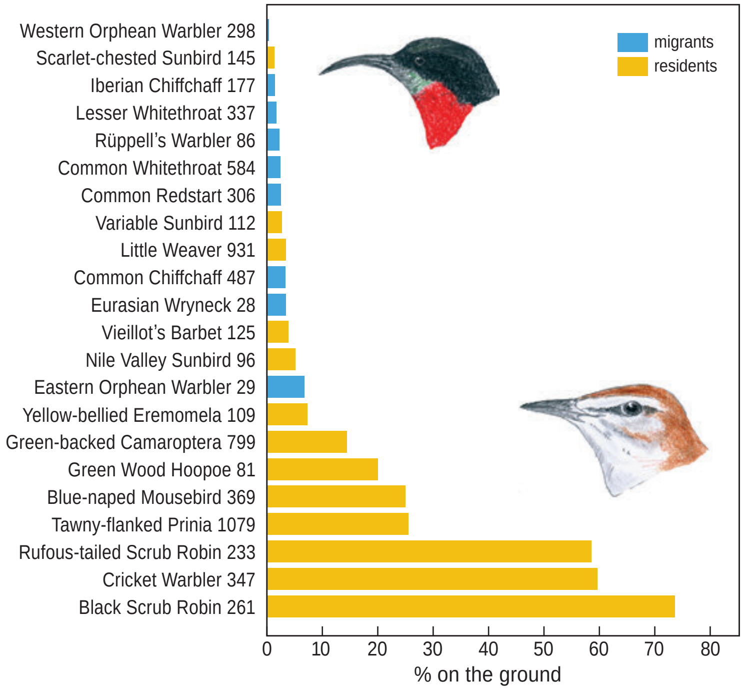

Figure 1. Percent of arboreal birds recorded in our study area as foraging on the ground (including herbaceous vegetation); strict canopy-dwellers are not shown. Total number of birds recorded are given next to their names. Mousebirds may feed on fruit that has fallen from the tree to the ground, while sunbirds were observed to feed on flowering legumes such as beans.

in open savannah and in farmland with few scattered shrubs and trees. The method was particularly time-consuming in woody sites, but – in contrast to relative counting methods relying on a mixture of sound and vision – all daylight hours could be used to find and identify birds because most were detected visually (Figure 11 in Zwarts & Bijlsma 2015). In most sites trees were standing apart and birds could be unequivocally assigned to a woody plant. Detecting birds in trees was usually easy since most trees either had open canopies, were small or had few or no leaves. When trees were closer together, the detection of individual birds was more difficult. Most arboreal birds had very small flight distances in a horizontal plane (even less so vertically), often only some metres, but birds feeding on the ground or present in the lower part of the canopy (such as Common Redstart *Phoenicurus phoenicurus*) were more wary, with an average flight distance of 20–40 m (see Figure 13 in Zwarts & Bijlsma 2015).

As extensively discussed by Zwarts & Bijlsma (2015), birds, including species leading a secretive life, were accurately counted by our time-consuming census method. Under exceptional conditions, especially under very high temperatures when birds were partly inactive (typically in March and April, periods mostly outside the time window of our surveys), some birds might have been overlooked (see also Bächler & Liechti 2007). We frequently checked by throwing stones or shaking branches after we finished counting birds in a particular tree to discover whether we had overlooked any birds, especially in densely-foliated trees where detection was difficult (Table 1). Of the trees covered in this study, <10% of woody plants in which birds were recorded had a dense crown, >90% possessing a more transparent crown enabling clear views into the canopy, thus making bird detection easy. Although we overlooked an estimated 7% of birds in trees with a dense crown (Table 1), we conclude that we missed less than a few percent of the arboreal birds overall because dense-canopied trees were scarce. For more details see Zwarts & Bijlsma (2015).

Table 1. The total number of birds detected in 420 woody plants with a dense crown, divided into birds detected during the standard procedure and overlooked birds that were flushed afterwards.

	Bird recorded		
	No	Yes	Sum
No bird present	349	0	349
Bird present	5	66	71
Sum	354	66	420

To assess the detectability of Wryneck *Jynx torquilla*, a particularly secretive species, an additional test was run in Chad from 14–16 February 2018 (between 6:41 and 16:07). For each leg of a transect (300 m) the song (a total of 10 plots, 52 broadcasts) or alarm call (7 plots, 40 attempts) was played back with a mobile phone, usually three times halfway through the transect and three times at the end of the transect. Simultaneously, we listened and looked for Wrynecks in the part of the transect ahead and the stretch already covered. In one instance, a Wryneck already detected in the plot responded immediately with song when song was broadcast. In another instance, a Wryneck approached from >150 m outside the plot when the alarm call was broadcast; this bird was agitated and alarm-called frequently. A silent Wryneck that had been flushed from a Desert Date *Balanites aegyptiaca* came back as soon as song (3×) and alarm-calls (10×) were played back; this bird remained silent. These trials suggest that (1) where playback was used to trigger a response, we had not missed Wrynecks that had been present, and (2) that Wrynecks responded to playback of song and – particularly – alarm calls, either by starting to call and/or by approaching the source of playback. Out of 30 records from the entire width of sub-Saharan Africa between 15 October and 18 February 2011–2019, only one bird was heard singing spontaneously, in Chad on 18 February 2018.

All Western Olivaceous Warbler *Iduna opaca* (*n* = 225) were seen West of 3°E and all Eastern Olivaceous Warbler *Iduna pallida* (*n* = 85) East of this longitude, except one bird in Gambia at 16.8°W (probably *Iduna pallida reiseri*). In the first years of our field work we did not differentiate between the two species. Despite some overlap in their distribution (see L. Gustafsson in Wilson & Cresswell 2010) and the presence of *Iduna pallida reiseri* in West Africa (Salewski & Herremans 2006), we categorised the 513 not specifically identified birds recorded West of 3°E as Western and 48 birds East of 3°E as Eastern Olivaceous Warbler.

Subalpine Warbler *Curruca cantillans* was recently split into three species: Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans* (Zuccon *et al.* 2020). We recorded them as one species, although we heard the characteristic rattle of Moltoni's Warbler in Chad, but not further West, where it is, according to Piot & Blanc (2017), indeed a rare bird compared to the Western Subalpine Warbler. No Subalpine Warblers were recorded in the sites in Sudan and Ethiopia, hardly surprising given the small source population of the Eastern Subalpine Warbler (southern Italy, Balkans, Greece, western Turkey; Zuccon *et al.* 2020).

Iberian Chiffchaffs *Phylloscopus ibericus* (*n* = 67) were recorded in Mauritania, Senegal, Gambia and Mali, all North of 13°N and West of 4°W, where it is a common species in flooded forests and wetlands. In the rest of West Africa and in Ethiopia we saw exclusively Common Chiffchaff *P. collybita* (*n* = 613). Within the range of the Iberian Chiffchaff, we also recorded 52 unspecified Chiffchaffs, mainly at 13–14°N, which in the analyses will be considered as Iberian Chiffchaff. Hence, Iberian Chiffchaff should be read in this paper as 'Iberian Chiffchaff with an unknown, but probably small, fraction of Common Chiffchaff'. The split into 2 species occurred relatively recently (Svensson 2001), and information on wintering ranges is still scarce (but see Isenmann *et al.* 2019, who roughly delineated the wintering range as lying between 10°N and 16°N and from coastal Senegal east to 1°W (covering Senegal, The Gambia, Mali and Burkina Faso)).

Woody plants

We counted, measured and identified all woody plants in the study sites, totalling 765,960 trees and shrubs of ≥1 m high. 304 woody plant species were identified, using mainly Bonnet *et al.* (2008) and Arbonnier (2019 and earlier editions), but also other sources, e.g. https://plants.jstor.org, Hawthorne & Jongkind (2006), Delvingt & Labão Tello (2004) and Harris *et al.* (2014) for the Central African Republic and Bekele-Tesemma (1993) and Fichtl & Adi (1994) for Ethiopia. On average, 2% of woody plants could not be identified, varying between 0.1% in sites with an average annual rainfall <800 mm, where we did most of our field work, and 18% in Ethiopia and 19% in the few sites beyond Ethiopia with an annual rainfall >1000 mm.

Using a laser rangefinder, we measured the height of each larger tree from a distance of at least twice the tree height. The height of trees <4 m was estimated by eye. The width of the canopy was also estimated by eye. We verified the estimated width of the canopy in large trees by pacing out the distance beneath the crown,

Photo 1. A narrow, densely wooded stream valley of only 10–30 m wide, with some water left in the middle of the dry season, is a bird paradise amidst dry and bird-poor wood- and farmland in southern Mali (18 January 2012). A birder selectively visiting only 'good spots' might mistakenly think that, for example, Pied Flycatchers are common birds occurring everywhere. Bird counts in random plots show the fallacy of non-random impressions.

and photographed trees to check the height-width ratio estimated in the field afterwards; details in Zwarts & Bijlsma (2015). The width of the canopy was used to calculate canopy surface for each woody plant, assuming circular crowns. The woody cover in a site is defined as the sum of the canopy surface of all trees and shrubs.

Analysis

Between 2011 and 2019 we counted only migratory arboreal birds in the study plots, but we started to systematically include insectivorous residents from 2012 onwards and frugivorous and nectarivorous residents after 2013. As a consequence, the average densities for migrants are based on 1901 sites, 8022 ha and 150 grid cells, for insectivorous residents on 1787 sites, 7316 ha and 150 grid cells, and for frugivorous and nectarivorous residents on 1613 sites, 6542 ha and 138 grid cells.

This paper analyses the distribution of birds in relation to the annual rainfall for the 50 most common arboreal bird species, i.e. 17 migrants (all insectivores) and 33 resident species (20 insectivores, 7 frugivores, 6 nectarivores). Distribution maps are produced for 34 bird species, exclucing species seen only in Ethiopia. The analyses of the distribution of bird species in relation to rainfall and woody cover exclude the data from the Ethiopian highlands (700–3500 m above sea level) as they are at variance with the rest of the data obtained in lower-lying flatlands. We used two selection criteria to construct the distribution maps: (1) to rule out seasonal variation in the distribution of birds, only data from 20 November to 10 March were used, and (2) non-random sites, usually pertaining to scarce habitat types (such as flooded forests), were discarded. Our stratified random sampling method is designed to reliably calculate the average density of common species. To arrive at a meaningful estimate of the average bird density for the entire region, the unequal distribution of grid cells within the region necessitated a correction. This is particularly evident for the desert, the humid woodlands and the eastern half of the region which were under-recorded (Supplementary Material 2 in Zwarts *et al.* 2023a). This problem is circumvented by calculating the average bird density for 11 rainfall zones in six longitudinal bands, using the surface area of the resulting 65 subregions (Figure S1 in Zwarts *et al.* 2023a) as a weighting factor to estimate the total number of birds. Density estimates are available for 53 of the 65 subareas. To estimate the bird density in the 12 missing subcategories, we averaged the measurements in two adjacent cells with a similar rainfall. Since habitat and birdlife of the Ethiopian highlands differ substantially from those of Sudan, we substituted adjacent values of Chad and the Central African Republic for missing values in Sudan cells. We used a split-half method (even and odd numbered sites) to assess the reliability of the population estimates.

RESULTS

Bird density and distribution

The overall density of arboreal birds was very low in the nearly treeless dry zone and increased in the semi-arid zone (Figure 2A) as woody cover increased (Figure 6B in Zwarts *et al.* 2023a). The density of insectivorous migrants was relatively high in the (semi) arid zone (200–600 mm rain/year), and much lower further south; Figure 2B) despite the fact that woody cover in the more humid zone was 20–30 times higher than in the arid zone (Figure 6B in Zwarts *et al.* 2023a). In contrast to the migrants, very few insectivorous residents were recorded in the (semi)-arid zone, but their density increased further south where they were more common in the humid zone than insectivorous migrants (Figure 2C). Nectarivorous and frugivorous residents (Figure 2D and 2E) showed more or less the same distribution as the insectivorous residents but were less common overall.

The average density of arboreal birds in the grid cells amounted to 140 birds per km^2, mostly insectivorous residents (61/km^2) and insectivorous migrants (42/km^2). Nectarivorous residents (22/km^2) and frugivorous residents (15/km^2) were least common (Figure 2). The most common arboreal bird species were:

- the insectivorous residents Tawny-flanked Prinia *Prinia subflava* (15.4/km^2; Figure S16) and Green-backed Camaroptera *Camaroptera brachyura* (11.1/km^2; Figure S17),
- the nectarivorous Pygmy Sunbird *Hedydipna platura* (8.8/km^2; Figure S29),
- the insectivorous resident Little Weaver *Ploceus luteolus* (7.8/km^2; Figure S34) and
- the insectivorous migrants Subalpine Warbler (8.8/km^2; Figure S24), Western Bonelli's Warbler *Phylloscopus bonelli* (6.8/km^2; Figure S10) and Lesser Whitethroat *Curruca curruca* (5.6/km^2; Figure S20).

The average density of 24 other species was <5/km^2; see Supplementary Material.

The lower density of arboreal birds in the arid zone was not the result of fewer birds visiting trees. On the contrary, the highest densities in trees and shrubs,

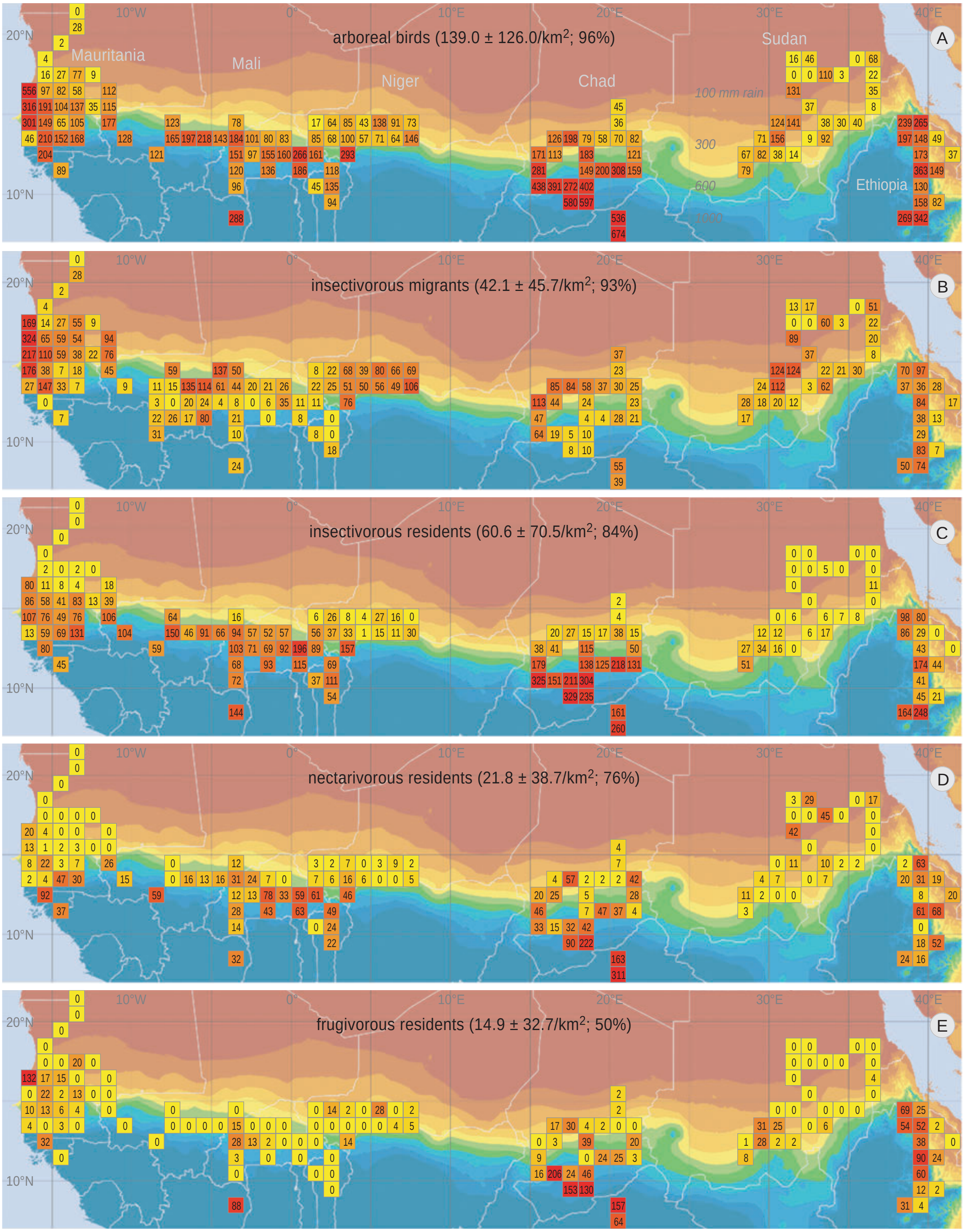

Figure 2. Density of 5 categories of arboreal birds/km^2 (n/km^2) in 138 (residents) and 150 (migrants) grid cells; average density (±SD) and presence in the grid cells (%) given between brackets. Background: rainfall (as Figure 4 in Zwarts *et al.* 2023a; simplified).

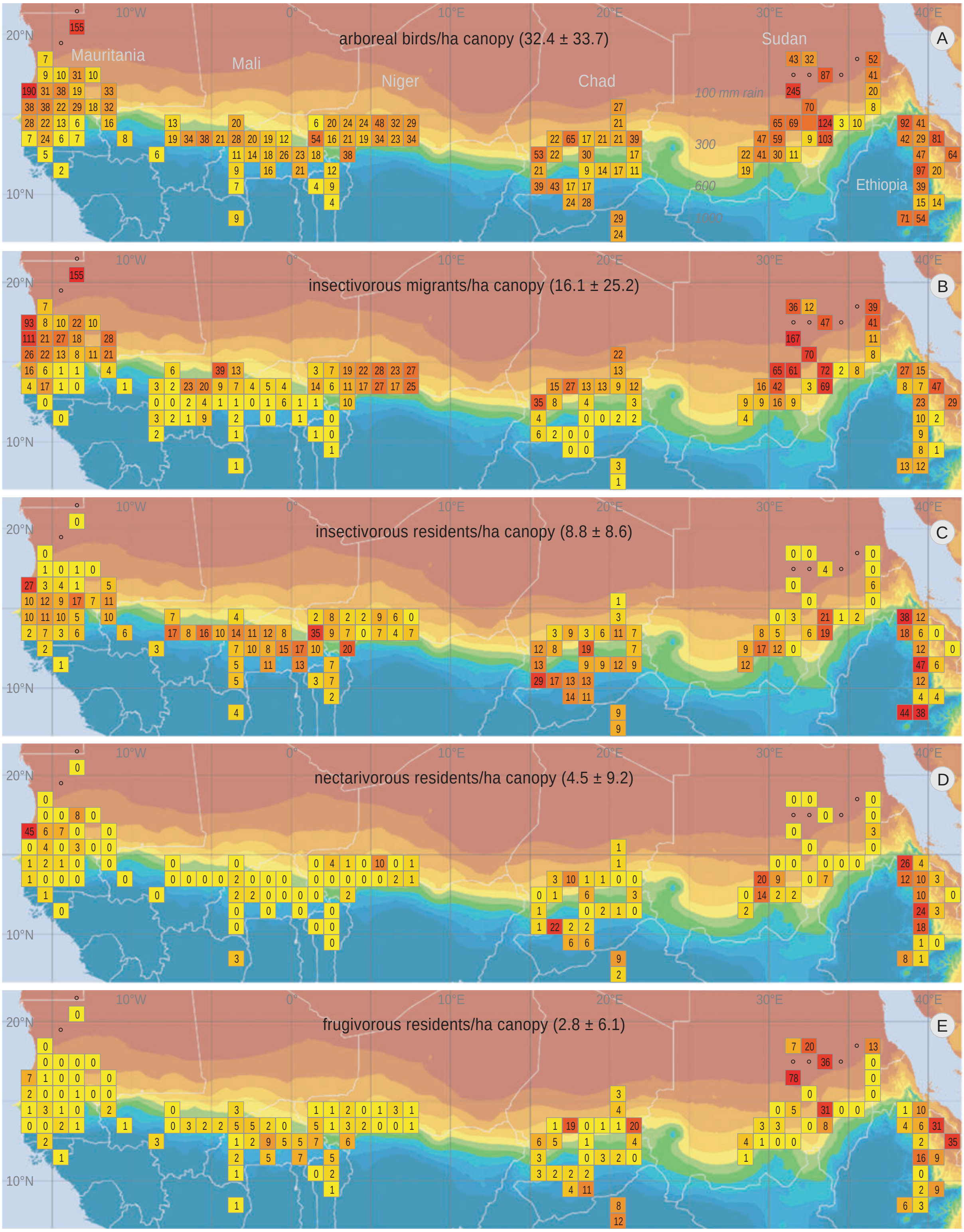

Figure 3. Density of 5 categories of arboreal birds in woody vegetation (n/ha per ha canopy) in 138 (residents) and 150 (migrants) grid cells; no bird density is given for six grid cells where woody cover was ≤ 0.1% (○). Background: rainfall (as Figure 4 in Zwarts *et al.* 2023a; simplified).

expressed as birds per hectare of canopy, were recorded in the arid zone (Figure 3A). Further south, with higher annual rainfall, the bird density in woody vegetation declined (Figure 3B). The decline was particularly evident among migrants and was only partly compensated by increases in insectivorous, nectarivorous and frugivorous residents (Figures 3C–E).

In contrast to ground-foraging bird species (Figure 12 in Zwarts *et al.* 2023a), none of the common arboreal bird species, except Blue-naped Mousebird *Urocolius macrourus*, foraged in flocks. Even in large trees, most species were solitary (Zwarts *et al.* 2023d) and only occasionally more than two individuals of the same species were recorded in the 4.5-ha sites when preferred tree species were dominant. On average, most arboreal species, when present, numbered one or two birds per site, irrespective of dietary preferences (Figure 4).

The most widely distributed arboreal species were the insectivorous residents Green-backed Camaroptera, Tawny-flanked Prinia and Little Weaver, which were recorded in 19, 18 and 12% of the sites and 54, 53 and 47% of grid cells, respectively (Figure S17, S16 and S34). The most widely distributed migrants were Subalpine Warbler, Common Whitethroat *Curruca communis* and Western Bonelli's Warbler, recorded in 21, 16 and 14% of the study sites and 38, 56 and 35% of the grid cells, respectively. The legends of the Figures in the Supplementary Material mention in how many grid cells the species was seen; see also Table S1 which provides information about the number of sites in which the different species were recorded.

Bird distribution, rainfall and woody cover

The distribution of bird species was restricted to specific rainfall zones, which mostly explains why bird species were encountered in only a fraction of the sites (Figure 5A), ranging from Spectacled Warbler *Curruca conspicillata* in the hyper-arid desert (95 mm rain/year) to African Golden Oriole *Oriolus auratus* in the hyper-humid woody zone (1244 mm rain/year). As woody cover increases with rainfall (see Figure 7 in Zwarts *et al.* 2023a), preferences of different bird species for a

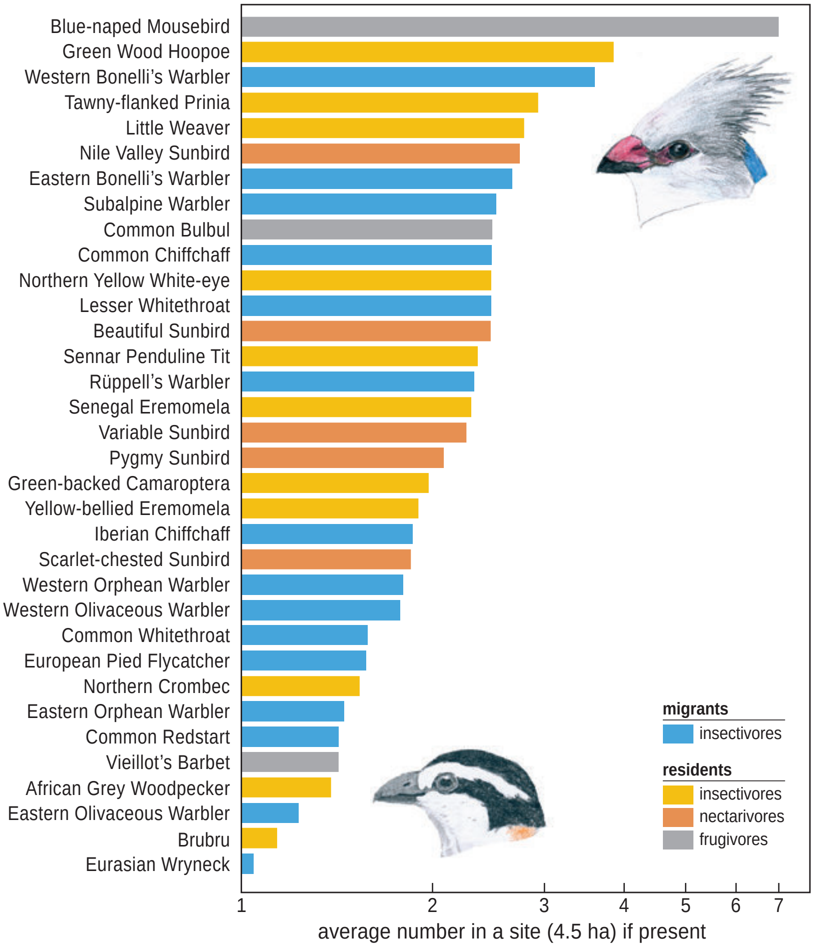

Figure 4. Average number of birds in 4.5-ha sites when present; note log scale.

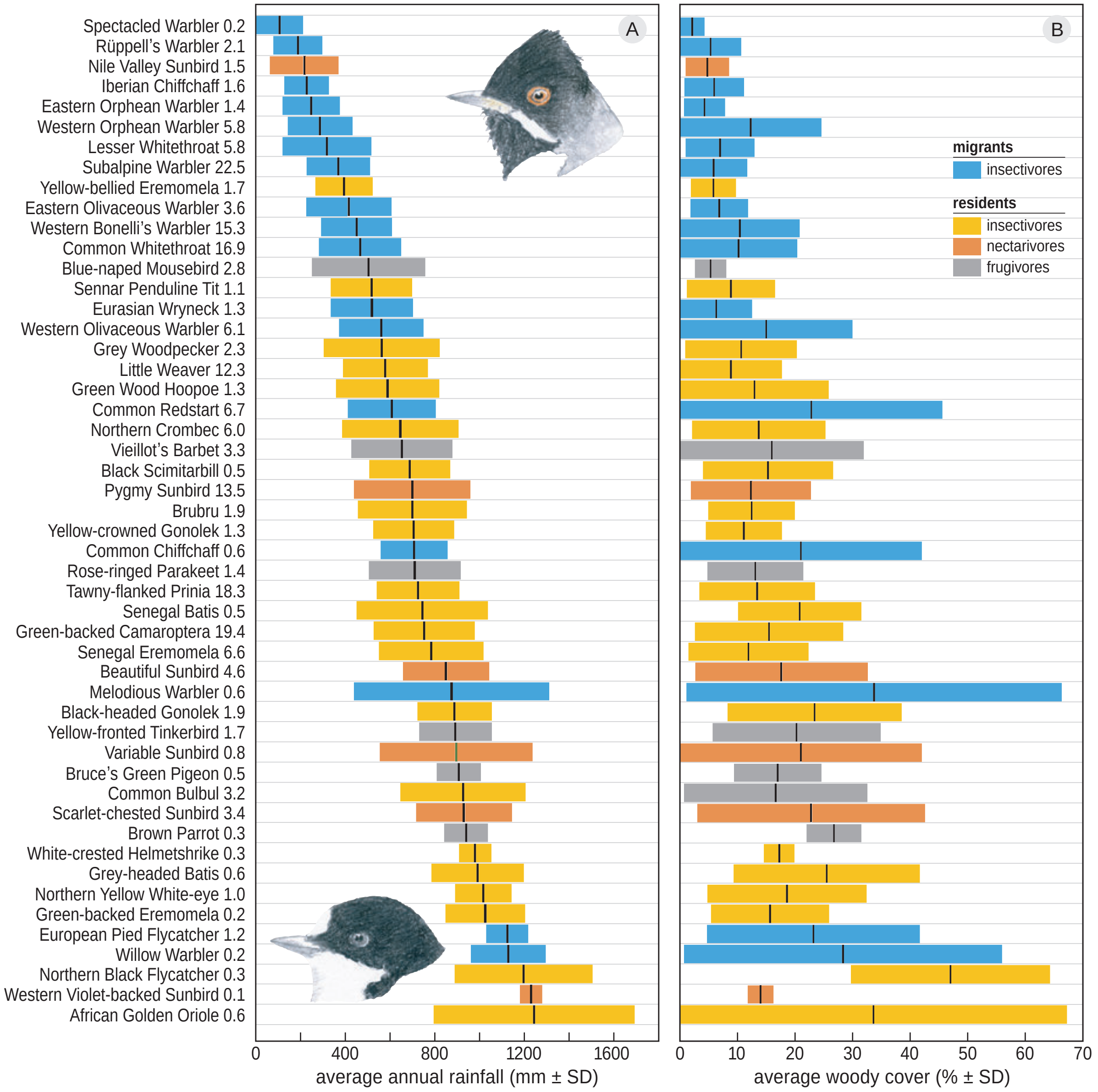

Figure 5. (A) Average annual rainfall and (B) average woody cover such as measured in study sites where a bird species was present, shown for 50 most common arboreal bird species: 17 insectivorous migrants and 33 residents (20 insectivores, 7 frugivores and 6 sunbirds). The species have been ranked according to the average rainfall. The numbers next to the bird names indicate in how many sites the species was present (%); sites from the Ethiopian Highlands (>700 m above sea level) are not included.

particular climate zone may depend on woody vegetation rather than rainfall. Preferences for open or less open habitats were, however, not very pronounced given the large standard deviations (Figure 5B). The SD of woody cover, as percentage of the average, amounted to 89%, for all 50 bird species combined (Figure 5B) against 37% for rainfall (Figure 5A). To investigate whether woody cover still has an impact on habitat selection of bird species, accounting for rainfall, average woody cover (Figure 5B) was regressed against average rainfall (Figure 5A). The relationship is very close and only deviates for species rarely recorded (Figure 6).

The 17 migratory species occurred, on average, in drier habitat (mean ± SD: 504 ± 305 mm rainfall/year) than the 33 residents (790 ± 232 mm), a highly significant difference (ANOVA based on data shown in Figure 5A; $P < 0.001$). The difference is much smaller when a similar comparison is made for the percent woody cover: 11.0 ± 9.3% for migrants and 16.5 ± 8.3% for residents (same data as in Figure 5B; $P = 0.04$). Differences between migrants and residents disappear when the high correlation between woody cover and rainfall (Figure 6) is taken into account (ANOVA based on data shown in Figure 5; $P = 0.38$). The difference in distribution of migrants and residents is therefore determined not by woody cover itself but by rainfall (and by variables related to rainfall such as the distribution of preferred woody species).

An analysis of covariance showed that, of the potential factors influencing bird distributions, i.e. woody cover, rainfall, longitude and land use (Table S1), it was rainfall rather than longitude that for most species had a larger impact on distribution. Since the interaction term is significant in half of the species, a closer look at the relationship between bird density and rainfall separately per longitudinal zone is needed. The raw data (bird densities per grid cell) are shown in Figures S1–S34.

The distribution of arboreal bird species varied greatly between species (Figures S1–S34). Nevertheless, insectivorous migrants were found, on average, further north than residents (Figure 7A). Apart from latitudinal variation in distributions associated with rainfall, distinct longitudinal variations in distribution were evident, particularly in species-complexes. The distributions of the seven *Curruca* species are a case in point (Figure 7B): Spectacled Warbler and Western Orphean Warbler *Curruca hortensis* were only found in the far west, Rüppell's Warbler and Eastern Orphean Warbler *Curruca crassirostris* exclusively in the eastern Sahara and north-eastern Sahel. The distribution areas of Subalpine Warbler in the western Sahel and of Lesser Whitethroat in the eastern Sahel were extensive and showed some overlap in Chad. Common Whitethroat was the only *Curruca* species recorded from the Atlantic Ocean in the west to the Red Sea in the east.

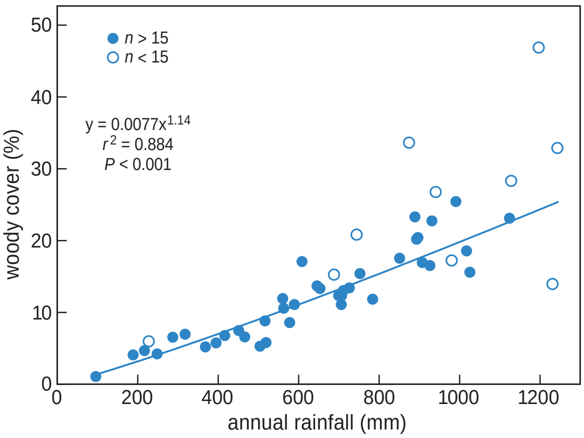

Figure 6. The relationship between woody cover (%) and average annual rainfall (mm), both averaged for the distribution areas of 50 arboreal bird species (same data as Figure 5). The rare species ($n < 15$) were disregarded in the calculation of the regression line.

The distribution of *Phylloscopus* species within sub-Saharan Africa was more restricted than that of the *Curruca* species (Figure 7C). Western Bonelli's Warbler was widely distributed from Senegal to western Chad, but Eastern Bonelli's Warbler *Phylloscopus orientalis* was limited to the Sahel from mid-Chad eastwards. Common Chiffchaff was abundant only in Ethiopia, but fairly rare in southern Senegal and Mali and absent between 5°W and 38°E. Iberian Chifchaff and Melodious Warbler *Hippolais polyglotta* were restricted to the western Sahel (east up to 4°W) where they occurred in the arid and humid zones, respectively. Willow Wabler *Phylloscopus trochilus* and Wood Warbler *P. sibilatrix* spend the northern winter mostly south of 7°N, and were rarely recorded between mid-November and early March in the southernmost rim of the sub-Saharan region covered by the present study.

Sunbirds also showed distinct species-specific variations in distribution (Figure 7D). Sunbirds were almost absent in the western Sahara north of 17°N, but in the eastern Sahara (north up to at least 16°N) and in the Danakil Desert, Nile Valley Sunbird *Hedydipna metallica* was quite common. Pygmy Sunbird was widely distributed between Senegal and Sudan. Other species also had a wide, but more irregular distribution, e.g. Scarlet-chested Sunbird *Chalcomitra senegalensis* in Burkina Faso and in Ethiopia.

The relationship between bird density and rainfall varied per longitudinal zone due to differences in the distribution of bird species (Figure 7). At the same time, a pronounced difference for nearly all bird species was found between the western and the central Sahel. In the western Sahel, migrants were remarkably common in the woody vegetation of the arid zone, whereas bird density of all species was very low in the humid zone. Although a similar but less pronounced latitudinal decline was recorded for residents in the central Sahel, resulting in a decline of overall bird density per ha canopy in relation to annual rainfall from 50 birds/ha in the hyper-arid to 2 birds/ha canopy in the hyper-humid zone, a greater contrast was that the central Sahel had far fewer migrants in the arid zone, but more residents in the humid zone. This resulted in about the same density of arboreal birds (20–25 birds/ha canopy) in the central Sahel across all ten rainfall zones (Figure 8).

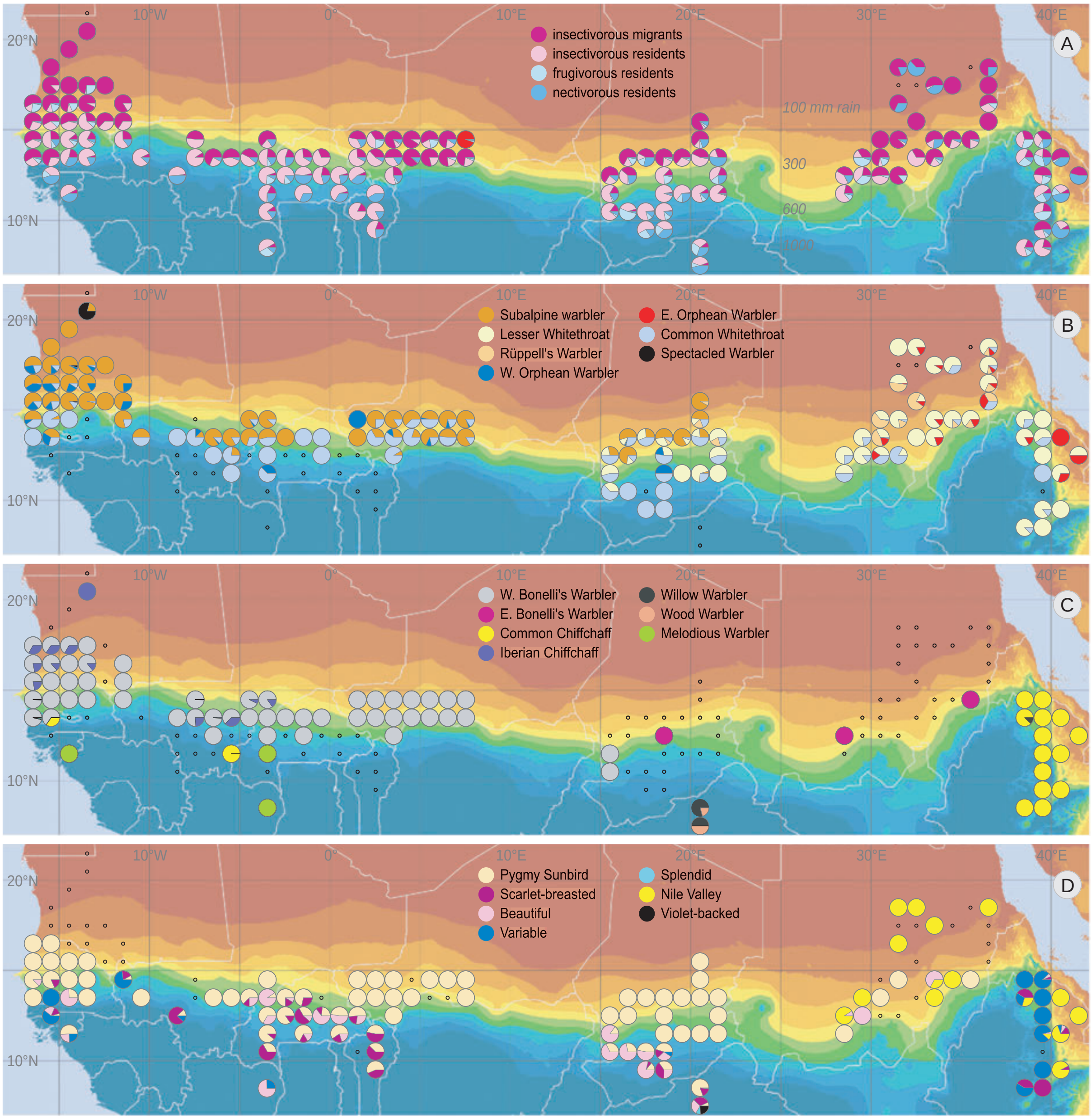

Figure 7. The relative occurrence of (A) migrants (all insectivorous) and residents (split up for insectivorous, frugivorous or nectarivorous species; data from Figure 3) in 138 grid cells; none (○) in 4 cells, (B) seven *Curruca* species in 150 grid cells; none in 33 cells, (C) seven *Phylloscopus* species in 150 grid cells; none in 73 cells and (D) seven sunbird species in 138 grid cells (not including three endemic species observed in Ethiopia); none in 34 cells.

Numbers

Average density and estimated total number of birds in the region were calculated for 34 bird species (see legends in Figure S1–S34). To assess the reliability of the population estimates, calculations were repeated for the same data split in halves, i.e. sites with an even or an odd numbered ranking. The correlation between the split-half averages of 34 bird species is extremely high, $R = 0.99$ ($P < 0.001$). This suggests that the population estimates are accurate but does not imply that all estimates are equally reliable. For example, the two estimates for Western Bonelli's Warbler scarcely differ: 30.0 and 30.2 million, deviating 0.3% of the population estimate (30.0 million) based on the full dataset. However, the deviation is very large in rare species, such as the Eastern Bonelli's Warbler: 0.0–1.0 million; deviating 100% from the estimate (0.5 million) based on the full dataset. The relation between % deviation and population size (in millions) estimated for 34 bird species is negatively exponential:

$$\%\text{deviation} = 48.3 \times \text{population}^{-0.406}$$
$$(r^2 = 0.424, n = 34, P < 0.001). \quad (1)$$

Three arboreal residents were much more common in the Sahel than any other species:

- Tawny-flanked Prinia (134 million; range 130–137 million; Figure S16),
- Green-backed Camaroptera (108 million; range 104–111 million; Figure S17),
- Pygmy Sunbird (91 million; range 73–109 million; Figure S29).

The three most common arboreal migrants were:

- Subalpine Warbler (63 million; range 51–75 million; Figure S24),
- Lesser Whitethroat (55 million; range 47–64 million; Figure S20),
- Western Bonelli's Warbler (30 million; range 30–30 million; Figure S10).

The total number of arboreal birds, including the 99 less common species not listed in Supplementary Material, was estimated at 1383 million birds, of which insectivorous residents (566 million) were more numerous than insectivorous migrants (354 million). The total number of nectar-feeding sunbirds was estimated at 286 million, and the total number of frugivores at 177 million (more details in Table 2).

Table 2. Population estimates (millions) of migrants and residents foraging on insects, fruit or nectar in sub-Saharan Africa between 7 and 22°N and between 17°W and 42°E. Minimum and maximum refer to two estimates based on half of the data. Deviation is a measure of reliability and defined as the average deviation of both split-half estimates from the estimate based on all data. See Supplementary Material 1 in Zwarts *et al.* (2023a) how the population size of bird species was estimated and partly interpolated.

Status	**Migrants**	**Residents**		
Food	Insect	Insect	Fruit	Nectar
Population	354	566	177	286
Interpolated	89	111	36	58
Minimum	324	522	171	252
Maximum	385	604	180	320
Deviation, %	8.6	7.2	2.5	11.9

Chiffchaffs categorised as Iberian were recorded west of 4°W and north of 14°N in Senegal (<600 mm rain/year) and north of 13°N in Mali (<800 mm rain/year; Figure 19). Assuming that unspecified Chiffchaffs recorded in this region were Iberian Chiffchaffs (see methods), we would arrive at a wintering population of 4.4 million birds. This estimate may be too high should the unidentified Chiffchaffs be Common Chiffchaffs. The total estimate of the Common Chiffchaff (18 million birds; Figure S12) might be, for the same reason, a bit too low. Acknowledging that Iberian Chiffchaff is a common bird in flooded forests along the Senegal River and in the Inner Niger Delta (5–80 birds/ha canopy; see Figure 14 in Zwarts *et al.* 2023g), not included in the present surveys, we assume that the actual winter population in West Africa might be about 5 million Iberian Chiffchaffs. The two other *Phylloscopus* species cannot be regarded as species wintering in the Sahel (also not when Sahel is used in the broader sense). Wood Warbler leaves the zone north of 7°N in November at the latest, and winters in more humid zones further south. The only wintering birds in our surveys were observed in the Central African Republic. Total number north of 7°N is estimated at 4.7 million, of which 0.8 are interpolated; range (split-half): 3.7–5.6 million. Willow Warbler is a common migrant in October–November, but most birds have disappeared by late November. The birds recorded in the Central African Republic in December (25 birds/km^2) are considered to represent the northernmost fringe of the wintering range. The total number north of 7°N is estimated at 12.2 million birds, of which 2.1 million interpolated, but the split-half estimates differ greatly: 3.9 and 20.4 million.

Six migratory arboreal bird species, either rare or limited in distribution, were not included in the Supplementary Material. The Melodious Warbler was common in Senegal and Mali in October, but most birds moved southwards in November and the few remaining birds were restricted to the southern zones (>500 mm rainfall/annum; maximal density 0.6 birds/km^2). The estimate of the numbers wintering north of 7°N (2.3 million birds; none interpolated) is not reliable given the large difference between the split-half estimates (0.5 and 4.1 million).

All but one Eurasian Blackcap *Sylvia atricapilla* were observed in Ethiopia, in the zone where rainfall exceeds 900 mm/year, with an average density of 9.5/km^2. The estimated total of 4.0 million birds is not reliable; the range of the split-half estimates is 0.0–7.5 million. Sardinian Warbler *Curruca melanocephala* winters north of the Sahara. The few birds recorded were observed in the rainfall zone 100–300 mm in Senegal and in Sudan. Estimated total: 0.6 million birds; range 0.3–0.9 million. Spectacled Warbler was recorded only in Mauritania where it reached maximal density in the hyper-arid zone (5.2/km^2 at <100 mm/year). The estimated total (1.6 million birds) is not reliable, ranging between 0.1 and 3.2 million.

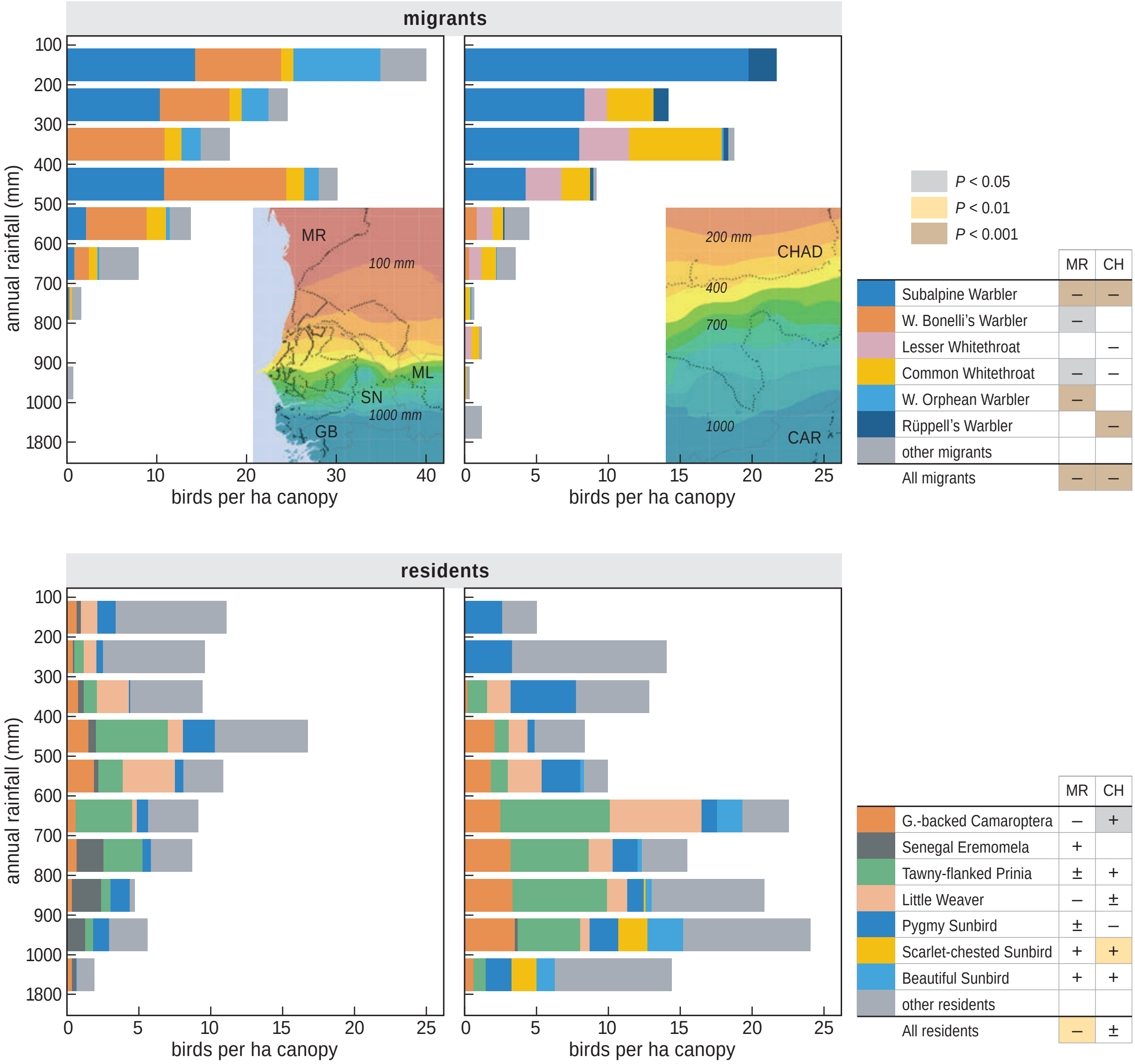

Figure 8. Density per ha canopy of arboreal birds between 20 November and 10 March in Mauritania, Senegal, West Mali and Guinea-Bissau (17–10°W; left) and in Chad and Central African Republic (15–21°E; right) per rainfall zone, shown separately for migrants (top) and residents (bottom). The maps show the regions with study sites and rainfall zones. Note that for the top left panel a different scale is used along the horizontal axis. Bird density is given separately for the six most common migrants and seven most common residents; all other species are taken together in one rest category. The legend shows whether the density in the western ('MR') or eastern ('CH') zone declined (–) or increased (+) with rainfall or without a clear trend (±); level of significance (second-degree curvilinear regression): is indicated with colours.

DISCUSSION

Comparison with previous quantitative studies in the same region

The bird densities given in the present paper may be compared to the few available quantitative studies performed in the region in the past. Browne (1982) measured bird densities in random plots in SW Mauritania in 1978–1982. He arrived at 2.6 Bonelli's Warbler/km^2, 2.3 Subalpine Warbler/km^2 and 1.3 Western Orphean Warbler per km^2. In the same region (between 16 and 19°N and west of 12°W) we covered 203 sites with, on average, 20 Bonelli's Warbler/km^2, 29 Subalpine Warbler/km^2 and 13 Western Orphean Warbler/km^2, thus about ten times higher. Given the loss of woody cover in the region since the early 1970s (Zwarts *et al.* 2018), a decline was to be expected. On the other hand, Browne did his counts in 1978–1982, when bird populations had fallen sharply after the start of a series of catastrophic dry years in 1969, while our surveys took place after the rainfall in the Sahel (and thus probably also the woody vegetation) had already recovered gradually. The large difference may also be a methodological artifact, contingent on the time spent in detecting birds. Browne worked alone and covered 30 ha per hour. In the same region our three-person group needed 171 hours to count all the birds on a surface area of 1050 ha, thus covering 6.1 ha per hour. Reducing searching time when counting arboreal birds has a major impact on numbers detected, especially for *Curruca* species that have, compared to *Phylloscopus* species, a more skulking and less flitting behaviour (Zwarts & Bijlsma 2015).

Jones *et al.* (1996) measured relative bird densities at ten non-random sites in northern Nigeria at about 13°N and 11°E in winter 1993/1994. We had no study sites in N Nigeria, but their measurements can be compared to 319 sites between 12 and 14°N in neighbouring countries (Burkina Faso, Niger, Chad). In Nigeria, the average number of birds/ha was much higher than in neighbouring countries: 2.19 vs. 0.43 arboreal migrants/ha, mainly on account of the two most common species: 1.59 vs. 0.12 Subalpine Warbler/ha and 0.29 vs. 0.12 Common Whitethroat/ha. The discrepancy finds its nemesis in the selection of random sites by us versus non-random bird-rich habitats by Jones *et al.* (one forest reserve, two riverine woodlands and two farmland plots with bird-rich *Faidherbia* trees). Cresswell *et al.* (2007) repeated the counts of Jones *et al.* (1996) from 1993/1994 in 2001/2002 and found no change in bird densities on farmland, but much lower densities in the forest reserve where tree density had declined by 82%, correlating with an 88% decline of Subalpine Warblers, from 5.9 to 0.7 birds/ha.

Wilson & Cresswell (2006) performed bird density counts in 16 sites in NE Nigeria at about 13°N and 11°E in 2002. The surveys were repeated in 2007 (Stevens *et al.* 2010). The sites in NE Nigeria were selected to have relatively high densities of birds, hence chosen in the vicinity of rivers and wetlands (Supplementary Material 3 in Zwarts *et al.* 2023a). Furthermore, the woody vegetation was dominated by Toothbrush Tree *Salvadora persica*, Desert Date *Balanites aegyptiaca* and three acacia species (Wilson & Cresswell 2006, Stevens *et al.* 2010), tree species known to attract birds, especially *Salvadora* (Zwarts *et al.* 2023c) but which nowadays has a very patchy distribution across the Sahel, and is even absent from large stretches. This background is important to keep in mind when comparing their surveys with our 43 same-latitudinal sites in SW Chad and 71 sites in SW Niger (12–14°N and 3–18°E); see also Supplementary Material 3 in Zwarts *et al.* 2023a. The most common migrants in NE Nigeria reached higher densities than in the surrounding countries: 0.40/ha in Nigeria vs. 0.28/ha in Chad + Niger for the Subalpine Warbler, 0.43/ha in Nigeria vs. 0.17/ha in Chad + Niger for the Common Whitethroat and 0.24/ha in Nigeria vs. 0.08/ha in Chad + Niger for Lesser Whitethroat. This difference can be attributed to the choice of non-random versus random plots.

Distribution and numbers

We arrive at 354 million arboreal migrants (split-half: 324 and 385 million) in Africa between 7 and 22°N (Table 2). The estimate is the same (355 million) using the estimated woody cover per tree species and average densities reached by the different migrant species in 304 tree species (Zwarts *et al.* 2023c). Although an impressive number in itself, it is only a fraction of the total number of arboreal migrants wintering in Africa. The most abundant arboreal migrant in Africa, the Willow Warbler (580–880 million birds), spends the winter farther south. Other migrants wintering south of 7°N are much less common (40–70 million Garden Warbler, 30–50 million Wood Warbler) (all estimates from Table 1 in Zwarts *et al.* 2023b). Including Sahelian species, as Common Whitethroat of which the wintering grounds extend far to the south in eastern Africa, the total number of arboreal migrants south of the 7°N may be roughly estimated at some 1 billion birds. This would equate to an average density of 67 birds per km^2, relatively high compared to the average density of 42 arboreal birds per km^2 in the region north

Photo 2. The distribution of tree-dwelling bird species during the dry season is restricted to specific rainfall zones (Figure 5A). *Curruca* species are found in scattered trees on the southern edge of the Sahara (photo A) and northern Sahel (photo B), but Willow Warbler and Pied Flycatcher, for instance, in hyper-humid woodlands (photo C) 500–1000 km further south. (Photo A: Mauritania, 19.45°N, 14.77°W, 30 Jan. 2017; Photo B: Mauritania, 17.15°N, 16.40°W, 2 Feb 2017; Photo C: Guinea-Bissau, 11.18°N, 15.51°W, 29 Jan 2014).

of 7°N (Figure 2B). Both estimates include, however, large areas where birds are absent. Disregarding the Sahara (rainfall <100 mm/year), the average density between 7 and 22°N would increase from 42 to 60 birds per km^2. Assuming that the migrants south of 7°N are scarce in the rainforest (2 million km^2) and in the Kalahari (0.9 million km^2), the average density would be 76 birds per km^2 in the rest of Africa south of 7°N . A validation of this density estimate is not easy as quantitative studies of migrants from southern and eastern Africa are thin on the ground. Ulfstrand & Alerstam (1977), for example, found in Zambia (15°S) an average density of 14 to 48 migrants per km^2 (mainly Willow Warblers) in miombo woodlands (dominated by *Brachystegia spiciformis*) and 80 migrants per km^2 in *Acacia* woody savannah. Large habitat-related differences were also found by Jones *et al.* (2010) in Zimbabwe, albeit at higher densities (sampling in Sengwa Wildlife Research Area in 1999/2000, at 18.10°S): Willow Warblers reached densities of 76–189 per km^2 in miombo (mainly *Brachystegia spiciformes* and *Julbernardia globiflora*), 19–75 per km^2 in mopane woodland (dominated by *Colophospermum mopane*) and 180/km^2 (but 715/km^2 during migration) in riverine *Acacia tortilis* woody savannah.

In the humid Guinean zone, migratory arboreal birds were recorded more often in derived savannah (farmland with scattered trees) than in closed woodland (Elgood *et al.* 1966, Jones 1998, Cresswell *et al.* 2009, Gatter 2016, Mallord *et al.* 2018). This suggests that arboreal migrants prefer a more open landscape than residents. Indeed, in our study most migrant species were found in open habitats and most residents in closed landscapes (Figure 5B). On the global scale, woody cover and rainfall are highly correlated (Figure 6), however. When this is taken into account, migrants and residents no longer differed in their selection of open or closed landscape, although Spectacled Warblers seemed to avoid sites with a woody vegetation. There were indeed few trees and shrubs in the Mauritanian sites where we recorded Spectacled Warbler, but instead *Schouwia purpurea*, an annual succulent herb of up to 90 cm high (and thus not registered by us as woody vegetation), covered large sections of sites where this species was registered (and where it probably bred, given the observed song and display flights). Heim de Balsac & Mayaud (1954, p. 330) and Bergier *et al.* (2020, p. 257) specifically mention herbaceous vegetations as the habitat for Spectacled Warbler, with fewer shrubs than normally favoured by *Curruca* species.

Some migratory bird species, mainly *Curruca* species, were exclusively found in the (semi) arid zone (<600 mm rainfall). Resident bird species, however, were absent from the most arid areas (Figure 5A), with the exception of the Nile Valley Sunbird which extends its distribution area to northernmost Sudan (Figure S30). In contrast, the humid zone (>1000 mm rainfall) is dominated by residents. The only migrants wintering, or temporarily so, in this zone are European Pied Flycatcher *Ficedula hypoleuca* (Figure S27), Melodious Warbler (which occurs in a rather wide range of rainfall zones; Figure 5A) and Willow Warbler (may largely depart from much of the region in midwinter, as found in NE Ivory Coast; Salewski *et al.* 2002). Between late November and early March, we recorded very small numbers of arboreal migrants which typically should winter farther south: Olive-tree Warbler *Hippolais olivetorum* in Sudan, Spotted Flycatcher *Muscicapa striata*, Wood Warbler *Phylloscopus sibilatrix* and Icterine Warbler *Hippolais icterina* in the Central African Republic and Garden Warbler *Sylvia borin* in Senegal and Mali.

The data summarised in this paper will be used to address various related questions, notably (1) can the observed distribution be explained by the distribution of their preferred woody plants, and (2) if not, what other factors may be involved (Zwarts *et al.* 2023c,e,f)?

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Zwarts L., Bijlsma R.G. & van der Kamp J. 2023e. Savannah trees attract more migratory bird species than residents, but why? Ardea 111: 189–206.

Zwarts L., Bijlsma R.G. & van der Kamp J. 2023f. The Gap of Chad, a dearth of migratory birds in the central Sahel. Ardea 111: 207–226.

Zwarts L., Bijlsma R.G. & van der Kamp J. 2023g. Seasonal shifts in habitat choice of birds in the Sahel: the importance of ‘refuge trees’ for surviving the dry season. Ardea 111: 227–250.

SAMENVATTING

Dit artikel beschrijft de verspreiding van vijftig in bomen en struiken foeragerende vogelsoorten in de Sahel, hier opgevat als de brede overgangszone tussen de Sahara in het noorden en de bos- en regenrijke Guinea-zone 1600 km zuidelijker. Het onderzoek werd uitgevoerd tussen 2011 en 2019. Van deze 50 soorten zijn er 17 insectenetende trekvogels. De overige 33 zijn ‘lokale’ soorten, waarvan 20 zich voeden met insecten, 7 met vruchten en 6 met nectar. Alle gegevens werden verzameld tussen november en maart, overeenkomend met de droge periode in de Sahel. In de regentijd van juli tot september valt er minder dan 50 mm neerslag per jaar aan de zuidrand van de Sahara, maar dat loopt op naar meer dan 1500 mm in de Guinea-zone. Er bestond een duidelijke verband tussen de verspreiding van vogelsoorten en de jaarlijkse regenval. De meeste trekvogels werden in de relatief droge zone aangetroffen, de lokale vogels juist in de meer natte zone. Rekening houdend met de nauwe correlatie tussen regenval en boombedekking (meer bomen in regenrijke gebieden en vice versa) is dit verschil in verspreiding niet te zien binnen eenzelfde regenvalzone. De gegevens werden gebruikt om het totale aantal boombewonende vogels in deze regio te schatten. De betrouwbaarheid van deze schattingen werd getoetst door de populatiegrootte afzonderlijk te berekenen voor even en oneven telvakjes. Op basis van die exercitie konden de geschatte populatiegroottes als nauwkeurig worden betiteld. De insectenetende lokale vogels waren het talrijkst (547 miljoen), gevolgd door insectenetende trekvogels (326 miljoen), honingzuigers (272 miljoen) en lokale vogelsoorten die vruchten eten (177 miljoen). De twee meest voorkomende vogelsoorten waren insecteneters: Roestflankprinia *Prinia subflava* (128 miljoen) en Mekkercamaroptera *Camaroptera brachyura* (103 miljoen). Onder de trekvogels waren de drie meest voorkomende soorten Baardgrasmus *Curruca iberiae + C. subalpina + C. cantillans* (62 miljoen), Braamsluiper *Curruca curruca* (48 miljoen) en Bergfluiter *Phylloscopus bonelli* (30 miljoen). Sommige insectenetende trekvogels werden uitsluitend in de (semi-)aride zone vastgesteld (denk vooral aan soorten in de grasmusfamilie *Curruca*), andere juist alleen in de natte zone waar ze feitelijk aan de noordgrens van hun winterverspreiding zaten (zoals Bonte Vliegenvanger *Ficedula hypoleuca* en Orpheusspotvogel *Hippolais polyglotta*).

RÉSUMÉ

Cet article présente la répartition de 50 espèces d'oiseaux arboricoles au sein de la vaste zone de transition appelée Sahel, qui s’étend entre le Sahara au Nord et les forêts humides de la zone soudano-guinéenne, 1600 km plus au Sud. Parmi ces espèces, 17 sont migratrices et insectivores. Les 33 autres sont des espèces sédentaires, dont 20 sont insectivores, 7 frugivores et 6 nectarivores. Toutes les données ont été collectées au cours de la saison sèche, entre novembre et mars. Il existe un lien direct entre la répartition des espèces et les précipitations annuelles, qui varient de moins de 50 mm/an sur la bordure sud du Sahara à plus de 1500 mm/an dans la zone soudano-guinéenne. La plupart des oiseaux migrateurs fréquentent la zone la plus sèche, tandis que les espèces locales préfèrent la zone plus humide. Compte tenu de l'étroite corrélation entre les hauteurs de précipitations et le couvert arboré, les espèces de la zone sèche fréquentent en moyenne des habitats plus ouverts que ceux de la zone humide, mais ces différences de répartition entre espèces en fonction du couvert arboré disparaissent si l’on considère des zones de pluviométrie homogène. Les comptages effectués au sein de carrés sélectionnés aléatoirement selon une méthode d’échantillonnage stratifié ont permis d’estimer les populations des espèces d’oiseaux arboricoles dans cette région. La fiabilité de ces estimations a été vérifiée en les comparant avec celles calculées en considérant séparément les carrés de comptage à numéros pairs et impairs. Les écarts obtenus selon les méthodes de calculs étant inférieurs à 10%, les populations estimées peuvent être considérées comme valides. Les insectivores sédentaires sont les plus abondants (547 millions), suivis des insectivores migrateurs (326 millions), des nectarivores (272 millions) et des frugivores (177 millions). Les deux espèces les plus abondantes sont insectivores : le Prinia modeste *Prinia subflava* (128 millions) et le Camaroptère à tête grise *Camaroptera brachyura* (103 millions). Parmi les migrateurs, les trois espèces les plus communes sont les Fauvettes du complexe « passerinette » *Curruca iberiae + subalpina + cantillans* (62 millions), la Fauvette babillarde *Curruca curruca* (48 millions) et le Pouillot de Bonelli *Phylloscopus bonelli* (30 millions). Certains migrateurs insectivores, telles les fauvettes du genre *Curruca*, n'ont été trouvés que dans la zone la plus aride, alors que d'autres tels le Gobemouche noir *Ficedula hypoleuca* et l'Hypolaïs polyglotte *Hippolais polyglotta* l’ont été uniquement dans la zone la plus humide où ils se trouvent à la limite nord de leur aire d'hivernage.

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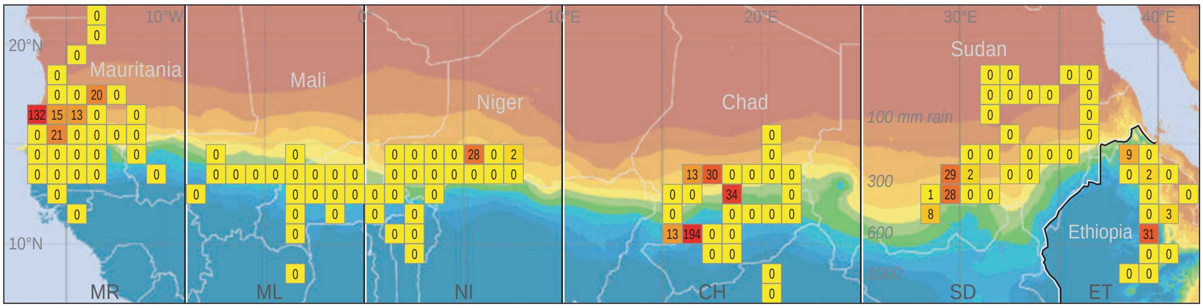
SUPPLEMENTARY MATERIAL: Distribution maps for 34 arboreal bird species

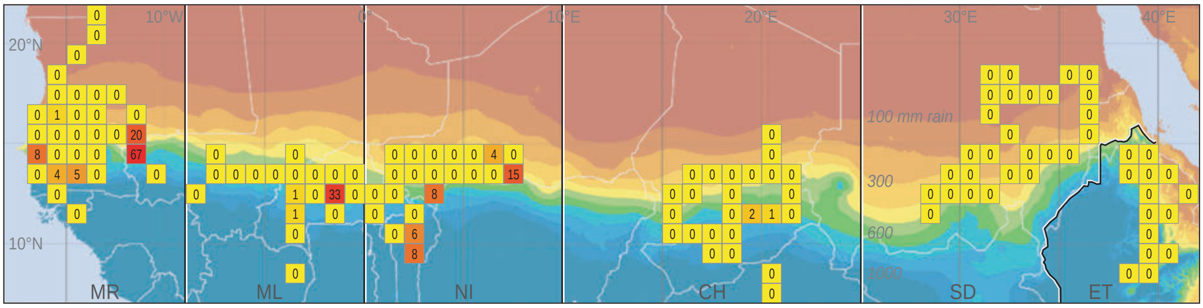
Table S1. Explained variance (r^2) in 34 covariance analyses with woody cover (w.cover) as covariate and longitude (longit.; 6 classes), rainfall (11 classes), land use (3 classes: farmland, savannah, woodland) as main effects and 4 interaction terms. Given in the last four columns: number of sites, % presence in sites, % presence and average density/km^2 in the grid cells (see Figures S2–S44). Level of significance: $P < 0.05$, $P < 0.01$, $P < 0.001$.

Fig.	Bird species	w.cover	longit.	rainfall	land use	long×rain	long×use	rain×use	l×r×u	all	sites	%cells	%sites	*n*/km^2
S1	Blue-naped Mousebird	0.001	0.000	0.001	0.000	0.009	0.001	0.002	0.012	0.063	1613	15	2.9	4.5
S2	Green Woodhoopoe	0.004	0.001	0.001	0.001	0.004	0.001	0.002	0.013	0.052	1613	12	1.2	1.3
S3	Vieillot's Barbet	0.011	0.002	0.001	0.003	0.008	0.001	0.002	0.008	0.064	1613	17	3.1	1.0
S4	Eurasian Wryneck	0.000	0.001	0.002	0.000	0.025	0.003	0.008	0.024	0.086	1901	11	1.2	0.3
S5	African Grey Woodpecker	0.002	0.001	0.007	0.001	0.028	0.017	0.014	0.025	0.081	1613	17	2.1	0.7
S6	Brubru	0.010	0.002	0.003	0.006	0.029	0.004	0.005	0.023	0.080	1613	11	2.2	0.8
S7	Sennar Penduline Tit	0.001	0.001	0.001	0.001	0.014	0.001	0.003	0.012	0.076	1613	9	1.1	0.5
S8	Common Bulbul	0.001	0.010	0.011	0.002	0.071	0.01	0.011	0.018	0.181	1613	28	4.5	5.3
S9	Northern Crombec	0.009	0.005	0.027	0.002	0.039	0.008	0.053	0.044	0.173	1787	38	5.9	2.7
S10	Western Bonelli's Warbler	0.017	0.020	0.032	0.005	0.038	0.014	0.028	0.033	0.262	1901	35	14.3	6.8
S11	Eastern Bonelli's Warbler	0.000	0.001	0.001	0.000	0.013	0.002	0.002	0.027	0.059	1901	2	0.2	0.1
S12	Common Chiffchaff	0.002	0.009	0.043	0.008	0.060	0.056	0.049	0.054	0.293	1901	11	0.4	2.2
S13	Iberian Chiffchaff	0.009	0.000	0.001	0.003	0.004	0.001	0.001	0.004	0.032	1901	9	3.7	0.8
S14	Eastern Olivaceous Warbler	0.004	0.029	0.035	0.006	0.100	0.027	0.040	0.076	0.195	1901	26	2.4	2.1
S15	Western Olivaceous Warbler	0.006	0.213	0.301	0.004	0.300	0.226	0.330	0.321	0.536	1901	26	2.7	1.8
S16	Tawny-flanked Prinia	0.004	0.043	0.029	0.002	0.076	0.008	0.011	0.028	0.344	1787	60	17.6	14.4
S17	Green-backed Camaroptera	0.031	0.031	0.024	0.008	0.140	0.021	0.023	0.082	0.361	1787	62	18.8	11.1
S18	Yellow-bellied Eremomela	0.000	0.001	0.002	0.001	0.019	0.001	0.003	0.017	0.070	1787	17	2.2	1.0
S19	Senegal Eremomela	0.001	0.010	0.020	0.004	0.043	0.016	0.016	0.034	0.158	1787	29	6.2	4.5
S20	Lesser Whitethroat	0.009	0.015	0.006	0.004	0.026	0.006	0.010	0.019	0.129	1901	33	6.9	5.6
S21	Western Orphean Warbler	0.015	0.006	0.078	0.000	0.023	0.004	0.100	0.006	0.216	1901	18	5.5	1.6
S22	Eastern Orphean Warbler	0.001	0.012	0.054	0.017	0.126	0.034	0.053	0.072	0.201	1901	11	1.1	0.5
S23	Rüppell's Warbler	0.001	0.066	0.084	0.005	0.220	0.016	0.054	0.048	0.306	1901	11	1.9	1.4
S24	Subalpine Warbler	0.021	0.008	0.029	0.007	0.027	0.007	0.012	0.015	0.229	1901	38	21.1	8.8
S25	Common Whitethroat	0.005	0.013	0.119	0.005	0.054	0.008	0.144	0.026	0.314	1901	56	16.1	4.9
S26	African Yellow White-eye	0.004	0.007	0.031	0.001	0.027	0.007	0.029	0.039	0.165	1901	9	0.9	1.3
S27	European Pied Flycatcher	0.000	0.011	0.009	0.001	0.041	0.007	0.008	0.054	0.208	1901	8	1.1	1.0
S28	Common Redstart	0.008	0.106	0.106	0.000	0.090	0.124	0.121	0.107	0.363	1901	43	6.7	2.6
S29	Pygmy Sunbird	0.003	0.004	0.018	0.004	0.034	0.013	0.020	0.036	0.196	1613	57	12.5	8.8
S30	Nile Valley Sunbird	0.003	0.002	0.012	0.001	0.034	0.002	0.001	0.004	0.106	1613	12	2.2	2.1
S31	Scarlet-chested Sunbird	0.006	0.014	0.027	0.001	0.031	0.009	0.013	0.020	0.154	1613	22	3.7	3.5
S32	Beautiful Sunbird	0.001	0.027	0.063	0.001	0.053	0.022	0.078	0.074	0.330	1613	20	4.4	4.0
S33	Variable Sunbird	0.002	0.002	0.003	0.001	0.029	0.002	0.007	0.022	0.115	1613	12	1.9	1.8
S34	Little Weaver	0.002	0.009	0.018	0.003	0.064	0.010	0.038	0.056	0.206	1613	56	12.5	7.8



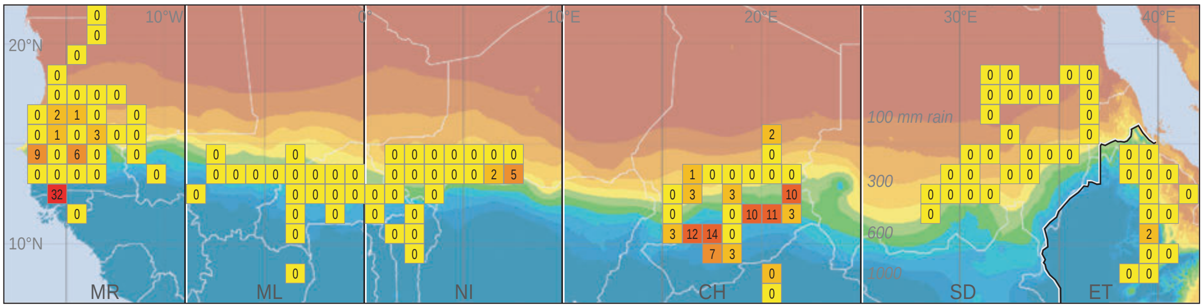
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	0.0
100–200	13.1	13.1	0.0	0.0	0.0	0.0
200–300	12.7	6.4	0.0	22.2	1.9	0.0
300–400	8.0	5.5	3.0	5.3	4.3	0.0
400–500	1.5	0.0	5.6	0.0	10.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	1.4
600–700	0.0	0.0	0.0	9.6	9.6	6.1
700–800	0.0	0.0	0.0	5.4	5.4	0.0
800–900	0.0	0.0	0.0	60.5	60.5	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	28.6

Figure S1. Blue-naped Mousebird *Urocolius macrourus* (*n*/km^2).
Frugivorous resident.
Present 15% of the 138 grid cells.
Average density (*n*/km^2, ±SD) in grid cells: 4.5 ± 20.8.
Estimated overall density: 4.2/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 41.7 million, of which 13.5 million birds are interpolated; range: 21.3–61.0 million (split-half).



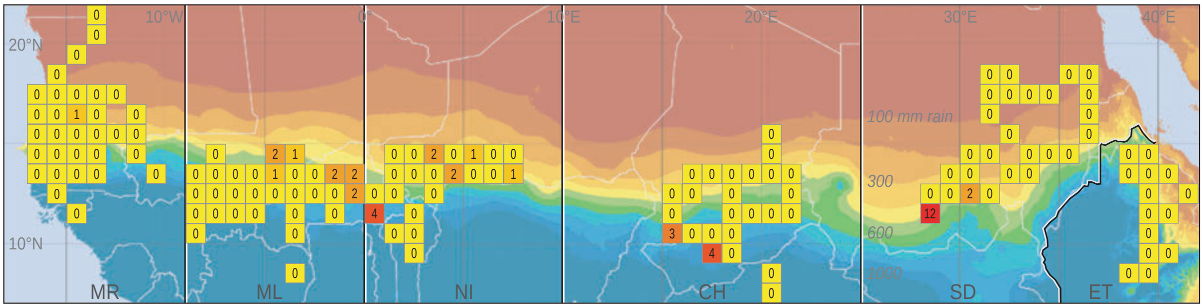
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	2.4	1.2	0.0	0.0	0.0	0.0
300–400	0.0	1.5	3.0	0.0	0.0	0.0
400–500	5.8	0.0	1.2	0.0	0.0	0.0
500–600	5.1	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.4	11.7	0.0	0.0	0.0
700–800	28.9	8.3	0.0	0.0	0.0	0.0
800–900	0.0	0.8	0.0	1.3	1.3	0.0
900–1000	1.1	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	10.1	0.0	0.0	28.6

Figure S2. Green Wood Hoopoe *Phoeniculus purpureus* (*n*/km^2).
Insectivorous resident.
Present in 12% of 138 grid cells.
Average density (*n*/km^2, ±SD) in grid cells: 1.3 ± 6.7.
Estimated overall density: 0.7/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 6.7 million, of which 0.4 million birds are interpolated; range: 5.6–7.9 million (split-half).



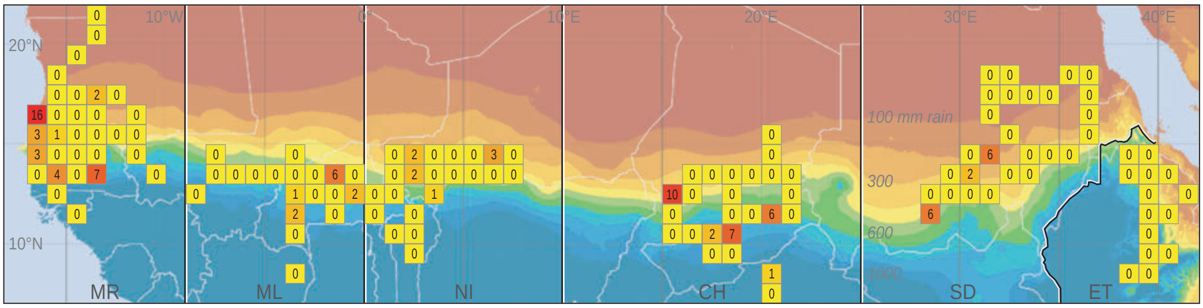
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.4	0.9	1.5	2.0	0.0	0.0
200–300	1.1	0.5	0.0	0.0	0.0	0.0
300–400	0.0	0.4	0.7	0.9	0.0	0.0
400–500	1.9	0.0	0.7	0.0	0.0	0.0
500–600	8.5	0.0	0.0	0.7	0.0	0.0
600–700	2.1	0.0	0.0	5.0	5.0	0.0
700–800	0.0	0.0	0.0	6.1	6.1	0.0
800–900	0.0	0.0	0.0	8.4	8.4	0.0
900–1000	0.0	0.0	0.0	6.3	6.3	0.0
>1000	13.2	0.0	0.0	0.0	0.0	1.5

Figure S3. Vieillot's Barbet *Lybius vieilloti* (n/km^2).
Frugivorous resident.
Present in 17% of the 138 grid cells.
Average density (n/km^2, ±SD) in grid cells: 1.0 ± 3.6.
Estimated overall density: 1.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 13.8 million, of which 3.5 million birds are interpolated; range: 8.9–18.7 million (split-half).



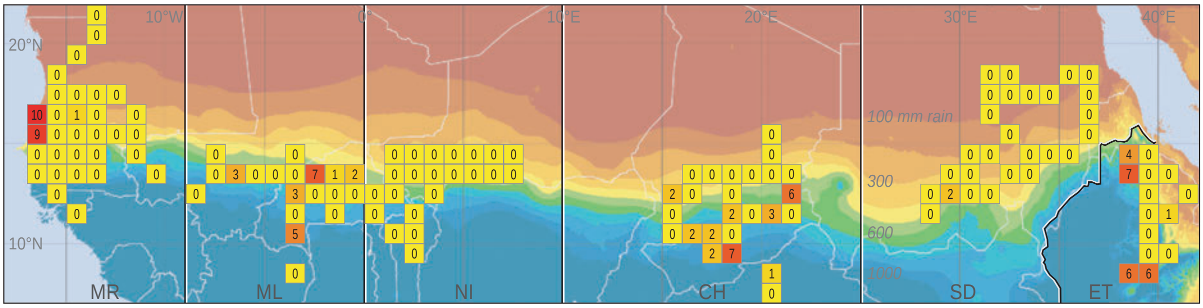
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.3	0.1	0.0	0.0	0.0	0.0
300–400	0.0	0.2	0.5	0.0	0.3	0.0
400–500	0.0	1.1	0.6	0.0	2.4	0.0
500–600	0.3	1.8	0.0	0.0	0.0	0.0
600–700	0.0	0.2	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.7	0.7	0.0
800–900	0.0	0.0	3.7	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	1.4	1.4	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S4. Eurasian Wryneck *Jynx torquilla* (n/km^2).
Insectivorous migrant.
Present in 11% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 0.3 ± 1.2.
Estimated overall density: 0.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 1.3 million, of which 0.2 million birds are interpolated; range: 1.0–1.7 million (split-half).



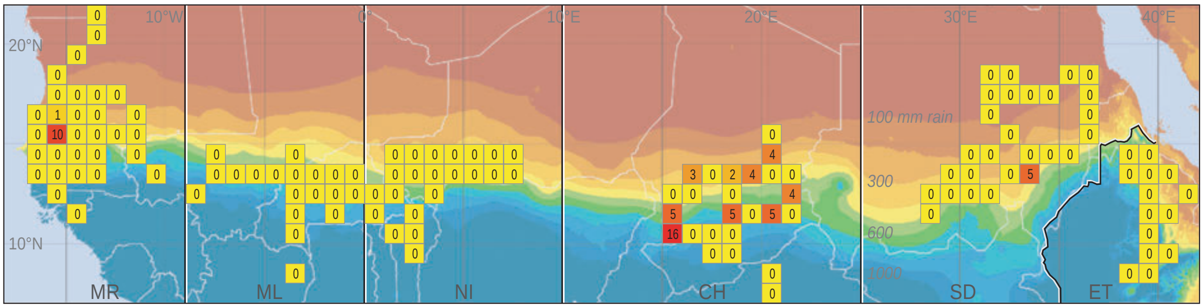
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.6	1.1	0.5	0.0	1.2	0.0
200–300	0.4	0.2	0.0	0.0	1.9	0.0
300–400	0.5	0.5	0.5	2.2	0.0	0.0
400–500	1.0	0.0	0.4	0.0	1.1	0.0
500–600	2.5	0.0	2.2	0.0	0.0	0.0
600–700	0.0	2.7	2.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	1.3	1.3	0.0
800–900	9.3	1.2	0.0	3.3	3.3	0.0
900–1000	1.1	0.0	0.0	0.8	0.8	0.0
>1000	0.0	0.0	0.0	0.3	0.3	0.0

Figure S5. African Grey Woodpecker *Dendropicos goertae* (n/km^2).
Insectivorous resident.
Present in 17% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 0.7 ± 2.1.
Estimated overall density: 0.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 4.1 million, of which 1.0 million birds are interpolated; range: 3.1–5.1 million (split-half).



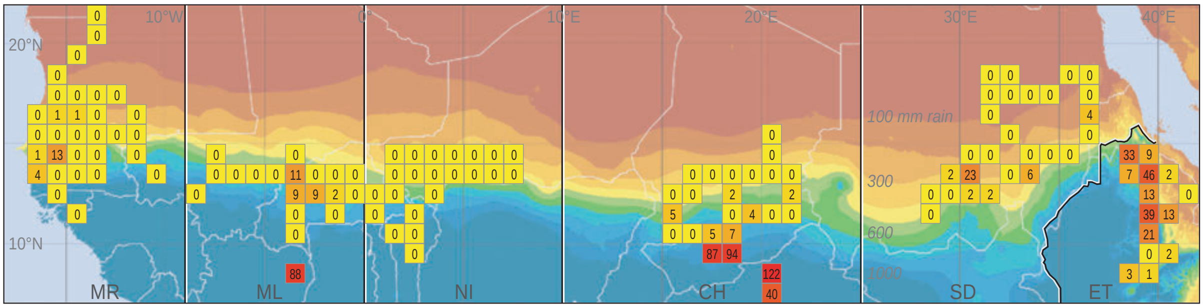
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.1	0.1	0.1	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.1	0.1	0.0	0.1	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.1	0.0
500–600	0.0	0.0	0.0	0.3	0.0	0.0
600–700	0.0	0.2	0.0	0.1	0.1	0.2
700–800	0.0	0.1	0.0	0.1	0.1	0.1
800–900	0.0	0.0	0.0	0.3	0.3	0.3
900–1000	0.0	0.0	0.0	0.7	0.3	0.2
>1000	0.0	2.0	0.0	0.1	0.0	0.0

Figure S6. Brubru *Nilaus afer* (n/km^2).
Insectivorous resident.
Present in 11% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 0.8 ± 2.9.
Estimated overall density: 0.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 5.9 million, of which 0.9 million birds are interpolated; range: 4.2–8.2 million (split-half).



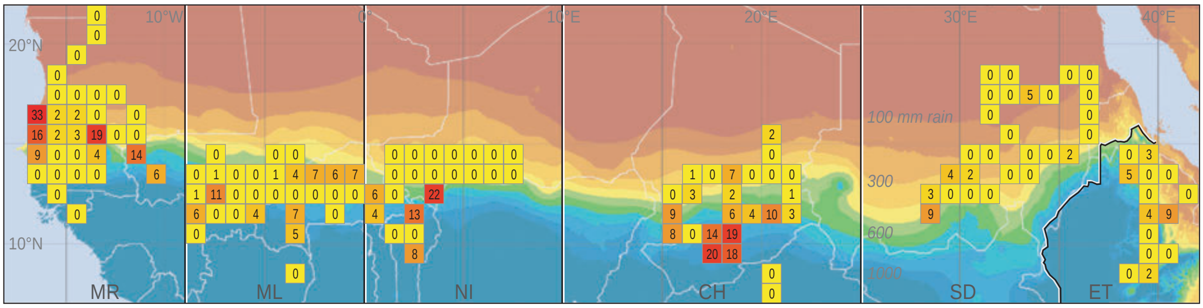
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.3	0.2	0.0	0.0	0.0	0.0
300–400	4.1	2.1	0.7	1.8	0.7	0.0
400–500	0.0	0.0	0.7	2.3	0.0	0.0
500–600	0.0	0.0	0.0	2.2	0.0	0.0
600–700	0.0	0.0	0.0	1.8	1.8	0.0
700–800	0.0	0.0	0.0	7.1	7.1	0.0
800–900	0.0	0.0	0.0	0.7	0.7	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S7. Sennar Penduline Tit *Anthoscopus punctifrons* (*n*/km^2).
Insectivorous resident.
Present in 9% of the 138 cells.
Average density (*n*/km^2, ±SD) in grid cells: 0.5 ± 1.9.
Estimated overall density: 0.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 3.6 million, of which 1.5 million birds are interpolated; range: 2.3–4.9 million (split-half).



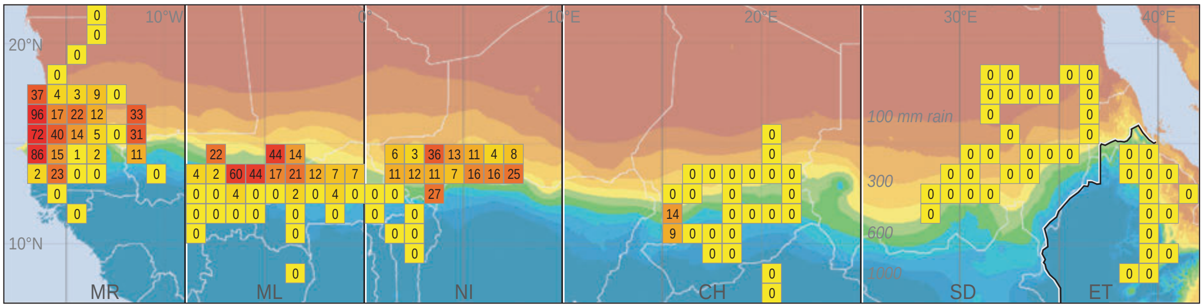
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	1.2	0.0
200–300	0.6	0.3	0.0	0.0	16.9	2.8
300–400	0.0	0.0	0.0	0.0	1.8	4.0
400–500	1.6	0.0	0.0	0.0	0.0	4.9
500–600	0.0	0.0	0.0	0.0	0.0	33.0
600–700	2.6	3.4	0.0	2.7	2.7	17.2
700–800	0.0	4.6	0.0	2.1	2.1	3.7
800–900	0.0	0.0	0.0	2.7	2.7	9.0
900–1000	0.0	0.0	0.0	75.3	75.3	6.5
>1000	0.0	5.5	0.0	81.2	81.2	29.8

Figure S8. Common Bulbul *Pycnonotus barbatus* (*n*/km^2).
Frugivorous resident.
Present in 28% of the 138 cells.
Average density (*n*/km^2, ±SD) in grid cells: 5.3 ± 17.8.
Estimated overall density: 7.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 75.5 million, of which 11.8 million birds are interpolated; range: 59.2–90.2 million (split-half).



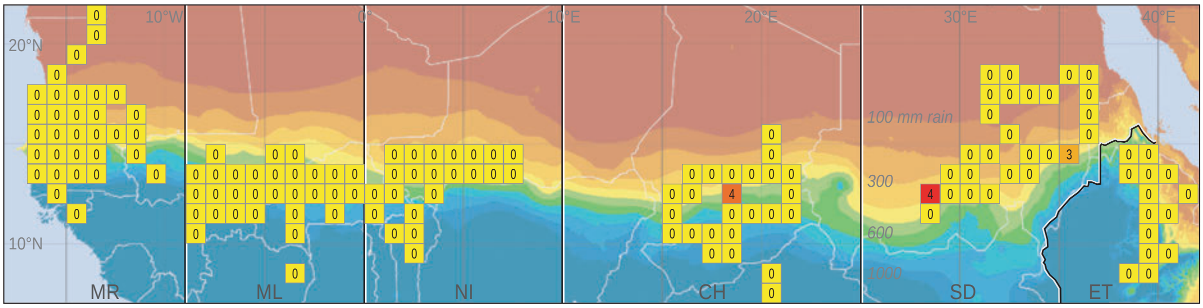
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.6	
100–200	0.7	1.2	1.7	2.2	0.0	0.0
200–300	3.8	1.9	0.0	0.0	0.0	0.0
300–400	5.4	2.7	0.0	2.2	1.0	2.0
400–500	9.5	0.0	0.0	0.0	2.8	0.0
500–600	8.4	2.2	0.0	5.9	2.2	5.7
600–700	4.0	2.5	32.3	2.6	2.6	2.2
700–800	1.5	0.5	3.0	5.9	5.9	0.0
800–900	0.0	4.2	3.7	10.8	10.8	0.0
900–1000	6.3	0.7	16.7	17.2	17.2	2.5
>1000	0.0	2.3	2.8	0.3	0.3	0.0

Figure S9. Northern Crombec *Sylvietta brachyura* (n/km^2).
Insectivorous resident.
Present in 38% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 2.7 ± 5.3.
Estimated overall density: 2.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 21.1 million, of which 5.2 million birds are interpolated; range: 21.1–21.3 million (split-half).



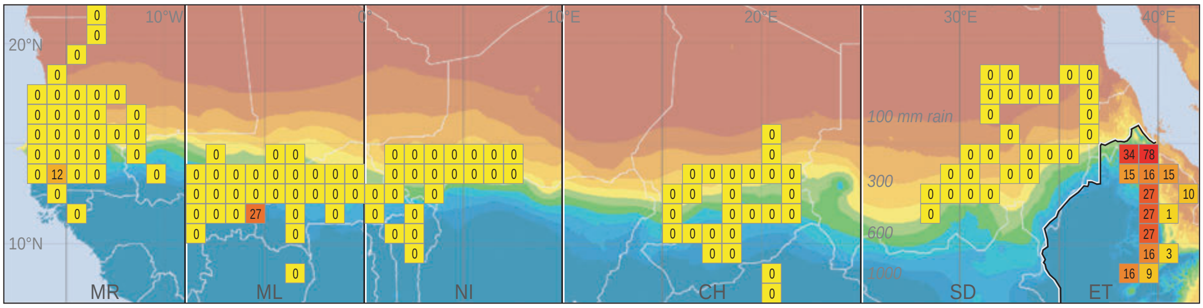
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	23.0	15.4	7.6	0.0	0.0	0.0
200–300	22.8	11.4	0.0	0.0	0.0	0.0
300–400	26.6	19.7	12.8	0.0	0.0	0.0
400–500	66.4	38.1	13.8	0.0	0.0	0.0
500–600	76.3	16.5	20.0	8.1	0.0	0.0
600–700	10.9	29.6	26.8	3.0	0.0	0.0
700–800	0.7	5.6	0.0	0.0	0.0	0.0
800–900	0.0	0.7	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S10. Western Bonelli's Warbler *Phylloscopus bonelli* (n/km^2).
Insectivorous migrants.
Present in 35% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 6.8 ± 15.4.
Estimated overall density: 3.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD 600–700 mm set to 0.
Estimated total number: 30.0 million, of which 6.2 million birds are interpolated; range: 30.0–30.2 million (split-half).



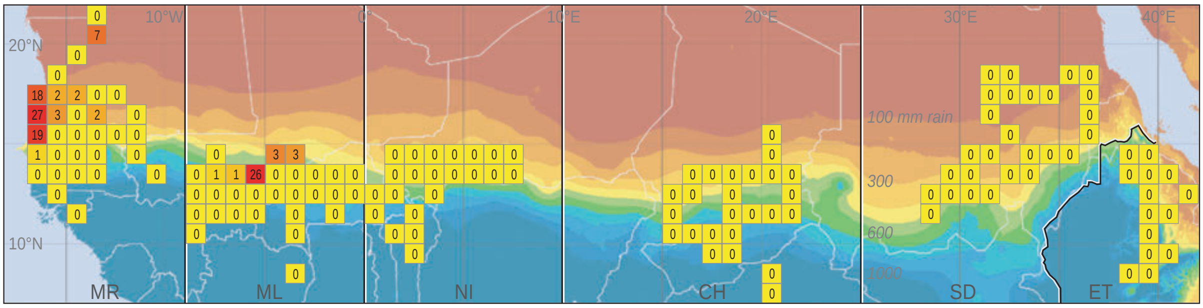
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.9	0.0
400–500	0.0	0.0	0.0	0.0	1.1	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.0	0.0	1.3	1.3	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.7	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S11. Eastern Bonelli's Warbler *Phylloscopus orientalis* (*n*/km^2).
Insectivorous migrant.
Present in 2% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 0.1 ± 0.5.
Estimated overall density: 0.05/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 0.50 million, of which 0.12 million birds are interpolated; range: 0–1.0 million (split-half).



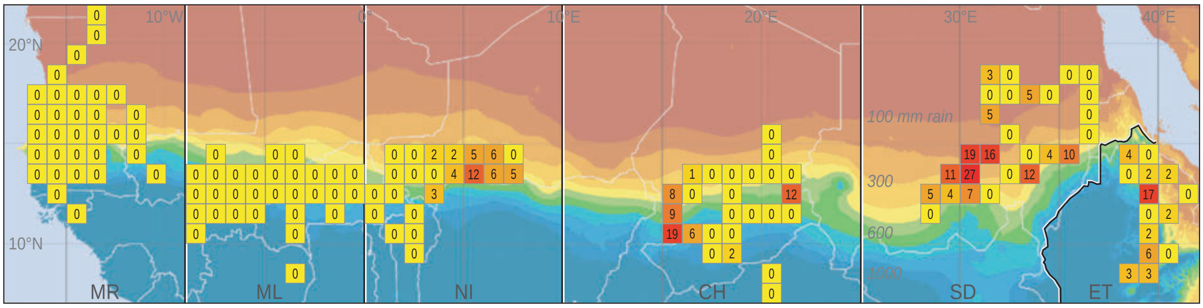
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	5.4
200–300	0.0	0.0	0.0	0.0	0.0	9.0
300–400	0.0	0.0	0.0	0.0	0.9	10.1
400–500	0.0	0.0	0.0	0.0	0.0	9.9
500–600	0.0	0.0	0.0	0.0	0.0	24.6
600–700	2.8	0.0	0.0	0.0	0.0	24.7
700–800	0.0	0.0	0.0	0.0	0.0	15.4
800–900	0.0	0.7	0.0	0.0	0.0	22.5
900–1000	0.0	0.0	0.0	0.0	0.0	21.3
>1000	0.0	4.0	0.0	0.0	0.0	29.6

Figure S12. Common Chiffchaff *Phylloscopus collybita* (*n*/km^2).
Insectivorous migrant.
Present in 11% of 150 the cells.
Average density (*n*/km^2, ±SD) in grid cells: 2.2 ± 8.6.
Estimated overall density: 1.7/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 16.8 million, of which no birds are interpolated; range: 9.3–23.6 million (split-half).



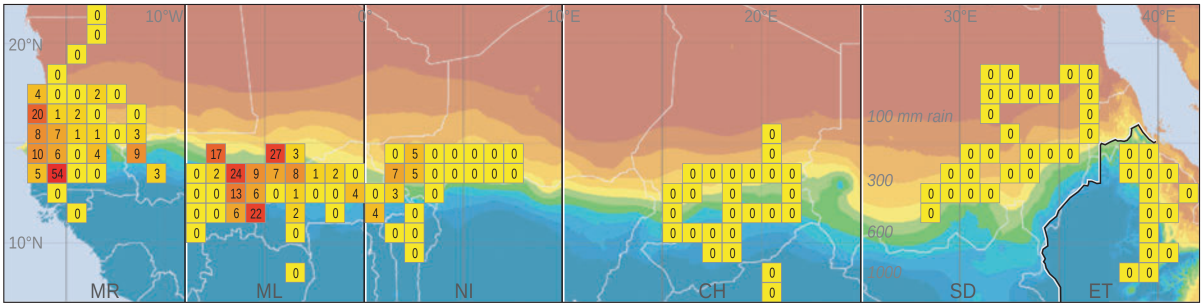
rain (mm)	MR	ML	NI	CH	SD	ET
<100	2.2	1.1	0.0	0.0	0.0	
100–200	6.5	3.3	0.0	0.0	0.0	0.0
200–300	3.2	1.6	0.0	0.0	0.0	0.0
300–400	9.3	4.6	0.0	0.0	0.9	0.0
400–500	0.0	4.2	0.0	0.0	0.0	0.0
500–600	0.7	0.0	0.0	0.0	0.0	0.0
600–700	0.0	6.0	0.0	0.0	0.0	0.0
700–800	0.0	0.2	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S13. Iberian Chiffchaff *Phylloscopus ibericus* (n/km^2).
Insectivorous migrant.
Present in 9% of 150 the cells.
Average density (n/km^2, ±SD) in grid cells: 0.8 ± 3.8.
Estimated overall density: 0.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; NI <200 set 0.
Estimated total number: 4.4 million, of which 1.4 million birds are interpolated; range: 1.8–6.9 million (split-half).



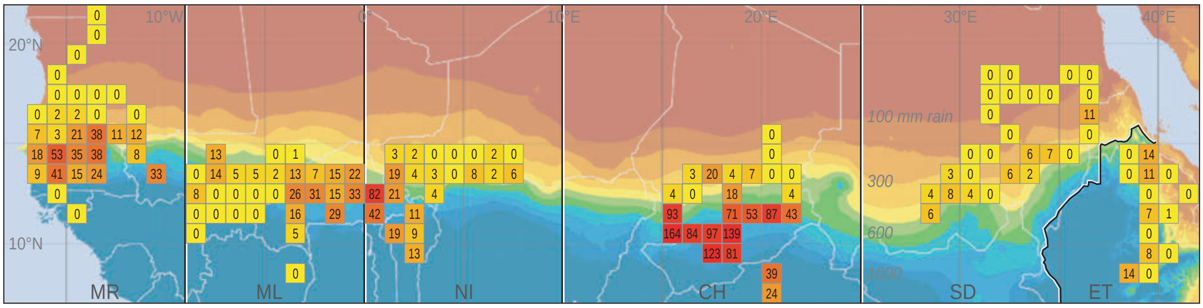
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	4.7	0.0
200–300	0.0	0.0	0.0	0.0	28.0	0.0
300–400	0.0	0.0	1.2	1.8	4.0	0.0
400–500	0.0	0.0	6.7	0.9	5.9	2.5
500–600	0.0	0.0	0.0	11.4	8.9	1.3
600–700	0.0	0.0	4.0	6.9	6.9	7.8
700–800	0.0	0.0	0.0	0.0	0.0	3.7
800–900	0.0	0.0	0.0	1.9	1.9	3.3
900–1000	0.0	0.0	0.0	0.8	0.8	0.0
>1000	0.0	0.0	0.0	0.2	0.2	5.9

Figure S14. Eastern Olivaceous Warbler *Iduna pallida* (n/km^2).
Insectivorous migrant (but also breeding in Niger).
Present in 26% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 2.1 ± 6.2.
Estimated overall density: 1.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set 0.
Estimated total number: 16.4 million, of which 1.1 million birds are interpolated; range: 12.0–21.0 million (split-half).



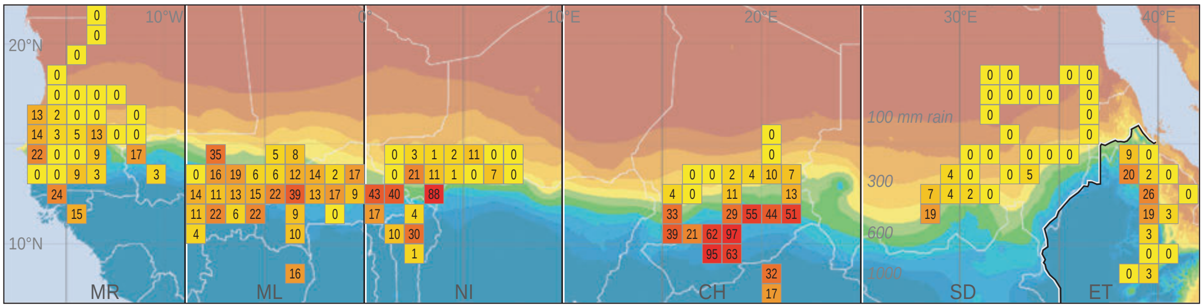
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	4.6	3.1	1.5	0.0	0.0	0.0
200–300	1.8	0.9	0.0	0.0	0.0	0.0
300–400	3.4	2.1	0.7	0.0	0.0	0.0
400–500	7.6	19.0	1.5	0.0	0.0	0.0
500–600	9.4	6.4	0.0	0.0	0.0	0.0
600–700	15.1	9.5	0.0	0.0	0.0	0.0
700–800	3.7	3.7	2.1	0.0	0.0	0.0
800–900	0.0	1.8	3.7	0.0	0.0	0.0
900–1000	0.0	1.8	0.0	0.0	0.0	0.0
>1000	0.0	3.6	0.0	0.0	0.0	0.0

Figure S15. Western Olivaceous Warbler *Iduna opaca* (n/km^2).
Insectivorous migrant.
Present in 26% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 1.8 ± 4.3.
Estimated overall density: 0.9/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 8.8 million, of which 1.4 million birds are interpolated; range: 5.6–11.1 million (split-half).



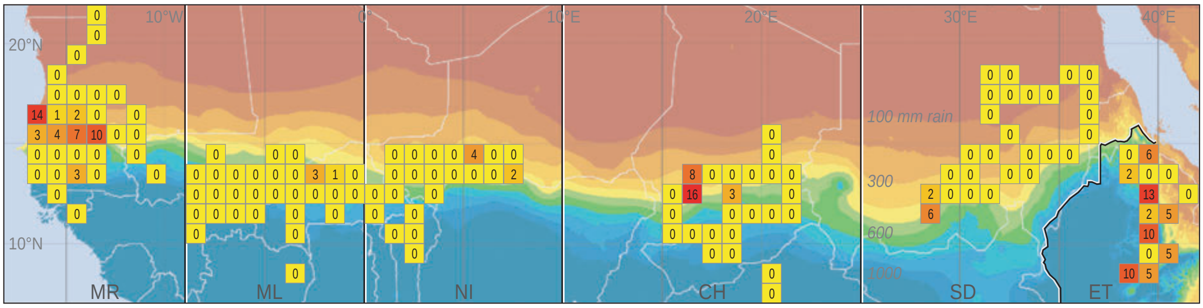
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	3.0	0.0
200–300	2.0	1.0	0.0	0.0	0.0	0.0
300–400	5.6	4.0	2.5	5.8	2.5	2.0
400–500	24.5	0.0	2.6	3.3	5.6	0.0
500–600	19.5	9.3	6.7	11.6	6.7	8.2
600–700	26.3	15.6	3.9	70.5	70.5	0.0
700–800	34.8	9.1	30.4	75.0	75.0	0.0
800–900	16.7	14.9	47.9	108.0	108.0	0.0
900–1000	15.9	10.1	25.0	94.9	94.9	6.2
>1000	0.0	1.4	14.5	31.2	31.2	14.8

Figure S16. Tawny-flanked Prinia *Prinia subflava* (n/km^2).
Insectivorous resident.
Present in 60% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 14.4 ± 27.4.
Estimated overall density: 13.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 133.7 million, of which 41.9 million birds are interpolated; range: 130.0–137.4 million (split-half).



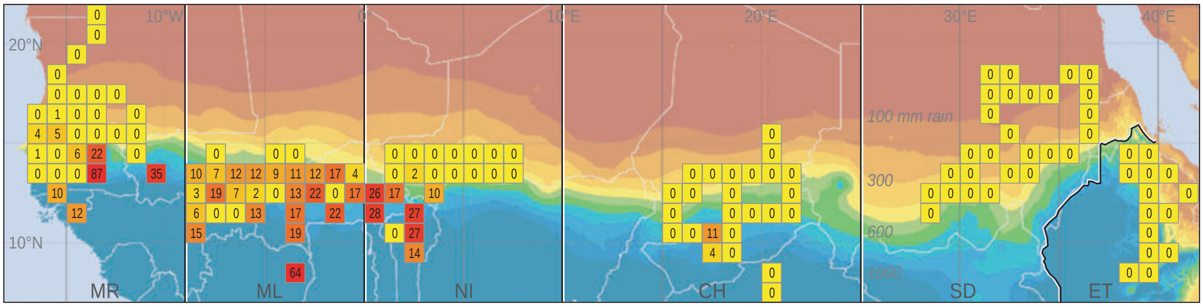
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.6	1.1	0.5	0.0	0.0	0.0
200–300	1.2	0.6	0.0	0.0	0.0	0.0
300–400	4.8	3.0	1.1	0.9	1.3	0.0
400–500	7.2	7.9	7.6	6.8	8.2	0.0
500–600	21.6	12.7	20.0	17.6	0.0	1.4
600–700	4.2	16.0	120.3	23.2	23.2	15.1
700–800	9.1	14.4	32.5	44.0	44.0	0.0
800–900	8.3	12.6	27.4	54.4	54.4	10.8
900–1000	0.0	10.6	0.0	75.5	75.5	1.2
>1000	18.8	12.6	13.5	24.5	24.5	16.5

Figure S17. Green-backed Camaroptera *Camaroptera brachyura* (*n*/km^2).
Insectivorous resident.
Present in 62% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 11.1 ± 17.6.
Estimated overall density: 10.8/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 107.8 million, of which 23.2 million birds are interpolated; range: 103.9–111.0 million (split-half).



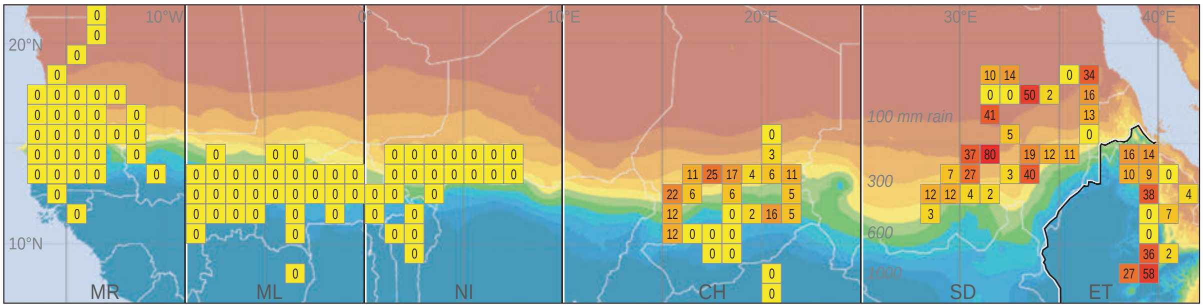
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.8	1.2	0.6	0.0	0.0	0.0
200–300	0.8	0.4	0.0	0.0	0.0	0.0
300–400	3.2	1.6	0.0	4.9	0.5	0.0
400–500	5.8	0.0	2.0	0.0	1.1	0.0
500–600	0.0	0.9	0.0	0.0	0.0	4.7
600–700	1.1	0.3	0.0	0.9	0.9	6.7
700–800	0.0	0.0	0.0	0.0	0.0	3.7
800–900	0.0	0.0	0.0	0.0	0.0	6.3
900–1000	0.0	0.0	0.0	0.0	0.0	1.2
>1000	0.0	0.0	0.0	0.0	0.0	11.0

Figure S18. Yellow-bellied Eremomela *Eremomela icteropygialis* (*n*/km^2).
Insectivorous resident.
Present in 17% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 1.0 ± 2.7.
Estimated overall density: 0.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 6.2 million, of which 0.6 million birds are interpolated; range: 3.0–9.1 million (split-half).



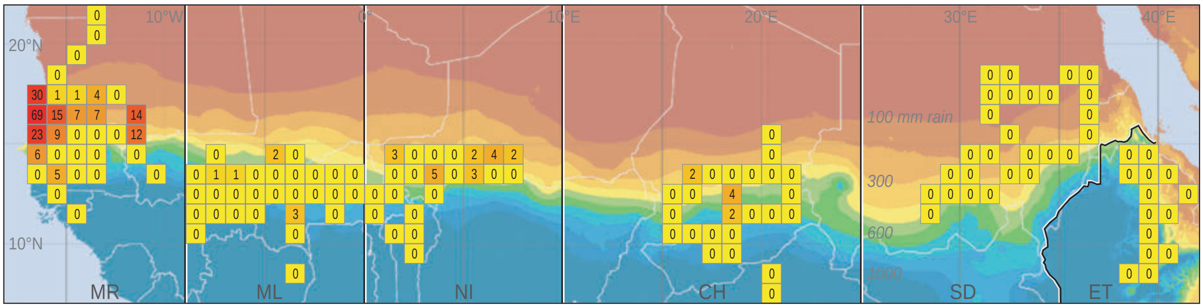
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.7	0.5	0.2	0.0	0.0	0.0
200–300	0.2	0.1	0.0	0.0	0.0	0.0
300–400	2.4	1.2	0.0	0.0	0.0	0.0
400–500	2.5	2.1	0.3	0.0	0.0	0.0
500–600	2.7	8.9	0.0	0.0	0.0	0.0
600–700	0.0	11.1	15.2	0.0	0.0	0.0
700–800	22.9	9.0	26.3	0.0	0.0	0.0
800–900	50.9	12.2	24.9	1.0	0.0	0.0
900–1000	36.2	8.8	33.3	4.0	0.0	0.0
>1000	11.5	10.4	10.5	0.0	0.0	0.0

Figure S19. Senegal Eremomela *Eremomela pusilla* (*n*/km^2).
Insectivorous resident.
Present in 29% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 4.5 ± 11.1.
Estimated overall density: 3.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD>600 mm set to 0.
Estimated total number: 29.5 million, of which 0.2 million birds are interpolated; range: 25.6–33.5 million (split-half).



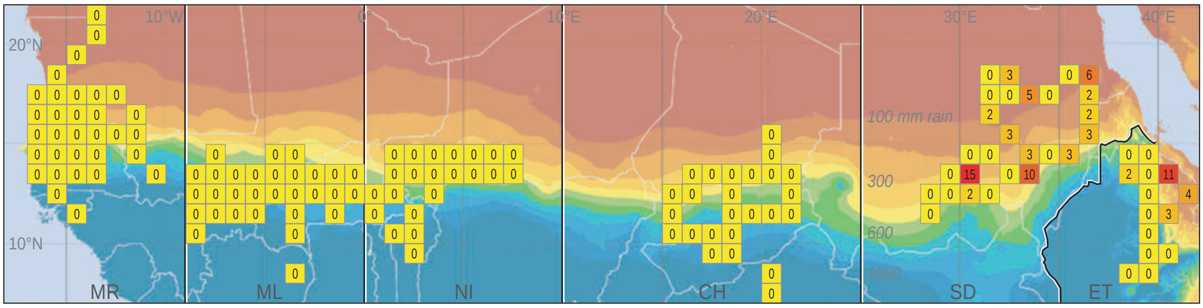
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	18.5	
100–200	0.0	0.0	0.0	0.0	27.6	0.0
200–300	0.0	0.0	0.0	3.6	33.3	6.3
300–400	0.0	0.0	0.0	15.2	10.6	4.0
400–500	0.0	0.0	0.0	8.2	10.2	2.5
500–600	0.0	0.0	0.0	10.8	15.6	3.1
600–700	0.0	0.0	0.0	8.0	8.0	16.7
700–800	0.0	0.0	0.0	1.4	1.4	79.0
800–900	0.0	0.0	0.0	7.2	7.2	20.2
900–1000	0.0	0.0	0.0	0.0	0.0	2.5
>1000	0.0	0.0	0.0	0.0	0.0	34.1

Figure S20. Lesser Whitethroat *Sylvia curruca* (*n*/km^2).
Insectivorous migrant.
Present in 33% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 5.6 ± 12.2.
Estimated overall density: 5.5/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; ML+NI+CH<100 set 0.
Estimated total number: 54.8 million, of which 2.1 million birds are interpolated; range: 47.1–63.7 million (split-half).



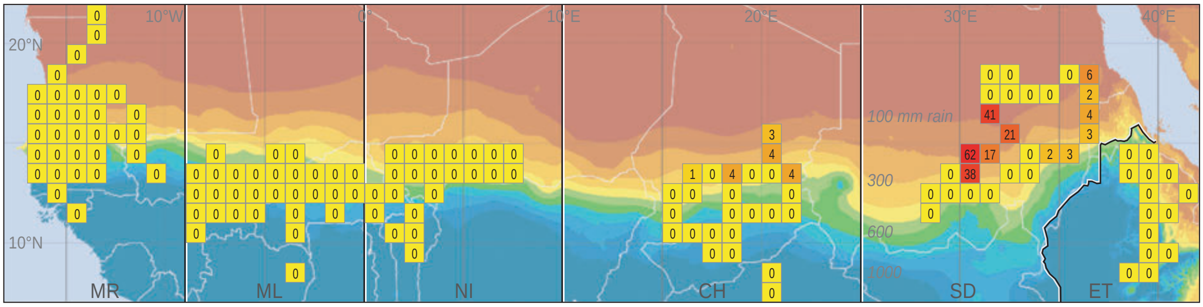
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	23.2	15.5	7.6	0.0	0.0	0.0
200–300	8.9	4.4	0.0	0.0	0.0	0.0
300–400	12.9	7.4	1.9	0.7	0.0	0.0
400–500	7.8	1.1	0.7	0.0	0.0	0.0
500–600	4.5	0.0	0.0	0.0	0.0	0.0
600–700	1.1	0.2	0.0	0.7	0.0	0.0
700–800	0.0	0.0	0.0	1.4	0.0	0.0
800–900	0.0	1.3	0.0	0.0	0.0	0.0
900–1000	0.0	1.2	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S21. Western Orphean Warbler *Sylvia hortensis* (*n*/km^2).
Insectivorous migrant.
Present in 18% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 1.6 ± 6.7.
Estimated overall density: 1.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD 600-800 mm set to 0.
Estimated total number: 10.8 million, of which 4.8 million birds are interpolated; range: 10.0–11.7 million (split-half).



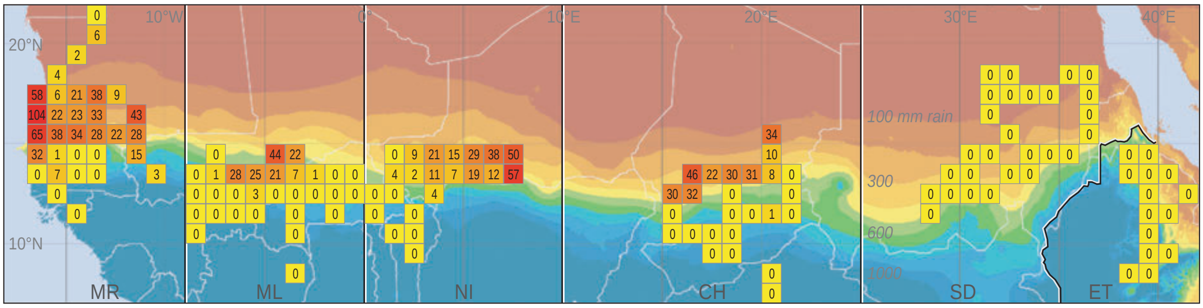
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	2.8	0.0
200–300	0.0	0.0	0.0	0.0	13.0	11.8
300–400	0.0	0.0	0.0	0.0	2.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	14.8
500–600	0.0	0.0	0.0	0.0	4.4	0.0
600–700	0.0	0.0	0.0	0.0	0.0	1.1
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S22. Eastern Orphean Warbler *Sylvia crassirostris* (*n*/km^2).
Insectivorous migrant.
Present in 11% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 0.5 ± 1.9.
Estimated overall density: 0.6/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set to 0.
Estimated total number: 5.8 million, of which no birds are interpolated; range: 4.8–6.9 million (split-half).



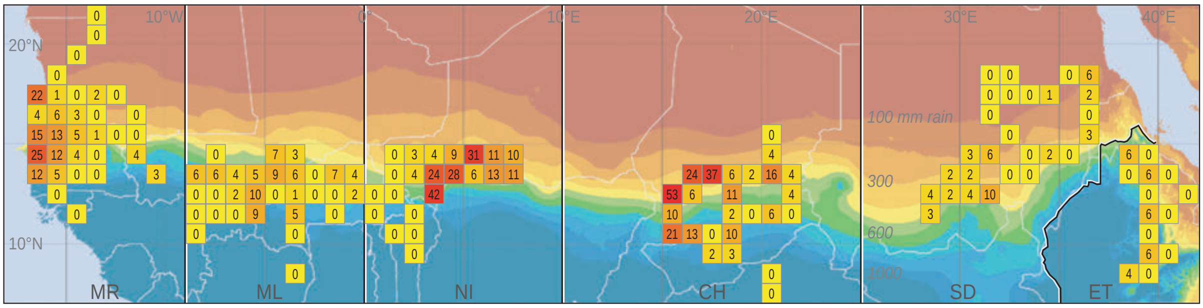
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	7.6	
100–200	0.0	0.0	0.0	3.4	9.9	0.0
200–300	0.0	0.0	0.0	2.5	56.0	0.0
300–400	0.0	0.0	0.0	1.3	0.0	0.0
400–500	0.0	0.0	0.0	0.8	0.0	0.0
500–600	0.0	0.0	0.0	1.2	6.7	0.0
600–700	0.0	0.0	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S23. Rüppell's Warbler *Sylvia ruppeli* (*n*/km^2).
Insectivorous migrant.
Present in 11% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 1.4 ± 7.1.
Estimated overall density: 2.4/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey: NI <200 and CH <100 mm set 0.
Estimated total number: 20.2 million, of which no birds are interpolated; range: 19.2–21.3 million (split-half).
Note that the unexpectedly high estimate of population size is based on high densities in some sub-regions in Sudan: clearly more counts are needed to validate whether indeed 9.8 million birds are present in SD 200–300 mm.



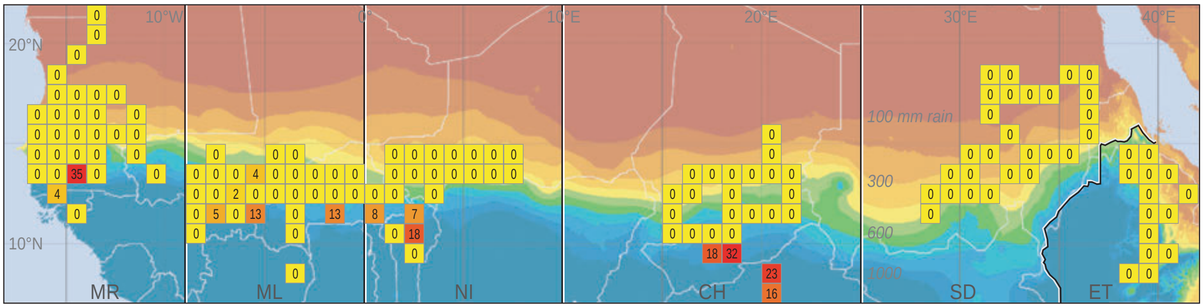
rain (mm)	MR	ML	NI	CH	SD	ET
<100	3.6	2.7	1.8	0.9	0.0	
100–200	34.1	34.1	34.0	34.0	0.0	0.0
200–300	30.1	29.7	29.3	19.1	0.0	0.0
300–400	39.8	32.9	26.1	35.0	0.0	0.0
400–500	52.4	39.7	21.1	14.2	0.0	0.0
500–600	23.3	11.5	6.7	0.0	0.0	0.0
600–700	5.4	13.8	0.0	0.0	0.0	0.0
700–800	3.0	2.2	0.0	0.0	0.0	0.0
800–900	0.0	0.2	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S24. Subalpine Warbler (now split up in three species Western and Eastern Subalpine Warbler *Sylvia iberae*, *S. cantillans*, and Moltoni's Warbler *S. subalpina*; *n*/km^2).
Insectivorous migrant.
Present in 38% of the 150 cells.
Average density (*n*/km^2, ±SD) in grid cells: 8.8 ± 16.5.
Estimated overall density: 6.3/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 62.5 million, of which 20.2 million birds are interpolated; range: 51.1–74.7 million (split-half).



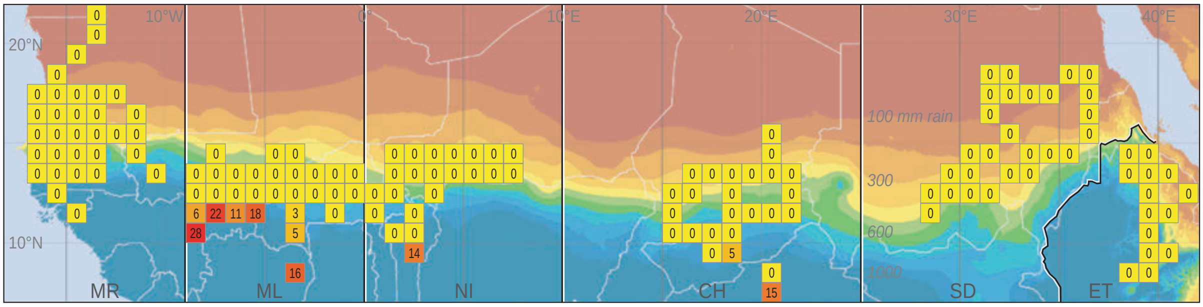
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.2	0.3	0.4	0.6	
100–200	3.3	2.2	1.1	0.0	2.4	0.0
200–300	3.9	6.6	9.4	7.4	3.7	0.0
300–400	11.6	9.7	7.8	28.0	2.3	0.0
400–500	9.5	3.2	20.7	6.6	3.3	0.0
500–600	24.3	5.7	17.8	6.6	0.0	2.4
600–700	6.3	3.6	43.4	9.2	9.2	3.3
700–800	3.0	3.9	0.0	3.9	3.9	7.4
800–900	0.0	5.3	0.0	8.7	8.7	0.0
900–1000	0.0	0.0	0.0	2.2	2.2	2.2
>1000	0.0	0.9	0.0	0.0	0.0	4.4

Figure S25. Common Whitethroat *Sylvia communis* (n/km^2).
Insectivorous migrant.
Present in 56% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 4.9 ± 8.3.
Estimated overall density: 3.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 30.0 million, of which 5.4 million birds are interpolated; range: 29.2–31.6 million (split-half).



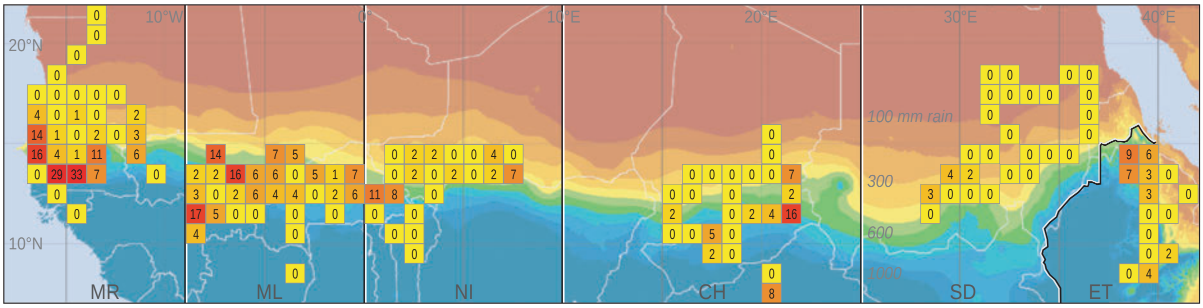
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.6	0.0	0.0	0.0	0.0
700–800	0.0	0.3	0.0	0.0	0.0	0.0
800–900	0.0	3.1	7.4	0.0	0.0	0.0
900–1000	24.8	0.7	8.3	21.1	21.1	0.0
>1000	0.0	2.3	5.6	19.5	19.5	0.0

Figure S26. Northern Yellow White-eye *Zosterops senegalensis* (n/km^2).
Insectivorous resident.
Present in 9% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 1.3 ± 5.1.
Estimated overall density: 2.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 19.3 million, of which 2.8 million birds are interpolated; range: 14.6–24.2 million (split-half).



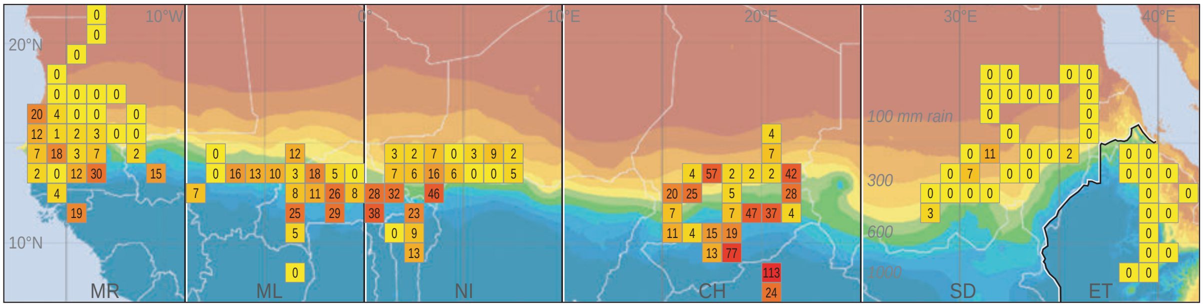
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.0	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	1.3	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	2.4	0.0	0.0
>1000	0.0	12.2	5.0	8.0	0.0	0.0

Figure S27. European Pied Flycatcher *Ficedula hypoleuca* (n/km^2).
Insectivorous migrant.
Present in 8% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 1.0 ± 3.9.
Estimated overall density: 1.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD>900 mm set to 0.
Estimated total number: 11.7 million, of which no birds are interpolated; range: 10.6–12.8 million (split-half).



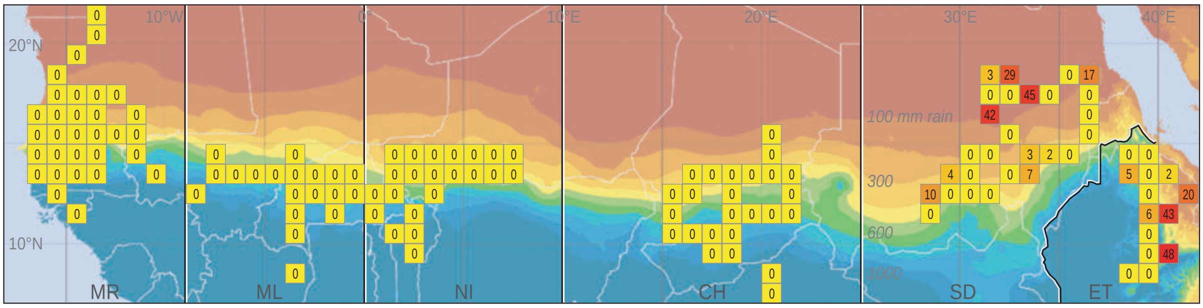
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.0	0.7	0.3	0.0	0.0	0.0
200–300	0.8	0.4	0.0	0.0	1.9	0.0
300–400	7.2	4.3	1.5	0.0	0.7	0.0
400–500	1.6	7.4	2.7	0.0	1.1	0.0
500–600	15.9	6.5	0.0	5.2	0.0	2.0
600–700	9.6	9.1	0.0	3.8	3.8	7.2
700–800	6.7	2.6	9.1	2.0	2.0	0.0
800–900	0.0	1.2	1.7	1.3	1.3	5.9
900–1000	18.3	1.7	0.0	1.4	1.4	0.0
>1000	0.0	2.7	0.0	3.9	3.9	0.0

Figure S28. Common Redstart *Phoenicurus phoenicurus* (n/km^2).
Insectivorous migrant.
Present in 43% of the 150 cells.
Average density (n/km^2, ±SD) in grid cells: 2.6 ± 5.0.
Estimated overall density: 1.3/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey
Estimated total number: 12.6 million, of which 1.8 million birds are interpolated; range: 10.4–14.7 million (split-half).



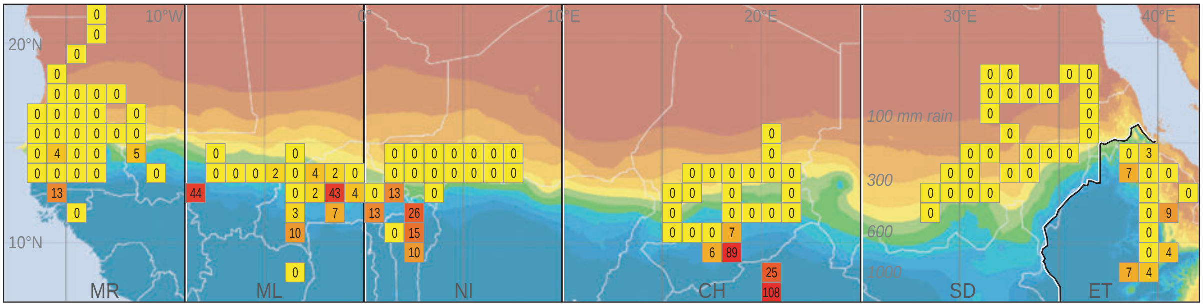
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	3.0	3.5	4.0	4.4	2.4	0.0
200–300	1.4	0.7	0.0	7.4	1.9	0.0
300–400	0.5	1.6	2.6	20.0	0.7	0.0
400–500	10.7	0.0	8.1	1.7	0.6	0.0
500–600	6.6	6.2	33.3	25.9	2.2	0.0
600–700	5.3	11.7	37.9	10.0	10.0	0.0
700–800	7.7	12.2	38.4	24.7	24.7	0.0
800–900	33.3	36.5	33.3	18.6	18.6	0.0
900–1000	32.9	3.5	25.0	44.3	44.3	0.0
>1000	3.7	4.2	10.6	68.3	68.3	0.0

Figure S29. Pygmy Sunbird *Hedydipna platura* (n/km^2).
Nectarivorous resident.
Present in 57% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 8.8 ± 15.6.
Estimated overall density: 9.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 90.7 million, of which 16.9 million birds are interpolated; range: 72.8–109.4 million (split-half).



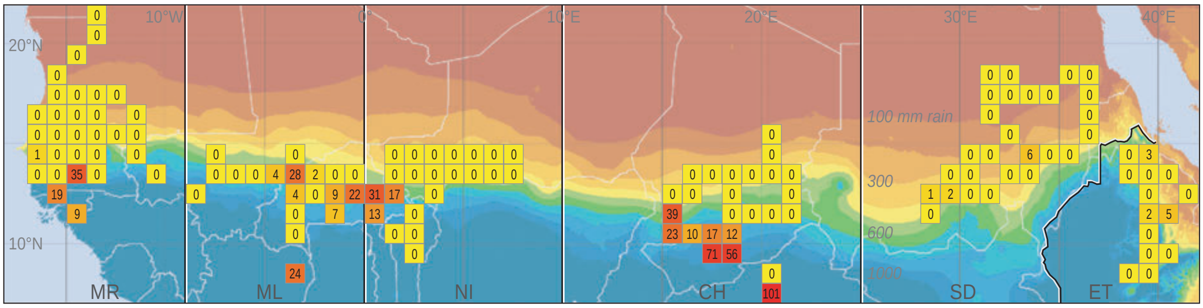
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	6.0
300–400	0.0	0.0	0.0	0.0	0.4	1.6
400–500	0.0	0.0	0.0	0.0	0.0	1.0
500–600	0.0	0.0	0.0	0.0	0.2	2.3
600–700	0.0	0.0	0.0	0.0	0.0	0.3
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.2
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

Figure S30. Nile Valley Sunbird *Hedydipna metallica* (n/km^2).
Nectarivorous resident.
Present in 12% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 2.1 ± 8.1.
Estimated overall density: 1.8/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set to 0.
Estimated total number: 17.4 million, of which no birds are interpolated; range: 13.7–21.1 million (split-half).



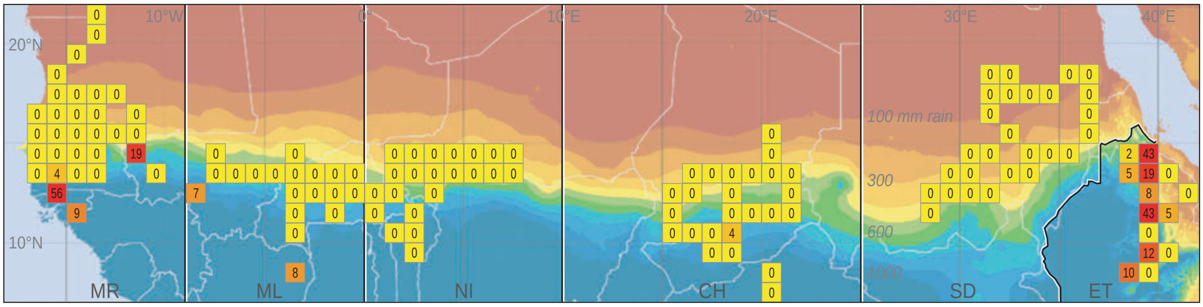
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.2	0.1	0.0	0.0	0.0	2.8
300–400	0.0	0.0	0.0	0.0	0.0	8.1
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.9	0.0	0.0	0.0	3.2
600–700	1.9	1.6	0.0	0.0	0.0	2.2
700–800	0.0	12.0	9.1	0.0	0.0	0.0
800–900	0.0	3.0	11.1	2.1	2.1	3.0
900–1000	0.0	24.6	16.7	43.4	43.4	4.4
>1000	5.6	8.3	10.4	66.9	66.9	0.0

Figure S31. Scarlet-chested Sunbird *Chalcomitra senegalensis* (*n*/km^2).
Nectarivorous resident.
Present in 22% of the 138 cells.
Average density (*n*/km^2, ±SD) in grid cells: 3.5 ± 13.3.
Estimated overall density: 6.0/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 59.0 million, of which 8.2 million birds are interpolated; range: 36.1–81.9 million (split-half).



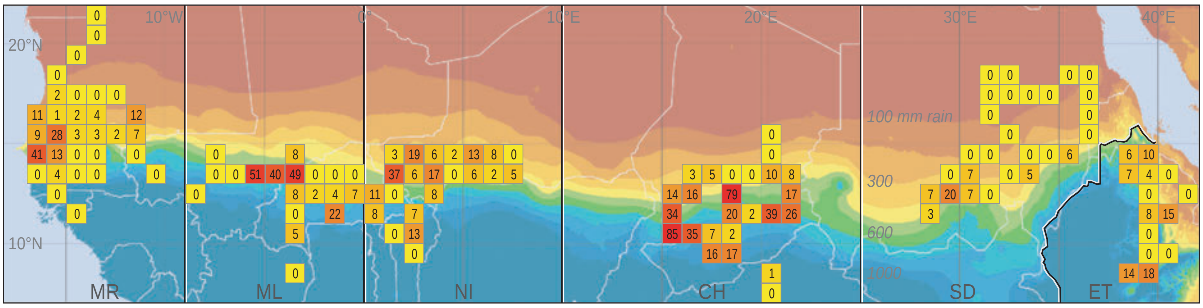
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.1	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.7	0.0
400–500	0.0	0.0	0.0	0.0	1.1	0.0
500–600	0.8	0.9	0.0	2.5	0.0	3.6
600–700	0.0	8.2	0.0	16.3	16.3	0.0
700–800	0.0	6.3	26.3	3.3	3.3	0.0
800–900	0.0	3.0	12.8	7.9	7.9	0.0
900–1000	31.6	0.0	0.0	54.5	54.5	1.2
>1000	8.0	1.5	0.0	50.4	50.4	0.0

Figure S32. Beautiful Sunbird *Cinnyris pulchellus* (*n*/km^2).
Nectarivorous resident.
Present in 20% of the 138 cells.
Average density (*n*/km^2, ±SD) in grid cells: 4.0 ± 13.0.
Estimated overall density: 5.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 50.5 million, of which 10.5 million birds are interpolated; range: 27.1–73.8 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.4	0.0	0.0	0.0	0.0	18.1
600–700	6.1	0.0	0.0	0.0	0.0	8.8
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	1.3	1.3	6.1
900–1000	12.7	3.5	0.0	0.0	0.0	4.9
>1000	21.2	0.5	0.0	0.0	0.0	46.2

Figure S33. Variable Sunbird *Cinnyris venustus* (n/km^2).
Nectarivorous resident.
Present in 12% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 1.8 ± 7.5.
Estimated overall density: 2.3/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 22.7 million, of which 0.2 million birds are interpolated; range: 20.5–23.8 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	2.7	1.8	0.9	0.0	0.0	0.0
200–300	2.5	1.3	0.0	0.0	5.6	11.1
300–400	13.5	11.0	8.6	7.1	3.3	6.1
400–500	5.0	0.0	9.0	4.3	6.0	0.0
500–600	40.6	5.2	13.3	22.2	8.9	4.7
600–700	2.1	16.9	0.0	59.0	59.0	8.6
700–800	0.0	12.0	0.0	22.6	22.6	3.7
800–900	0.0	11.3	11.1	23.1	23.1	9.5
900–1000	0.0	3.5	8.3	13.6	13.6	12.4
>1000	0.0	0.0	4.2	0.4	0.4	0.0

Figure S34. Little Weaver *Ploceus luteolus* (n/km^2).
Insectivorous resident.
Present in 56% of the 138 cells.
Average density (n/km^2, ±SD) in grid cells: 7.8 ± 13.9.
Estimated overall density: 5.1/km^2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number: 50.6 million, of which 15.1 million birds are interpolated; range: 46.9–54.3 million (split-half).

Distribution and relative density of raptors in the sub-Sahara during the dry season

Rob G. Bijlsma[1,*], Jan van der Kamp[2] & Leo Zwarts[2]

Bijlsma R.G., van der Kamp J. & Zwarts L. 2023. Distribution and relative density of raptors in the sub-Sahara during the dry season. Ardea 111: 103–117. doi:10.5253/arde.2023.a6

The sub-Sahara between the Atlantic Ocean and Red Sea and between 5°N (Guinean vegetation zone) and 20°N (southern Sahara) was visited on 466 days during 15 dry seasons (late September – early March) in 1996–2019. Using a combination of field methods, ranging from road counts to surveys of single sites (non-random and random-stratified), a total of 22,696 raptors of 62 species were identified. These were allocated to 1° latitude-longitude grid cells. Palearctic migrants accounted for 13% of the total. Two Afrotropical raptors were by far the most common, Yellow-billed Kite *Milvus aegyptius* (46%) and Hooded Vulture *Necrosyrtes monachus* (25%). Diversity and density were lowest in the arid and semi-arid zones but increased with increasing annual rainfall and vegetation cover. Palearctic migrants almost exclusively occupied the driest zones (100–500 mm rainfall per year), African raptors were commonest in the more humid zones. Migrants were concentrated in the western and eastern sections of the sub-Sahara, in longitudinal agreement with the main crossing points on either side of the Mediterranean for the large majority of Palearctic migrants. Comparatively few migrants were encountered in the central Sahel (Mali-Niger-Chad), suggesting that most Palearctic raptors remained either in West or in East Africa upon entering the continent. Even harriers *Circus* spp., known to cross the full width of the Mediterranean Sea, showed a distinct East Africa bias in their distribution. Afrotropical raptors were more evenly distributed across the width of the sub-Sahara within the 100–1000-mm rainfall zone.

Key words: Sahel, birds of prey, bird distribution, relative density

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The diversity of raptors in Africa is seasonally enriched with tens of Eurasian species. Via the eastern flyway, namely Turkey, Caucasus, Middle East and Arabian Peninsula, several million raptors from Europe and Asia pour into Africa (Jobson *et al.* 2021). The western route via the Iberian Peninsula is a floodgate for migratory raptors from western and northern Europe. A trickle of raptor species with low wing-loading crosses the full width of the Mediterranean in between the two bottlenecks (Panuccio *et al.* 2021). Except for European Honey Buzzard *Pernis apivorus*, which typically winters in humid forests in western and central Africa (Vansteelant *et al.* 2015), and Osprey *Pandion haliaetus*, which winters in coastal and inland wetlands, most common migratory raptor species from Eurasia spend the non-breeding period in savannah-like ecosystems (including derived savannah) in the sub-Sahara and southern Africa (Thiollay 1978a, Brown *et al.* 1982).

In the recent past, attempts to describe distributional and seasonal patterns in the dry zones of Africa were mostly restricted to analyses of observations of resident ornithologists (e.g. in Nigeria by Elgood *et al.* 1973). Road counts were used to cope more quantitatively with diversity and abundance across large regions, notably in West Africa (Mali, Burkina Faso, Niger and northern Cameroon; Thiollay 1978a, 2006), and in East and southern Africa (with a preliminary overview by Brown 1970: 284–295). Many more road surveys have seen the light of day since then (McClure *et al.* 2021), albeit rather few from the Sahelian-

Sudano-Guinean zone (but see e.g. Rondeau *et al.* 2007, Anadon *et al.* 2010, Buij *et al.* 2013, Angelov & Hashim 2019). The advent of satellite-tracking has fine-tuned distributional patterns and movements within wintering ranges in Africa, especially when concurrent field studies were carried out to quantify habitat use and food resources *in situ* (Schlaich *et al.* 2016). Similarly, ornithologists and birders have not remained idle in the 50 years since Brown's (1970) overview was published. Many open questions regarding biology and ecology of raptors in Africa have been resolved through fieldwork and telemetry. Still, much work on raptors is concentrated on certain species, be they threatened or large, such as vultures, or limited to specific habitats (wetlands, forests) and regions (National Parks; e.g. Smeenk 1974, Thiollay 1998). This leaves much scope for publishing data on raptor guilds, irrespective of conservation directives.

During fieldwork between 1996 and 2019, raptors were routinely recorded across the full width of sub-Saharan Africa north of 5°N. The longitudinal and latitudinal distribution of common Afro-Palearctic migratory raptors are compared to those of Afro-tropical raptor species (including intra-African migrants). The study complements those covering ground-foraging and arboreal birds, with the caveat that densities per 1° latitude × 1° longitude grid cells used in the present study are relative (rather than absolute, as in Zwarts *et al.* 2023a, 2023b).

METHODS

The material for this overview was collected across the Sahelian-Sudano-Guinean zone between Atlantic Coast and Red Sea in 15 dry seasons (late September – early March) over the years 1996–2019. Three major sources of data were tapped. Raptors were recorded during road trips, stays at a single site (e.g. Bijlsma 2001), and stratified-random plot-sampling (Zwarts *et al.* 2023a). Additionally, raptors were registered whenever encountered and identified during fieldwork. Out of 22,696 raptors observed, 83% were recorded in December–February, i.e. midway through the dry season when within-African displacements are small or non-existent (hence the qualification 'residents' for Afrotropical species).

Road counts were opportunistic, insofar as raptors were identified and counted from the passenger's seat, with or without the help of other passengers, along roads and dirt tracks. Road counts were made on day-long journeys (Mali, Ghana, Nigeria) and on much shorter trips (usually the 11-km stretches between successive sites forming part of the stratified-random survey of the wider Sahel; Zwarts *et al.* 2023a). Vehicle speed varied substantially between slow-moving and full speed (up to 90 km/h) depending on the terrain. Only rarely were stops made to better examine flocks or individuals. Raptors were categorized as recorded within or further than 100 m from the road or observation site (Table S1, for % recorded at >100 m). Except for the width of the band, counts were not standardized (in terms of McClure *et al.* 2021). The road surveys were probably biased towards large and/or exposed species.

Single site studies were available for Nigeria (Boje-Ebakken, 6.63°N, 9.08°E, 2 × 3 km, 2604 mm rainfall/year near Ikom), Mali (Inner Niger Delta, 15.15°N, 4.23°W, 100 × 50 km), Ghana (Kintampo, 7.97°N, 1.73°W, 1 × 1 km and Damongo, 9.08°N, 1.77°W, 50 ha, respectively, 1351 mm and 1082 mm rainfall/year, averaged over 2001–2011; Ouwehand 2016: 27) and Ivory Coast (Comoé National Park, 8.75°N, 3.78°E, 1 × 1 km, 1000 mm rainfall/year; Ouwehand *et al.* 2023).

The site in Nigeria consisted of rainforest in the foothills of Afi Mountain, where an observation post in a *Pennisetum*-covered gap on the hillside provided an unobstructed view over forest and valley. Systematic daily observations of raptors were performed from elevated positions between 31 January and 21 February 2001 (Bijlsma 2001), and small forest raptors were netted incidentally during the capture of roosting Barn Swallows *Hirundo rustica* in early morning and evening (Bijlsma & van den Brink 2005).

Two study sites in Ghana near Kintampo and Damongo were situated in wooded savannah and consisted of dry forest remnants amidst farmland (for a detailed description, see Ouwehand 2016). Sites were alternately visited for 7–12 days to study European Pied Flycatchers *Ficedula hypoleuca*, and raptors were opportunistically recorded whilst surveying the forest and nearby fields, including occasional captures of small forest raptors during targeted netting of flycatchers (Ouwehand 2016). Prolonged stays at specific sites and where the forest was broken (clearcuts, small fields) achieved better than average detection of secretive raptors in these sites, whether by sight or hearing. In addition, raptor observations were available from several sites across Ghana that were visited between 10 December and 3 January 1996/1997 as part of a survey of Barn Swallow roosts. These included Keta Lagoon, Akuse Dam, Owabi Dam, Bosumtwi and Ayensudo (see van den Brink *et al.* 1998, for a description of sites).

The site in Comoé National Park in Ivory Coast consists of wooded savannah with two small forest islands and gallery forest along the Comoé River. Raptor observations were mostly carried out in the afternoons, whilst walking transects on the savannah, along the Comoé River and in the edges of forest islands. Fieldwork was conducted before the annual burning of savannah grasses was started (in 2018, the first fires were lit by late December).

The sub-Sahara between 7°N and 22°N and between 17°W and 42°E was systematically surveyed between 2007 and 2019 during the dry season from 26 September up to and including 10 March (see Figures 3–4 in Zwarts *et al.* 2023a). We used a stratified random sampling regime, covering a total of 2144 sites of 4.5 ha each (occasionally smaller when they were particularly labour-intensive). The sites were at least 5.5 km, but most often 11 km apart, and located along longitudinal and latitudinal transects traversing 14 countries between the Atlantic Ocean and the Red Sea. The field methods were specifically developed to collect absolute quantitative data from sunrise to sunset on ground-foraging and arboreal birds, while simultaneously obtaining detailed descriptions of the woody vegetation within plots (Zwarts & Bijlsma 2015). This time-consuming approach involved close and prolonged examination of individual trees, rather than scanning the sky. Consequently, many flying raptors, especially when high overhead, must have been overlooked, unlike those residing within the site boundaries of three legs of 300 × 50 m each. When moving by car from one site to the next, raptors were recorded as usual (within and beyond 100 m of the road).

Overall, the observations form a disparate collection based on repeatable (stratified-random) and non-repeatable methods. Of common raptor species (>500 records; Table S1), only a few were frequently observed beyond 100 m, namely Hooded Vulture *Necrosyrtes monachus* (38%), Black Kite *Milvus migrans* (36%), Yellow-billed Kite *M. aegyptius* (35%) and White-backed Vulture *Gyps africanus* (24%). For the present paper, we combined all observations, irrespective of distance from the observer. The data are condensed into species-specific numbers per 1° latitude × 1° longitude grid cells (111 × c. 104 km), corrected for observer effort (field days spent in grid cells; Figure 1). 83 out of 154 grid cells were visited during just a single day (54%; yellow squares in Figure 1) and only 9 grid cells for more than 10 days (red squares in Figure 1; sometimes across several years, and restricted to Senegal, Mali, Ivory Coast, Ghana and Nigeria). Each raptor observation is also consigned to a site-specific value of mean annual rainfall (based on Hijmans *et al.* 2005). During the 15 dry seasons of observation, rainfall was below or well below the calculated average for 1950–2000 in 1996, 2000, 2004, 2008 and 2011 (dry years), about average in 2003, 2005, 2010 and 2013–2017, and well above in 2018–2019 (wet years; see Supplementary Material 4, in Zwarts *et al.* 2023a).

RESULTS

Species and relative abundance

During 466 field days spent in 14 sub-Saharan countries in 1996–2019 a total of 22,696 raptors of 62 species were recorded (Table S1). Just two species, Yellow-billed Kite (46.0%) and Hooded Vulture (25.2%), accounted for the bulk of the observations. Twenty species were recorded 10 times or fewer, partly because of their secretive life-style, as for several *Accipiter* species and Long-tailed Hawk *Urotriorchis macrourus*, or partly because they had a genuinely rare presence in the sub-Sahara north of 5°N (e.g. White-

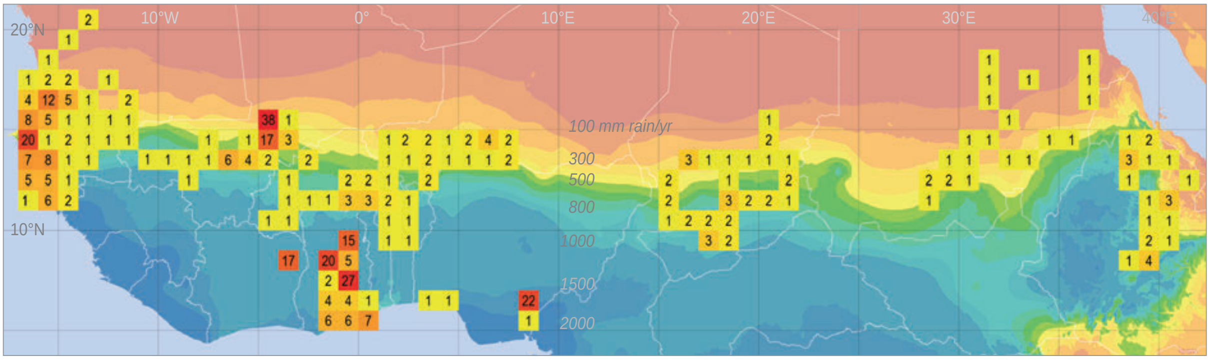

Figure 1. Number of days spent in grid cells (on average 111 × 104 km) across the sub-Sahara in 1996–2019, against a backdrop of rainfall isolines between <100 mm in the north (dark red) and >2000 mm in the south (dark blue).

headed Vulture *Trigonoceps occipitalis*, Eastern Imperial Eagle *Aquila heliaca*, Greater Spotted Eagle *Clanga clanga* and Red-footed Falcon *Falco vespertinus*), or because they had a limited distribution (e.g. Bearded Vulture *Gypaetus barbatus* confined to the Ethiopian Highlands). Sparsely recorded raptor species were less frequently encountered than expected within their distributional range than species that were commonly recorded (Figure 2). Overall, migrants were vastly outnumbered by residents (the latter including intra-African migrants), only 13.4% being migrants among the 22,696 raptors recorded.

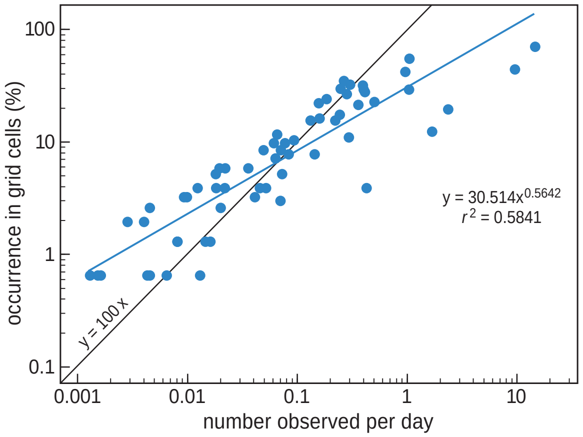

Figure 2. Encounter rate of 62 raptor species (dots) recorded within the grid cells encompassing their distributional range in the sub-Sahara as a function of their abundance, based on data collected in the dry seasons between 1996 and 2019. For raw data see Table S1.

Rainfall and latitudinal variation in distribution

Migratory raptors were mostly concentrated in the driest zones within the sub-Sahara (Table S2). Many species were typically confined to desert (<100 mm rainfall per annum), Sahel and the northern Sudan zone (<500 mm rainfall), notably Montagu's *Circus pygargus* and Pallid Harrier *C. macrourus*, Black Kite, Short-toed Snake Eagle *Circaetus gallicus*, Booted Eagle *Hieraaetus pennatus*, Egyptian Vulture *Neophron percnopterus* and Lesser Kestrel *Falco naumanni* (Figure 3). In the arid zones migrants were about as numerous as residents, but they outnumbered Afrotropical species when rainfall was 200 mm per year or less (Figure 4).

Residents covered a wider range of rainfall zones, were scarce in the most arid zones (<200 mm) and were most common when rainfall exceeded 1000 mm. Ecologically closely related species differed in their latitudinal range, with migratory species wintering north of the residents on average, as in Egyptian Vulture (although those in the East mostly refer to local breeding birds) versus Hooded Vulture, Black Kite versus Yellow-billed Kite and Short-toed Snake Eagle versus Black-chested *Circaetus pectoralis* and Brown Snake Eagle *C. cinereus*.

The highest diversity of raptors was found in the humid Guinean zone, with a mixture of forests, farmland and derived savannah. This diversity was under-recorded given the fact that many species lead a secretive life in cover and are hard to detect. The few raptors observed in deserts and semi-deserts in the dry season were most notably the bird-hunting Lanner Falcon *Falco biarmicus* and the scavenging Egyptian Vulture (mostly in the Afar region in eastern Ethiopia) and Yellow-billed Kite near human settlements, with acridivorous raptors during occasional outbreaks of grasshoppers and locusts (Black Kite and Lesser Kestrel) and species profiting from large floodplains in the Sahel (especially Western Marsh Harrier *Circus aeruginosus*, e.g. in Inner Niger Delta and Lake Chad).

Longitudinal variation in distribution

Migratory raptors within the wider Sahel showed distinct concentrations in the east and west, and least so in the central Sahel (Niger-Chad; Figure 5, Table S3). Overall numbers were highest in the eastern Sahel (notably Montagu's and Pallid Harrier, Short-toed Snake Eagle and Booted Eagle). Black Kite was slightly more common in the west than in the east (Table S3).

Numbers of resident raptor species (including intra-African migrants) were more evenly spread across the width of the sub-Saharan region, except Sudan and Chad where numbers were much smaller. High densities were typically encountered in regions with a dense human population and large cities, as in W Senegal, S Ghana and Ethiopia, where until recently urban scavengers, such as Hooded Vulture and Yellow-billed Kite, abounded.

DISCUSSION

The Gap of Niger-Chad

The vast majority of thermal-using migratory raptors bypass the Mediterranean Sea via Iberia and the Middle and Near East. Species that routinely cross the Mediterranean Sea have low wing loadings, notably harriers, or are powerful fliers (falcons). Facultatively soaring species, such as Osprey and – to a lesser extent – European Honey Buzzard, are known to profit from thermal uplift of the seascape (Duriez *et al.* 2019,

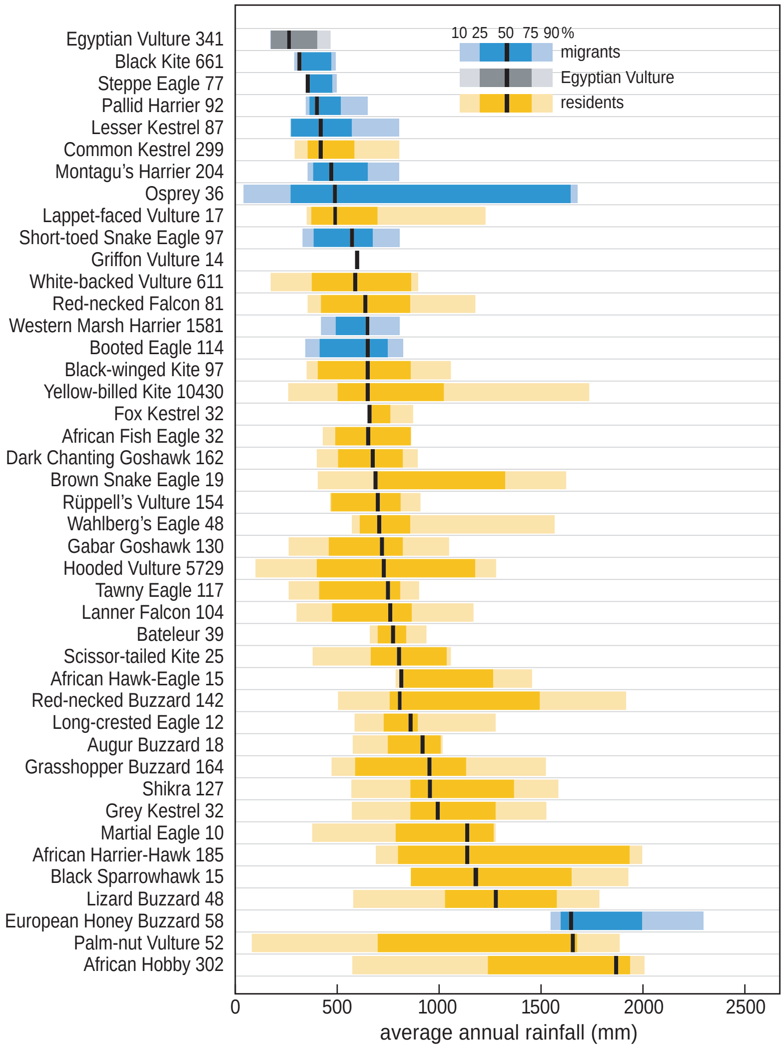

Figure 3. Average annual rainfall for the sites in the sub-Sahara where migratory and resident raptor species (including intra-African migrants) were recorded in this study (with >10 observations in 1996–2019, totals included). Egyptian Vultures are represented by (mostly) residents and some Palearctic migrants.

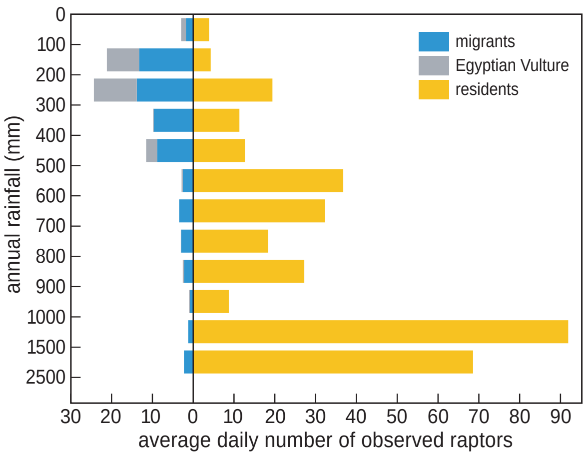

Figure 4. Latitudinal distribution of migratory, intra-African migratory and resident raptors in the dry season in the sub-Sahara (1996–2019), in terms of 100-mm annual rainfall bands (from desert to humid forests), but 500- and 1000-mm bands in the hyper-humid region. Egyptian Vulture mostly relates to residents in Ethiopia), with some Palearctic migrants (mostly in West Africa). Averages based on mean densities in 154 grid cells (Figure 1). ANOVA: migrants NS, $r^2 = 0.09$; Egyptian vulture: NS, $r^2 = 0.09$; residents $r^2 = 0.21$, $P < 0.001$.

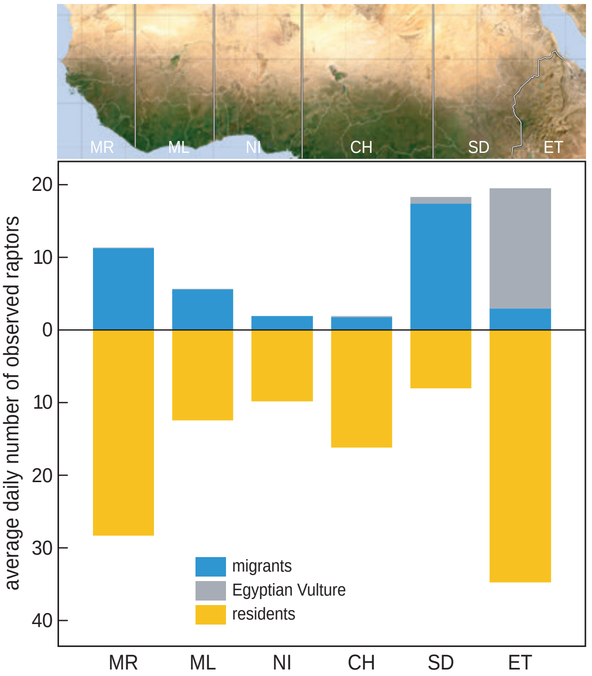

Figure 5. Relative density of migratory and resident raptors across six longitudinal bands in the sub-Sahara (1996–2019); Egyptian Vulture in East Africa mostly refers to local residents. Averages based on mean densities in 118 grid cells where annual rainfall varied between 100 and 1000 mm (Figure 1). ANOVA: migrants $r^2 = 0.11$, $P < 0.02$; Egyptian vulture: $r^2 = 0.21$, $P < 0.001$; residents $r^2 = 0.10$, $P = 0.03$.

Nourani *et al.* 2020) and to perform direct flights across the Central Mediterranean. Soaring raptors using the eastern gateway easily surpass 2 million birds (combining bottlenecks in Caucasus, Middle East and Yemen; Table 1), whereas the western bottleneck in the Gibraltar region probably accounts for less than 400,000 raptors (comprehensive overviews for this site are lacking, or make use of outdated, anecdotal or relative data; e.g. de Juana & Garcia 2015, Panuccio *et al.* 2021).

The higher number of migratory raptors encountered during our surveys in the eastern sub-Sahara compared to the western half, and the relative scarcity of Palearctic raptors in Niger-Chad (as found in passerines; Zwarts *et al.* 2023c), are coincident with the respective hinterlands and general migration pattern. It furthermore suggests that movements from West Africa eastwards or from East Africa westwards are limited in scope. Several species entering Africa in the east continue migration into southern Africa, as do Common Buzzard *Buteo buteo vulpinus*, Lesser Spotted Eagle *Clanga pomarina*, Red-footed Falcon and Lesser Kestrel. These species – except Lesser Kestrel that has a large wintering population in West Africa (with 24,000 at a single roost in Senegal in 2007; Rodriguez *et al.* 2009) – were sparsely recorded during our surveys.

The discrepancy between the small numbers of Eurasian Egyptian Vultures entering Africa via the eastern bottleneck and the spike in occurrence in eastern Ethiopia hinges on the local population in mainly the Afar region, which numbered at least 1082–1424 birds in 2009–2013 (Arkumarev *et al.* 2014, McGrady *et al.* 2018). In Ethiopia we recorded 261 Egyptian Vultures in 1–24 February 2019, mostly in the region of Mekele-Logya where a single communication tower at 13.315°N and 39.982°E held 83 roosting birds on 17 February. A total of 153 out of 261 birds were aged: 99 (sub)adults, 25 immature (second and third plumage) and 29 juveniles. The proportion of 19% juveniles was much lower than the 32% among c. 1282 (90% age-identified of 1424) birds in the Afar region in 2009–2013 (Arkumarev *et al.* 2014).

The case of the harriers

Raptor species with low wing-loading, notably harriers, are known to cross the Mediterranean Sea in a broad front. An assessment of systematic counts across the northern Mediterranean during autumn migration of Montagu's Harriers suggested a preponderance of migrants crossing via Spain (23%), Aegean Archipelago (22%) and the Middle East (52%), but relatively few taking the Central Mediterranean (Trierweiler & Bijlsma 2010). The combined tracks of 145 birds equipped with transmitters partly confirmed the concentrated passage of western European Montagu's Harriers via SE Spain, but eastern European breeding

Table 1. Maximum count of long-distance migratory raptor species in autumn at bottlenecks in the Western Mediterranean (Gibraltar region) and in the East Mediterranean plus the Arabian Peninsula (Batumi^{1}, Belen Pass^{2}, Suez^{3}, Bab el Mandeb^{4}; after Jobson *et al.* 2021, Panuccio *et al.* 2021), known to winter largely in the sub-Sahara excluding humid forests.

Species	West	East
Egyptian Vulture *Neophron percnopterus*	4000	1000^{3}
Short-toed Snake Eagle *Circaetus gallicus*	12,000	13,000^{2}
Booted Eagle *Hieraaetus pennatus*	31,000	7370^{1}
Steppe Eagle *Aquila nipalensis*	0	141,000^{3,4}
Western Marsh Harrier *Circus aeruginosus*	8000	6500^{1}
Montagu's Harrier *Circus pygargus*	6500	7000^{1}
Pallid Harrier *Circus macrourus*	0	1500^{1}
Black Kite *Milvus migrans*	224,000	221,000^{1}

birds crossed the Mediterranean via Corsica-Sardinia, the Italian mainland and the Aegean Sea. Eastern European birds ended up in the central Sudano-Sahel (with a concentration in the drainage basin of the Sokoto River in northern Nigeria), from where the birds redistributed themselves westwards in the course of the dry season (Schlaich & Klaassen in Panuccio *et al.* 2021: 152–159). Montagu's Harriers have not yet been tagged with transmitters in the Russian breeding range between Belarus and Kazakhstan (birds from Kazakhstan were found to winter in India; Panuccio *et al.* 2021: 155), and their distribution in Africa is not yet clear. Our observations suggest wintering grounds in eastern Africa, without much of a westward redistribution into the central Sudano-Sahel.

Pallid Harriers were largely confined to the eastern Sudano-Sahel (in Chad-Sudan-Ethiopia), as expected from the position of their Central Asian breeding grounds. Although telemetry showed some birds (2 out of 6; Limiñana *et al.* 2015) to shift their midwinter distribution from East to Central Sahel, our data indicate that Pallid Harriers are sparse west of Chad (Table S3). Orthopterans and rodents constitute major food resources, but granivorous birds may become an alternative food when such prey are scarce (Buij 2013). Within the Sudano-Sahel seed-eating birds were found to be most abundant in Chad, but they have declined significantly in West Africa (Zwarts *et al.* 2018, 2023c, 2023d). Numbers of Red-billed Quelea *Quelea quelea*, for example, an important prey of Pallid Harriers in northern Cameroon (Buij 2013), have crashed by 47–85% between the 1960s and 2010s, and other granivorous birds (at least in NW Senegal) by 39–97% (Zwarts *et al.* 2023d). When orthopterans and rodents are scarce, West Africa has not much to offer Pallid Harriers in the form of large flocks of granivorous birds, except locally near wetlands (notably Waza Logone in the Lake Chad Basin, a local magnet for Palearctic raptors; Thiollay 1978b, Buij & Croes 2013).

Western Marsh Harriers were typically concentrated within or near floodplains and other wetlands, especially in the delta and valley of the Senegal River, the Inner Niger Delta in Mali and Keta Lagoon in S Ghana (Zwarts *et al.* 2009). Of sex-identified adult Western Marsh Harriers, 98% of 95 females were recorded in wetlands, compared to 76% of 246 males; the latter were frequently recorded in savannah and cropland. Lake Chad is known to also hold a substantial wintering population (Buij *et al.* 2012), where Western Marsh Harrier is the most common Palearctic raptor species in the inundation zone with a mean dry season abundance of 23 birds per 100 km transect (Buij & Croes 2014).

Latitudinal distribution and rainfall

The latitudinal separation between migrants and residents, with the former residing in the (semi-)arid strata north of the residents, showed little overlap between both groups of raptors (as already noted by Thiollay 1978a, 1989). Our survey methods were inadequate to show seasonal latitudinal movements in the course of the dry season. A gradual southward shift in conjunction with declining food availability in the arid and semi-arid Sahel and Sudan zone has been shown for Montagu's Harrier between September and April (Trierweiler *et al.* 2013, Schlaich *et al.* 2016). Similar shifts have been noted for most Afrotropical and Palearctic raptor species (Brown 1970, Elgood *et al.* 1972). In very poor rainy seasons, as in 1972, birds left the Sahara and Sahel earlier, and their movements extended 200–300 km farther to the south, than in normal years (Thiollay 1978a). During our surveys, mostly in December–February, halfway through the dry season, local Afrotropical raptors had already moved into the more humid regions of the sub-Sahara, so that residents vastly outnumbered migrants south of 500 mm rainfall. Within the zone of overlap, residents were largely confined to urbanized regions (notably Yellow-billed Kite, with smaller numbers attending large wetlands such as the Inner Niger Delta, where breeding had commenced and food consisted of fishes, amphibians, rodents and offal (Bijlsma *et al.* 2005). The migratory Black Kite roamed the savannahs and farmland in small flocks, their movements being itinerant in response to local outbreaks of grasshoppers and locusts. Long-distance displacements were at great height (Thiollay 1978a).

Whether the latitudinal separation hinges on competition for resources between migrants and residents (as alluded to by Thiollay 1978a), or is the result of differences in diet and the concurrent habitat choice, or a combination of these and other factors, is unknown. Local studies showed clear differences in preferred habitats in winter, with Palearctic migrants occupying savannahs and exploiting cropland and rice fields after harvest (rodents and lizards), whereas residents profited from habitat fragmentation in the humid Guinean zones where a wider range of habitats, ecozones and foraging niches are available (Buij *et al.* 2013, Rodrigues *et al.* 2020). The semi-arid regions provide fewer contrasts between habitats, and in terms of food are especially productive regarding seed (attracting seed-eaters, and hence passerine-hunting raptors) and locusts and grasshoppers (attracting acridivorous raptors, like falcons, kites and harriers).

Shifting prospects

In the sub-Sahara, a study period of almost a quarter of a century is sufficiently long for large changes in climate and land use to occur. Well before our study took place, Thiollay (2006) had demonstrated vast declines in most raptor species in the Sudano-Sahelian zone of Mali, Burkina Faso, Niger and N Cameroon between 1969–1973 and 2003–2004. African vultures and eagles showed particularly steep declines in the late 1900s, but smaller African species were also affected (and Palearctic migrants less so). Outside protected zones declines were rampant. This general trend has largely continued unabated in later decades, notably in vultures (Di Vittorio *et al.* 2018, Henriques *et al.* 2020). Our study was not designed to monitor trends, but it is likely that within the quarter of a century covered by our survey raptors have been the subject of further changes, not just in vultures and eagles but also in medium-sized and small raptor species. Apart from declines, these changes also include some increases related to improving fortunes of some Palearctic raptor species. For example, juveniles and immatures of the booming Iberian population of Griffon Vultures *Gyps fulvus* began to winter in Senegal and at present locally outnumber White-backed Vultures (Ouweneel 2021). Similarly, the population of western Palearctic Osprey has increased from 5500 in the 1980s to 9500–11,500 pairs in the early 2000s (Schmidt-Rothmund *et al.* 2014), which must have resulted in higher numbers wintering in West Africa.

At the same time, several Palearctic raptor species are in the process of shifting their wintering range to the north within Europe and Africa, as evident in Common Buzzard *Buteo buteo*, for example, which de

Outbreaks of locusts, like this flock of *Schistocerca gregaria* alighting from *Acacia tortilis* in semi-arid Mauritania (18.970°N, 15.314°W) on 27 January 2017, and roving grasshopper bands are lodestones to raptors, in this particular instance mostly Black Kites, Eurasian Kestrels and Lesser Kestrels.

facto has ceased to cross the Straits of Gibraltar in spring. This is attributed to a decreased migratory tendency in European breeding birds since the 1970s (Bensusan *et al.* 2007, Holte *et al.* 2017). Shifts are also evident among Palearctic-African migrants which until recently almost exclusively wintered in Africa. Black Kites are now routinely wintering in substantial numbers in southern Europe, although partly consisting of the eastern *Milvus migrans lineatus* (Zwarts *et al.* 2023d), as are Western Marsh Harriers and Booted Eagles (also in substantial numbers, e.g. 180–220 Booted Eagles on just Sicily in winter 2022; Surdo *et al.* 2022). To a smaller extent, the same tendency is noted in Pallid Harrier (Ollé *et al.* 2015) and Osprey (Martín *et al.* 2019).

Of African raptors, apart from vultures and some eagles, much less is known regarding trends, migratory shifts or shifting breeding and wintering ranges. The overall decline among seed-eating passerines in savannah-like habitats, as quantified by Zwarts *et al.* (2018, 2023a, 2023b, 2023d), has resulted in a substantial decline in food supply of bird-eating raptors. On the other hand, the conversion of savannah into farmland and floodplains into rice fields will, temporarily at least, favour rodent-eating raptors (Anadon *et al.* 2010, Buij *et al.* 2012, 2013, Augiron *et al.* 2015, Shaw *et al.* 2019). The overall effect of changing landscapes on raptors in the sub-Sahara, especially on small and medium-sized species, is presently an enigma but in the long run augurs large changes (Amar *et al.* 2018).

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SAMENVATTING

In vijftien winters tussen 1996 en 2019 werden 466 dagen in het veld doorgebracht in veertien landen ten zuiden van de Sahara en ten noorden van 5°N, in regencijfers uitgedrukt van <100 mm tot 2650 mm regenval per jaar. Het onderzoek bestreek de volle breedte van Afrika, van Atlantische Oceaan tot Rode Zee. Het veldwerk was niet per se gericht op roofvogels, maar deze werden niettemin zoveel mogelijk genoteerd tijdens autotochten, *in situ* veldwerk aan andere soorten en tijdens een gestratificeerd-random onderzoek naar bomen en vogels van West- tot Oost-Afrika. Het allegaartje van 22.696 waarnemingen van 62 soorten roofvogels werd ingedikt tot aantal waarnemingen per gradenhok (1° breedte- × 1° lengtegraad, 111 × c. 104 km), omgerekend naar het aantal waargenomen per dag doorgebracht in het betreffende hok. Van 154 hokken was aldus informatie beschikbaar, waarbij in 54% van de hokken slechts één dag werd gekeken (en in negen hokken >10 dagen). In de jaren van onderzoek lag de regenval in de voorafgaande natte tijd acht maal rond het gemiddelde berekend over 1950–2000, vijf maal er (duidelijk) onder en twee maal er duidelijk boven. De verspreiding, dichtheid en diversiteit van roofvogels was mager in de aride en semi-aride gebieden van zuidelijke Sahara, Sahel en Soedanzone. Juist in deze band met <800 mm regenval per jaar zaten verreweg de meeste Palearctische trekvogels. Meer naar het zuiden werden die uitgesproken schaars, en in de meest humide zone (>1500 mm regenval per jaar) werd slechts één Palearctische soort vastgesteld, de Wespendief *Pernis apivorus*. Op het totale aantal waargenomen roofvogels namen de Euraziatische soorten maar 13.4% voor hun rekening (vooral Zwarte Wouw *Milvus migrans* en Bruine Kiekendief *Circus aeruginosus*, die laatste sterk gebonden aan vloedvlaktes, rivierdalen en -delta's); de rest betrof Afrotropische roofvogels inclusief intra-Afrikaanse trekvogels. De Afrikaanse roofvogels waren schaars in de droge gebieden en hun dichtheid en verscheidenheid namen sterk toe naarmate de regenval toenam. De Afrotropische Geelsnavelwouw *Milvus aegyptius* en Kapgier *Necrosyrtes monachus* namen resp. 46.0% en 25.2% van alle roofvogels voor hun rekening. Ook over de breedte van de sub-Sahara bleken roofvogels verre van willekeurig verspreid voor te komen. Palearctische soorten hielden zich vooral in het Westen of Oosten op (binnen de zone met 100 tot 1000 mm regenval), overeenkomend met de twee flessenhalzen die de bulk van de thermiek gebruikende Euraziatische roofvogels gebruiken (resp. Gibraltar en Turkije-Kaukasus-Midden-Oosten en Arabische Schiereiland. De schaarste aan Palearctische roofvogels in de centrale Sahel (Mali-Niger-Tsjaad-Soedan) laat zien dat verhoudingsgewijs weinig roofvogels zich vanuit het westen of oosten naar het hart van de Sahel bewegen. Bij de Afrikaanse soorten werd een minder prominente 'leegte' in de centrale Sahel opgemerkt. Het materiaal was van onvoldoende kwaliteit om iets te kunnen zeggen over habitatgebruik, invloed van voedselaanbod op verspreiding en dichtheid en aantalsveranderingen in de loop van de tijd. Maar zeker is dat de door ons waargenomen roofvogelfauna een slap aftreksel is van wat de eerste helft van de vorige eeuw heeft laten zien. Ook in de sub-Sahara, net als in het achterland van de aldaar overwinterende Palearctische soorten, gaan de veranderingen snel.

RÉSUMÉ

Pendant les 15 hivers entre 1996 à 2019 et en 466 jours d'observations de terrain effectués dans 14 pays différents au sein de la bande comprise entre le Sud du Sahara et la latitude 5°N, nous n'avons observé qu'une seule espèce d'origine paléarctique : la Bondrée apivore *Pernis apivorus*. Par ailleurs, les espèces paléarctiques n'ont représenté que 13,4% du nombre total de rapaces observés. Il s'agit principalement du Milan noir *Milvus migrans* et du Busard des roseaux *Circus aeruginosus*, ce dernier étant fortement lié aux estrans, aux vallées fluviales et aux deltas. Les rapaces sédentaires et les migrateurs intra-africains sont donc dominants. Les rapaces africains sont rares dans les zones arides et leur densité et diversité augmentent fortement avec l'accroissement des précipitations. Deux espèces sédentaires, le Milan d'Afrique *Milvus aegyptius* et le Vautour charognard *Necrosyrtes monachus*, représentent respectivement 46,0 % et 25,2 % de tous les rapaces. Nous avons également constaté que la répartition des rapaces est loin d'être aléatoire sous les latitudes subsahariennes. Les espèces paléarctiques sont principalement présentes aux extrémités Ouest et Est de la zone (avec 100 à 1000 mm précipitation per an), ce qui correspond aux deux principaux axes migratoires qui empruntent respectivement le Delta de Gibraltar à l'Ouest, le Caucase et le Moyen-Orient à l'Est. La rareté des rapaces paléarctiques dans le Sahel central (Mali-Niger-Tchad-Soudan) montre que peu d'entre eux se déplacent de l'Ouest ou de l'Est vers le cœur du Sahel. Pour les espèces africaines, la zone de moindre densité dans le centre du Sahel est moins étendue. La qualité des données collectées ne permet pas de tirer de conclusions sur l'utilisation de l'habitat, l'influence de la disponibilité alimentaire sur la répartition des rapaces ou sur l'évolution dans le temps de leur densité et de leur nombre. Mais ce qui est certain, c'est que les populations de rapaces que nous avons observées ne représentent qu'une fraction de ce qu'elles étaient lors de la première moitié du siècle dernier. Les changements sont rapides en Afrique subsaharienne, comme dans les pays d'origine des espèces paléarctiques qui y hivernent.

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SUPPLEMENTARY MATERIAL

Table S1. Number of raptors observed in the sub-Sahara in 15 dry seasons between 1996 and 2019, subdivided in migrants (blue), residents (yellow) and the partly Palearctic Egyptian Vulture (grey), with % observed >100 m, % of 154 grid cells (1° longitude × 1° latitude) occupied, average number observed per field day, average group size and average annual rainfall (mm) for all sites where the species was observed.

Species		*n*	>100m%	% grid	*n*/day	*n*/obs	avg. rain
Osprey	*Pandion haliaetus*	36	14	12	0.07	1.0	727
Black-winged Kite	*Elanus caeruleus*	97	5	27	0.28	1.4	769
Scissor-tailed Kite	*Chelictinia riocourii*	25	16	8	0.08	1.2	602
African Harrier-Hawk	*Polyboroides typus*	185	3	16	0.16	1.3	1575
Palm-nut Vulture	*Gypohierax angolensis*	52	4	8	0.05	1.3	1501
Bearded Vulture	*Gypaetus barbatus*	4	0	1	0.02	1.3	943
Egyptian Vulture	*Neophron percnopterus*	341	3	12	1.69	3.7	310
European Honey Buzzard	*Pernis apivorus*	58	12	6	0.04	1.1	1613
African Cuckoo-Hawk	*Aviceda cuculoides*	8	0	4	0.01	1.1	1158
Hooded Vulture	*Necrosyrtes monachus*	5729	38	44	9.60	11.5	1169
White-backed Vulture	*Gyps africanus*	611	24	29	1.04	3.5	632
Rüppell's Vulture	*Gyps rueppelli*	154	48	11	0.30	2.9	629
Griffon Vulture	*Gyps fulvus*	14	14	1	0.00	4.7	588
White-headed Vulture	*Trigonoceps occipitalis*	9	0	4	0.02	1.5	720
Lappet-faced Vulture	*Torgos tracheliotos*	17	12	6	0.02	1.5	638
Short-toed Snake Eagle	*Circaetus gallicus*	97	13	30	0.25	1.1	606
Beaudouin's Snake Eagle	*Circaetus beaudouini*	6	0	4	0.02	1.0	816
Black-chested Snake Eagle	*Circaetus pectoralis*	2	100	1	0.01	1.0	802
Brown Snake Eagle	*Circaetus cinereus*	19	21	10	0.08	1.0	876
Western Banded Snake Eagle	*Circaetus cinerascens*	6	0	2	0.00	1.2	1356
Bateleur	*Terathopius ecaudatus*	39	11	10	0.09	1.2	891
Martial Eagle	*Polemaetus bellicosus*	10	10	3	0.01	1.1	1029
Long-crested Eagle	*Lophaetus occipitalis*	12	8	5	0.02	1.0	995
Lesser Spotted Eagle	*Clanga pomarina*	6	33	1	0.01	2.0	738
Greater Spotted Eagle	*Clanga clanga*	2	50	1	0.01	1.0	545
Wahlberg's Eagle	*Hieraaetus wahlbergi*	48	16	8	0.07	1.4	1278
Booted Eagle	*Hieraaetus pennatus*	114	6	32	0.30	1.1	585
Tawny Eagle	*Aquila rapax*	117	21	23	0.50	1.4	729
Steppe Eagle	*Aquila nipalensis*	77	25	4	0.43	2.8	454
Eastern Imperial Eagle	*Aquila heliaca*	1	0	1	0.01	1.0	750
Verreaux's Eagle	*Aquila verreauxii*	2	0	1	0.01	2.0	574

Table S1. Continued.

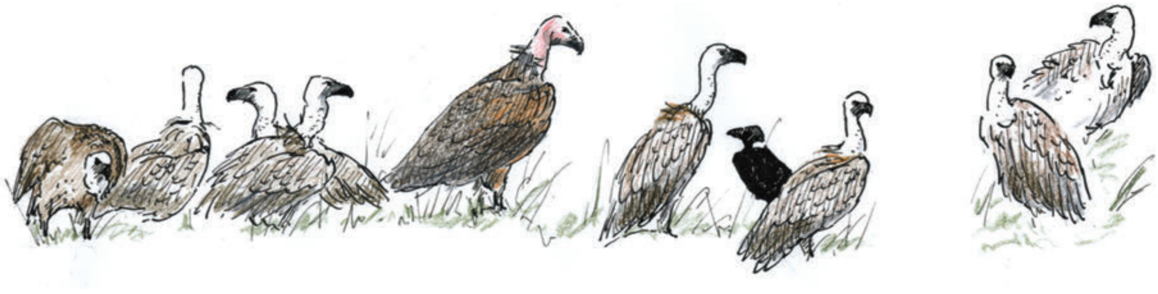
Species		*n*	>100m%	% grid	*n*/day	*n*/obs	avg. rain
African Hawk-Eagle	*Aquila spilogaster*	15	20	7	0.06	1.2	1034
Lizard Buzzard	*Kaupifalco monogrammicus*	48	0	10	0.06	1.2	1184
Gabar Goshawk	*Micronisus gabar*	130	2	32	0.40	1.1	704
Dark Chanting Goshawk	*Melierax metabates*	162	3	28	0.41	1.1	664
Long-tailed Hawk	*Urotriorchis macrourus*	1	0	1	0.00	1.0	1170
African Goshawk	*Accipiter tachiro*	7	0	3	0.01	1.0	1406
Shikra	*Accipiter badius*	127	2	24	0.18	1.2	1063
Red-thighed Sparrowhawk	*Accipiter erythropus*	4	0	1	0.00	1.0	1059
Ovambo Sparrowhawk	*Accipiter ovampensis*	8	0	4	0.05	1.1	898
Eurasian Sparrowhawk	*Accipiter nisus*	1	0	1	0.00	1.0	706
Black Sparrowhawk	*Accipiter melanoleucus*	15	0	3	0.00	1.1	1650
Western Marsh Harrier	*Circus aeruginosus*	1581	2	42	0.96	2.2	425
Pallid Harrier	*Circus macrourus*	92	12	21	0.36	1.0	456
Montagu's Harrier	*Circus pygargus*	204	3	29	0.40	1.1	509
Black Kite	*Milvus migrans*	661	36	19	2.37	5.2	463
Yellow-billed Kite	*Milvus aegyptius*	10430	35	70	14.60	10.3	802
African Fish Eagle	*Haliaeetus vocifer*	32	9	6	0.02	1.2	689
Grasshopper Buzzard	*Butastur rufipennis*	164	3	18	0.24	1.8	1027
Long-legged Buzzard	*Buteo rufinus*	7	14	3	0.04	1.0	405
Common Buzzard	*Buteo buteo vulpinus*	5	0	3	0.02	1.0	703
Red-necked Buzzard	*Buteo auguralis*	142	3	16	0.13	1.3	1491
Augur Buzzard	*Buteo augur*	18	39	5	0.07	1.0	833
Lesser Kestrel	*Falco naumanni*	87	18	16	0.22	1.0	560
Common Kestrel	*Falco tinnunculus*	299	5	55	1.05	1.9	482
Fox Kestrel	*Falco alopex*	32	6	4	0.05	1.1	620
Grey Kestrel	*Falco ardosiaceus*	32	3	3	0.07	1.5	1233
Red-necked Falcon	*Falco chicquera*	81	0	22	0.16	1.2	596
Red-footed Falcon	*Falco vespertinus*	4	0	1	0.00	1.5	1050
African Hobby	*Falco cuvierii*	302	1	8	0.14	1.2	1758
Lanner Falcon	*Falco biarmicus*	104	2	35	0.27	1.2	837
Peregrine Falcon	*Falco peregrinus*	3	0	2	0.00	1.0	640

Table S2. Number of raptors observed per day (for species with >10 records) in the sub-Sahara subdivided per 100-mm rainfall zones (0 = 0–100 mm … 1000 = 1000–1500, 1500 = 1500–2500/annum). Palearctic migrants in yellow, African species in blue and Egyptian Vulture in grey (mixture of both). The last line gives the average number of species observed per day. *P* = statistical significance of the difference between the twelve rainfall zones: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one-way ANOVA).

Species	0	100	200	300	400	500	600	700	800	900	1000	1500	avg	*P*
Osprey	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1	***
Black-winged Kite	0.0	0.0	0.4	0.2	0.4	0.1	0.2	0.1	0.6	0.0	0.7	0.0	0.3	
Scissor-tailed Kite	0.0	0.0	0.0	0.2	0.0	0.1	0.4	0.2	0.0	0.0	0.0	0.0	0.1	
African Harrier-Hawk	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.3	0.0	0.5	0.8	0.2	*
Egyptian Vulture	1.1	7.9	10.6	0.1	2.7	0.3	0.0	0.1	0.3	0.2	0.0	0.0	1.7	
Hooded Vulture	0.0	0.8	0.1	0.8	1.2	5.8	11.2	2.8	9.3	0.6	44.8	20.9	9.6	***
White-backed Vulture	0.1	0.5	0.6	1.7	0.7	2.0	0.9	1.6	1.5	0.3	0.7	0.9	1.0	
Rüppell's Vulture	0.0	0.0	0.0	0.1	0.4	0.3	0.0	1.1	0.7	0.0	0.1	0.0	0.3	
Short-toed Snake Eagle	0.0	0.1	0.3	0.6	0.2	0.4	0.9	0.1	0.3	0.0	0.0	0.1	0.2	***
Brown Snake Eagle	0.0	0.0	0.0	0.1	0.0	0.0	0.2	0.1	0.4	0.0	0.0	0.1	0.1	
Bateleur	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.3	0.1	0.0	0.0	0.1	
Wahlberg's Eagle	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.2	0.0	0.1	0.0	0.1	0.1	**
Booted Eagle	0.1	0.0	0.1	0.5	0.7	0.2	0.6	0.2	0.4	0.0	0.1	0.1	0.3	**
Tawny Eagle	0.0	0.1	0.0	0.2	0.3	0.4	0.2	1.3	2.4	0.0	0.1	0.0	0.5	*
Steppe Eagle	0.0	0.0	0.0	2.3	0.8	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.4	
African Hawk-Eagle	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.3	0.1	
Gabar Goshawk	0.1	0.0	0.1	0.1	0.4	0.8	1.5	0.2	0.7	1.1	0.3	0.0	0.4	***
Dark Chanting Goshawk	0.0	0.0	0.1	0.3	0.4	0.7	0.6	0.7	1.2	0.1	0.2	0.0	0.4	*
Shikra	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.4	0.8	0.6	0.0	0.2	***
Western Marsh Harrier	0.0	0.3	1.0	2.7	1.0	0.7	1.3	0.4	1.2	0.4	0.5	0.9	1.0	
Pallid Harrier	0.0	0.1	0.5	1.3	0.8	0.4	0.1	0.1	0.2	0.0	0.0	0.0	0.4	**
Montagu's Harrier	0.0	0.4	0.3	1.6	0.4	0.3	0.3	0.2	0.1	0.1	0.2	0.1	0.4	***
Black Kite	1.3	11.8	11.2	0.2	4.4	0.3	0.0	1.0	0.0	0.4	0.2	0.0	2.4	
Yellow-billed Kite	3.3	1.0	16.9	4.7	6.1	25.4	14.5	7.7	7.8	4.5	41.4	42.1	14.6	*
African Fish Eagle	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	
Grasshopper Buzzard	0.1	0.0	0.1	0.0	0.1	0.1	0.1	0.4	0.2	0.5	1.0	0.0	0.2	
Red-necked Buzzard	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.2	0.1	0.0	0.4	0.5	0.1	
Augur Buzzard	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.1	0.2	0.2	0.0	0.1	
Lesser Kestrel	0.3	0.6	0.2	0.3	0.5	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.2	
Common Kestrel	0.3	1.4	1.1	2.4	2.2	0.4	1.2	0.6	0.4	0.4	0.3	0.2	1.1	***
Fox Kestrel	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.2	0.0	0.0	0.0	0.1	
Red-necked Falcon	0.0	0.0	0.1	0.2	0.2	0.1	0.3	0.2	0.2	0.0	0.2	0.1	0.2	
African Hobby	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3	2.0	0.1	*
Lanner Falcon	0.1	0.4	0.0	0.2	0.1	0.2	0.4	0.4	0.3	0.2	0.4	0.1	0.3	
Residents	3.9	4.3	19.4	11.4	12.7	36.8	32.4	18.4	27.2	8.8	92.0	68.6	29.9	***
Migrants	1.8	13.3	13.8	9.7	8.9	2.6	3.4	3.0	2.3	0.9	1.2	2.2	5.5	
no. of species	2.4	3.5	7.2	8.3	7.3	8.7	9.8	9.8	10.1	5.5	12.0	7.7	8.4	***

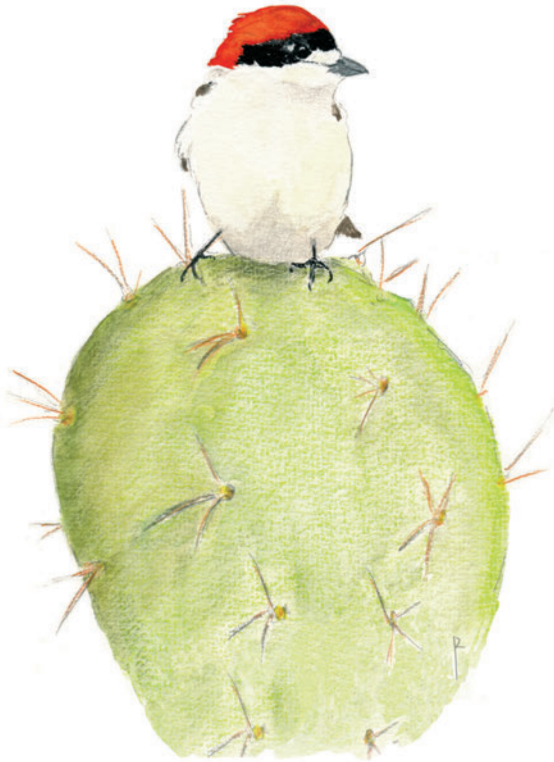
Table S3. Number of raptors observed per day (species with >10 records) in the sub-Sahara subdivided per longitudinal zone (Mauritania, Mali, Niger, Chad, Sudan, Ethiopia; see Figure 4). Palearctic migrants in orange, African species in blue and Egyptian Vulture in grey (mixture of both). The last line gives the average number of species observed per day. P = statistical significance of the difference between the six zones: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one-way ANOVA).

Species	MR	ML	NI	CH	SD	ET	Total	*P*
Osprey	0.2	0.0	0.0	0.0	0.1	0.0	0.1	
Black-winged Kite	0.2	0.3	0.5	0.1	0.3	0.2	0.3	
Scissor-tailed Kite	0.0	0.2	0.1	0.1	0.0	0.0	0.1	
African Harrier-Hawk	0.2	0.2	0.2	0.2	0.0	0.1	0.2	
Egyptian Vulture	0.1	0.1	0.0	0.1	1.1	15.4	1.7	***
Hooded Vulture	11.6	23.8	7.2	2.3	0.5	5.8	9.6	
White-backed Vulture	1.7	0.2	0.2	2.8	0.2	1.4	1.0	***
Rüppell's Vulture	0.2	0.0	0.0	0.0	0.0	2.6	0.3	***
Short-toed Snake Eagle	0.3	0.3	0.1	0.2	0.5	0.2	0.2	
Brown Snake Eagle	0.1	0.0	0.1	0.2	0.1	0.0	0.1	
Bateleur	0.0	0.0	0.0	0.5	0.0	0.0	0.1	***
Wahlberg's Eagle	0.0	0.0	0.1	0.3	0.0	0.1	0.1	*
Booted Eagle	0.1	0.3	0.3	0.2	0.5	0.5	0.3	
Tawny Eagle	1.0	0.1	0.0	0.8	0.0	1.6	0.5	*
Steppe Eagle	0.0	0.0	0.0	0.0	3.0	0.4	0.4	*
African Hawk-Eagle	0.2	0.0	0.1	0.0	0.0	0.0	0.1	
Gabar Goshawk	0.3	0.6	0.3	0.8	0.3	0.1	0.4	
Dark Chanting Goshawk	0.3	0.2	0.2	1.3	0.0	0.9	0.4	***
Shikra	0.1	0.3	0.2	0.4	0.1	0.0	0.2	
Western Marsh Harrier	1.0	2.5	0.6	0.2	0.5	0.5	1.0	*
Pallid Harrier	0.1	0.0	0.0	0.4	1.8	0.4	0.4	***
Montagu's Harrier	0.3	0.2	0.3	0.2	1.4	0.2	0.4	***
Black Kite	7.2	0.1	0.1	0.2	4.5	0.3	2.4	
Yellow-billed Kite	14.0	21.9	18.3	4.4	4.4	23.2	14.6	
African Fish Eagle	0.0	0.0	0.0	0.0	0.0	0.1	0.0	
Grasshopper Buzzard	0.2	0.6	0.2	0.2	0.1	0.0	0.2	
Red-necked Buzzard	0.1	0.3	0.2	0.1	0.0	0.0	0.1	
Augur Buzzard	0.0	0.0	0.0	0.0	0.0	0.7	0.1	***
Lesser Kestrel	0.4	0.0	0.1	0.3	0.6	0.0	0.2	
Common Kestrel	0.8	0.1	1.5	1.6	1.6	1.0	1.1	***
Fox Kestrel	0.0	0.0	0.1	0.1	0.0	0.1	0.1	
Red-necked Falcon	0.1	0.2	0.3	0.2	0.1	0.0	0.2	
African Hobby	0.0	0.1	0.6	0.0	0.0	0.0	0.1	
Lanner Falcon	0.1	0.6	0.3	0.2	0.2	0.2	0.3	**
Residents	31.4	49.0	30.3	16.2	7.6	38.6	29.9	*
Migrants	9.4	3.7	1.6	1.8	13.2	2.9	5.5	**
no. of species	9.0	10.4	6.3	9.0	5.6	10.2	8.4	



Revisiting published distribution maps and estimates of population size of landbirds breeding in Eurasia and wintering in Africa

Leo Zwarts[1,*], Rob G. Bijlsma[2] & Jan van der Kamp[1]



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For 30 Afro-Palearctic bird species, the size of the breeding population in Europe is compared to the numbers wintering in the northern dry belt of Africa south of the Sahara, the Sahel. As the distribution of most of these species is wider than just Europe and the Sahel, the estimates are adjusted based on known breeding and wintering ranges. Eight Palearctic species recorded sparsely in the Sahel appeared to winter mainly beyond our delimited study area and so were excluded from the analyses. Species with a wide breeding distribution invariably had larger breeding than wintering ranges, but the opposite was true for species with limited breeding distributions. This outcome was at least partly due to underestimation of the breeding range of species with a small breeding area and an overestimation of the wintering range in species having a large wintering area. Our systematic survey of the Sahel revealed that bird species wintering in the northern and driest part of the Sahel actually wintered further north than indicated on published distribution maps, whereas species from the southern, humid zone wintered further south. The Sahel surveys indicate that the total population size of species breeding mainly in southern Europe, such as Masked Shrike *Lanius nubicus*, Western Bonelli's Warbler *Phylloscopus bonelli*, Subalpine Warbler *Curruca iberiae* + *C. subalpina* + *C. cantillans* and Rüppell's Warbler *Curruca ruppeli*, have so far been underestimated, but that population sizes of Common Redstart *Phoenicurus phoenicurus* and Common Whitethroat *Curruca communis* have probably been overestimated.

Key words: Sahel, bird distribution, bird population estimates

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The Palearctic-Afrotropical migration system is one of the largest avian migration systems on Earth (Newton 2008). Altogether 215 bird species from the boreal and temperate zone annually cross the Sahara or the Arabian Desert further east to spend the northern winter in sub-Saharan Africa (Moreau 1972, Curry-Lindahl 1981, Walther & Rahbek 2002, Newton 2008). Taxonomic splits subsequent to these references have increased the total beyond 215. For the most common Afro-Palearctic migrant, Willow Warbler *Phylloscopus trochilus*, the breeding area stretches across the whole of Eurasia as far as easternmost Siberia, from which they undertake twice yearly a 13,000 km flight between eastern Siberia and southern Africa, using the eastern Sahel and Ethiopia as stopover sites (Sokolovskis *et al.* 2018). The most spectacular transcontinental migration is that of the remotest population of Northern Wheatear *Oenanthe oenanthe*, which from Alaska migrates east across Asia to spend the northern winter in Sudan (Bairlein *et al.* 2012). The Northern Wheatear populations of eastern Canada and Greenland fly southeast across the North Atlantic to Mauritania, which lies some 5000 km west of Sudan (Delingat *et al.* 2011, Bairlein *et al.* 2012). Adding the migrant populations of

Northern Wheatear breeding in Europe and Asia, a total of some 100 million might be found wintering in African drylands south of the Sahara Desert (BirdLife International 2022).

Moreau (1972) speculated that some five billion migratory birds annually departed Eurasia for sub-Saharan Africa in winter. Bruno Bruderer (in Newton 2008) estimated that 3.5–4.5 billion migrants cross just the Mediterranean, to which should be added unknown numbers from Asia crossing Arabia. For 68 migratory species of passerines and near-passerines breeding in Europe west of the Urals, 1.5 to 2.9 billion are estimated to spend the northern winter south of the Sahara (Hahn *et al.* 2009), but that total omits the migrants from Asia. Thus, half a century after his daring proposal, Moreau's 1972 rough guess of five billion migrants has been validated, not disproved. However, if we consider the massive population declines experienced by more than a few species since 1970, he may actually have underestimated his 1970s figures by a significant margin.

The numbers of some migratory species from the northern continents spending the winter in Africa, like storks and raptors, can be measured directly by systematic autumn counts at migratory bottlenecks (Panuccio *et al.* 2021). Other species concentrate in a limited number of wintering sites, where counts of absolute numbers suffice to cover entire breeding populations, such as the millions of arctic waders present along the African coast in its few large intertidal areas (van de Kam *et al.* 2004, Wetlands International 2006, Oudman *et al.* 2020). Counts of migratory waterbirds in large Sahelian wetlands showed that wintering numbers of some species exceeded breeding population size in Europe, indicating the presence of large numbers of birds from Asia, examples being Squacco Heron *Ardea ralloides*, Garganey *Anas querquedula*, Ruff *Calidris pugnax* and Gull-billed Tern *Gelochelidon nilotica* (Zwarts *et al.* 2009).

Direct counting methods are not an option for the majority of bird species, because they do not concentrate during migration or on the wintering grounds. For less concentrated distributions, the total number of birds can be estimated only by measuring densities on samples of the wintering grounds. In this way, Herremans (1998a) determined the size of the world population of Lesser Grey Shrike *Lanius minor* spending the northern winter in southern Africa. Zwarts *et al.* (2023a,b) used bird counts in stratified plots to estimate the numbers of common bird species present in the transition zone between the Sahara in the north and the humid tropical forest farther south, covering 997 million ha between 7°N and 22°N, equivalent to 30% of the total surface of Africa. In the present paper we use these data to compare the estimated breeding and wintering ranges of 30 Afro-Palearctic, tree-dwelling or ground-feeding bird species. Using their densities, we also compare the population size of bird species breeding in Europe with their wintering numbers in the northern dry belt of Africa. Breeding and wintering ranges for many of these species extend beyond just Europe and northern sub-Saharan Africa, which required additional estimates of the numbers breeding beyond Europe and wintering outside northern sub-Saharan Africa, and a reassessment of distribution ranges in Europe, Africa and Asia.

METHODS

Population size derived from breeding numbers

Tucker & Heath (1994) were the first to attempt an estimate of European breeding bird populations, based on national estimates of the constituent countries. Their estimates included the European part of Russia and Kazakhstan (following the Ural Mountains and the Ural River down to the Caspian Sea) and the Asian part of Turkey. This exercise was repeated and updated by BirdLife International (2000, 2004, 2015, 2021), to additionally include the three southeastern most European countries of Georgia, Armenia and Azerbaijan, the total European area being 1154 million ha. These estimates of population sizes referred to mature individuals upon the assumption of a balanced sex ratio of 1:1 to calculate breeding pairs (but see Donald 2007, Loonstra *et al.* 2019).

To make a fair comparison of a breeding population with its wintering population, three additional estimates are needed: the number of birds that do not breed, the number of first-year birds produced over the spring and summer, and their mortality after the breeding season. We follow Hahn *et al.* (2009) who estimated the non-breeding fraction at 15% relative to the breeding population and who listed for 68 Afro-Palearctic species the number of fledglings per nest of which an estimated 60% survived their first summer. This information allowed us to estimate population size at the start of the autumn migration, which was, on average, 2.12 times the number of breeding birds (SD = 0.49), varying between species from 1.0 to 3.4 (Table 1: column 1). Numbers during the northward return migrations will obviously be smaller than 6 to 8 months previously, due to mortality during autumn migration and on the wintering grounds. Winter mortality in Africa differs per migratory bird species and per year and is higher for juveniles than for adults (Figure 235, 251, 256, 261 in Zwarts *et al.* 2009). We assume that, on average, bird populations in spring equal the number of breeding birds in the previous breeding season plus 15% non-breeders. We further assume that the winter population, such as derived from counts in the breeding area, is midway between estimated autumn and spring numbers.

Most European species spending the northern winter in sub-Saharan Africa also breed in northern Africa and/or in Asia. To estimate the total population size including the non-European part of the range we used the digitised distribution maps of the breeding birds compiled by BirdLife International and Handbook of the Birds of the World (2021) and the most recent estimation of the total number of birds in Europe (BirdLife International 2021). We assume that the average species-specific densities in the breeding range outside Europe were similar to those found in Europe.

Population size derived from bird counts in the Sahel

Estimates of the total number of birds present in Africa between 7 and 22°N and between 17°W and 42°E during the dry season (November–March) are given by Zwarts *et al.* (2023a,b). This region represents a gradual shift from desert in the north (30 mm/year) to humid forests in the south (>1200 mm/year). Our data were collected mostly in the Sahel climate zone covered by 100–600 mm/year. In this paper we use the term Sahel in a broad sense to include the entire region between 7 and 22°N.

The estimates of bird numbers present in the Sahel were based on bird counts between 2011 and 2019 during the dry season (20 November – 10 March) in 1901 random sites of usually 4.5 ha each. Maps with bird densities averaged for 150 grid cells (with >10 random sites) of 1° latitude × 1° longitude are given by Zwarts *et al.* (2023a,b). The 150 grid cells represented 18% of the total land surface area between 7 and 22°N and between 17°W and 42°E (997 million ha), taking into consideration that each grid cell measured 1.2 million ha. Zwarts *et al.* (2023a) discussed at length whether the random sites were representative for grid cells and whether grid cells were representative for the region as a whole. The main conclusion was that the random sites were indeed a representative sample of the grid cells. However, for the region between 7 and 22°N the 150 grid cells themselves were not representative, especially because grid cells from the desert and the humid forests were underrepresented. This bias was corrected by calculating the average density for 11 rainfall zones and then using these density estimates as the basis for extrapolation. As bird densities not only varied latitudinally per rainfall zone, but also longitudinally across the entire Sahel (Zwarts *et al.* 2023c), and as grid cells were overrepresented in the western Sahel, the 11 rainfall zones were further subdivided into six longitudinal bands. Estimates of bird density were available for 53 of the 65 sub-regions. To estimate bird density in the 12 missing sub-regions, the measurements in two adjacent cells with similar rainfall were averaged and used for estimation purposes. For the missing cells in southern Sudan, we substituted values from Chad and Central African Republic, rather than from the adjacent Ethiopian Highlands (the latter representing a very different ecozone). The total number of birds present between 7 and 22°N was calculated from the measured or interpolated bird density in the 65 sub-regions multiplied by surface area (Figure S1 in Zwarts *et al.* 2023a).

The split-half method was used to assess the reliability of the estimated totals (Zwarts *et al.* 2023a,b). Even and odd numbered sites were selected to repeat the calculations, as described above, to arrive at an estimate of the total number present. Estimates for even and odd sites were highly correlated (Figure 1). For all bird species combined, the split-half estimates deviated, on average, 18.8% from the average based on the full

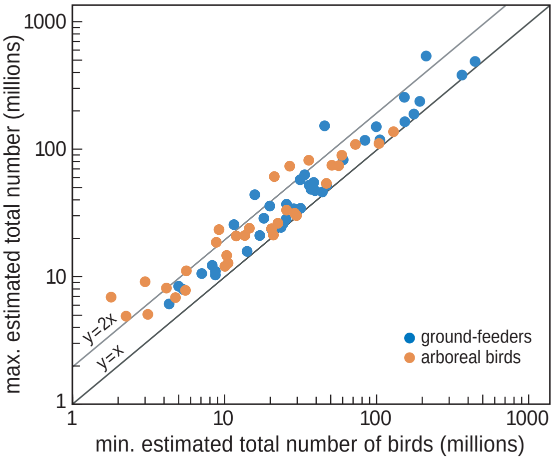

Figure 1. Maximum and minimum estimate of the population size of 75 Afro-Palearctic and Afro-tropical bird species present in Africa during the dry season (November–March) between 7 and 22°N and between 17°W and 42°E, using a split-half method. Shown here is the higher estimate plotted against the lower estimate, both on a log scale. The raw data are given in Zwarts *et al.* (2023a: Supplementary Material 1; 41 ground-feeding bird species) and in Zwarts *et al.* (2023b: Supplementary Material; 34 arboreal bird species).

data set. The relative deviation was, on average smaller for Palearctic migrants (17.5%) than for Afro-tropical residents (19.3%). As expected, the estimates were better for species that were common and widely distributed: the relative deviation depended on population size ($r = -0.25$, $n = 75$, $P = 0.01$), showing a negative exponential decline (from 27 to 6.5% deviation at population sizes of 1 and 467 million birds, respectively) and on frequency of occurrence in the 1901 sites ($r = -0.35$, $n = 75$, $P = 0.001$), from 21 to 6.4% deviation when the species were recorded in 1 and 25% of the sites, respectively. The actual error of estimate may be larger because the split-half method was applied to sites within grid cells; the total estimate might have been different had other grid cells been chosen.

For the present exercise, 30 migratory species were selected, but Eastern Bonelli's Warbler *Phylloscopus orientalis* was excluded from some analyses because we lacked an accurate estimate of the population size. Although Subalpine Warbler *Curruca cantillans* has recently been split into three species, we here maintained the lumped name for Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans*. The same applies for Black-eared Wheatear *Oenanthe hispanica*, now split into Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*.

RESULTS

Distribution in the Sahel

The presence of most bird species in 150 grid cells in Africa between 7 and 22°N and their winter distribution (BirdLife International and Handbook of the Birds of the World 2021) in general showed a good fit (Figure 2–30). A closer look, however, revealed many systematic differences, some small, some greater. Eight bird species wintered farther north in the Sahel than shown on published distribution maps. The difference was conspicuous in Eurasian Wryneck (Figure 2) and Iberian Chiffchaff *Phylloscopus ibericus* (Figure 9), where two thirds of the occupied grid cells were north of the described distribution range, and in Common Redstart *Phoenicurus phoenicurus* (Figure 23), where one third of the occupied grid cells was north of the published distribution. To quantify the latitudinal distribution range, we calculated the average latitude based on the bird counts in the grid cells (column 5 in Table 1) and the centroid of the latitudinal distribution between 7 and 22°N based on the maps (column 6 in Table 1). Eurasian Wryneck (Figure 2), Woodchat Shrike *Lanius senator* (Figure 3), Iberian Chiffchaff (Figure 9) and Eastern Orphean Warbler (Figure 19) spent the winter in the Sahel zone about 300 km further to the north than indicated on the maps, and Common Redstart 200 km (Figure 23). In other species

Table 1. Estimated population size of 30 Afro-Palearctic bird species, derived from counts of breeding numbers in Europe and from counts in the Sahel during the northern winter. Explanation:
Column 1. Ratio used to convert breeding numbers into mid-winter population (based on Hahn *et al.* 2009; further explanation in text).
Column 2. Figure number of the map.
Column 3. Percent of grid cells ($N = 150$) in which the species was observed (from Zwarts *et al.* 2023a,b).
Column 4. As 3, but corrected for the unequal distribution of the grid cells over the 11 rainfall zones and six longitudinal bands.
Column 5. Average latitude, based on counts in the grid cells, weighted for the average density in the grid cells (from Zwarts *et al.* 2023a,b).
Column 6. Average latitude, calculated as the centroid of the distribution range between 7 and 22°N (see Figure 2–30 based on BirdLife International and Handbook of the Birds of the World 2021).
Column 7. Surface area of the breeding range in Europe, derived from Keller *et al.* (2020); further explanation in text.
Column 8. Surface area of the breeding range in Europe, derived from maps (Figure 2–30).
Column 9. As 8, but for the entire world (see maps; Figure 2–30).
Column 10. Surface area of the distribution range during the northern winter between 7 and 22°N (see maps).
Column 11. As 10, but for the entire world.
Column 12 and 13: Minimum and maximum population size in Europe (based on BirdLife International 2021) using the ratio given in column 1 to convert breeding numbers in mid-winter population size.
Column 14 and 15. Extrapolated minimum and maximum world population, derived from number in Europe (column 12 and 13) and the ratio between breeding range worldwide and in Europe (column 8 and 9).
Column 16 and 17. Minimum and maximum population size in the Sahel (from Zwarts *et al.* 2023a,b).
Column 18 and 19. Extrapolated minimum and maximum world population, derived from number in the Sahel (column 16 and 17) and the ratio between range of the distribution during the northern winter worldwide and in the Sahel (column 11 and 10).
The 30 bird species have been divided into three groups: those wintering in the Sahel and breeding in southern Europe ($n = 14$); or in most of Europe ($n = 8$), and those that appear to winter rarely or not at all in the Sahel ($n = 8$). The total number of birds in the three groups are given in the last row of the table.

the differences were small, between –100 and +100 km, but, on average, Isabelline Wheatear *Oenanthe isabellina* (Figure 26) occurred 180 km further to the south than expected on the basis of published maps. That difference was still larger for Eastern Bonelli's Warbler (200 km), Rüppell's Warbler (240 km; Figure 18) and Whinchat *Saxicola rubetra* (390 km; Figure 24). Two bird species with a winter distribution south of 7°N were completely absent from the Sahel, except in the southernmost rim: Wood Warbler *Phylloscopus sibilatrix* (Figure 6) and Willow Warbler (Figure 7). The Common Chiffchaff *Phylloscopus collybita* was restricted largely to the Ethiopian Highlands; very few were encountered elsewhere, all in the western Sahel (Figure 8). We saw only a single Eurasian Blackcap *Sylvia atricapilla* (Figure 14) outside Ethiopia.

Species common in the northern Sahel, such as Woodchat Shrike (Figure 3), Western Bonelli's Warbler

Column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
			Sahel				**Range** (million ha)					**Bird numbers** (millions)							
	Ratio	Fig	Grid			Map	Summer			Winter		Europa		World		Sahel		World	
Common name			%	%	N°	N°	Europa		Total	Sahel	Total	Min	Max	Min	Max	Min	Max	Min	Max
Eurasian Wryneck	3.0	2	11	5	12.30	9.91	677	760	1764	377	1270	4.7	9.0	10.4	20.0	1.0	1.7	3.5	5.9
Woodchat Shrike	1.9	3	39	17	14.40	11.54	198	170	258	555	709	7.2	11.6	10.9	17.6	8.8	10.4	11.2	13.3
Masked Shrike	2.7	4	13	9	12.94	13.98	50	22	35	188	195	0.2	0.6	0.3	0.9	3.4	6.4	3.5	6.6
Greater Short-toed Lark	2.0	5	11	17	15.48	15.50	185	273	928	233	789	18.5	34.7	63.0	118	100	151	309	465
Wood Warbler	1.9	6	1	5	8.08	9.51	560	626	636	254	590	30.3	53.2	30.8	54.1	3.7	5.6	8.5	12.9
Western Bonelli's Warbler	1.9	10	35	13	14.72	13.49	117	80	112	231	231	9.3	12.3	13.0	17.2	30.0	30.2	30.0	30.2
Eastern Bonelli's Warbler	1.9		2	2	13.09	14.92	31	29	32	68	68					0.0	1.0	0.0	1.0
Willow Warbler	2.2	8	3	5	8.67	9.89	636	688	1585	231	1329	235	356	581	881	9.2	14.4	53.8	84.2
Common Chiffchaff	1.8	7	11	7	12.55		839	738	757	708	1468	129	203	132	208	9.3	23.6	20.2	51.4
Iberian Chiffchaff	1.8	9	9	7	15.91	13.04	41	23	30	45	45	1.6	2.7	2.1	3.6	1.8	6.9	1.8	6.9
Eastern Olivaceous Warbler	1.8	11	26	23	13.12	12.50	133	156	479	365	673	11.5	24.1	29.9	62.4	12.0	21.0	22.1	38.7
Western Olivaceous Warbler	1.8	12	26	10	13.88	12.67	15	5	48	136	136	0.0	0.0	0.2	0.2	5.6	11.1	5.6	11.1
Melodious Warbler	1.8	13	5	4	12.13	9.67	150	132	171	167	222	7.5	12.4	9.5	15.7	0.6	4.2	0.8	5.6
Eurasian Blackcap	1.0	14	1	1	10.60		813	812	863	292	629	85	132	101	158	0.0	7.5	0.0	16.7
Garden Warbler	1.8	15	0	0		10.26	702	785	965	175	1097	42.0	70.5	42.7	71.7	0.0	0.0	0.0	0.0
Lesser Whitethroat	1.9	16	33	35	13.64	14.35	691	789	2110	324	870	18.6	31.8	49.7	85.1	56.6	74.6	152	200
Western Orphean Warbler	1.9	17	18	9	15.92	14.98	54	51	104	162	162	0.5	0.9	1.0	1.9	10.1	12.1	10.1	12.1
Eastern Orphean Warbler	1.6	19	11	14	14.67	12.05	66	70	149	118	263	0.2	0.6	0.4	1.4	4.8	6.9	10.7	15.3
Rüppell's Warbler	1.8	18	11	17	14.97	17.04	20	23	24	183	200	0.4	1.9	0.4	1.9	19.2	21.3	21.0	23.2
Subalpine Warbler	2.4	20	38	30	15.01	15.07	124	91	145	315	349	17.2	26.4	27.5	42.2	51.1	75.0	56.6	83.0
Common Whitethroat	2.4	21	56	38	13.47	12.28	841	915	1412	504	916	94.5	143	146	220	29.2	31.6	53.0	57.4
European Pied Flycatcher	2.4	22	8	13	10.23	9.01	530	581	734	153	355	37.1	59.6	46.9	75.3	10.6	12.8	24.6	29.6
Common Redstart	3.4	23	43	23	13.23	11.34	767	874	1449	435	622	35.3	65.9	58.5	109	10.4	14.7	14.9	21.0
Whinchat	2.0	24	2	5	7.62	11.10	692	797	1024	472	803	30.8	42.2	39.6	54.2	0.5	7.4	0.9	12.6
Northern Wheatear	3.1	25	51	28	13.67	13.35	851	984	2787	667	996	33.0	89.5	83.2	226	25.5	28.4	38.0	42.4
Isabelline Wheatear	2.5	26	31	26	13.18	14.85	156	193	1171	435	1198	11.4	32.7	69.3	198	28.7	34.3	79.0	94.4
Black-eared Wheatear	2.7	27	21	18	15.16	16.02	159	193	353	373	373	6.9	19.9	12.7	36.4	7.1	10.7	7.1	10.7
Western Yellow Wagtail	2.1	28	26	17	11.88	11.22	792	914	1950	559	2027	56.4	76.1	118	159	23.6	24.4	86.4	89.3
Tawny Pipit	2.0	29	21	8	14.22	13.38	341	464	1118	343	845	4.5	8.1	10.8	19.5	5.0	8.4	12.3	20.7
Tree Pipit	2.3	30	10	11	10.96	10.77	812	780	1535	383	1240	88.6	160	175	314	11.5	15.3	37.3	49.6
South Europe–Sahel, *n*=14												85	169	231	502	283	398	568	811
entire Europe–Sahel, *n*=8												284	483	523	914	162	197	385	467
entire Europe–no Sahel, *n*=8												648	1029	1112	1757	35	78	122	233
TOTAL												**1017**	**1680**	**1866**	**3173**	**479**	**672**	**1074**	**1511**

(Figure 10) and Subalpine Warbler (Figure 20), were less frequently encountered in the south of the Sahelian zone, each showing a north-south density gradient. Four species largely confined to the eastern Sahel were not observed at all, or rarely, in the westernmost part of their distribution range: Masked Shrike *Lanius nubicus* (Figure 4), Greater Short-toed Lark *Calandrella brachydactyla* (Figure 5), Lesser Whitethroat *Curruca curruca* (Figure 16) and Isabelline Wheatear (Figure 26). In contrast, two species common in the western Sahel were observed less often within their distribution range in the eastern Sahel, Common Whitethroat *Curruca communis* (Figure 21) and Northern Wheatear (Figure 25). These examples show that species were more common in the centre of their distribution range and less common at the fringes.

The distributions of Palearctic bird species across the Sahel differed considerably. Some species were widespread, like Common Whitethroat (in 56% of the grid cells) and Northern Wheatear (51%), others were much more limited, like Eastern Bonelli's Warbler and Iberian Chiffchaff, each in only 3% of the grid cells (column 3 in Table 1). The size of the wintering ranges, relative to the 997 million ha available between 7 and 22°N, varied accordingly on the distribution maps, from the range of Northern Wheatear covering 67% of the Sahel's total surface area, to less than 5% for Eastern Bonelli's Warbler and Iberian Chiffchaff (column 9 in Table 1). On average, Palearctic bird species were present in 19% (SD = 16) of the 150 investigated grid cells and this declines to 14 ± 10% after correcting for the unequal distribution of the grid cells over the region (column 3 and 4 in Table 1, respectively). The distribution maps in Figures 2 to 30 assigned greater ranges (by 32 ± 17%) to most of the 30 species (surface area given in column 10 of Table 1, converted to percent relative to total surface, 997 million ha). Eight species were observed exclusively along the southern fringe of the region and/or in Ethiopia, representing only a tiny northern fraction of their more southerly wintering ranges, yet the published maps indicated that these species would occupy some 20 to 70% of the Sahel (7–22°N; 17°W–42°E). For the remaining 22 bird species, their actual distribution within the Sahel region is smaller, on average, than the wintering range indicated on the maps, especially for widely distributed bird species (Figure 31).

Numbers

Of the bird species analysed here, the Iberian Chiffchaff (Figure 9) is the only one exclusively breeding in Europe and exclusively wintering in the Sahel. The wintering range of Western Bonelli's Warbler *Phylloscopus bonelli* (Figure 10), Western Orphean Warbler (Figure 19) and Subalpine Warbler (Figure 20) are also restricted to the Sahel, but their breeding ranges encompass Europe and Northern Africa. Nearly all Rüppell's Warblers *Curruca ruppeli* (Figure 18) breed in Europe and most winter in the Sahel. The other species have a distribution area larger than Europe in summer and/or a distribution area larger than the Sahel during the northern winter. This complicates a comparison between population sizes as derived from bird counts in the Sahel and on the breeding grounds in Europe. The population estimates have therefore been enlarged with estimated numbers beyond Europe in summer and beyond the Sahel in winter, based on extent of the breeding and wintering range (given as bars in Figs 2–30; see also column 12–19 in Table 1).

Many migratory Palearctic bird species winter mainly or exclusively south of 7°N, which is south of the region covered in this study. For example, our density estimate for European Pied Flycatcher *Ficedula hypoleuca* (Figure 22) refers to the northern fringe of the distribution area. The extrapolated winter numbers are therefore less reliable, especially when we take into account the usually lower than average densities along the edges of distributions (see above). The same applies for Wood Warbler (Figure 6), Willow Warbler (Figure 8), Melodious Warbler *Hippolais polyglotta* (Figure 13), Garden Warbler *Sylvia borin* (Figure 15) and Whinchat (Figure 24), all of which winter in regions south of 7°N. Common Chiffchaff (Figure 7) and Eurasian Blackcap (Figure 14) have become an enigma in the Sahel (except in Ethiopia), being either absent or extremely scarce where they were once common as winter visitors (Urban *et al.* 1997). On published maps all these species are depicted with wide distributions north of 7°N (covering 18–71% of the Sahel region), but our field work shows that actual distributions north of 7°N are extremely small (11% of grid cells occupied by Tree Pipit *Anthus trivialis*, 7% by Common Chiffchaff), smaller still for six other species and 0% for Garden Warbler (Figure 31; column 4 in Table 1)). To correct for this error, distributional ranges north of 7°N should be adjusted, but even so the extrapolation would remain crude given the tiny fraction of wintering ranges of some species north of 7°N. The extrapolations are given for the sake of completeness, but a blue arrow is added in the graphs of 8 species to indicate substantial underestimation of the wintering numbers.

Four species occurring in the Sahel had estimated wintering numbers of less than half of the population size derived from counts of breeding birds: Eurasian Wryneck *Jynx torquilla* (Figure 2), Common Whitethroat (Figure 21), Common Redstart (Figure 23) and Northern Wheatear (Figure 25). The winter estimates for the Sahel were at least twice as high as the population size derived from the European breeding birds in nine species: Masked Shrike (Figure 4), Greater Short-toed Lark (Figure 5), Western Bonelli's Warbler (Figure 10), Western Olivaceous Warbler *Iduna opaca* (Figure 12), Lesser Whitethroat (Figure 16), Rüppell's Warbler (Figure 18), Western Orphean Warbler *Curruca crassirostris* (Figure 17), Eastern Orphean Warbler (Figure 19) and Subalpine Warbler *Curruca cantillans* (Figure 20). In eight species the two estimates broadly agreed: Woodchat Shrike (Figure 3), Iberian Chiffchaff (Figure 9), Eastern Olivaceous Warbler (Figure 11), European Pied Flycatcher (Figure 22), Isabelline and Black-eared Wheatear (Figure 26–27), Western Yellow Wagtail *Motacilla flava* (Figure 28) and Tawny Pipit *Anthus campestris* (Figure 29).

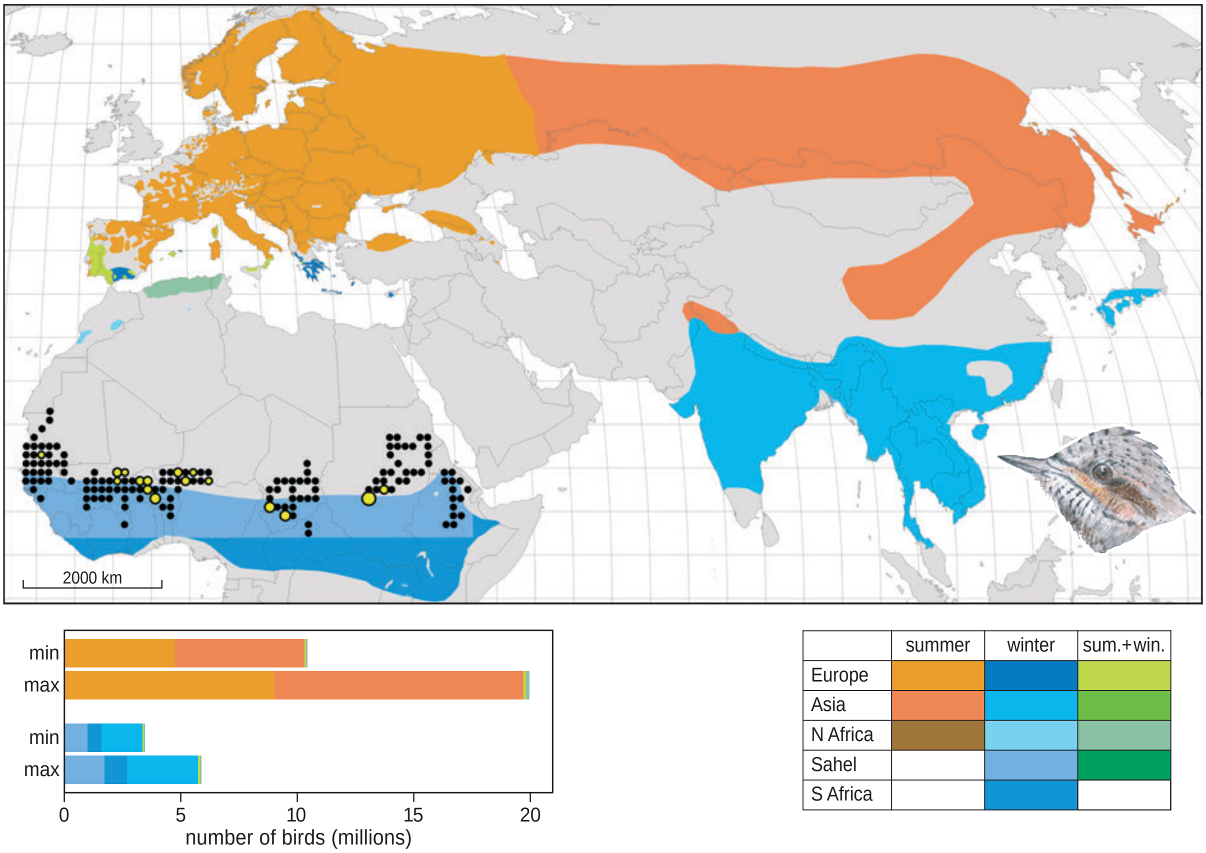

Figure 2. Eurasian Wryneck *Jynx torquilla*. **Map**: Bird density in the Sahel region shown for 150 grid cells (yellow symbols differing in size; black: no birds; see for the field periods Table S4 in Zwarts *et al.* 2023a). Distribution area in winter (shades of blue), summer (shades of red-brown) and both (shades of green) shown in different colours for Europe, Asia and in Africa for the zone between 7 and 22°N and between 17°W and 42°E (our 'Sahel'), and the area north or south of this area. Map based on: BirdLife International and Handbook of the Birds of the World (2021).
Graph: Population estimates for the Sahel are based on Zwarts *et al.* (2023a,b) and given as light blue; extrapolated numbers, based on the surface areas of the wintering ranges, are added in various other shades of blue. Similarly, estimates for the breeding population in Europe are given as ochre, based on BirdLife International (2021); additional red-brown colours denote extrapolated numbers based on the surface areas of the breeding ranges in Asia and Africa. This colour key applies to Figures 2 to 30.

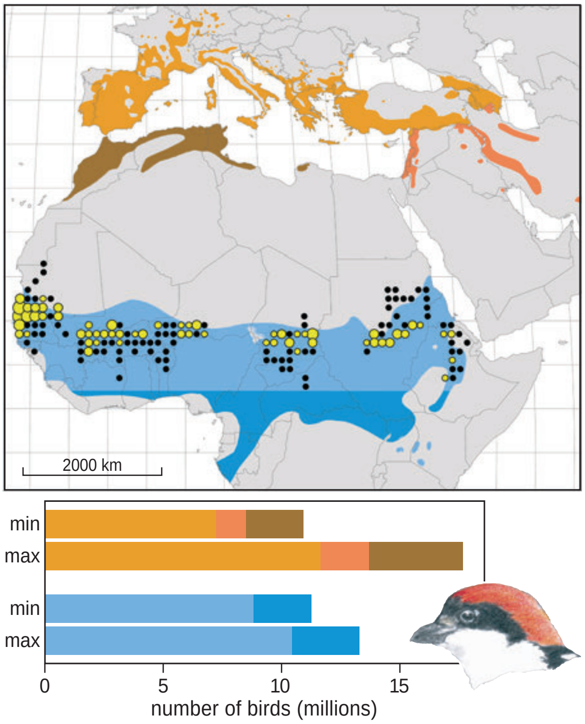

Figure 3. Woodchat Shrike *Lanius senator*; explanation in Figure 2; see also Figure S13 in Zwarts *et al.* (2023a).

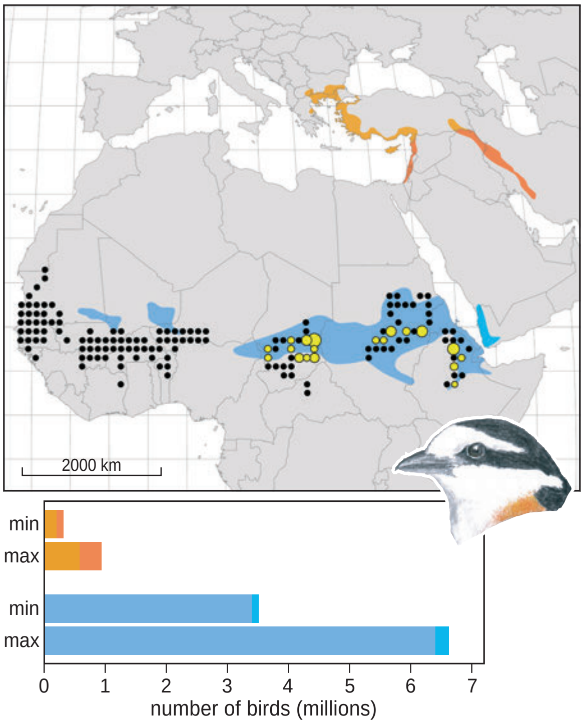

Figure 4. Masked Shrike *Lanius nubicus*; explanation in Figure 2; see also Figure S14 in Zwarts *et al.* (2023a).

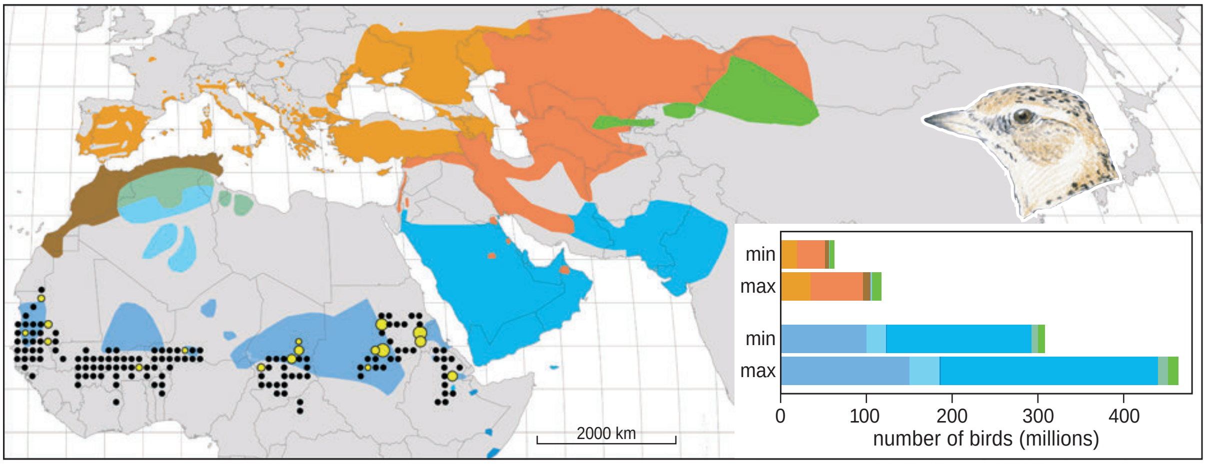

Figure 5. Greater Short-toed Lark *Calandrella brachydactyla*; explanation in Figure 2; see also Figure S18 in Zwarts *et al.* (2023a).

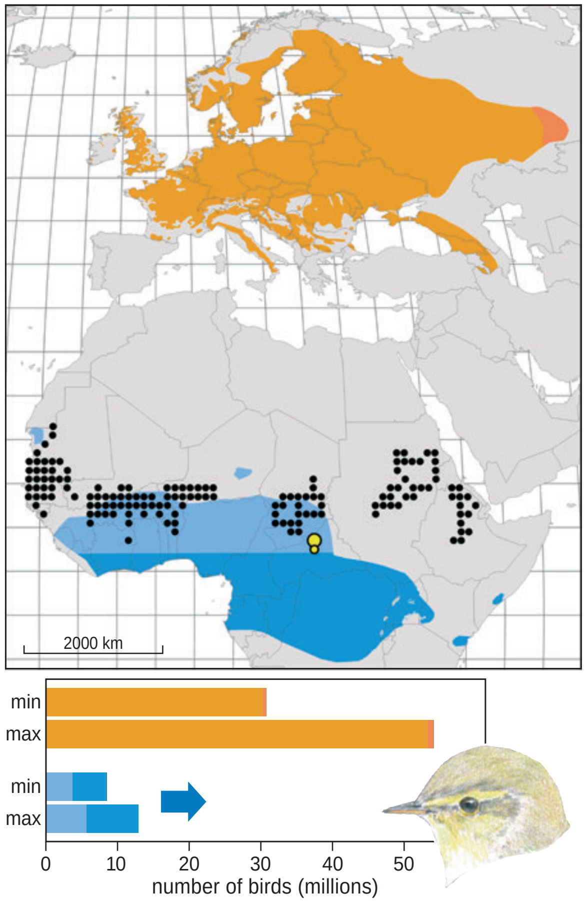

Figure 6. Wood Warbler *Phylloscopus sibilatrix*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

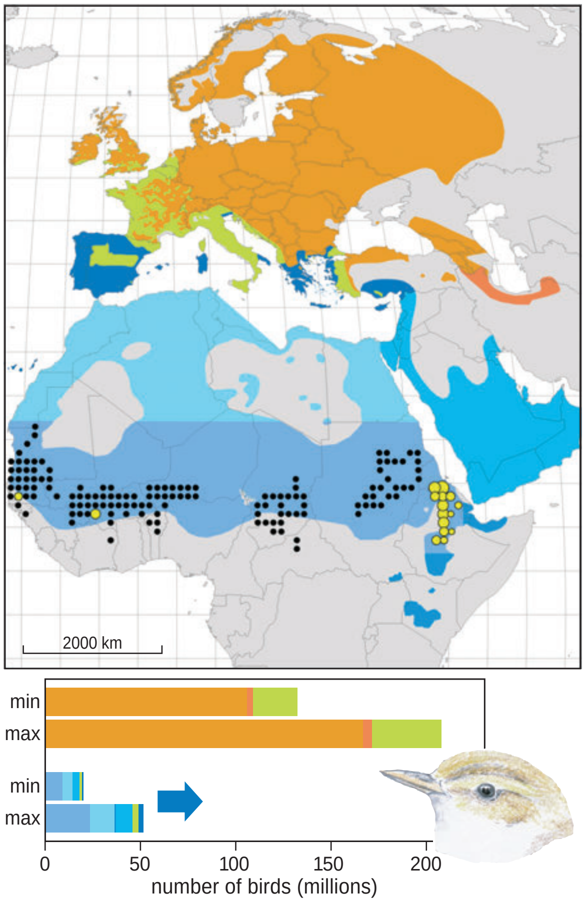

Figure 7. Common Chiffchaff *Phylloscopus collybita*; explanation in Figure 2; see also Figure S12 in Zwarts *et al.* (2023b). Arrow added to indicate underestimation of the extrapolated winter population.

Common Chiffchaff is abundant in acacia trees in Ethiopia, but not elsewhere in the Sahel zone.

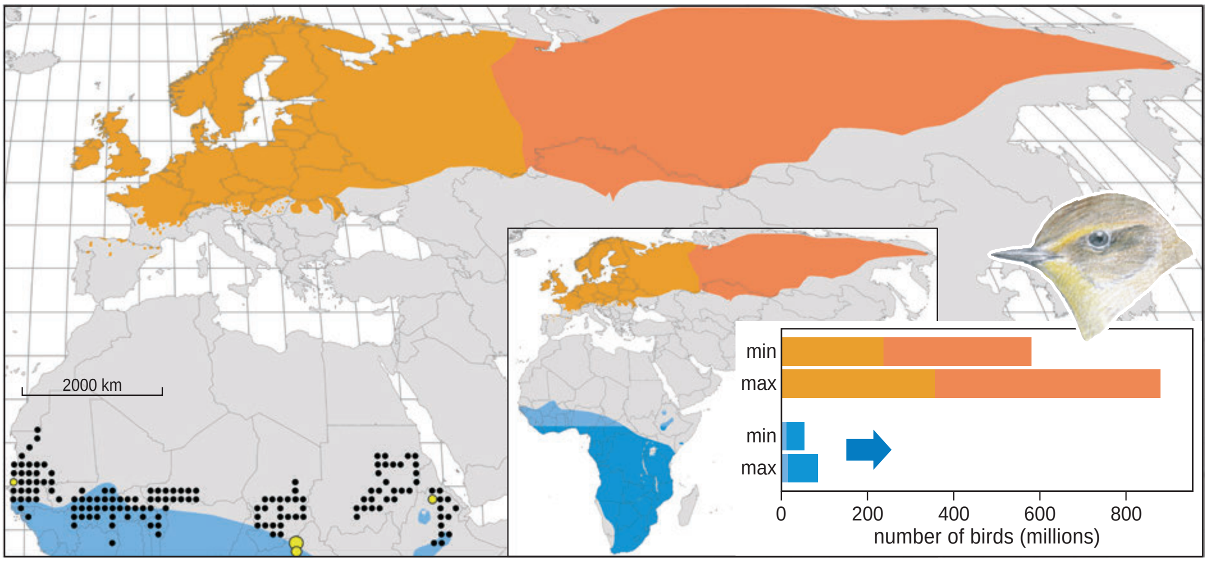

Figure 8. Willow Warbler *Phylloscopus trochilus*; inset figure shows entire breeding and wintering range; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

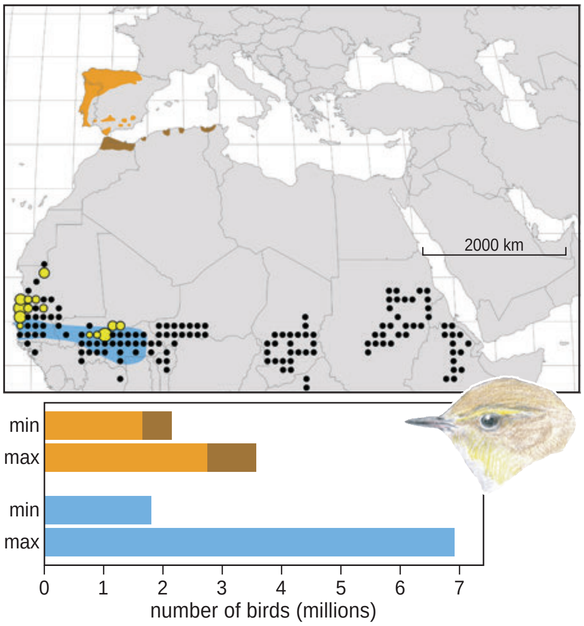

Figure 9. Iberian Chiffchaff *Phylloscopus ibericus*; explanation in Figure 2; see also Figure S13 in Zwarts *et al.* (2023b).

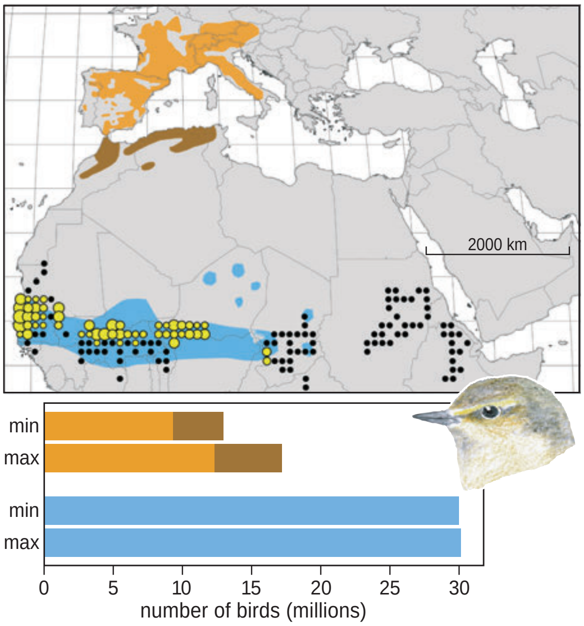

Figure 10. Western Bonelli's Warbler *Phylloscopus bonelli*; explanation in Figure 2; see also Figure S10 in Zwarts *et al.* (2023b).

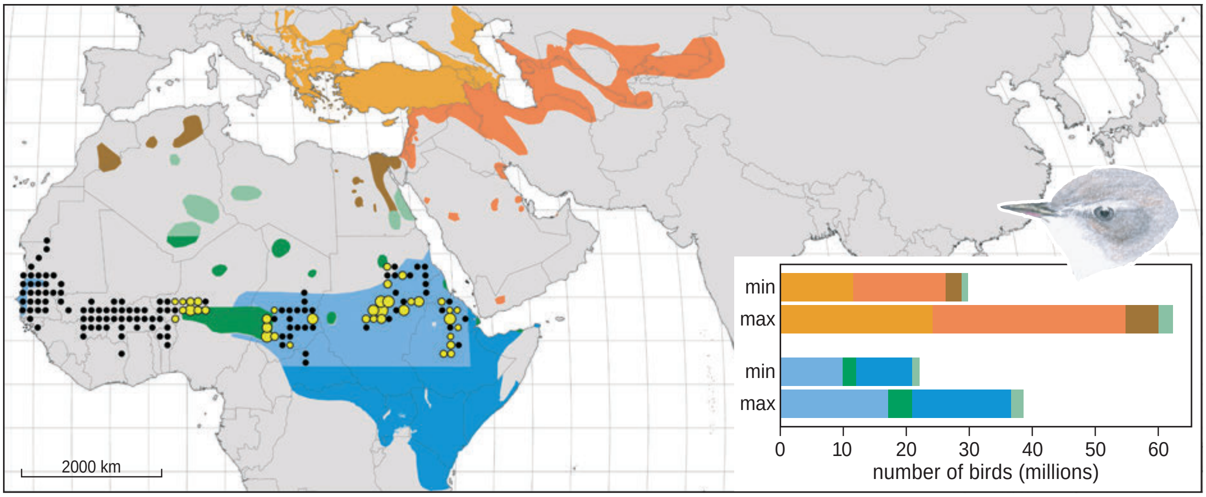

Figure 11. Eastern Olivaceous Warbler *Iduna pallida*; explanation in Figure 2; see also Figure S14 in Zwarts *et al.* (2023b).

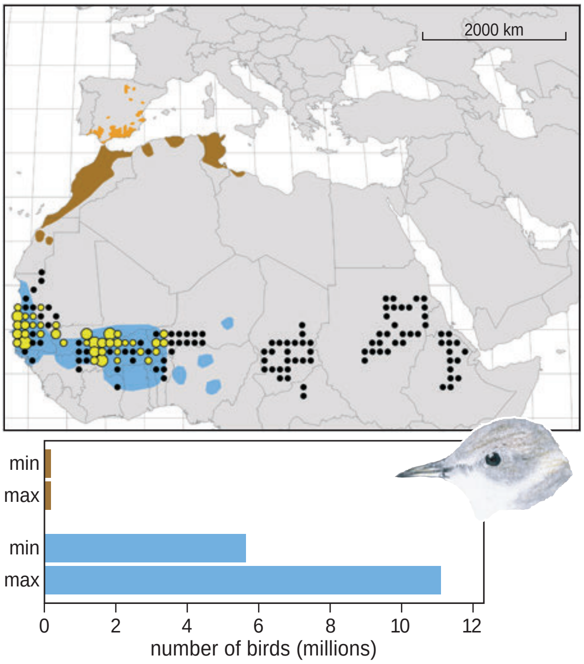

Figure 12. Western Olivaceous Warbler *Iduna opaca*; explanation in Figure 2; see also Figure S15 in Zwarts *et al.* (2023b).

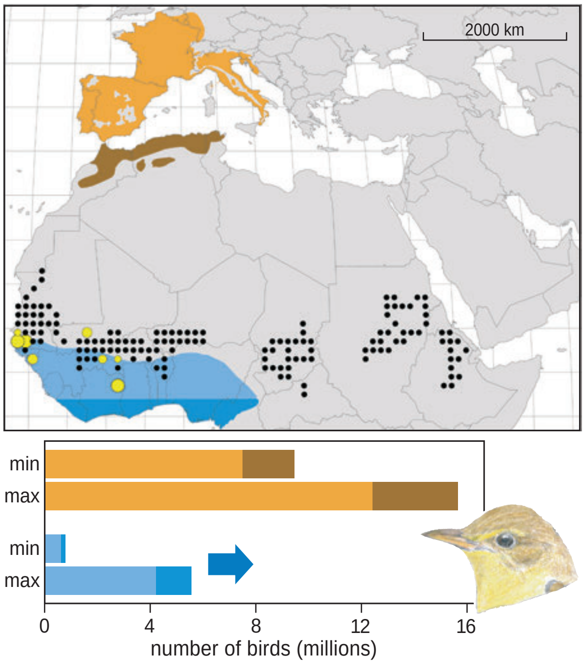

Figure 13. Melodious Warbler *Hippolais polyglotta*; explanation in Figure 2.

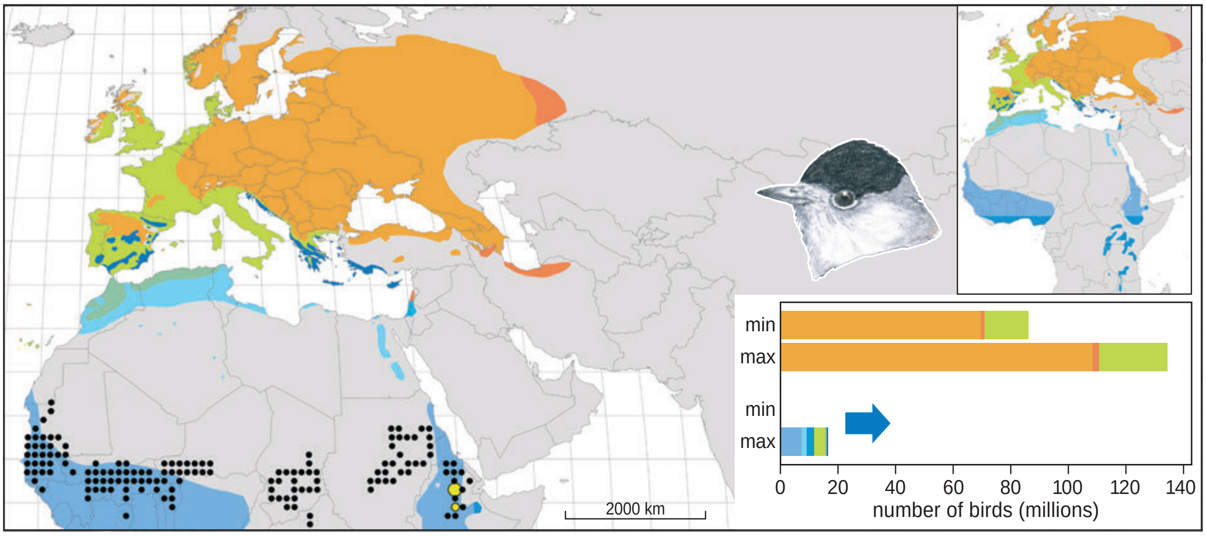

Figure 14. Eurasian Blackcap *Sylvia atricapilla*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

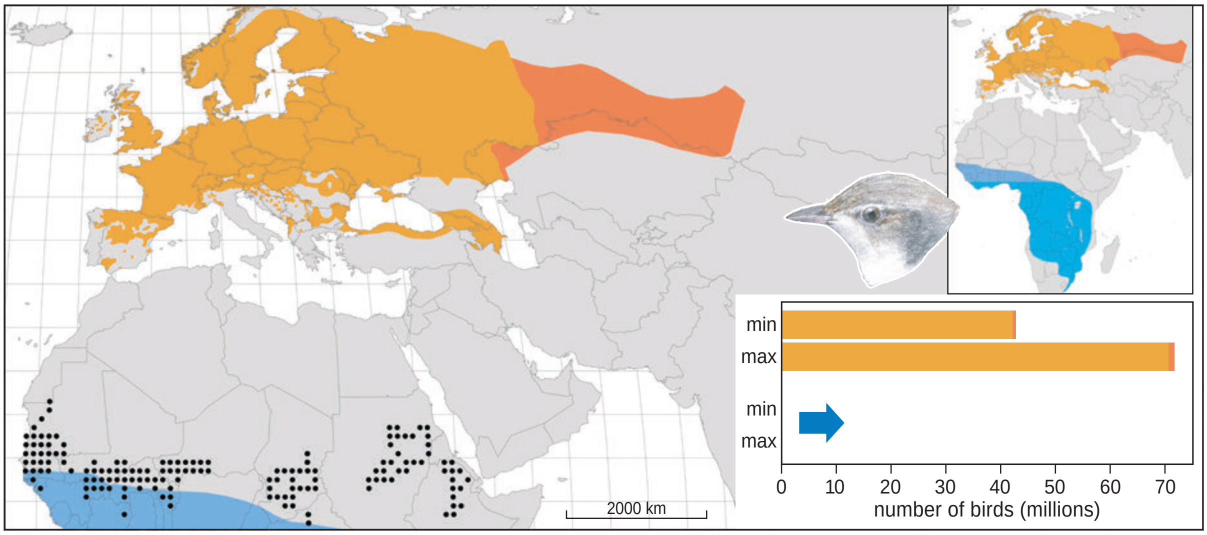

Figure 15. Garden Warbler *Sylvia borin*; explanation in Figure 2; inset map shows entire breeding and wintering range. Arrow added to indicate underestimation of the extrapolated winter population.

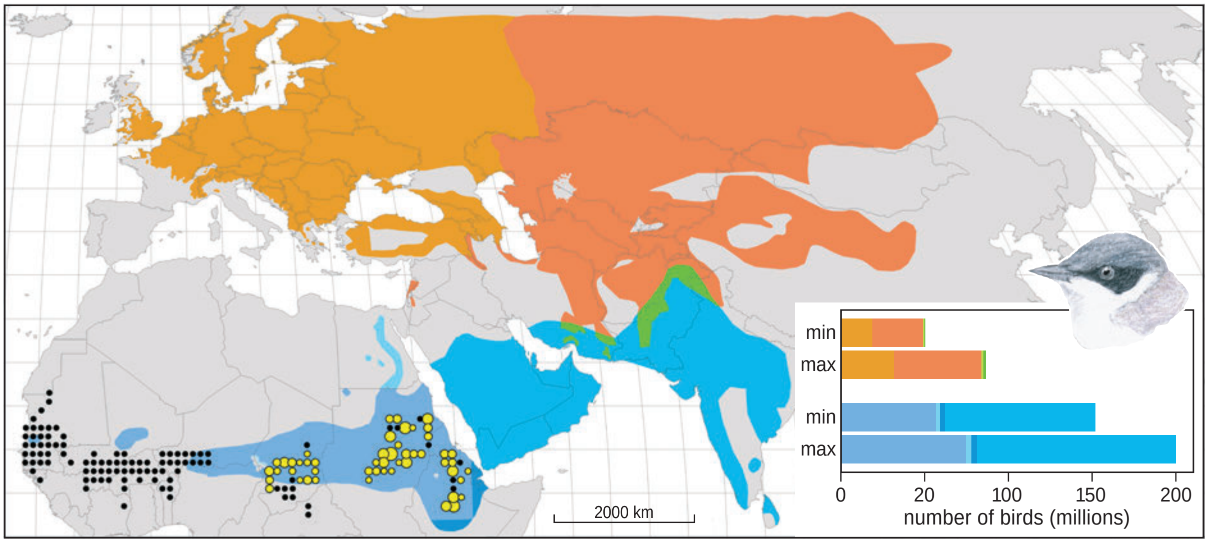

Figure 16. Lesser Whitethroat *Curruca curruca*; explanation in Figure 2; see also Figure S20 in Zwarts *et al.* (2023b).

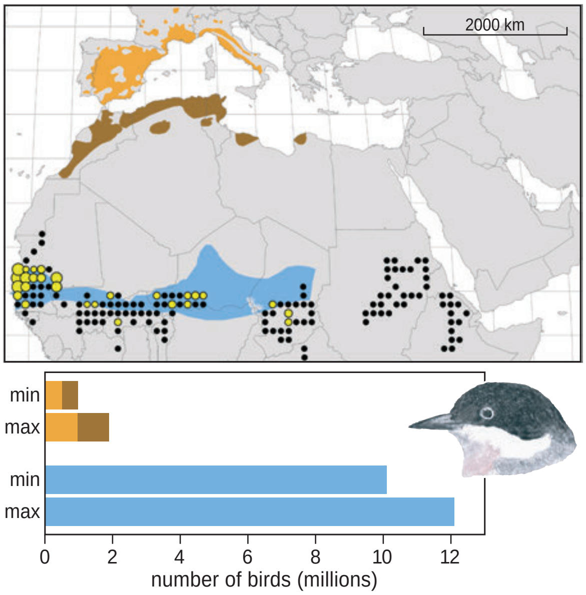

Figure 17. Western Orphean Warbler *Curruca hortensis*; explanation in Figure 2; see also Figure S21 in Zwarts *et al.* (2023b).

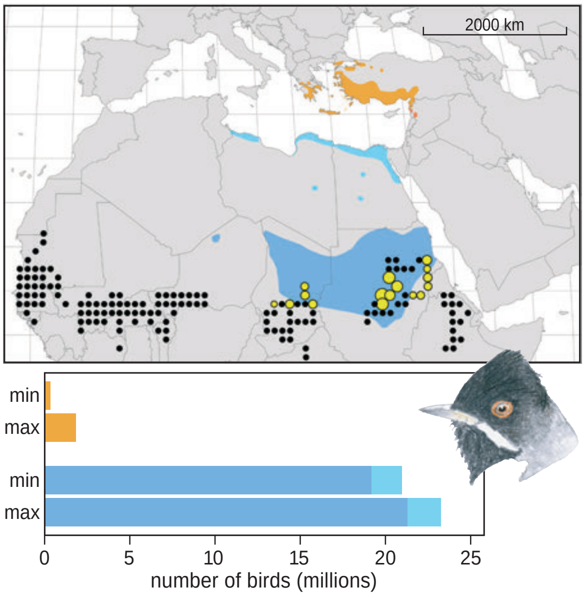

Figure 18. Rüppell's Warbler *Curruca ruppeli*; explanation in Figure 2; see also Figure S23 in Zwarts *et al.* (2023b).

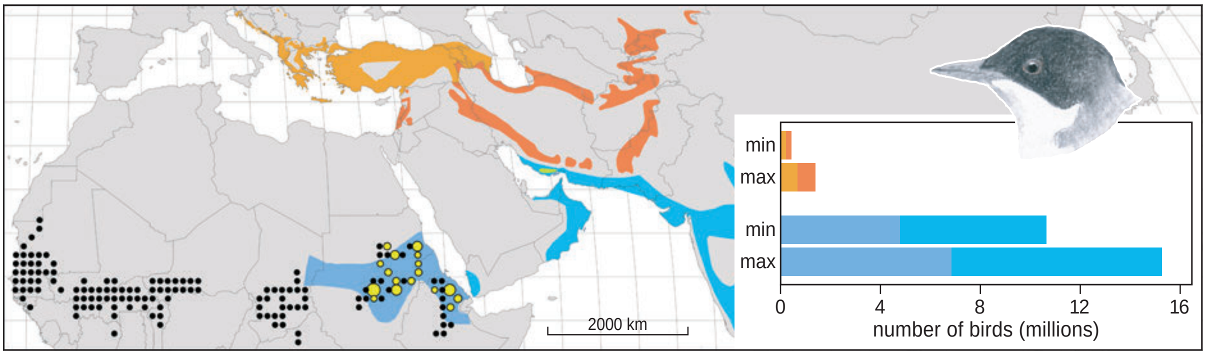

Figure 19. Eastern Orphean Warbler *Curruca crassirostris*; explanation in Figure 2; see also Figure S22 in Zwarts *et al.* (2023b).

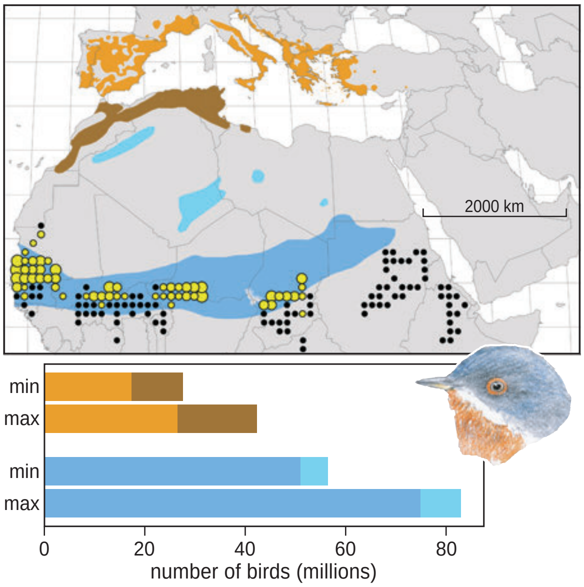

Figure 20. Subalpine Warbler (Western Subalpine Warbler *Curruca iberiae* + Moltoni's Warbler *C. subalpina* + Eastern Subalpine Warbler *C. cantillans*); explanation in Figure 2; see also Figure S24 in Zwarts *et al.* (2023b).

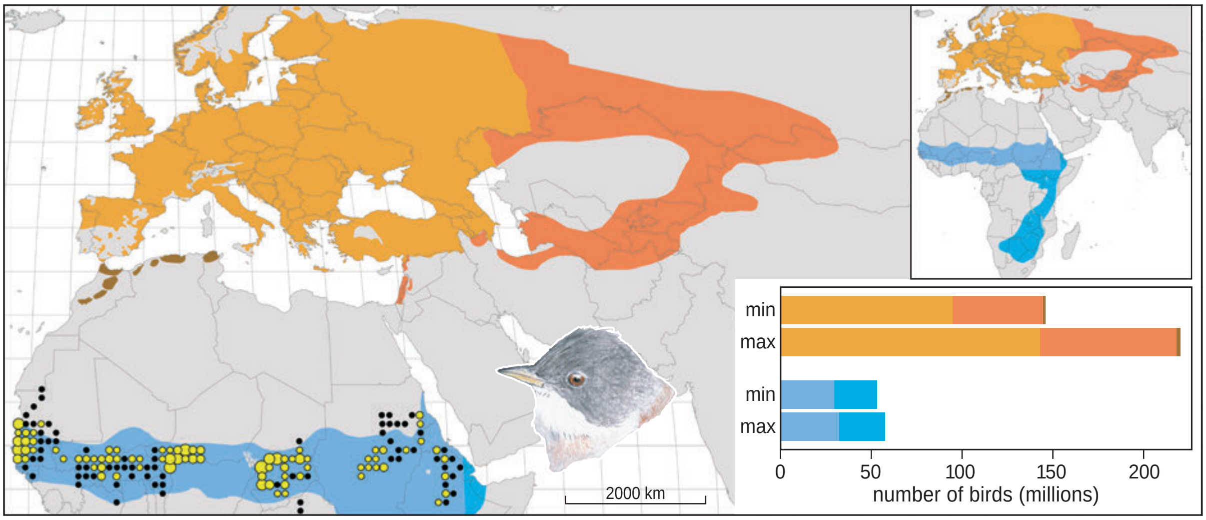

Figure 21. Common Whitethroat *Curruca communis*; inset map shows entire breeding and wintering range; explanation in Figure 2; see also Figure S25 in Zwarts *et al.* (2023b).

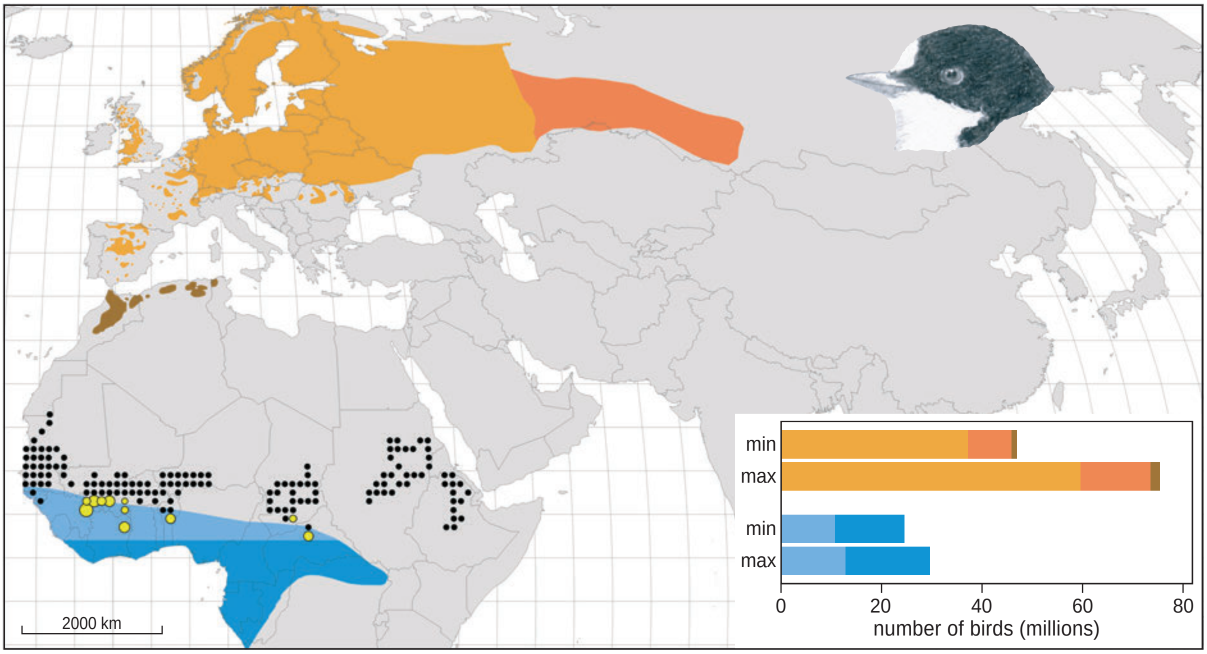

Figure 22. European Pied Flycatcher *Ficedula hypoleuca*; explanation in Figure 2; see also Figure S27 in Zwarts *et al.* (2023b).

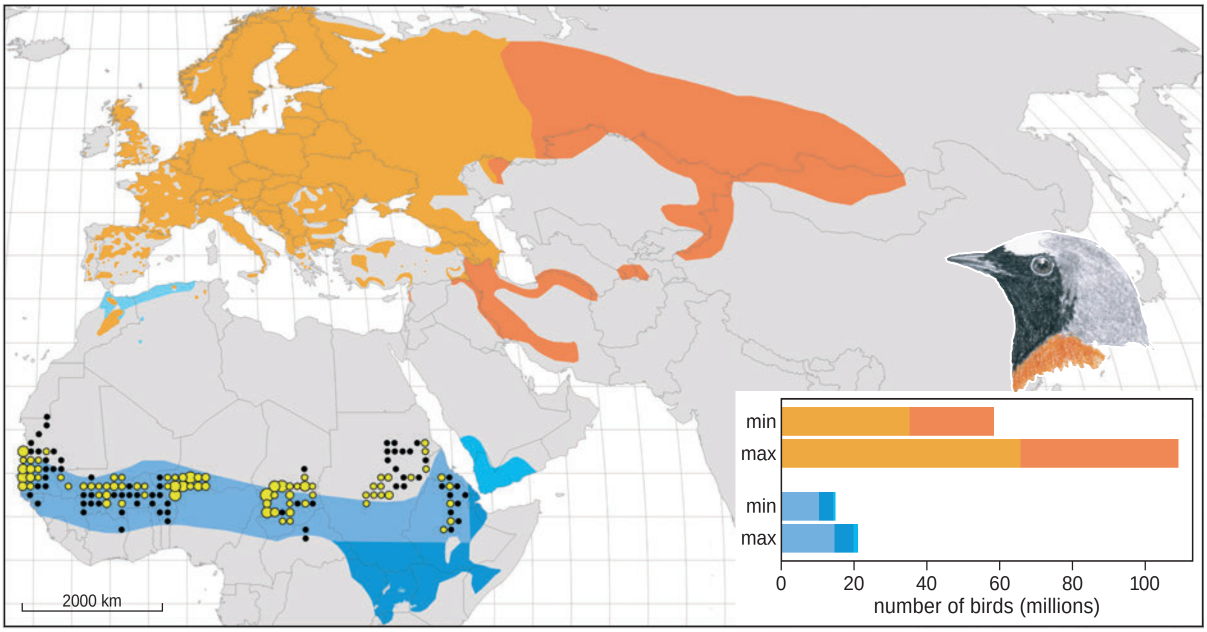

Figure 23. Common Redstart *Phoenicurus phoenicurus*; explanation in Figure 2; see also Figure S28 in Zwarts *et al.* (2023b).

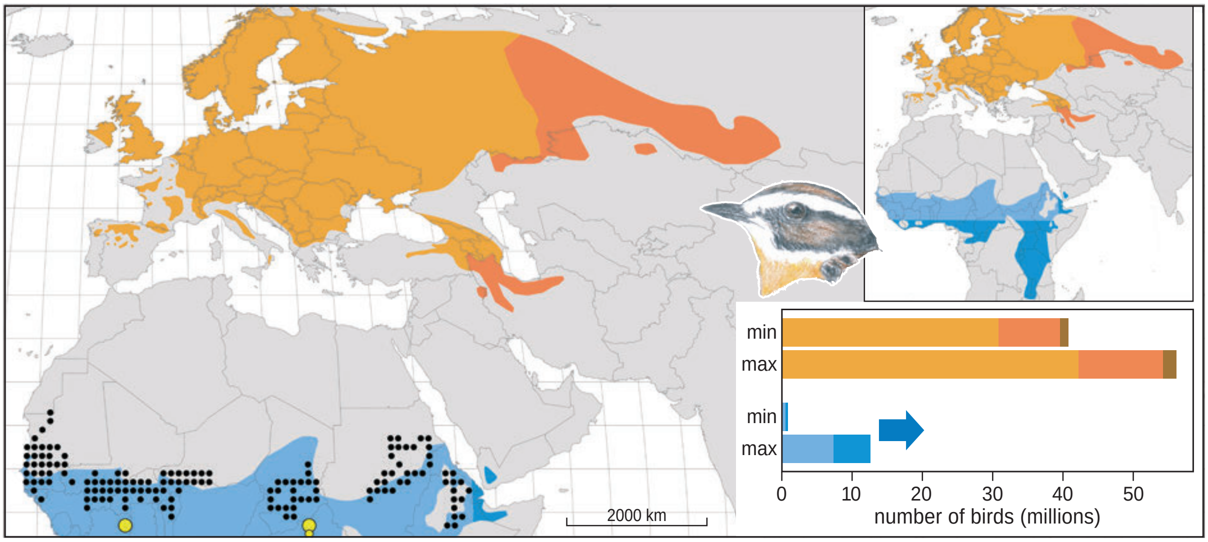

Figure 24. Whinchat *Saxicola rubetra*; inset map shows entire breeding and wintering range; inset map shows entire breeding and wintering range; explanation in Figure 2.

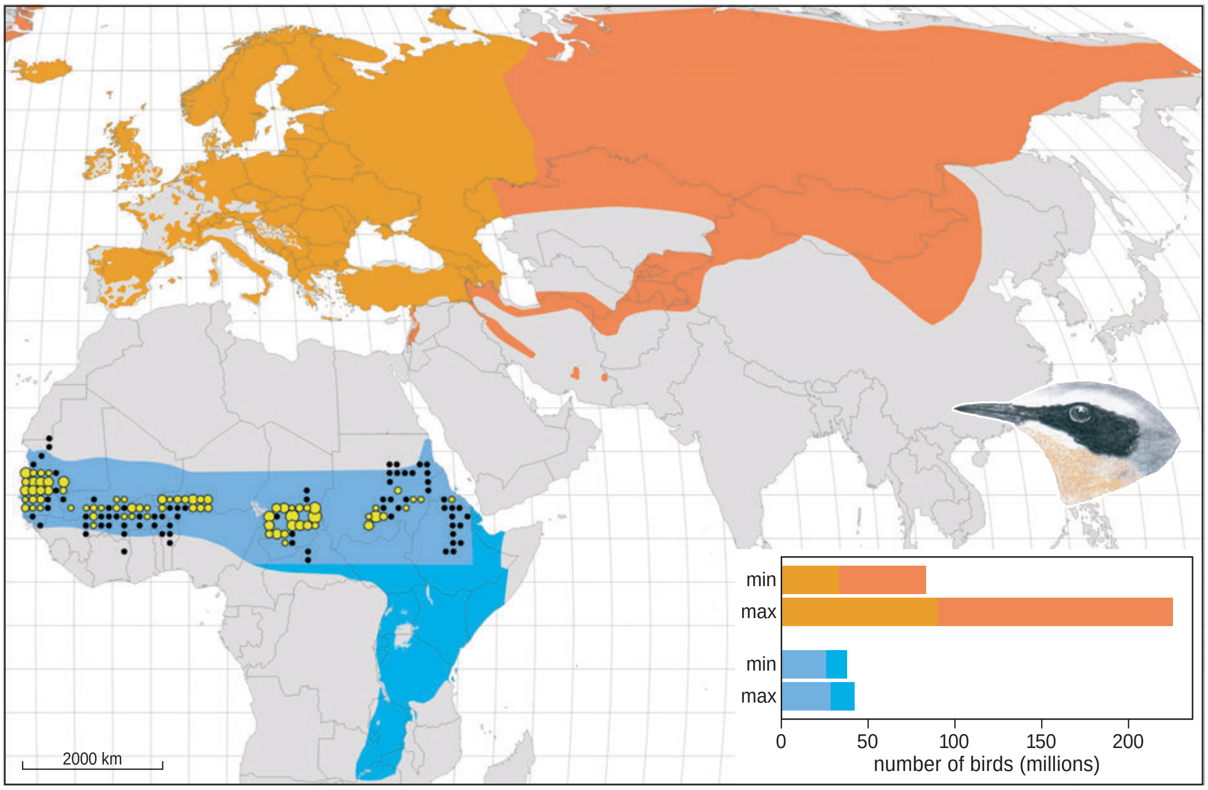

Figure 25. Northern Wheatear *Oenanthe oenanthe*; explanation in Figure 2; breeding grounds in Alaska, Canada and on Greenland are not shown; see also Figure S27 in Zwarts *et al.* (2023a).

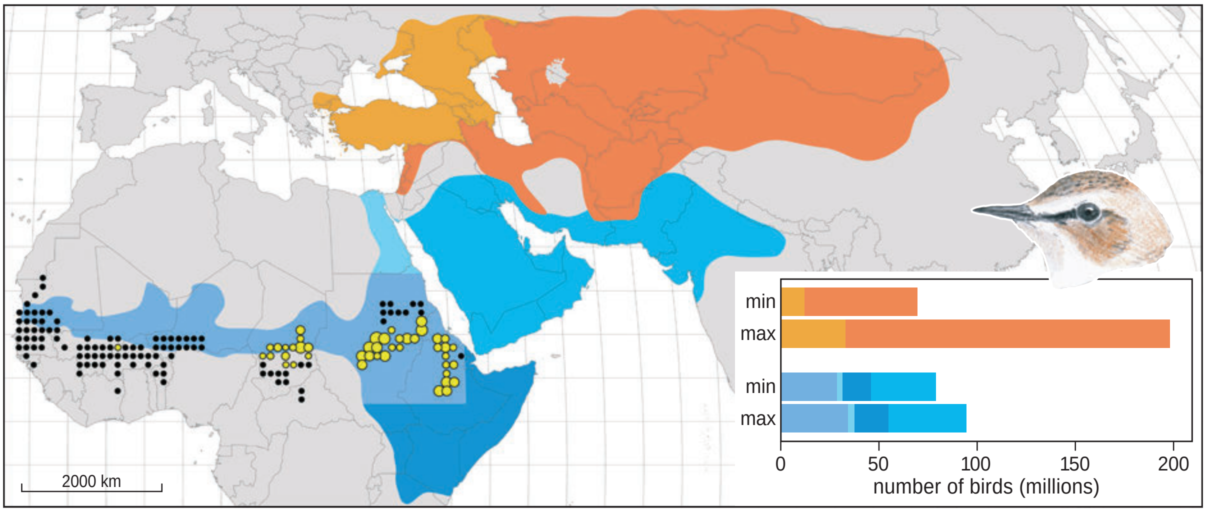

Figure 26. Isabelline Wheatear *Oenanthe isabellina*; explanation in Figure 2; see also Figure S28 in Zwarts *et al.* (2023a).

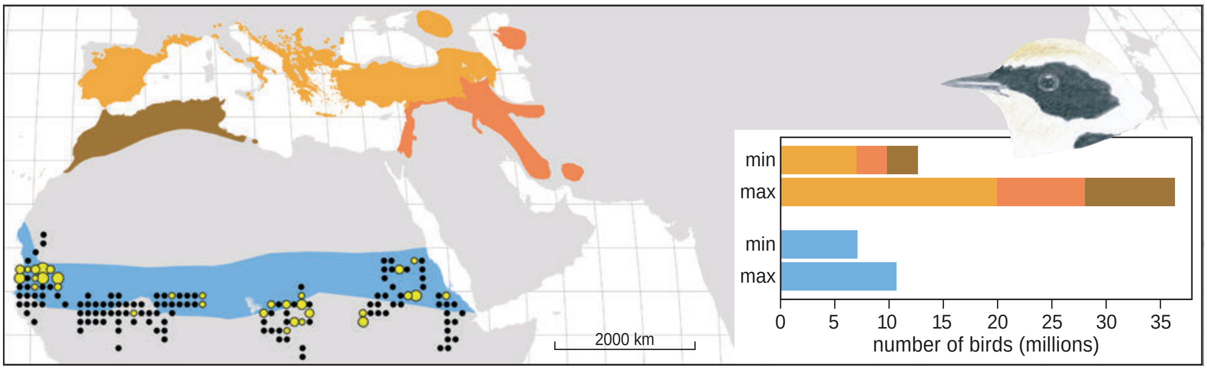

Figure 27. Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*; explanation in Figure 2; see also Figure A29 in Zwarts *et al.* (2022b).

Western Black-eared Wheatear using a small tree to avoid heat stress when ground temperature exceeds 50°C.

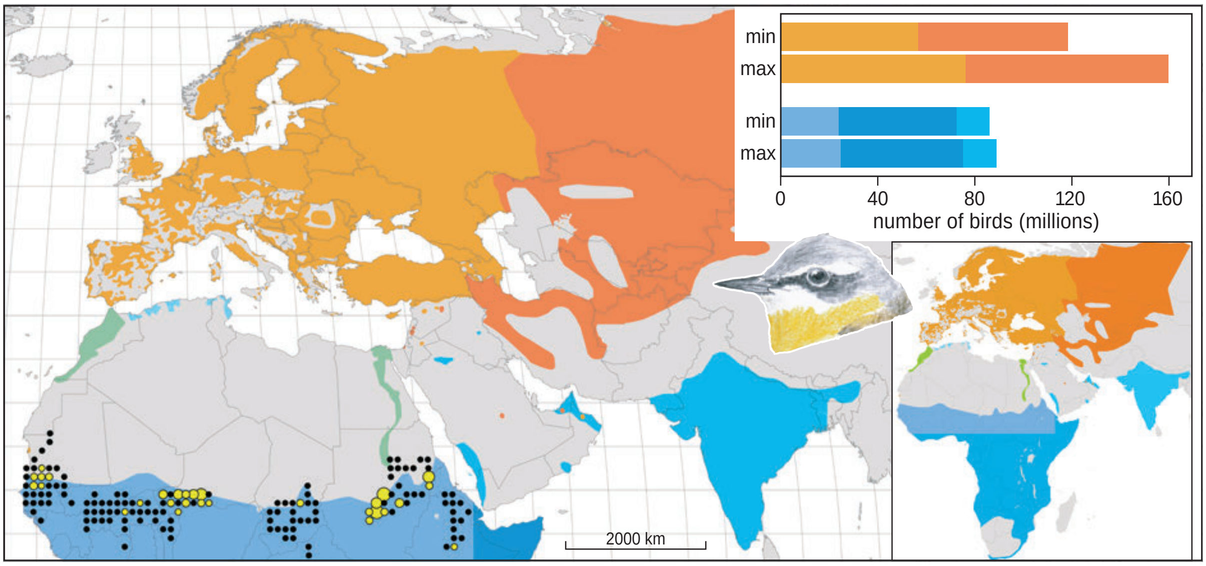

Figure 28. Western Yellow Wagtail *Motacilla flava*; explanation in Figure 2; inset map shows entire breeding and wintering range; see also Figure S41 in Zwarts *et al.* (2023a).

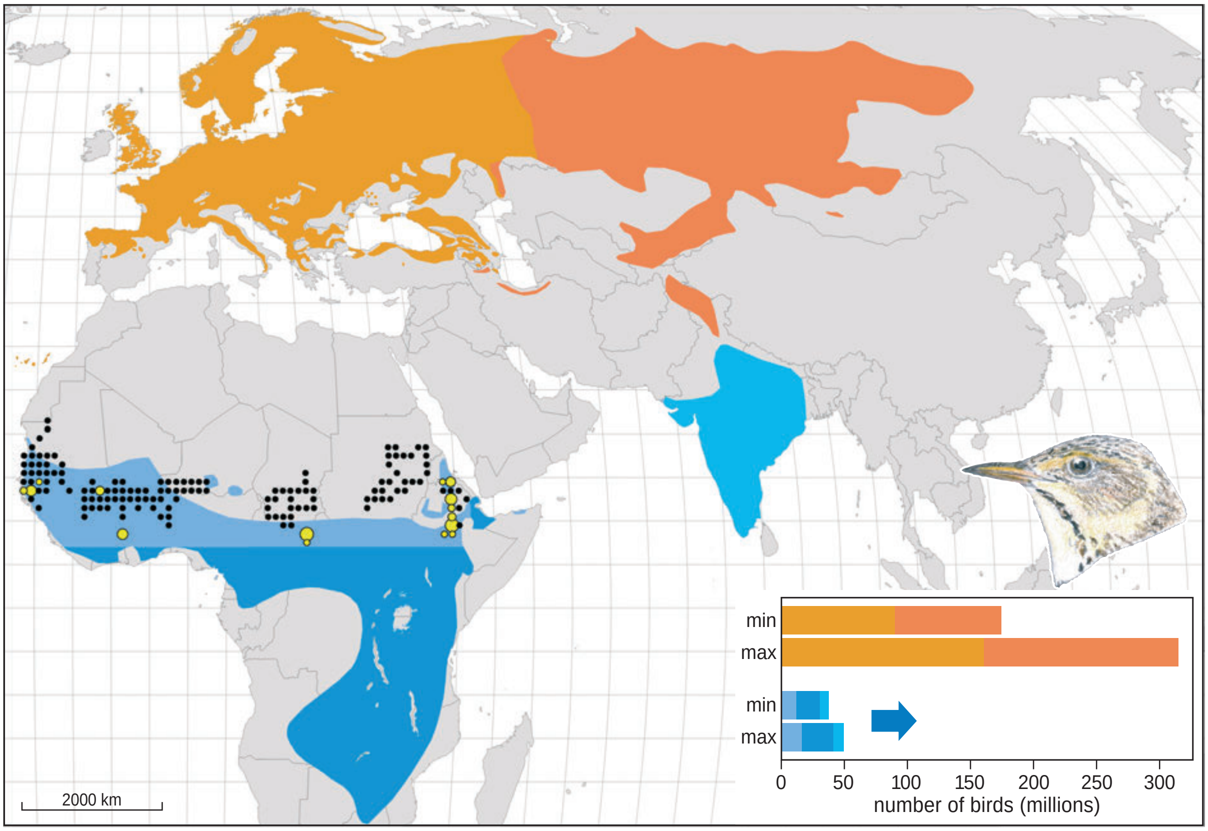

Figure 29. Tree Pipit *Anthus trivialis*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population; see also Figure S43 in Zwarts *et al.* (2023a).

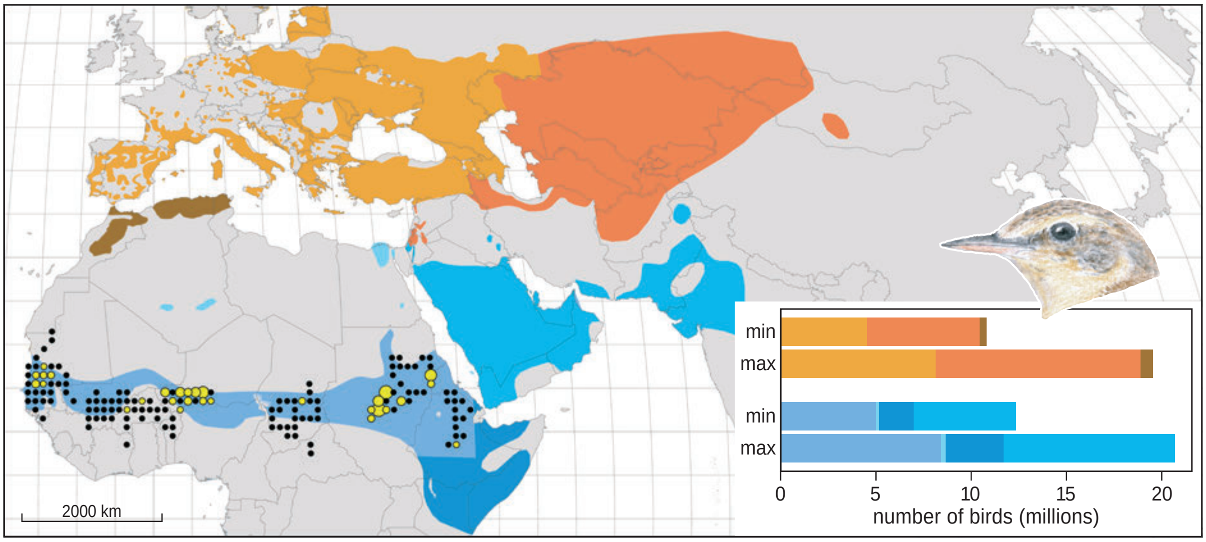

Figure 30. Tawny Pipit *Anthus campestris*; explanation in Figure 2; see also Figure S42 in Zwarts *et al.* (2023a).

DISCUSSION

Breeding and wintering range

Distribution maps of birds are the accumulated work of generations of ornithologists, summarised for Africa by Moreau (1972) and later enhanced by Curry-Lindahl (1981) and further improved in The Birds of Africa (Urban *et al.* 1986, 1997, Keith *et al.* 1992 and Fry & Keith 2004), and specifically for the sub-Saharan region by Nikolaus (1987), Morel & Morel (1990), Borrow & Demey (2004), Redman *et al.* (2009), Dowsett-Lemaire & Dowsett (2014, 2019) and Languy (2019). Even so, Borrow & Demey (2004) warned that their distribution maps "reflect the known or inferred distribution of a species in areas of suitable habitat within a broadly defined range. As locality data remain scant for many species in our region, the maps should not necessarily be taken as providing a true reflection of actual distributions and must therefore be used with caution and common sense". Additionally, distributional boundaries are based on arbitrary choices on which bird observation should be classified as "within the range" or not. Distribution areas will become less detailed (and thus likely larger) when coverage is fragmented or based on time-constrained surveys by but a few people. Note, for instance, the detailed and often patchy breeding ranges of birds in Europe, the many gaps truthfully depicting unsuitable habitats, in stark contrast to Asia where coverage is much less intensive than in Europe, and presence of bird species is therefore assumed to be continuous within rough distribution areas (e.g. Figures 23, 25 and 28 for Common Redstart, Northern Wheatear and Western Yellow Wagtail).

The European Breeding Bird Atlases (Hagemeijer & Blair 1997, Keller *et al.* 2020; see also https://ebba2.info/maps/) quantified the distribution of breeding birds by recording their presence in 50 by 50 km squares. The second Atlas (Keller *et al.* 2020) covered 5110 squares, in total 1108 million ha, equivalent to 96% of the total land surface of Europe. We used these data to calculate the total breeding range of the 30 bird species selected by us (in million ha; column 7 in Table 1). The breeding areas derived from the counts in these squares closely matched the surface area of the breeding ranges as given on the distribution maps (Figure 32), but with a systematic deviation: the surface areas on the maps were, on average 15% larger in species with a very wide distribution and, on average, 30% smaller in species with a small breeding range.

The above bias concerning breeding ranges is also applicable to wintering ranges where information is lacking from huge tracts of inhospitable or infrequently visited regions across Africa. Data-deficient distribution maps will be crude, showing an overestimated presence in terms of surface area. An obvious example is the Common Chiffchaff, which is shown to occur widely across the Sahara and the Arabian Peninsula (Figure 8), despite its much patchier distribution so strongly linked to oases and wadis. The latter comprise just about one percent of arid regions (Lövei 1989). Wintering areas depicted in handbooks and field guides are also inflated because many bird species shift seasonally or annually between regions depending on local conditions, resulting in temporal and geographical variations in presence/absence (Pearson & Lack 1992, Herremans 1998b, Jones 1999). At any moment in time, actual wintering ranges are usually smaller than indicated. Our Sahel data reveal that overestimation of the actual wintering range is larger in species with a wide distribution (Figure 32).

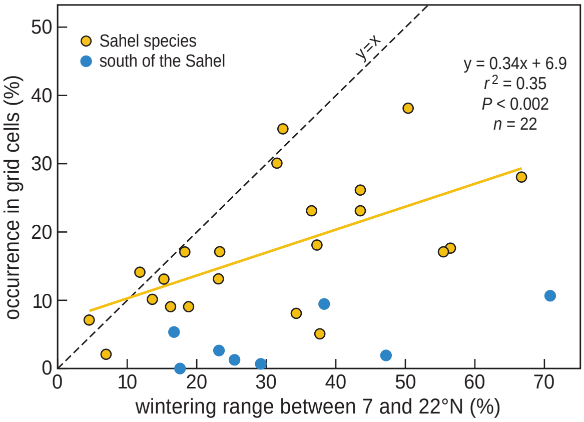

Figure 31. Relative occurrence of mapped species found in the Sahel (yellow dot) and mapped species not found in the Sahel (blue dot). The presence (%) in 150 grid cells is compared to the wintering range (%), given on the maps (Figure 2–30). The eight species with blue symbols, also marked blue in Table 1, were supposed to have a wide distribution in the Sahel, but were in fact absent or encountered in a relatively small number of grid cells during our fieldwork. Raw data given in Table 1 (column 4 and 10).

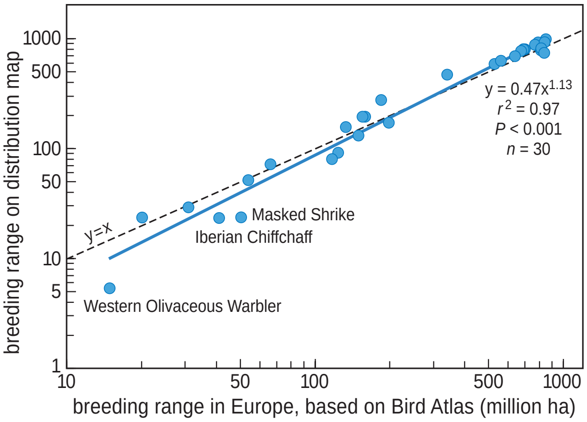

Figure 32. Breeding range in Europe (in million ha) in 30 bird species on distribution maps (Figures 2–30) compared to the breeding range as derived from the 5110 grid cell data in Keller *et al.* (2020). Raw data in Table 1 (column 8 and 7).

The size of the distribution ranges differed substantially between species, on the breeding grounds (between 20 million and 2787 million ha for Rüppell's Warbler and Northern Wheatear, respectively) and on the wintering grounds (between 45 million and 2027 million ha for Iberian Chiffchaff and Western Yellow Wagtail, respectively; Table 1: column 9 and 11). For 57 Afro-Palearctic landbirds breeding in Eurasia and wintering in Africa, Newton (1995) found that wintering ranges were smaller than breeding ranges in 69% of the species; for all species combined the wintering ranges were on average one-third smaller. In the 30 species investigated in this paper, the size of breeding and wintering ranges were highly correlated (Figure 33). Typically, breeding ranges were larger than wintering ranges only in species with large wintering and breeding ranges, as exemplified by the Northern Wheatear, whose total breeding range of 2787 million ha is three times larger than its wintering range. In contrast, breeding ranges were smaller than wintering ranges in species with a small breeding range, with the Rüppell's Warbler as a typical example. Its wintering range (183 million km^2) is eight times larger than the breeding range. Newton (1995) speculated that birds occurred in a higher density on the wintering grounds because they might need more space in the breeding areas and/or that the available land area might be smaller in winter than in summer. That is reasonable, but why should this not hold for species occurring over smaller breeding or wintering ranges?

From the above, we tentatively conclude that breeding ranges usually are larger than wintering ranges in bird species with a wide breeding distribution, but smaller in species with limited breeding distribution (Figure 33). This is at least partly due to an underestimation of the breeding range in species with a small distribution area (Figure 32) and an overestimation of the wintering range in species with a wide distribution (Figure 31). Consequently, bird numbers extrapolated from the size of breeding or wintering ranges, should be treated with caution.

Distribution in Africa

As expected, the distribution on the African wintering grounds between 7 and 22°N, as indicated on published maps and compared to our surveys in 150 grid cells, showed several disparities. Typical Sahelian migrants were found to winter farther north than maps indicated. There are two possible explanations. First, migratory bird species wintering in the northern Sahel are less common farther south (Figure 8 in Zwarts *et al.* 2023b), but apparently sufficiently common to be included within the general distribution range of the species. Second, our data were collected in 2011–2019 during a series of relatively wet years (Supplementary Material 5 in Zwarts *et al.* 2023a), concomitant to a distributional shift to the north into drier habitats (e.g. for Northern Wheatear, although probably not for Tawny Pipit; Zwarts *et al.* 2023d). Whether rainfall explains why birds were observed farther north than previously published maps indicate remains difficult to say, because it is unknown to what degree the distribution maps are based on field observations from the 1970s and 1980s (when droughts prevailed) or from the 1950s and 1960s (series of extremely wet years).

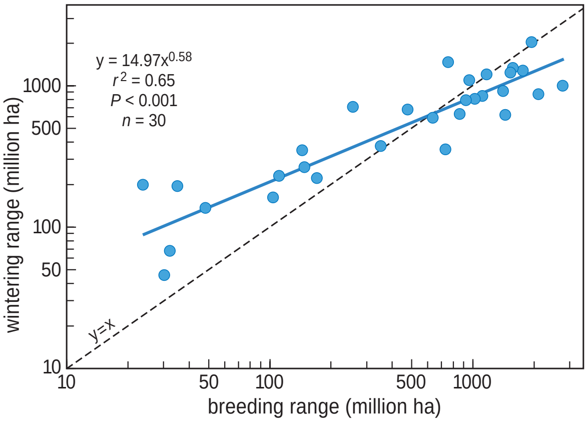

Figure 33. Relation between size of wintering and breeding range in 30 Afro-Palearctic species. Raw data in column 9 and 11 of Table 1.

Migrants wintering in the Guinea vegetation zone cross the Sahel during migration, using stopover areas between Sahara and Guinean wintering sites with >1000 mm rainfall per year. Thus, published maps may include observations from migratory periods, with a subsequent extension of the mapped winter distribution. When stopover and wintering areas are spatially separated, such as for Spotted Flycatchers *Muscicapa striata* wintering in Central Africa and passing the Sahel in October, or for European Pied Flycatchers staging temporarily in acacia forests in NW Senegal in October, the distinction is obvious, because their wintering sites are situated more than 500 km farther to the south, becoming occupied from November onwards. The distinction is less clear in itinerant species that stay north of 8°N until mid-November or even December, before a subsequent movement shifts the mid-winter distribution to regions farther south, such as for Willow Warbler (Salewski *et al.* 2002, Lerche-Jørgensen *et al.* 2017, Zwarts *et al.* 2023d). This might explain the inclusion of the Sahel as a wintering area on maps, despite these birds' complete departure in, or even before, November.

Estimates of population size

Bird population estimates derived from counts on the breeding and wintering grounds are crude and rely on multiple assumptions. This applies specially to birds whose breeding and wintering populations extend beyond Europe and the Sahel respectively, and to bird species with a large discrepancy between the sizes of their breeding and wintering ranges. Take, for instance, the tiny European population of Western Olivaceous Warbler (10,000 birds with a small breeding range of 5 million ha). Its breeding range in North Africa is nearly nine times larger (43 million ha), totalling almost 100,000 birds (assuming the same density as in Europe). All Western Olivaceous Warblers winter in the Sahel, where our surveys arrived at 5.6–11.1 million birds. The discrepancy by two orders of magnitude between breeding and wintering numbers may reflect an overestimate of wintering numbers, but more likely an underestimate of breeding numbers. In fact, the latest survey of European breeding birds suggests a breeding range 2.6 times larger than the distribution map (Keller *et al.* 2020; Table 1: column 7 and 8).

Although our Sahel survey and additional extrapolations may help to improve existing population estimates, prudence and common sense should prevail in the face of so many unknowns. For instance, an estimated 8.8–10.4 million Woodchat Shrikes spend the winter in the Sahel, but since their wintering range extends farther south, the total winter population was extrapolated to 11.2–13.2 million birds. Within the confines of the Sahel, the density declines from north to south (Figure 3), suggesting lower densities further south. As in all other species, however, our extrapolation is based on the assumption that the density is the same as in the Sahel. Similarly, extrapolations for the breeding grounds may be incorrect. To estimate the world population of Common Wheatear, the number estimated for Europe (23–62 million birds) was multiplied by 2.8 to estimate the world population based on the assumption that the density on the European breeding grounds (984 million ha) is equal across the entire range (2787 million ha). The density on the Arctic breeding grounds of Greenland and Northern America (300 million ha) is much lower, however, than in Europe (Dunn *et al.* 2020); the estimated world population of 57–155 million birds is therefore likely too high.

Surprisingly, the most common arboreal migrants in the Sahel were Lesser Whitethroat and Subalpine Warbler, not, as we had expected, Common Whitethroat; the latter was about as common as Western Bonelli's Warbler. Even more surprising, given their respective breeding ranges, was that Rüppell's Warbler turned out to be commoner than Common Redstart. Our surveys showed that 14 bird species (marked light yellow in Table 1) that breed in southern Europe were estimated to have total wintering numbers of 570–810 million birds in the Sahel, some twice as many as the 200–420 million total derived from breeding birds.

The opposite was found for eight species breeding across Europe (Sahel counts: 380–470 million, counts in Europe: 520–910 million; species marked brown in Table 1). An independent check of the estimates of Sahel numbers is not possible, but the European Breeding Bird Atlas (Keller *et al.* 2020) offers the opportunity of evaluating the estimates for European breeding birds. In general, the relationship between breeding range according to the Bird Atlas and general distribution maps is tight (Figure 34), but with clear differences per species. An extreme example is the Masked Shrike for which the breeding range in the Bird Atlas is twice as large as on the distribution map (50 and 23 million ha, respectively). This discrepancy suggests that the species is more common than previously thought and may also explain why the population size based on breeding birds (0.2–0.7 million birds) is so much lower than estimated for wintering numbers (3.5–6.6 million). In contrast, the European breeding range of the Common Redstart is 12% smaller in the Atlas (767 million ha) than on the distribution map (874 million ha), perhaps also indicating a lesser abundance, which may explain why the estimated number of breeding birds (40–73 million birds) is higher than the estimate based on Sahel counts (15–21 million birds). Figure 34 plotted the ratio of the estimated population size based on counts on the breeding or wintering grounds against the ratio of the European breeding range such as determined on the Atlas and the distribution maps. The relationship is shown for 10 species, disregarding eight bird species wintering south of the Sahel and 11 species for which the breeding range in Europe is less than 50% of the total breeding range (and thus less reliable). The Sahel counts arrived at a larger population than the summer counts in six species, of which five have a larger range in the European Breeding Bird Atlas than on published distribution maps (Masked Shrike, Iberian Chiffchaff, Western Bonelli's Warbler, Subalpine Warbler and Woodchat Shrike; the exception is Rüppell's Warbler). The Sahel counts were lower than the summer counts in four species, all with a smaller range in the Bird Atlas (Common Whitethroat, European Pied Flycatcher, Common Redstart and Black-eared Wheatear).

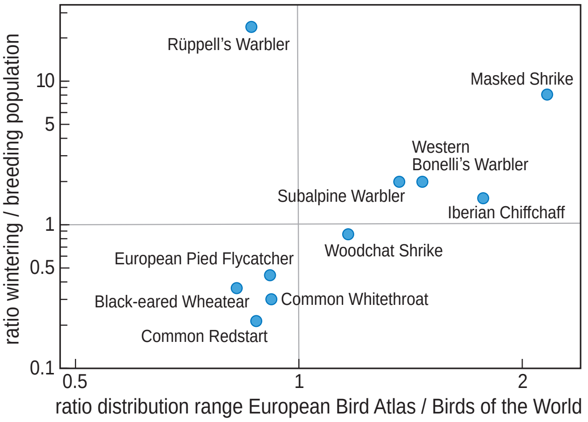

Figure 34. The larger the breeding ranges in the European Bird Atlas (Keller *et al.* 2020) relative to those indicated on distribution maps, the larger the population size, derived from wintering numbers relative to those based on breeding birds. Selection made of species occurring in the Sahel of which the total breeding range is less than twice the breeding range in Europe. Raw data in Table 1 (*y*-axis: ratio of average population size, from column 18–19 and 14–15; *x*-axis: ratio of breeding ranges, from column 7 and 8).

We conclude that the breeding populations of southern European species have so far been underestimated, especially for Masked Shrike, Western Bonelli's, Subalpine and Rüppell's Warbler, but that widespread species such as Common Redstart and Common Whitethroat most likely have been overestimated. The latter two species were much more common in their breeding ranges before 1969, at which time their populations collapsed due to a series of drought years in the Sahel (e.g. Winstanley *et al.* 1974, Zwarts *et al.* 2009). After annual rainfall patterns recovered in the Sahel, their population sizes increased again from 1992 onwards, but without reaching pre-1969 levels.

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SAMENVATTING

Over de zomer- en winterverspreiding van vogelsoorten is de afgelopen decennia veel bekend geworden. Regionale, nationale en zelfs wereldwijde populatieschattingen zijn in toenemende mate gebaseerd op gestandaardiseerde tellingen in plaats van aannames en ruwe schattingen. Maar hoe nauwkeurig zijn die verspreidingskaarten en populatieschattingen? Met onze gestratificeerde (en absolute, in plaats van relatieve) tellingen in de Sahel hebben we een handvat om schattingen te maken vanaf de andere kant van het spectrum, namelijk vanuit de winterpopulatie. Het is een unieke kans om schattingen in de broedgebieden te toetsen op betrouwbaarheid. Voor toetsing van de verspreiding in de noordelijke helft van Afrika zijn onze gegevens ook heel geschikt, wederom vanwege de gestratificeerde opzet van het onderzoek en onder gebruikmaking van betrouwbare dichtheidsverschillen binnen de regio. In dit artikel vergelijken we voor 30 vogelsoorten die in Europa en Azië broeden en in Afrika overwinteren, de winterverspreiding volgens het Handbook of Birds of the World met vogeldichtheden die gemeten zijn verspreid over de hele Sahel, een gebied van 10 miljoen km^2. De meeste vogelsoorten die in het noordelijke en droogste deel van de Sahel overwinteren, bleken in werkelijkheid wat noordelijker te verblijven dan op de gepubliceerde verspreidingskaarten is aangegeven. Uit de vogeltellingen bleek ook dat vogelsoorten die normaliter ten zuiden van de Sahel overwinteren, dat zuidelijker deden dan verwacht en daardoor nauwelijks, of zelfs niet, bleken voor te komen in de zuidelijkste rand van de Sahel zone (met >1000 mm regenval per jaar). Op basis van onze tellingen blijken de kaartenmakers in handboeken en avifauna's het daadwerkelijke wintergebied van vooral wijdverbreide vogelsoorten te overschatten. De systematische vogeltellingen in de Sahel werden gebruikt om een totaalschatting te maken van het aantal trekvogels dat daar overwintert. Die schattingen werden vergeleken met de geschatte broedpopulaties van diezelfde vogelsoorten in Europa. Aangezien veel soorten niet alleen in Europa broeden en ook niet alleen in de Sahel overwinteren, zijn de wereldpopulaties geschat aan de hand van de totale oppervlakte van broed- en overwinteringsgebieden. Uit de systematische inventarisatie in de Sahel blijkt dat de totale populatieomvang van soorten die hoofdzakelijk in Zuid-Europa broeden, sterk wordt onderschat. Dat is in het bijzonder het geval bij Maskerklauwier *Lanius nubicus*, Bergfluiter *Phylloscopus bonelli*, Baardgrasmus *Curruca iberiae + C. subalpina + C. cantillans* en Rüppell's Grasmus *Curruca ruppeli*. Daarentegen lijken de broedpopulaties van Gekraagde Roodstaart *Phoenicurus phoenicurus* en Grasmus *Curruca communis* te worden overschat.

RÉSUMÉ

Au cours des dernières décennies, les connaissances sur la répartition des espèces d'oiseaux ont beaucoup progressé. Les estimations de populations se sont affinées grâce l'utilisation de résultats de comptages standardisés. Mais dans quelle mesure les aires de répartition et les estimations de population actuelles sont-elles précises? Les inventaires basés sur une méthode d'échantillonnage stratifié réalisés en période hivernale dans l'ensemble Sahel offrent une occasion unique de tester la fiabilité des estimations basées sur les effectifs reproducteurs. Dans cet article, nous comparons les populations nicheuses de 30 espèces d'oiseaux d'origine paléarctique hivernant en Afrique avec les populations hivernales calculées sur la base des densités rencontrées dans les 10 millions de km^2 de la zone sahélienne. Nos résultats montrent que les espèces qui hivernent dans la partie septentrionale du Sahel (la plus sèche) fréquentent des zones un peu plus au nord que celles figurant dans les cartes de répartition publiées. Cet écart peut être lié à des précipitations plus abondantes pendant notre période d'observation (2011–2019) que pendant les années précédentes, notamment durant la grande sécheresse de 1969 à 1992. Les effets négatifs de la sécheresse sur la végétation sahélienne ont donc été moins prononcés. Par ailleurs, les espèces qui hivernent principalement dans les zones tropicales humides plus au Sud n'ont été que très peu rencontrées dans la partie méridionale de la zone sahélienne, bien que celle-ci reçoive plus de 1000 mm de pluie par an. Les aires de répartition hivernales publiées semblent donc surestimées, en particulier pour les espèces les plus répandues. Les estimations de populations obtenues à partir des comptages hivernaux au Sahel ont été comparées à celles basées sur les populations reproductrices en Europe. De nombreuses espèces ne se reproduisant pas uniquement en Europe et n'hivernant pas uniquement au Sahel, les populations mondiales ont été estimées en appliquant les densités rencontrées au Sahel à la superficie totale des aires de reproduction et d'hivernage. Les résultats montrent que les populations des espèces qui se reproduisent principalement en Europe du Sud sont largement sous-estimées. C'est notamment le cas de la Pie-grièche masquée *Lanius nubicus*, du Pouillot de Bonelli *Phylloscopus bonelli*, des fauvettes du complexe « passerinette » *Curruca iberiae + C. subalpina + C. cantillans* et de la Fauvette de Rüppell *Curruca ruppeli*. En revanche, les populations nicheuses du Rougequeue à front blanc *Phoenicurus phoenicurus* et de la Fauvette grisette *Curruca communis* semblent être surestimées.

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Selection by birds of shrub and tree species in the Sahel

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The Sahel is thinly covered by trees, but nevertheless forms an important habitat for millions of tree-dwelling birds. We describe tree availability and tree selection of 14 insectivorous Afro-Palearctic migrants and 18 Afro-tropical residents (10 insectivores, 3 frugivores and 5 nectarivores) inhabiting the Sahel from the Atlantic to the Red Sea. Of the 304 woody species identified across the region during systematic fieldwork in stratified plots, we noted height and canopy surface of 760,000 individual woody plants. Birds present in trees and shrubs were recorded separately per individual woody plant. 99.5% of the birds were concentrated in only 41 woody species. For 20 out of 32 bird species, Winter Thorn *Faidherbia albida* was the tree species most often used. Two other important tree species were Umbrella Thorn *Acacia tortilis* and Desert Date *Balanites aegyptiaca*. Representing only 11% of the total woody canopy cover, these three species attracted 89% of Western Bonelli's Warblers *Phylloscopus bonelli* and 77% of Subalpine Warblers *Curruca iberiae* + *subalpina* + *cantillans*. High selectivity for particular woody species was typical for migrants and residents, irrespective of their diet. Bird species feeding in shrubs used a larger variety of woody species than bird species feeding in tall trees. The highest bird densities (80–160 birds/ha canopy) were found in three shrubs with a limited distribution in the southern Sahara and northern Sahel: the berry-bearing Toothbrush Tree *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua* and the small tree *Maerua crassifolia*. Other bird-rich woody species were without exception thorny (*Balanites aegyptiaca*, various species of acacia and ziziphus). In contrast, the five woody species most commonly distributed across the region (Cashew *Anacardium occidentale*, African Birch *Anogeissus leiocarpus*, *Combretum glutinosum*, *Guiera senegalensis* and Shea Tree *Vitellaria paradoxa*), representing 27% of the woody cover in the study sites, were rarely visited by foraging birds. In this sub-Saharan region, it is not total woody cover per se that matters to birds, but the presence of specific woody species. This finding has important implications: remote sensing studies showing global increase or decline of woody vegetation without identifying individual species have little value in explaining trends in arboreal bird populations. Local people have a large impact on the species composition of the woody vegetation in the Sahel, with positive and negative consequences for migrants wintering in this region. *Faidherbia albida*, the most important tree for birds in the sub-Saharan dry belt, is highly valued by local people and has the distinction of leafing in winter and being attractive to arthropods. On the other hand, migratory and African bird species have been negatively affected by the rapidly expanding cashew plantations since the early 1980s.

Key words: arboreal birds, Sahel, tree selection, Cashew, Shea Tree, *Faidherbia*

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Birds foraging in woody vegetation are highly selective in their choice of trees and shrubs. Frugivores are concentrated in the few trees where they can find their preferred fruit (e.g. Levey 1988, Herrera 1998, Jordano 2015) and nectarivores select nectar-producing flowering trees (e.g. Feinsinger 1976, Pettet 1977, Symes *et al.* 2008). The same principle applies to the many insectivorous tree-dwelling bird species (Zwarts *et al.* 2015). In West Africa, arboreal birds are concentrated in only 20 out of the 56 most common woody plant species. Woody species disregarded by foraging birds have coriaceous leaves, leaves with latex and/or leaves with a high crude fibre content (Zwarts *et al.* 2015). These traits have evolved as a defence mechanism against herbivorous insects, explaining the scarcity of insectivorous birds foraging in such woody species. Most insectivorous bird species are instead found in woody species with thorns or spines, such as acacias: these woody species have evolved mechanical defences against grazing by large herbivores, at the expense of chemical defences against arthropods. The consequence of this strategy is higher insect loads, precisely why many thorny trees are attractive to insectivorous tree-dwelling birds (Greenberg & Bichier 2005).

In African savannahs, the grazing pressure of large herbivores on woody plants has always been high but became even higher after domesticated herbivores, mostly cattle, sheep and goats, replaced the indigenous grazing fauna during the 20th century (at least in the Sahel; on the East African savannahs herbivore species-richness has remained very high (Prins & Olff 1998). In regions with an annual rainfall >800 mm, however, large herbivores are mostly absent due to the occurrence of the Tsetse Fly *Glossina morsitans*, which is the vector of tripanosomes responsible for causing sleeping sickness (Buxton 1955). This explains why acacias and other thorny shrubs and trees dominate the semi-arid and arid zone (100–600 mm rain/year) and are replaced in the more humid zone by non-thorny woody plants with better defences against arthropods. The humid zone looks greener and lusher than the adjacent more arid Sahel, superficially suggesting a richer food supply, but in fact it is the opposite: trees from savannahs are rich in arthropods and attract more insectivorous birds than trees from the adjacent humid zone (Zwarts *et al.* 2023b).

To unravel the intricate relationships between birds and their Sahelian habitat, Zwarts *et al.* (2015) counted birds per individual woody plant and measured for each woody plant its canopy surface, thus allowing calculation of bird density per ha of canopy and ranking of the attractiveness of woody species for birds. Densities ranged from 0 to 122 birds/ha canopy in the 56 most common tree and shrub species. The initial analysis was restricted to West Africa but covered a wide array of climate zones, where woody species as well as bird species experienced different levels of rainfall. Distributions of tree and bird species rarely overlap one-on-one, which complicates any assessment of tree preference by birds. Tree selection by bird species is therefore described only for woody species that are within the bird's distribution. The present analysis includes and expands upon the data used in Zwarts *et al.* (2015), and covers the entire transient zone south of the Sahara between Atlantic Ocean and Red Sea. Using this much larger data set, we quantify: (1) the distribution of the woody species across the region, (2) tree choice of bird species (species, height), (3) density of bird species foraging in woody species, (4) variation in bird density per woody species relative to traits of woody species presumed to be related to species-specific food supplies (tree size, presence of leaves, flowers, fruit and thorns, production of latex, whether tree is indigenous or exotic), (5) total woody cover of different shrubs and trees, and (6) total number of birds present in the different woody species.

METHODS

The methods used to count birds and woody plants are described in great detail by Zwarts & Bijlsma (2015) and briefly again in Zwarts *et al.* (2023a,b). In summary, birds and woody plants were counted between 2011 and 2019 at 1901 randomly selected study sites (each 4.5 ha) in Africa between 7° and 22°N and between 17°W and 42°E. We used data collected during the dry season (20 November – 10 March), a period during which tree-bird relationships are relatively stable (Zwarts *et al.* 2023d).

We counted and measured all trees and shrubs in the study sites and used the width of the canopy to calculate canopy surface per individual woody plant. Using a laser rangefinder, we measured the height of each larger tree at a distance of at least twice the tree height. The height of trees <4 m was estimated by eye. The width of the canopy was estimated by eye as fraction of the height which was checked in large trees by pacing steps beneath the crown and by taking pictures. A total of 765,960 woody plants with a combined canopy surface of 4,312 million m^2 were registered. Altogether we identified 304 woody species. We scored individual woody plants regarding their opacity on a five-point scale from 'leafless' to 'very dense crown'

(Zwarts & Bijlsma 2015); in this paper we only use the proportion of leafless woody plants. For each study site we calculated the total woody cover per woody species and for all woody species combined. The latter may overestimate the actual woody cover if shrubs occur underneath trees. Indeed, in one site, our method indicated a total woody cover of 105%, but this was an exception because the woody cover in most sites was so low that canopies of different woody plants did not overlap.

Birds present in trees and shrubs were recorded separately per individual woody plant. Each tree and shrub was examined for as long as necessary to detect all birds present (Zwarts & Bijlsma, 2015). This enabled the calculation of absolute bird density per tree species, expressed as birds per ha of canopy. The counts of birds and woody plants were converted into densities per study site, after which average densities were calculated for sites in 150 1° latitude × 1° longitude grid cells. In addition, for each bird species we also determined total woody cover within its distributional range, based on the grid cells where the species occurred. Most bird species were found in about a quarter of the grid cells and the most widely distributed species in half of the grid cells (Zwarts *et al.* 2023b). Distribution maps of the most common arboreal bird species are given as Supplementary Material in Zwarts *et al.* 2023b. The presence of a bird species in the 150 grid cells is used here to define the distribution area of the 32 most common bird species, of which 14 are Afro-Palearctic species (from now on called migrants) and 18 are Afro-tropical species (referred to as residents).

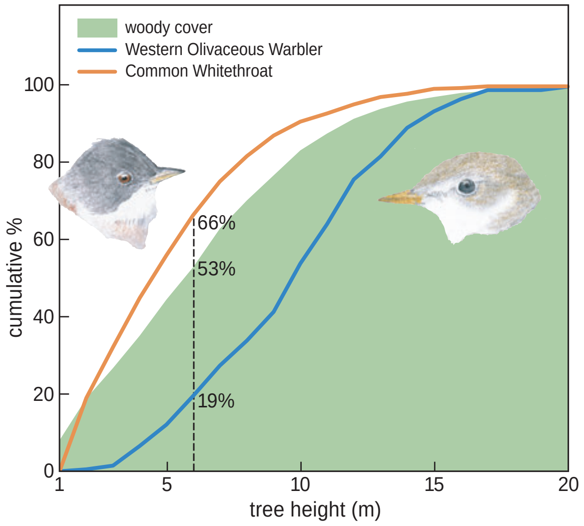


Figure 1. The cumulative frequency distribution of woody cover (%) as a function of height of woody plants ≥1 m used by two bird species compared to the height of all trees and shrubs in the sites where both species were recorded.

For each study site, we determined the average annual rainfall in the period 1950–2000 (Hijmans *et al.* 2005) and used this information to ascertain the average annual rainfall for each site and each grid cell. The grid cells span a range of climate zones from Sahara to Guinean forests, with an annual rainfall between 30 and 1800 mm (see Figure 4 in Zwarts *et al.* 2023a). Strictly, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a) but we use the term Sahel here in a wider sense as the transition zone between Sahara in the north and the humid forests in the south.

In dry areas, the height of the woody vegetation tends to be far lower than in humid areas (Figure S9C). Even when excluding all shrubs ≤ 1 m, there is still a linear increase of the average height (H) of the woody vegetation from 3 m in the hyper-arid zone (<100 mm rainfall/year) to 6 m in the hyper-humid zone (>1200 mm rainfall/year):

$$H = 0.00166 \times \text{rain} + 2.9$$
$$(r^2 = 0.87, n = 16, P < 0.001), \qquad (1)$$

where H = average height (m) of the woody vegetation and rain = annual rainfall (mm); regression line based on average values per rainfall classes of 100 mm over the range 0 to 2400 mm; rainfall classes 1300–2400 were combined in three categories in order to have >1000 woody plants in all categories.

The linear increase of tree height with rainfall explains why bird species confined to arid regions dwell in smaller trees than species typical of humid zones, as for example respectively Eastern Orphean Warbler *Sylvia crassirostris* (recorded in trees 4.7 m high, on average) and Northern Yellow White-eye *Zosterops senegalensis* (8.2 m; see Figure 5A in Zwarts *et al.* 2023b for the distribution of bird species along the rainfall gradient). Within the same rainfall zone, bird species may also differ in foraging height, as exemplified by Western Olivaceous Warbler *Iduna opaca* and Common Whitethroat *Curruca communis*. Western Olivaceous Warbler is typically a canopy-hugging passerine that was not recorded in woody plants <4 m tall, whereas 66% of all Common Whitethroats were detected in shrubs and trees <4 m tall. Had these species not been selective of their feeding niche, 53% of both species would have been expected to use trees up to and including 6 m high (Figure 1), where it was in fact respectively 19% and 66%. In this paper the 6-m threshold is used to discriminate bird species feeding in low and high woody vegetation.

Since the grid cells were unevenly distributed across the region, we calculated the average woody cover for 11 rainfall zones in six longitudinal bands for the region shown on Figure 2 (i.e. Africa between 7° and 22°N and between 17°W and 42°E, in total 10 million km^2) and used the surface area of the subregions (given in Figure S1 of Zwarts *et al.* 2023a) as weighting factors to estimate average woody cover and total woody cover in the region. We applied a split-half method (even and odd numbered sites) to assess the reliability of the estimated total woody cover (see Supplementary Material).

For the analyses of tree use by birds, shrub and tree species were selected in which >0.5% of arboreal birds were found. Tree preference by bird species was quantified with the proportion of birds observed in different woody species compared to the canopy cover of all woody species within the distribution area of each bird species (Table 1). The density of all bird species combined is calculated for 112 woody species, each with >2000 m^2 canopy cover in our sample, for the 29 most common woody species, each >0.9% of the canopy surface relative to the total cover of all woody plants, and separately per bird species (Table 2). Again, bird densities in the various woody species refer to the woody species present within the distribution areas of the bird species. These averages cannot be used to estimate the density of all birds together since most bird species occupy only a proportion of the woody species' distributions, and in differing proportions per bird species. Simply adding densities would, on average, result in an overestimate by a factor of two. Therefore, bird densities per woody species for all species together were calculated for all woody plants in the entire region.

RESULTS

Distribution of woody plants

The total woody cover increased from <1% in the desert to >15% in the humid zone (annual rainfall > 1000 mm) and averaged 9% for the entire region between 7° and 22°N (Figure S1). The five most common woody species each contributed 5–6% to the total woody cover. African Birch *Anogeissus leiocarpus* (Figure S6), *Combretum glutinosum* (Figure S7) and *Guiera senegalensis* (Figure S8) were widely distributed and found in about half of the grid cells though *Guiera* was largely restricted to the less humid zone. Cashew *Anacardium occidentale* (Figure S5) and Shea Tree *Vitellaria paradoxa* (Figure S9) were locally common, but large regional differences were apparent. Cashew was restricted to the more humid zone, being the dominant tree species in Guinea-Bissau and southern Mali but rare in the same humid zone of Central African Republic and southern Chad. Whereas Shea Tree was absent in the humid zone of Senegal and Guinea-Bissau, it was very common in the same climate zone in Mali and Burkina Faso. For *Anogeissus* it was the other way round: widely distributed in the Central African Republic and Chad but an erratic distribution in West Africa. The common denominator for these very common tree species was the scarcity of birds (see below).

Of all tree species available within the range of our study area, very few were preferred by foraging birds. Some of these were scarce or patchy in distribution and therefore, despite being highly attractive to birds, harboured a minor proportion of the overall bird population. Only Umbrella Thorn *Acacia tortilis*, Winter Thorn *Faidherbia* (=*Acacia*) *albida* and Desert Date *Balanites aegyptiaca* were rich in birds as well as widely distributed (Figures S2–S4). All three occurred throughout the region from Senegal to Ethiopia, with *A. tortilis*

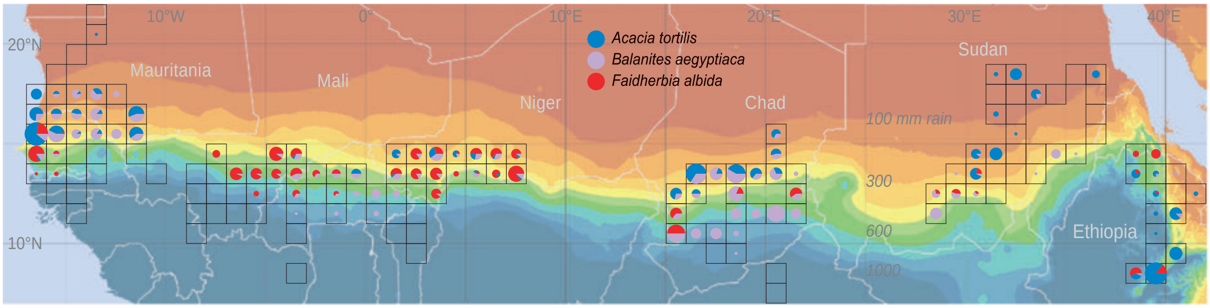


Figure 2. Relative woody cover of three bird-rich woody species combined (data from Figure S2–S4) in 150 grid cells. Woody cover of the three species, relative to woody cover of all species combined, amounts to 8.4%, on average, varying between 0 and 55% per grid cell. The three species were present in 83% of the grid cells.

Table 1. The percentage of the recorded birds found in 41 woody plants shown for the 32 most common bird species. Colours indicate which woody plants attract most birds (rank 1: orange, rank 2: yellow, rank 3: grey). Names of thorny shrubs and trees are shown in bold.

	Insectivorous migrants														Insectivorous residents										Frugivores			Nectarivores				
	Eurasian Wryneck	Iberian Chiffchaff	Common Chiffchaff	Eastern Olivaceous Warbler	Western Olivaceous Warbler	Western Bonelli's Warbler	Western Orphean Warbler	Eastern Orphean Warbler	Lesser Whitethroat	Subalpine Warbler	Rüppell's Warbler	Common Whitethroat	European Pied Flycatcher	Common Redstart	Green Wood Hoope	Grey Woodpecker	Sennar Penduline Tit	Northern Crombec	Yellow-bellied Eremomela	Senegal Eremomela	Green-backed Camaroptera	Tawny-flanked Prinia	Northern Yellow White-eye	Little Weaver	Blue-naped Mousebird	Vieillot's Barbet	Common Bulbul	Pygmy Sunbird	Nile Valley Sunbird	Scarlet-chested Sunbird	Beautiful Sunbird	Variable Sunbird
Acacia asak			7															1				1							2			13
Acacia ataxacantha														2				1		1	10	2						1			1	
Acacia ehrenbergiana		2	1	1		1	1	7	2	1	2							1											4	1		
Acacia etbaica								4	2		10							1											1			
Acacia mellifera			2	3					2									1	3										19	2		
Acacia nilotica			3	12		2		4	7	1	1	3	8	3	2		5	1		2	1	3		2	1	1					2	
Acacia senegal		7	1	2		3	10	11	2	1	4	1		1	2		8	1	1	2	1	1		4		1		3	9	2		
Acacia seyal		2	8	4	9	2	1	4	4		4	6		7	2		8	14	13	1	2	9		6		6		6	2	1	5	13
Acacia sieberiana													5							1	1	1		2		1	3			5	1	
Acacia tortilis	9	28	2	17	8	27	49	26	23	20	26	12		6	2	23	20	9	32	4	1	1		9	6	9	3	3	40	2	2	6
10 OTHER ACACIA's			13						3					2				1				3	2									4
Albizia amara	4													1		2		2			2	1				4		1	1			
Anogeissus leiocarpa													8	1				5		4	2	2		1		6	3	2		3	1	
Azadirachta indica		4		2	5									1							1				24	3	7			1	1	
Balanites aegyptiaca	30	12		6	3	6	13	4	12	26	5	12		5		8	48	13	20	14	11	22	2	13	26	11	2	9	1	2	6	
Bombax costatum																2				3						1		2		9	1	1
Boscia senegalensis							1			1		4		1					4		2											
Capparis decidua		1	2	1				15	7	4	11	6						1	1									2	8			
Commiphora africana			9																3													
Combretum glutinosum				1					1	1		3	5	2	13	2		7	8	10	5	6		1		3	1	19		11	24	1
Combretum micranthum	4											2		5				1		3	10	1						1			2	
Daniellia oliveri													3					1		2			16	1		1	6	3		8	3	3
Diospyros mespiliformis					1									1	2	2					1		7		5	4	2			1	3	
Euphorbia balsamifera		11			1							4		1					3	1										5		
Faidherbia albida	13	12	30	43	49	56	13	11	24	30	11	16		25	21	23		10		8	6	7	7	48	1	14	3	10	1	3	12	9
Ficus exasperata																											28					
Ficus sycomorus															2											4	2					
Ficus thonningii																										10	4					
Guiera senegalensis										1		3							3	1	3	3						1			1	3
Isoberlina doka													8		3												1			2		1
Maerua crassifolia								4	2	1	19	1		1											1			5	1			
Mangifera indica		2			7								8	2		2					1									2		
Mitragyna inermis														3	2	4					1						4			1		
Parkia biglobosa													8		2			1		7		1	18				4	1		2	1	
Piliostigma reticulatum	30		3	1	1		2		1	3		7		6	8	6		1	1	4	6	10	2	1				4	3	1	5	
Prosopis juliflora		4	1												11																	
Pterocarpus lucens														2				4		2	1	1				3	1					
Salvadora persica		4		1			4			2		3										1		1	16			1	2			
Sclerocarya birrea				1			1		1			1		2	7	6		5		4	1	2		1		4		3		2	3	
Tamarindus indica							1							2	8	6		2		3	3	3	5	1		4	4	2		5	3	
Vitellaria paradoxa													3	1		4		6		9	1	1	2	2				6		14	6	
Ziziphus mauritiana					6	1	1	4		1	4	2		7			5			1	5	5		3								2
SUM	91	89	82	94	90	97	96	93	92	94	96	87	57	88	86	92	93	86	93	85	77	85	61	92	80	93	78	82	95	84	79	57
A.tort.+Balanites+Faid.	52	52	32	66	60	89	76	41	59	77	42	40	0	36	23	54	68	32	52	26	19	30	9	70	33	34	8	21	42	7	20	14
all 21 Acacia species	22	51	67	82	66	90	75	67	68	54	57	38	14	47	28	46	40	38	49	19	22	28	9	70	8	33	9	22	78	16	22	45
all 26 thorny species	52	68	79	89	75	97	89	89	87	86	76	59	14	58	39	54	93	52	73	33	38	54	11	85	34	44	11	32	87	18	28	47

Table 2. Birds/ha canopy for the 32 common arboreal bird species, shown for the 29 most common trees and shrubs (each >0.9% of the total woody cover measured in the random study sites during winter) and 13 uncommon trees and shrubs in which birds reach a relatively high density. Five bird species and 5 woody species from the dry zone (<300 mm rainfall/year) are highlighted in dull yellow and 3 bird species and 5 woody species from the humid zone (>900 mm rainfall/year) marked blue. Names of thorny species are in bold. The bird densities are calculated for woody plants present in all sites within the grid cells where the bird species occur (Figures A2 – A34 in Zwarts *et al.* 2022b). Bird density is zero when the cell is empty. A cell is marked with • when a woody species did not occur, or scarcely so, within the distribution area of a bird species (i.e. surface area of the canopy <1000 m^2). Colours indicate common woody plant species in which birds reach their highest densities (rank 1: orange, rank 2: bright yellow).

	Insectivorous migrants														Insectivorous residents										Frugivores			Nectarivores				
29 common species	Eurasian Wryneck 518	Iberian Chiffchaff 227	Common Chiffchaff 707	Eastern Olivaceous Warbler 415	Western Olivaceous Warbler 560	Western Bonelli's Warbler 450	Western Orphean Warbler 287	Eastern Orphean Warbler 247	Lesser Whitethroat 318	Subalpine Warbler 368	Rüppell's Warbler 188	Common Whitethroat 466	European Pied Flycatcher 1124	Common Redstart 608	Green Wood Hoope 589	Grey Woodpecker 562	Sennar Penduline Tit 517	Northern Crombec 646	Yellow-bellied Eremomela 394	Senegal Eremomela 783	Green-backed Camaroptera 752	Tawny-flanked Prinia 725	Northern Yellow White-eye 1017	Little Weaver 579	Blue-naped Mousebird 503	Vieillot's Barbet 652	Common Bulbul 926	Pygmy Sunbird 699	Nile Valley Sunbird 216	Scarlet-chested Sunbird 930	Beautiful Sunbird 850	Variable Sunbird 896
Acacia nilotica			7.3	6.2	0.7	7.3		1.6	8.5	7.4	2.1	4.0	27	2.7	2.6		2.2	0.4		5.6	2.2	5.5		2.7	3.3	0.7		0.3			4.6	
Acacia senegal		4.0	3.4	0.5	0.5	5.6	8.6	2.0	1.0	4.0	1.5	1.1	•	0.3	1.4		2.1	0.2	0.3	0.5	0.7	2.3	•	3.3		0.5		2.4	5.7	2.5		
Acacia seyal			7.9	0.8	2.3	1.9	0.3	1.3	1.1	0.5	0.7	1.4	•	0.9	0.1		0.4	1.4	4.4	13	0.8	2.9	•	1.9		0.4		1.4	0.5	0.5	1.4	1.6
Acacia tortilis	1.0	2.6	0.7	2.4	1.7	23	7.4	2.7	8.3	13	4.9	3.6	•	0.9	0.4	2.2	1.4	1.4	1.9	2.0	0.6	0.6	•	3.8	1.9	1.1	0.5	1.1	14	0.7	4.1	2.7
Albizia amara	2.7	•				•			0.2		•	0.3	•	0.5		0.6		0.5		•	1.5	0.7	•	0.3		0.8		0.7	6.2			
Anacardium occidentale			•					•	•		•		0.9		5.9		•			0.5	0.7				•				•		0.9	
Anogeissus leiocarpus			•		0.2	1.0		•		0.7		0.2	0.5	0.2				0.5		1.5	0.5	0.9		0.2		0.4	0.2	0.4	•	0.4	0.1	
Azadirachta indica				2.6	3.6	0.4		•		1.6	•	0.3		0.8							1.0	0.9		0.5	22	3.2	5.7		•	0.7	0.7	
Balanites aegyptiaca	1.3	1.2		1.2	0.5	3.7	1.8	2.5	3.6	13	1.2	2.4		0.5		0.5	2.0	1.2	1.3	4.8	3.4	6.8	3.2	3.2	6.6	0.7	0.3	1.8	1.0	0.6	2.2	
Boscia senegalensis			•				0.3		0.7	1.5		3.9	•	0.2					0.9		2.7	0.7	•									
Calotropis procera		1.0	•				0.4			0.6		0.2	•						0.5			0.3	•					1.8	12	1.3		•
Combretum glutinosum				0.4	0.1	0.2		•	3.2	0.9		1.1	1.5	0.2	1.8	0.2		1.2	2.1	2.0	1.4	2.1		0.9		0.4	0.4	4.8	•	3.8	8.8	0.5
Combretum micranthum	0.4		•		0.1			•	•		•	1.0	•	0.9			•	0.5		0.9	5.8	0.9		0.3	•			0.9	•		1.4	
Detarium microcarpum		•	•			•	•	•	•		•	0.2					•		•		0.4	0.2		0.2	•			0.4	•			1.0
Eucalyptus spp.			1.8	0.6	0.8			•			•	1.0	•				•				0.2	0.3		0.6			0.3	0.8			0.5	
Faidherbia albida	0.2	0.6	23	5.7	5.3	24	1.8	13	22	14	61	3.2	•	2.0	1.7	1.2		1.5		1.7	1.8	2.6	4.4	15	1.2	1.3	0.4	2.4	4.0	1.6	2.6	1.1
Guiera senegalensis								•		0.4	•	0.6							0.4	0.1	0.8	0.8						0.2	•		0.2	1.3
Hyphaene thebaica		•	•																		0.8	1.3		1.1	•	1.2			•		0.4	•
Isoberlina doka	•	•	•			•		•	•	•	•		1.0		5.0		•		•	0.4	0.5				•		2.1	0.7	•	1.4		2.2
Lannea acida	2.4		•	1.0				•			•				6.2				•				•					1.4	•			
Leptadenia pyrotechnica			•				0.3			1.4	2.3	0.8	•					1.4									1.6		•		•	•
Parkia biglobosa						1.2		•	•	0.7	•	0.3	1.0				•	0.5	•	2.4	0.2	0.9	2.8	0.6	•			1.2	•	0.6	0.3	
Piliostigma reticulatum	2.2	2.1	1.3	0.4	0.6	0.5	1.5	•	1.9	7.3	•	4.3		1.6	2.4	1.0		0.2	0.6	1.8	4.3	7.8	1.0	0.4				2.3	•	0.4	1.9	
Pterocarpus lucens			•					•			•			0.7	•		•	1.5		1.4	1.2	1.0			•	1.9	1.3	0.3	•			
Sclerocarya birrea			•	0.7		0.7	0.4	•	0.7	0.5	•	0.6		0.4	6.1	1.0		1.0		2.2	0.7	1.5		0.4		0.7		1.4	•	1.4	2.0	
Sterculia setigera			•					•	•		•	0.4				1.7				0.5		0.5		0.9	•	0.6		0.6	•			
Tamarindus indica			•		0.5	2.5	1.6	•		2.2	•	0.2		0.7	4.8	1.5		0.6		2.3	2.4	3.1	1.1	0.6		0.8	0.9	1.3	•	1.8	1.0	
Vitellaria paradoxa					0.1			•	•		•		0.2	0.1		0.7	•	0.9		1.3	0.3	0.4	0.1	1.2	•			2.2	•	2.0	1.5	
Ziziphus mauritiana		2.5	2.6		5.0	2.4	1.4	•	0.9	6.2	25	3.4	•	4.4			3.4			1.7	9.7	12		5.2	20	0.7	•	4.2	•			
13 bird-rich species																																
Acacia ataxacantha			•					•		2.5	•			1.6				0.7		1.5	21	6.5						5.3			1.7	
Acacia ehrenbergiana	•	2.8	3.6	4.1	•	9.1	3.0	6.7	11	12	5.2	8.5	•	•	•	•	•	1.9	•				•	1.2				5.5	13	5.4		
Acacia etbaica	•	•	•	•	•	•	•	2.8	16	•	25	3.6	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•
Bauhinia rufescens		•	•					•		15	•	7.1	•	2.1		9.4		3.5	9.4		5.7	6.7		5.6						•	•	•
Bombax costatum	•		•					•	•		•	1.6				3.3				5.8	0.7	2.3			•			6.2	•	22	3.9	2.6
Capparis decidua	•	•	•	2.4				28	26	51	34	39	•	•	•			3.6	4.6				•	1.7				10	70	•	•	•
Daniellia oliveri		•	•			•	•	•	•	•	•		0.8					0.7	•	3.2	0.8	1.1	6.6	2.1	•	0.9	4.4	5.7	•	5.8	3.7	3.2
Diospyros mespiliformis				2.3				•			•	1.0		2.1	2.1	2.1			•		4.2	2.2	8.4		•	7.1	2.6	0.7	•	1.4	5.4	
Ficus thonningii		•	•	•			•	•			•		•					1.5	•		2.8	6.8			•	13	8.8	3.9	•	1.9	2.1	
Maerua crassifolia	•	•	•				•		24	32	80	18	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	7.5	•	•	•
Salvadora persica	•	17	•	3.7			24	•		47		26	•	•	•	•				•		12	•	8.8	98		•	13	•	•	•	•
Ziziphus mucronate			•	•		3.7		•	•	7.6	•	2.8	•				•		•	3.7	10	10	•	3.6	•				•	•		
Ziziphus spina-christi		•		3.0	5.6	3.6	4.5		7.6	14.		1.6	•	1.5		•	•		2.1		6.2	8.5	•	6.5				2.0				

in drier habitats than *Faidherbia* and *Balanites* (Figure 2). The three species were present in 31–59% of the grid cells (Figures S2–S4). Their average woody cover in each grid cell varied mostly between 2 and 3% of the total woody cover in the zone with 100 to 600 mm rainfall per year.

Usage of woody plant species

As a first step to quantify the use of trees and shrubs by the 32 common arboreal bird species, we calculated their relative numbers counted in woody species that were most often frequented by birds (Table 1). Among the woody plants most important for birds were several of the 11 acacia species, including *Faidherbia albida*. There were 10 other acacia species with smaller distribution areas (e.g. only in Ethiopia: *Acacia abyssinica*, *Acacia lahai*, or only in Sudan and Ethiopia: *Acacia oerfota*) that were also attractive to arboreal birds, such as Common Chiffchaff *Phylloscopus collybita* in Ethiopia (lumped in Table 1). In terms of bird numbers, the 21 acacia species harboured 57% of the 14 migrant bird species and 35% of the resident bird species. Thorny tree species in general, not just acacia species, were very important to migrants (73% of the 14 migrants were found in 26 thorny species; in bold highlighted in Table 1), but less so to residents, at 46%.

Tree choice varied enormously between bird species, from highly specific to wide-ranging. For example, 99% of Western Bonelli's Warbler *Phylloscopus bonelli* were observed in just eight woody species and mostly in *Faidherbia albida* (56%). *Faidherbia* was the outstanding choice of tree for nine other bird species, for five species the second choice, and for six more species the third choice of tree. For 21 out of the 32 bird species, the choice for *Faidherbia* stands out from the tree species available, only matched in significance by *Acacia tortilis* and *Balanites aegyptiaca*. These three tree species are of prime importance for the insectivorous residents (except African Yellow-White-eye), and even more so for the insectivorous migrants (except for European Pied Flycatcher *Ficedula hypoleuca*, whose wintering grounds lie south of the distribution of *Faidherbia*, as they do for the resident African Yellow White-eye; see Figures S26 and S27 in Zwarts *et al.* 2023b). Of the insectivorous migrants (excluding Pied Flycatcher), 32–89% of the birds were concentrated in *Faidherbia*, *Acacia tortilis* and *Balanites* (56%, on average), as were 19–70% (41%, on average) of the insectivorous residents (excluding African Yellow White-eye). Three frugivorous species and five sunbirds were also frequently found in the same three woody species, but with lower relative numbers (25 and 21%, on average, respectively). Sunbirds were mainly recorded in woody species that flower during the dry season (e.g. *A. tortilis*, *Combretum glutinosum*) or species (e.g. Shea Tree) that host flowering parasites (*Tapinanthus* spp.). The frugivores were seen mainly in five fruit-bearing trees: Neem *Azadirachta indica*, *Balanites* and three *Ficus* species.

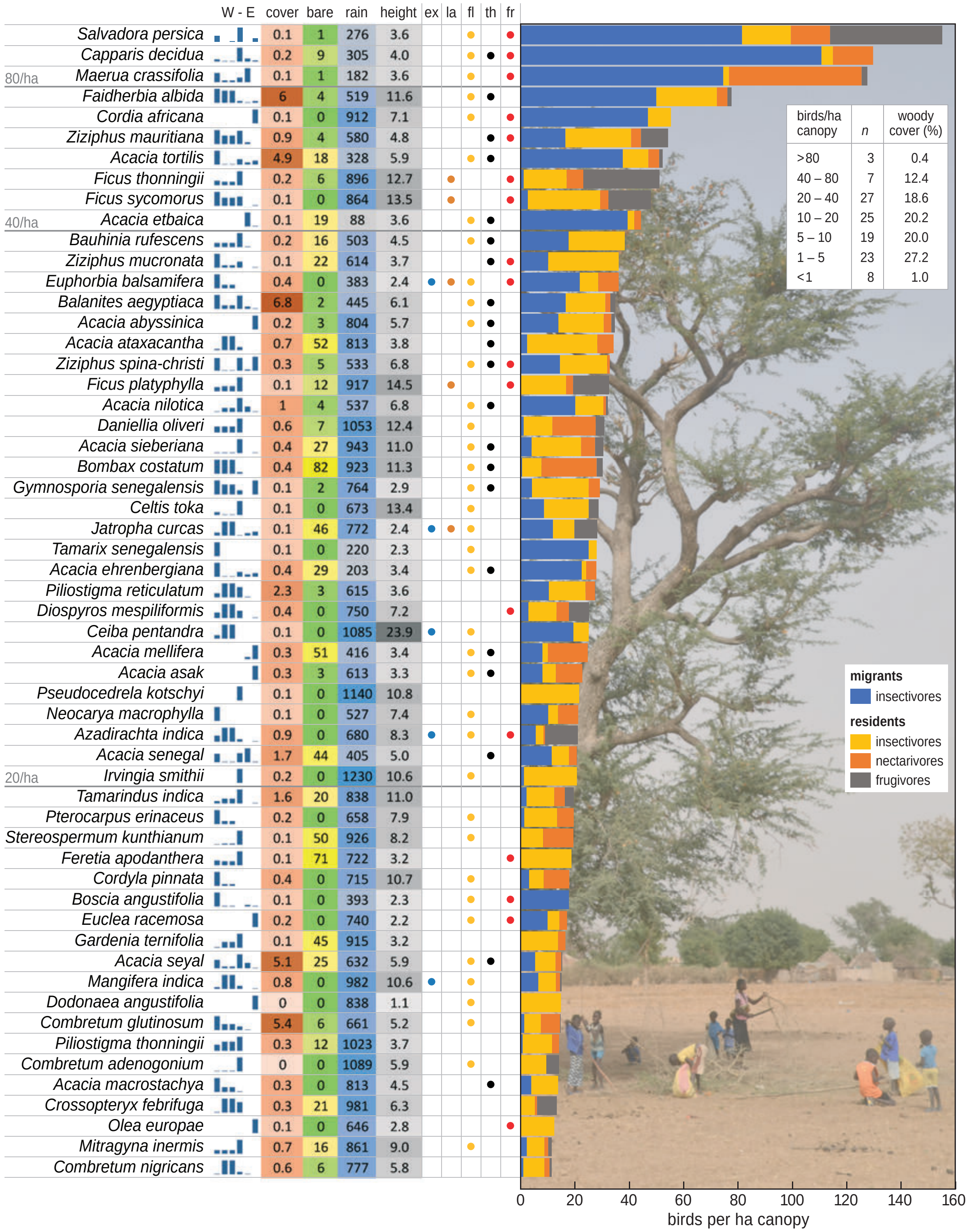
Bird density per woody plant species

In our study sites across the width of sub-Saharan Africa, we identified 304 woody species, of which more than half were relatively rare or had a patchy distribution. Only 144 woody species had a total canopy surface area of larger than 1000 m^2 (measured in a horizontal plane: 1000 $m^2 = 0.023\%$ per tree species of the total woody cover measured in the study sites). Most bird species also occurred in just a part of the study area. The number of woody species with a canopy surface >1000 m^2 within the range of the different bird species varied between 24 (Eastern Orphean Warbler *Curruca crassirostris*) and 128 (Green-backed Camaroptera).

A wide distribution and high relative density of trees did not necessarily equate to high numbers of birds in those trees. Indeed, the most widespread among trees and shrubs, *Guiera senegalensis*, a shrub usually 1–2 m tall, is the commonest species, comprising 7% of the total woody cover measured in all study sites combined (Figure S8). Even so, 20 out of 29 bird species were never recorded in *Guiera* (taking into account that *Guiera* does not occur within the range of three bird species mentioned in Table 2). Several other common tree species, notably *Combretum glutinosum*, Shea Tree and Cashew, characteristically held few birds, if any. In the same vein, tree species able to grow to majestic size, like *Albizia amara* and African locust bean tree *Parkia biglobosa*, were often remarkably poor in birds during the dry season.

Nearly all acacia species were rich in birds to the extent that all 32 bird species covered here were recorded in *A. tortilis* and all but two in *Faidherbia*. Clearly, these tree species are not just attractive to generalists but also to specialists. Ten bird species reached their highest density in *Faidherbia* (orange cells in Table 2) and nine in four other acacia species: *A. tortilis* (3 bird species), *A. nilotica* (2), *A. seyal* (2) and *A. senegal* (2). Seventeen of the 24 insectivorous species (71%) reached their maximal density in these five acacia species, but only two of the five sunbirds and, not surprisingly, none of the three frugivores.

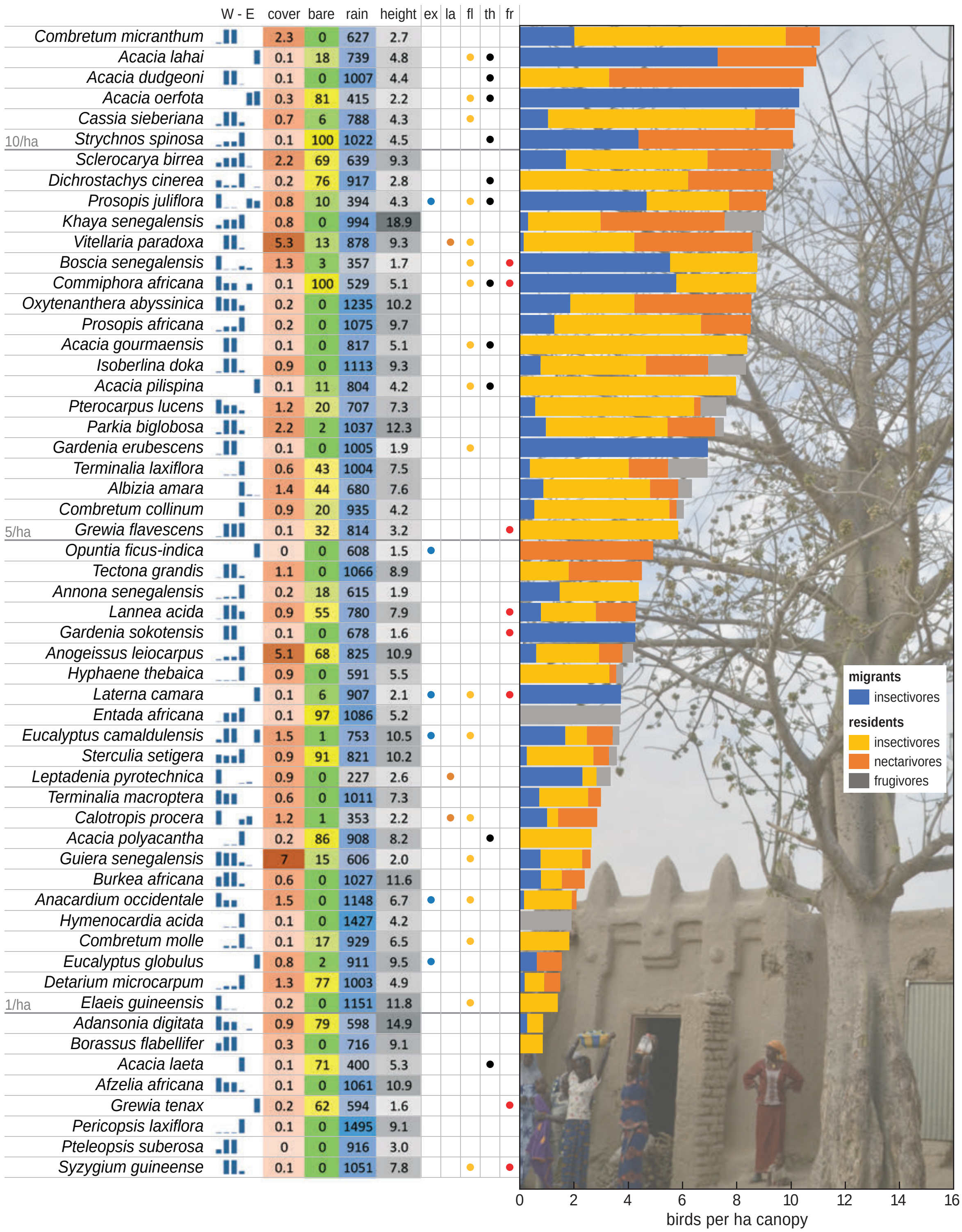
The 29 most common woody species contribute, in total, 74.8% to the total woody cover. Among the other



	W - E	cover	bare	rain	height	ex	la	fl	th	fr
Salvadora persica		0.1	1	276	3.6			●		●
Capparis decidua		0.2	9	305	4.0			●	●	●
Maerua crassifolia		0.1	1	182	3.6			●		●
Faidherbia albida		6	4	519	11.6			●	●	
Cordia africana		0.1	0	912	7.1			●		●
Ziziphus mauritiana		0.9	4	580	4.8				●	●
Acacia tortilis		4.9	18	328	5.9			●	●	
Ficus thonningii		0.2	6	896	12.7		●			●
Ficus sycomorus		0.1	0	864	13.5		●			●
Acacia etbaica		0.1	19	88	3.6			●	●	
Bauhinia rufescens		0.2	16	503	4.5			●	●	
Ziziphus mucronata		0.1	22	614	3.7				●	●
Euphorbia balsamifera		0.4	0	383	2.4	●	●	●		●
Balanites aegyptiaca		6.8	2	445	6.1			●	●	
Acacia abyssinica		0.2	3	804	5.7			●	●	
Acacia ataxacantha		0.7	52	813	3.8				●	
Ziziphus spina-christi		0.3	5	533	6.8			●	●	●
Ficus platyphylla		0.1	12	917	14.5		●			●
Acacia nilotica		1	4	537	6.8			●	●	
Daniellia oliveri		0.6	7	1053	12.4			●		
Acacia sieberiana		0.4	27	943	11.0			●	●	
Bombax costatum		0.4	82	923	11.3			●	●	
Gymnosporia senegalensis		0.1	2	764	2.9			●	●	
Celtis toka		0.1	0	673	13.4			●		
Jatropha curcas		0.1	46	772	2.4	●	●	●		
Tamarix senegalensis		0.1	0	220	2.3			●		
Acacia ehrenbergiana		0.4	29	203	3.4			●	●	
Piliostigma reticulatum		2.3	3	615	3.6					
Diospyros mespiliformis		0.4	0	750	7.2					●
Ceiba pentandra		0.1	0	1085	23.9	●		●		
Acacia mellifera		0.3	51	416	3.4			●	●	
Acacia asak		0.3	3	613	3.3			●	●	
Pseudocedrela kotschyi		0.1	0	1140	10.8					
Neocarya macrophylla		0.1	0	527	7.4			●		
Azadirachta indica		0.9	0	680	8.3	●		●		●
Acacia senegal		1.7	44	405	5.0				●	
Irvingia smithii		0.2	0	1230	10.6			●		
Tamarindus indica		1.6	20	838	11.0					
Pterocarpus erinaceus		0.2	0	658	7.9			●		
Stereospermum kunthianum		0.1	50	926	8.2			●		
Feretia apodanthera		0.1	71	722	3.2					●
Cordyla pinnata		0.4	0	715	10.7			●		
Boscia angustifolia		0.1	0	393	2.3			●		●
Euclea racemosa		0.2	0	740	2.2			●		●
Gardenia ternifolia		0.1	45	915	3.2			●		
Acacia seyal		5.1	25	632	5.9			●	●	
Mangifera indica		0.8	0	982	10.6	●		●		
Dodonaea angustifolia		0	0	838	1.1			●		
Combretum glutinosum		5.4	6	661	5.2			●		
Piliostigma thonningii		0.3	12	1023	3.7					
Combretum adenogonium		0	0	1089	5.9			●		
Acacia macrostachya		0.3	0	813	4.5				●	
Crossopteryx febrifuga		0.3	21	981	6.3					
Olea europae		0.1	0	646	2.8					●
Mitragyna inermis		0.7	16	861	9.0			●		
Combretum nigricans		0.6	6	777	5.8					

birds/ha canopy	*n*	woody cover (%)
>80	3	0.4
40 – 80	7	12.4
20 – 40	27	18.6
10 – 20	25	20.2
5 – 10	19	20.0
1 – 5	23	27.2
<1	8	1.0

Figure 3. Birds per ha of canopy in 112 woody species ranked from bird-rich to bird-poor with the rightmost panel listing woody species with relatively low densities. Note that a different scale is used on the x-axis in both panels. Columns next to the names of woody species: W-E = relative occurrence along the west-east gradient for six longitudinal categories (17–9°W, 9–0°W, 0–8°E, 15–22°W, 28–37°E and 38–42°E), cover = % woody cover relative to the total woody cover in the study sites, bare = % of the woody plants without leaves, rain = average annual rainfall (mm), height = average height of the woody species (m),



		W - E	cover	bare	rain	height	ex	la	fl	th	fr
	Combretum micranthum		2.3	0	627	2.7					
	Acacia lahai		0.1	18	739	4.8			●	●	
	Acacia dudgeoni		0.1	0	1007	4.4				●	
	Acacia oerfota		0.3	81	415	2.2			●	●	
	Cassia sieberiana		0.7	6	788	4.3			●		
10/ha	*Strychnos spinosa*		0.1	100	1022	4.5				●	
	Sclerocarya birrea		2.2	69	639	9.3					
	Dichrostachys cinerea		0.2	76	917	2.8				●	
	Prosopis juliflora		0.8	10	394	4.3	●		●	●	
	Khaya senegalensis		0.8	0	994	18.9					
	Vitellaria paradoxa		5.3	13	878	9.3		●	●		
	Boscia senegalensis		1.3	3	357	1.7			●		●
	Commiphora africana		0.1	100	529	5.1			●	●	●
	Oxytenanthera abyssinica		0.2	0	1235	10.2					
	Prosopis africana		0.2	0	1075	9.7					
	Acacia gourmaensis		0.1	0	817	5.1			●	●	
	Isoberlina doka		0.9	0	1113	9.3					
	Acacia pilispina		0.1	11	804	4.2			●	●	
	Pterocarpus lucens		1.2	20	707	7.3					
	Parkia biglobosa		2.2	2	1037	12.3					
	Gardenia erubescens		0.1	0	1005	1.9			●		
	Terminalia laxiflora		0.6	43	1004	7.5					
	Albizia amara		1.4	44	680	7.6					
	Combretum collinum		0.9	20	935	4.2					
5/ha	*Grewia flavescens*		0.1	32	814	3.2					●
	Opuntia ficus-indica		0	0	608	1.5	●				
	Tectona grandis		1.1	0	1066	8.9					
	Annona senegalensis		0.2	18	615	1.9					
	Lannea acida		0.9	55	780	7.9					●
	Gardenia sokotensis		0.1	0	678	1.6					●
	Anogeissus leiocarpus		5.1	68	825	10.9					
	Hyphaene thebaica		0.9	0	591	5.5					
	Laterna camara		0.1	6	907	2.1	●		●		●
	Entada africana		0.1	97	1086	5.2					
	Eucalyptus camaldulensis		1.5	1	753	10.5	●		●		
	Sterculia setigera		0.9	91	821	10.2					
	Leptadenia pyrotechnica		0.9	0	227	2.6		●			
	Terminalia macroptera		0.6	0	1011	7.3					
	Calotropis procera		1.2	1	353	2.2		●	●		
	Acacia polyacantha		0.2	86	908	8.2				●	
	Guiera senegalensis		7	15	606	2.0			●		
	Burkea africana		0.6	0	1027	11.6					
	Anacardium occidentale		1.5	0	1148	6.7	●		●		
	Hymenocardia acida		0.1	0	1427	4.2					
	Combretum molle		0.1	17	929	6.5			●		
	Eucalyptus globulus		0.8	2	911	9.5	●				
	Detarium microcarpum		1.3	77	1003	4.9					
1/ha	*Elaeis guineensis*		0.2	0	1151	11.8			●		
	Adansonia digitata		0.9	79	598	14.9					
	Borassus flabellifer		0.3	0	716	9.1					
	Acacia laeta		0.1	71	400	5.3				●	
	Afzelia africana		0.1	0	1061	10.9					
	Grewia tenax		0.2	62	594	1.6					●
	Pericopsis laxiflora		0.1	0	1495	9.1					
	Pteleopsis suberosa		0	0	916	3.0					
	Syzygium guineense		0.1	0	1051	7.8			●		●

Figure 3 (continued). ex = exotic, la = latex-producing, fl = flowering in dry season, th = thorns or spines and fr = wet fruit in dry season. The inset table in the left panel gives the number of woody species (*n*) and the relative contribution to the total woody cover (set to 100%) for the seven density classes; see *y*-axis which woody species belong to these classes. Photo: Winter Thorn *Faidherbia albida* after pruning (left) and a Kapok Tree *Ceiba pentandra*, 26-year-old, planted by our deceased friend Sine Konta in the yard of his house in Akka (Inner Niger Delta) in 1984 (right).

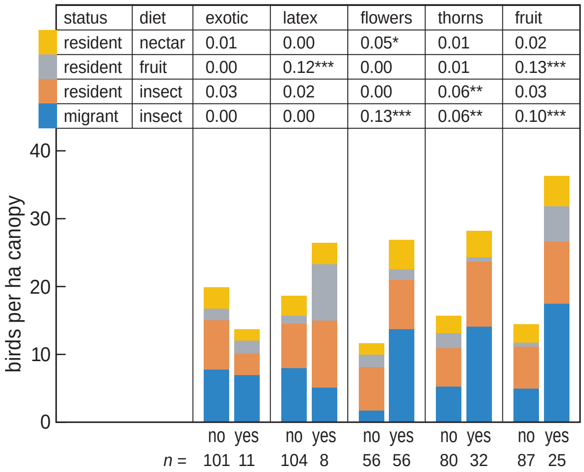
275 less common woody species, only 13 stand out because of their high bird density (listed at the bottom of Table 2). Four of these 13 woody species occurred in the most arid part of our study area, which explains why many bird species, having a distribution area in the less arid zone, are lacking. However, the bird species in the arid zone reached exceptionally high densities in these small trees and shrubs. Toothbrush Tree *Salvadora persica* is particularly attractive because of its berries, not just for Blue-naped Mousebird *Urocolius macrourus*, a frugivore, but also for the insectivorous *Curruca* species.

The highest bird densities (80–160 birds/ha) were recorded in three shrubs that have a limited distribution in the semi-arid zone (400–600 mm rainfall/year), mainly in Chad and Sudan: the berry-bearing *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua* and the low tree *Maerua crassifolia*. Most other bird-rich woody species were thorny (acacias and ziziphus; Figure 3). To investigate whether bird density is related to properties of woody species, Figure 3 gives several traits of the woody plants which are thought to have an impact on the food supply of the birds: the fraction of the woody plants being leafless, average height, average yearly rainfall (based on Hijmans *et al.* 2005) and whether the woody plant is exotic, produces latex, has flowers or fruit during the dry season, or has thorns. The percentage of bare woody plants and average plant heights are based on our own measurements. The other categories are based, apart from own observations, on Arbonnier (2019) and de Bie *et al.* (1998) for flowers and Schmidt *et al.* (2013) for fruit. Most frugivores take small fleshy fruit, therefore dry fruit and fruit >20 mm were excluded (except *Ficus sycomorus*, where birds were recorded eating from ripe figs of 2–6 cm).

Whether birds visit certain tree species was clearly associated with traits of the trees (Figure 4), which – insofar relevant to birds – are interrelated. For instance, woody species from the arid zone are more often thorny (correlation between rain and thorn is negative: $r = -0.33$) and small (correlation between rain and tree height is positive: $r = +0.42$). Whether trees occur solitarily or in continuous stands appears to have no impact on tree use by birds (Zwarts *et al.* 2018).

How strong is the preference for most intensively used tree species?

In terms of usage, the three most important species for insectivorous birds were *A. tortilis*, *Balanites* and *Faidherbia* (Table 1). The relative contribution of these species to the total woody cover in the distribution areas of bird species varied between 0.0 and 22.6% (green bars in Figure 5). Had birds not been selective as to the choice of tree, we would have expected a random distribution among the tree species available. For many bird species the opposite was true (compare yellow with green bars in Figure 5). In fact, the fraction of birds recorded in the three favoured tree species was often much higher than expected (76%, or 71 out of the 93 comparisons made in Figure 5). The preferences differed per bird and tree species. On average, migrants were three times more common than expected in *Faidherbia*, 1.7 times more common in *A. tortilis* and showed no preference for *Balanites* (1.0 times). Insectivorous residents were 2.2 times more common than expected in *Faidherbia*, 2.0 times in *Balanites* and 1.7 times in *A. tortilis*. Sunbirds preferred *Faidherbia* (ratio 1.2) and *A. tortilis* (ratio 1.5), but not *Balanites* (ratio 0.7). Frugivores occurred less frequently than expected in the three woody species, with average ratios of 0.7 in *Faidherbia*, 0.9 in *Balanites* and 0.8 in *A. tortilis*.



	status	diet	exotic	latex	flowers	thorns	fruit
🟨	resident	nectar	0.01	0.00	0.05*	0.01	0.02
⬜	resident	fruit	0.00	0.12***	0.00	0.01	0.13***
🟧	resident	insect	0.03	0.02	0.00	0.06**	0.03
🟦	migrant	insect	0.00	0.00	0.13***	0.06**	0.10***

Figure 4. Average total bird density/ha canopy in woody plants that are exotic or indigenous, or have (yes) latex flowers, thorns or berries, or (no) lack them (number of woody species is given along x-axis). Data from Figure 3. The inset table gives the explained variance (r^2) in 20 one-way analyses of variance; significance level: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $n = 112$.

Some bird species are more selective than others

Western Bonelli's Warblers were recorded in very few woody species, whereas Green-backed Camaropteras were seen in more than half of the available common woody species (Table 1). This does not necessarily imply that Bonelli's Warblers are more selective than Green-backed Camaropteras, because the diversity of woody species might differ within the distribution areas of both bird species (see green bars in Figure 5). For instance, most Western Bonelli's Warblers (56%) were recorded in *Faidherbia* (12% of the woody cover within the distribution area of this bird species). When *A. tortilis* was added, this proportion increased to 83% of the birds in 18% of the woody cover, and after *Balanites* was added: 92% of the birds in 29% of the woody cover (Figure 6). Several other insectivores also showed high selectivity, clearly deviating from random tree use (the $y=x$-line for 'no preference' in Figure 6), although none as extreme as Western Bonelli's Warbler.

The fraction of birds found in 50%, 80% and 90% of the woody cover for all 32 bird species showed that, on average, 50% of the individuals were found in only 19.9% of the woody cover and 3.9 woody species, 80% of the birds in 38.2% of the woody cover and in 9.5 tree species, and 90% of the birds in 48.5% of the woody cover and in 15.3 tree species.

The 32 bird species were observed in 30.6 woody species on average, varying between 7 and 77 woody species. As expected, common birds were seen in more tree species than rare ones ($r = 0.62$, $P < 0.001$; bird numbers given along vertical axis in Figure 7). Tree selectivity did not differ much between migrants and residents, nor between species with different diets: 80% of the migrants were found in 36.9 ± 9.5% (mean ± SD) of the woody cover, against insectivorous residents in 40.5 ± 14.6%. Corresponding figures for frugivores were 32.2 ± 14.3% and for sunbirds 40.7 ± 7.9%.

Selection for tree height

As described above, Common Whitethroats preferred low trees (66% in woody vegetation ≤6 m high) compared to the canopy-hugging Western Olivaceous Warbler which preferred taller trees (only 19% in trees ≤6 m high). Without selection 53% of both species would have used trees ≤6 m high (Figure 1). Similar calculations were made for 38 arboreal bird species (Figure 8). Four residents were even more selective for trees >6 m than Western Olivaceous Warbler, and 5 bird species, all residents, selected woody plants ≤6 m more often than Common Whitethroat. The tall-tree dwellers partly belonged to species that used treetops to advertise their presence (like Brubru *Nilaus afer*) but more often because their feeding was largely restricted to the canopy of trees. The latter included flower-visitors, like sunbirds, leaf-gleaners (passerines, both migrants and residents) and trunk and branch users. On the other hand, species preferring to forage in low trees and shrubs were mostly skulkers among twigs and

Photo 1. The woody cover was estimated by measuring the diameter of all individual shrubs and trees (South Mauritania, 16.476°N, 11.453°W, 25 January 2017; mainly Desert Date *Balanites* and Umbrella Thorn *Acacia tortilis*).

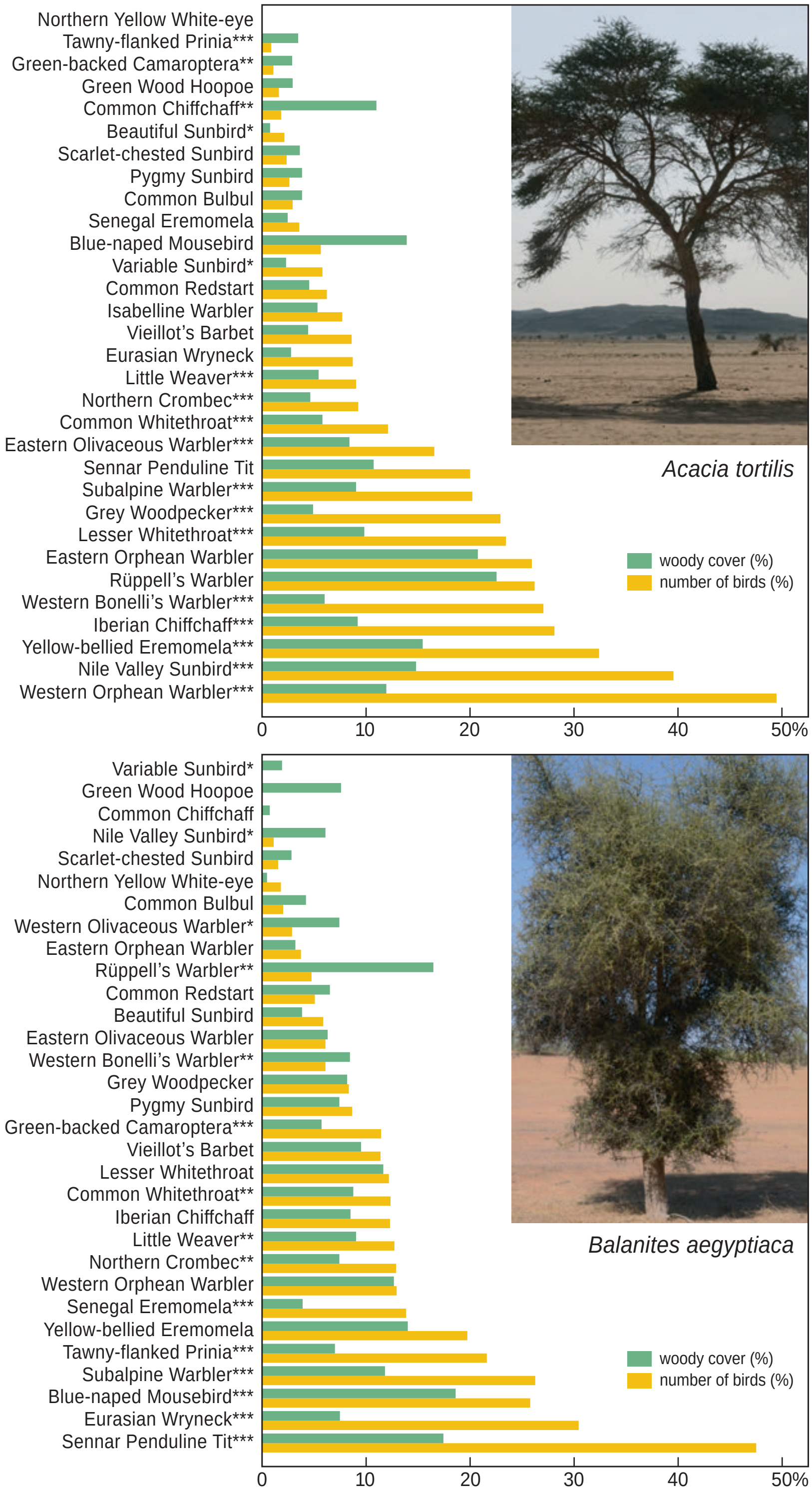


Figure 5. The contribution (%) of *Acacia tortilis*, *Balanites aegyptiaca* or *Faidherbia albida* to total woody cover (set at 100%) within the grid cells of occurrence of 36 bird species (see Supplementary Material of Zwarts *et al.* 2023b), compared to the percentage of the birds recorded in the three woody species. Green bars show the % contribution of each woody species and yellow bars the % of individual birds recorded in that woody species. Significance level in a χ^2_1 test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. The observed number of birds varied between 24 and 1009 and amounted to, on average, 256 birds per species.

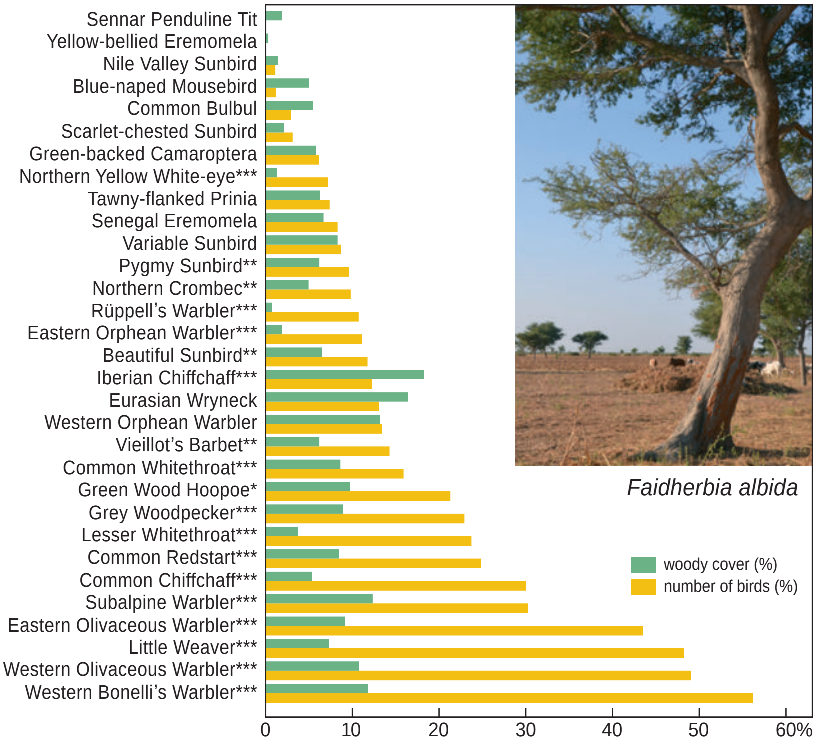


Figure 5. Continued.

leaves, often also actively foraging on, or near to, the ground (McLean 2018, Figure 1 in Zwarts *et al.* 2023b). Residents were especially well represented among this group. The species without a clear preference for foraging height showed an admixture of foraging strategies, using all parts of woody plants including the ground beneath trees, and were represented by African as well as migratory species. In the rest of this paper, we excluded six bird species: three feeding more than half of the time on the ground (marked G in Figure 8), two species using woody plants as a perch (marked P in Figure 8) and one for which the sample size was too small (Brubru). Some bird species always foraged in the tree canopy, others in low vegetation (Figure 4 in Zwarts *et al.* 2015). Their presence in low woody vegetation was, as expected, negatively correlated with the height above the ground where individual birds were detected, averaged per bird species:

$$H = 5.2 - 0.065 \times V,$$
$$(r^2 = 0.57, n = 29, P < 0.001), \qquad (2)$$

where H is the average height at which the bird species was observed (m above the ground; Figure 4 in Zwarts *et al.* 2015) and V = relative occurrence in low woody vegetation (% ≤ 6m; Figure 8).

For instance, Rufous-tailed and Black Scrub Robin, and among migrants Common Whitethroat, Woodchat Shrike, Eurasian Wryneck *Jynx torquilla* and Iberian Chiffchaff *Phylloscopus ibericus*, not only selected low woody vegetation, but were also often foraging in the lower part of tall trees. In contrast, migrants such as Western Olivaceous and Western Bonelli's Warbler selected tall trees and mainly foraged in the upper part of the canopy (Figure 4 in Zwarts *et al.* 2015; Figure 8).

Food supply and bird density

Watching the almost ceaseless foraging activity of birds in trees from sunrise to sunset, there can be no doubt that obtaining food is of paramount importance and – by default – that arthropod abundance must be the overriding factor explaining the selection of woody plants as described above for insectivorous birds. Unfortunately, we lack quantitative data on food supply per woody species to show variations in tree-specific food abundance. For insectivorous species, however, we have an indirect measure of feeding success: the fraction of recorded prey items being large, and for that reason presumed highly profitable. While searching for

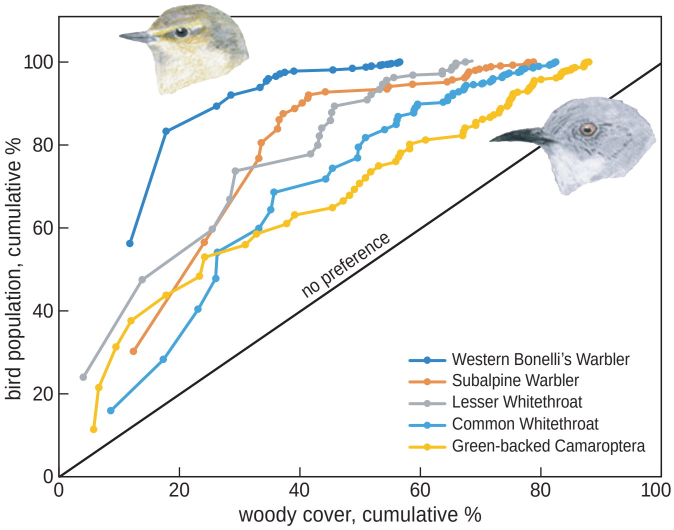


Figure 6. Cumulative percentage of five bird species occurring in different woody species as a function of the cumulative percentage of the woody cover of those woody species. The woody species are for each bird species ranked from most to least used. The total woody cover in the distribution area of each bird species is set to 100%. A random distribution would have resulted in the 'no preference' line.

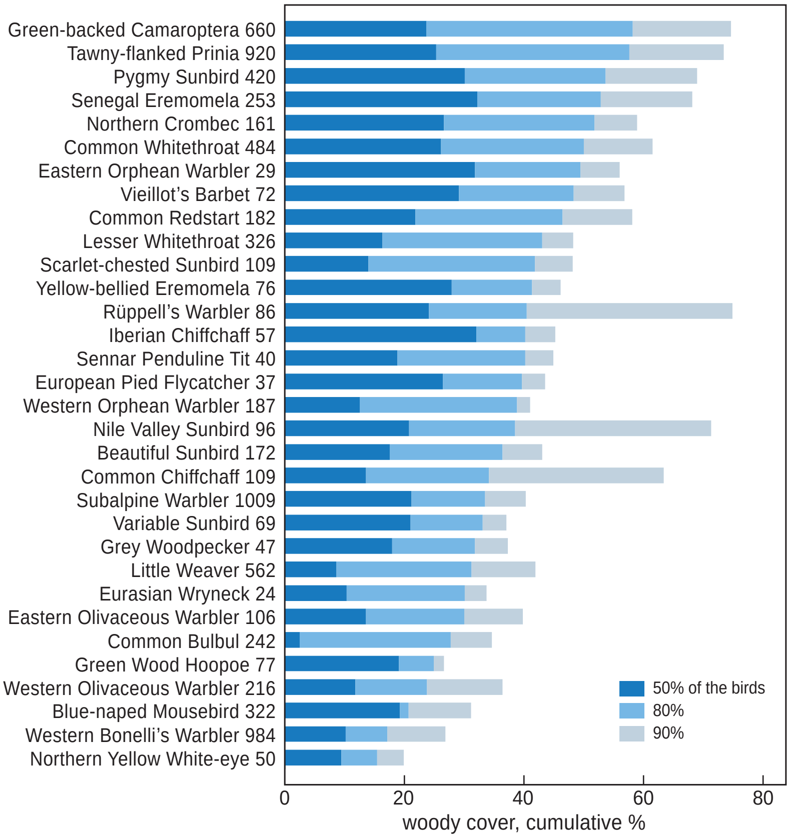


Figure 7. Thirty-two bird species ranked regarding their selectivity for woody species. Species with relatively low values of cumulative woody cover are more selective of woody species. The bars show woody cover (%) where 50%, 80% and 90% of the individuals of a bird species were found; total number of birds recorded given next to the bird's name. Same data are shown in more detail for five bird species in Figure 6.

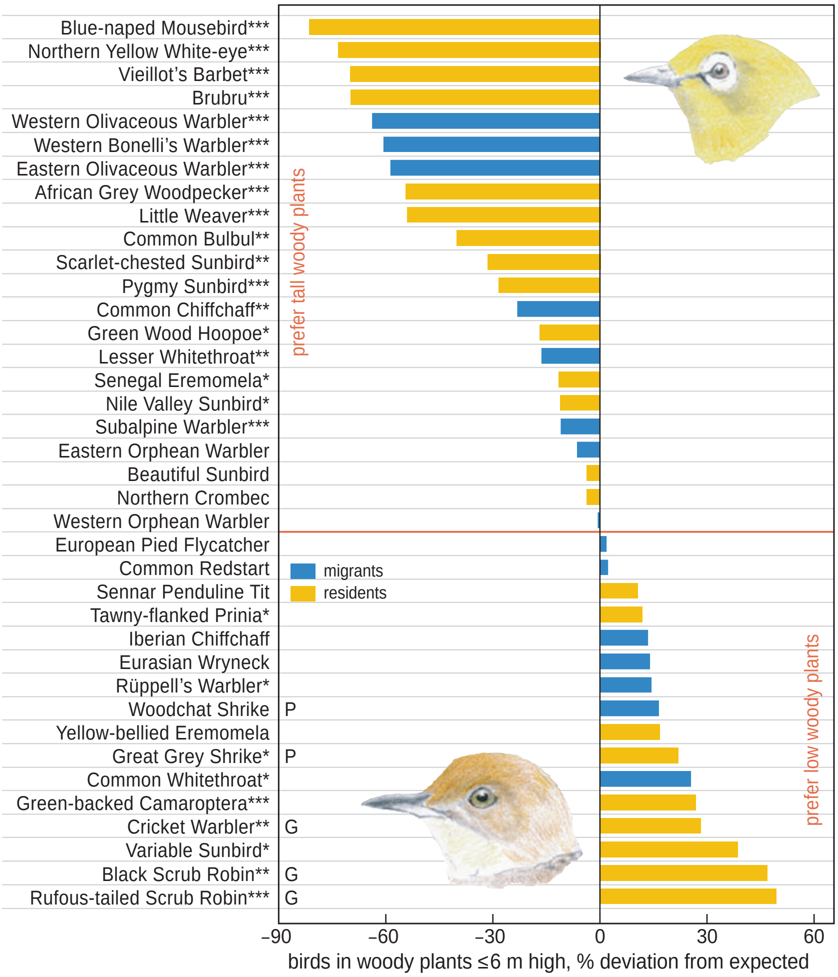


Figure 8. The occurrence of 38 bird species foraging in woody plants ≤6 m, given as percent deviation from expected, where the expectation is based on the fraction of the woody cover of all trees and shrubs being 1–6 m high within the distribution areas of the bird species. Two bird species use woody plants as perches (P) and in three species, more than 50% of the birds forage on the ground (G); see Figure 1 in Zwarts *et al.* 2023b. Significance level in a χ^2_1 test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. The observed number of birds varied for the different species between 23 and 1005, on average 215 birds.

birds in trees, we made notes about captured prey, which were usually too small to be identified (e.g. ant, or even smaller: aphid). Larger prey took more time to handle, providing opportunities to identify prey to species group (dragonfly, locust, caterpillar, etc.). This was systematically noted from October 2012 onwards. After October 2012 we registered 13,447 insectivorous birds, of which 232 birds (1.7%) were handling a large prey item, most often a moth (15%) or a caterpillar (70%). The fraction of birds seen with large prey varied per woody species, from highest in *Faidherbia* to lowest in tree species without thorns (Figure 9). The fraction of large prey in the five categories shown in Figure 9 is correlated with the average density/ha canopy of insectivorous birds ($r = +0.88$, $P = 0.02$).

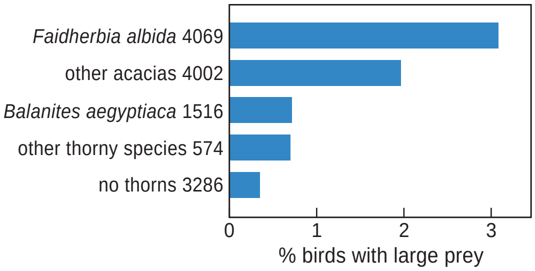


Figure 9. Percent of insectivorous birds handling a large insect during standard bird counts, given separately for *Faidherbia*, other acacias, *Balanites*, other thorny non-acacia species and all woody species without thorns. The number of birds observed is given next to the tree name. The difference is highly significant ($\chi^2_4 = 222$, $P < 0.0001$).

DISCUSSION

Selection for height in woody vegetation

The vertical stratification of foraging birds that we found (Figure 8) has already been described for birds in Africa (Cody 1985, Salewski *et al.* 2003, Wilson & Cresswell 2006, Mclean 2018) and is also known from other continents (Pearson 1971, Hinno *et al.* 2002, Walther 2002, Utschick 2006, Böhm & Kalko 2009, Hinsley *et al.* 2009). Leisler (1992) suggested that migrants and residents would be ecologically separated by feeding in different vertical layers of the woody vegetation. Our study shows, however, that within woody vegetation the vertical stratification is, on average, not different for migrants or residents (ANOVA: $r^2 = 0.02$, $n = 38$, $P = 0.44$), although the nine species showing the strongest preference for high or low woody vegetation were all residents (Figure 8).

The preference for vegetation height is not related to body mass of the 38 bird species, varying between 7 and 45 g (body mass taken from Urban *et al.* 1997, Fry& Keith 2000, 2004; see Figure 4 in Zwarts *et al.* 2015). Species with a higher body mass, i.e. African Grey Woodpecker *Dendropicos goertae* and Eurasian Wryneck, foraged on trunks and thick branches and might for that reason select larger trees than sunbirds and warblers feeding among leaves and flowers by hovering and making sallies or jump-flights. However, the expected negative relation between body mass and occurrence in low woody vegetation was not found (linear regression: $r^2 = 0.01$, $n = 38$, $P = 0.24$).

There are other reasons to expect that arboreal birds may prefer to feed in older woody plants. Young woody plants do not normally have flowers or fruit. Furthermore, at a young age tree architecture is still simple, lacking horizontal branches and a well-leafed canopy. The absence of shadow in small trees is probably an additional disadvantage at high ambient temperatures when birds actively seek protection from the sun (Walsberg 1993, Martin *et al.* 2015). Indeed, twice as many bird species were found in high than in low woody vegetation (omitting five bird species which preferred low woody vegetation because they use woody plants as perches or spend more than half of their time feeding on the ground; Figure 8).

Tree preference of birds across the Sahel

A first attempt to calculate tree preferences and densities of birds was restricted to data collected in West Africa (Zwarts *et al.* 2015, see their Figure 6 and Supplementary Material). The much larger dataset presented here covers the entire width of the Sahel, which enables a similar attempt that takes into account variations in the distribution and density of bird species in step with the distribution of trees and shrubs. In general, woody species rich or poor in birds in West Africa showed the same pattern across the entire Sahel. Some woody species that are rare in West Africa but much more common in the central and eastern Sahel proved to be highly attractive to birds, notably *Maerua crassifolia*, *Capparis decidua* and *Bauhinia rufescens*. Geographic differences were also found, especially regarding the average density of migrants (but not of residents) in most woody species: higher in the western than in central and eastern Sahel. This difference hinges intrinsically on a systematic longitudinal variation in bird density in migrants (Zwarts *et al.* 2023c).

Photo 2. Green-backed Eremomela *Eremomela canescens* feeding on insects in a Desert Date *Balanites aegyptiaca* (Ethiopia, 7.983°N and 38.623°E; 27 February 2019). This tree species has straight spines up to 10 cm long arranged in spirals which deter large grazers from browsing. Leafing in *Balanites* occurs from May through December, followed by partial defoliation in the latter part of the dry season. The investment of this tree species in mechanical defence against grazers instead of chemical defence against herbivorous arthropods explains why *Balanites* belongs to the tree species attracting insectivorous birds.

Closely related bird species often showed similar preferences for tree species, even when their distributions did not (appreciably) overlap. Eastern Bonelli's Warbler *Phylloscopus orientalis* replaced Western Bonelli's Warbler in Chad and Sudan, where all birds were found in acacia species (though based on only 9 birds), similar to the tree preferences of Western Bonelli's Warbler (90% in acacia species). In both subregions, Western and Eastern Olivaceous Warbler *Iduna pallida* were found in high numbers in *Faidherbia*

(43 and 49%, respectively), but rarely in *Balanites* (6 and 3%, respectively). For six *Curruca* species, *A. tortilis* was on average more important than *Faidherbia* (26% and 18%, respectively), but in three *Phylloscopus* species it was the other way round (18% in *A. tortilis* and 33% in *Faidherbia*). In *Balanites*, *Curruca* species were more common than *Phylloscopus* species (12 and 6%, respectively). Whether this is due to systematic differences in food supply in the different tree species (Morel 1968, Stoate 1998, Vickery *et al.* 1999), the diet of these bird species (Stoate 1997, 1998, Stoate & Moreby 1995, Wink 1981), their foraging modes or a combination of these factors is unknown.

The distinct preference for acacia trees by migrants, and less so by residents, may be illustrated by a bird count we did in the southern, humid part of Mali (11.600°N, 5.838°W; average annual rainfall 1073 mm), where nearly all trees in the site were *Acacia nilotica*, a tree usually found in the zone with an annual rainfall between 200 and 800 mm. The *A. nilotica* plantation (woody cover 8550 m^2) attracted, apart from 3 Green-backed Camaropteras, 5 migratory species (6 Common Chiffchaffs, 5 Western Olivaceous Warblers, 4 European Pied Flycatchers, 2 Common Whitethroats and 1 Melodious Warbler *Hippolais polyglotta*, amounting to 20 migrants per ha of canopy). Elsewhere in the humid zone densities rarely exceeded 1–2 birds per ha of canopy (Figure 3B in Zwarts *et al.* 2023b). Farther south in Ghana (Dowsett-Lemaire & Dowsett 2014) and in Togo + Benin (Dowsett-Lemaire & Dowsett 2019), the few Sahelian migrants were observed in – for that zone – equally rare Sahelian trees, e.g. Western Bonelli's Warbler in *Faidherbia* and *Balanites*; Subalpine Warbler in *A. nilotica* and Common Whitethroat in *A. seyal*.

Most arboreal birds in the Sahel feed on insects, but data are lacking about temporal and spatial variations in insect abundance per tree species. When trees attracted a lot of insects, as when flowering, standing in water or having a large well-leafed canopy, more birds were recorded (Figures 7, 15 and 18 in Zwarts & Bijlsma 2015). Birds taking large prey were recorded more often in thorny trees than in non-thorny trees. Figure 9 shows that the frequency at which birds take large prey is lowest in non-thorny woody species and high in acacia species, especially in *Faidherbia*. We hypothesize that the total food intake is high when more large prey can be taken, because large prey are more profitable. A bird must eat about 100 or 500 aphids (0.2 mg) to have a food intake equal to a single moth of 2 cm (dry weight: 20 mg) or a caterpillar of 3 cm (100 mg), respectively.

Variations on the overriding theme of rainfall and tree characteristics are abundant, each explicable by specific local conditions. Take for example sunbirds, a largely nectarivorous group of birds that usually avoids

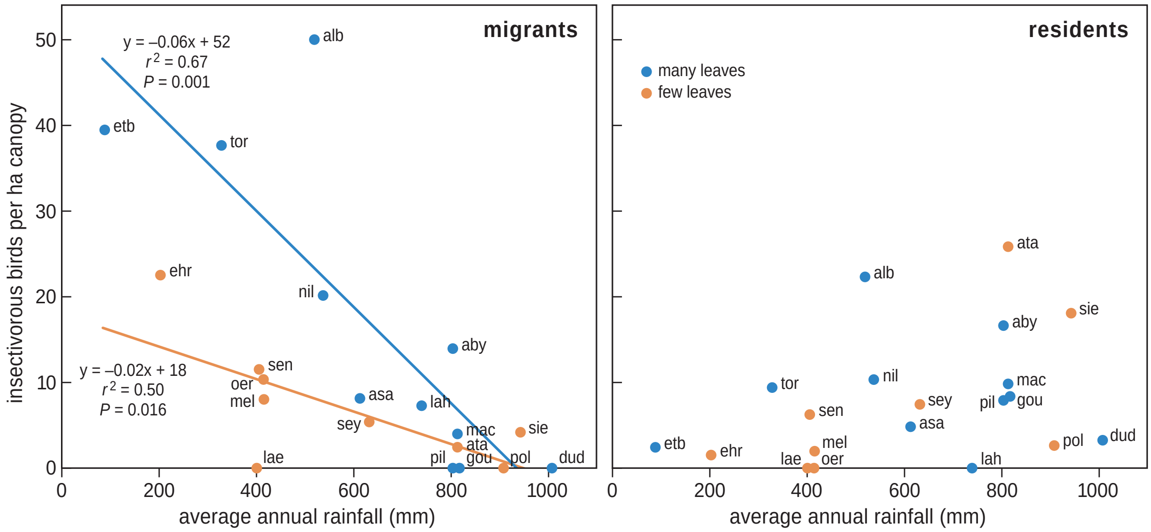


Figure 10. Average bird density of insectivorous migrants (left) and residents (right) during the dry season in twenty *Acacia* species as a function of average rainfall, separately for *Acacia* species with few leaves (range 0–47 %, on average 21%, of the woody plants being leafless) and many leaves (range 51–95%, on average 76%). All data from Figure 3, which also gives the full name of the *Acacia* species indicated here with three letters. In migrants, bird density in acacia trees declines significantly with rainfall and differs for trees with few or many leaves. In residents, the increase in bird density is not significant: it is also not significant for *acacias* with few or many leaves.

woody species without flowers (even when foraging for insects). However, they also avoid the majority of flowering species (not all tree species produce nectar when flowering, or only at night, or in different amounts; e.g. Adgaba *et al.* 2016). This explains the small difference between the average density of sunbirds in flowering and non-flowering species (Figure 4). Similar deviations from the general pattern can be found in the other categories, as for example in thorny trees. The average feeding density of migrants in thorny species was three times larger than in non-thorny species, but within the range of thorny species, four were found to contain no migrants at all. Two factors appear to have an impact on the density of migrants in acacia species: annual rainfall (acacias in humid zones were least attractive) and whether the species is leafless during the dry season (if so, devoid of migrants; Figure 10). Insectivorous resident bird species occurred at lower densities than insectivorous migrants and were indifferent to whether trees carried leaves or not. They were indifferent also to average rainfall (even to the point of showing a non-significant increase with rainfall; Figure 10).

There are several other possible explanations as to why some bird species were found in a wider variety of woody species than others (Figures 6 and 7). First, bird species with a larger range (i.e. found in more grid cells; see Supplementary Material in Zwarts *et al.* 2023b) are more likely to encounter a wider range of tree species. This effect was indeed found ($r = +0.46$, $P < 0.01$). The impact of the size of the distribution area is statistically independent of tree height since the two are not correlated ($r = 0.00$). Second, bird species in the humid zone encounter more tree species than those residing in the dry zone, because of the much higher tree diversity in the more humid region:

$$N_{\text{tree}} = 0.035 \times \text{rain}^{0.880} \ (n = 140 \text{ grid cells, excluding Ethiopian highlands; } r = +0.78, P < 0.0001), \quad (3)$$

where N_{tree} = number of woody species in the random sites, averaged per grid cell and rain = average annual rainfall (mm).

However, the correlations between the 50%, 80% and 90% selection criteria shown in Figure 7 and annual rainfall in the distribution area of the bird species (shown in Figure 5A in Zwarts *et al.* 2023b) were close to zero and thus far from significant. In other words, despite the increase of tree diversity with rainfall, bird species from the humid zone were concentrated in the same number of woody species as the bird species bound to the dry zone.

Third, birds gleaning prey from leaves may be more selective in their choice of tree species than those hovering for their prey, as found in North American forests by Holmes & Robinson (1981). Nearly all species from Figure 7 are foliage gleaners, but Western Bonelli's Warblers, and to a lesser degree also Eastern Olivaceous Warblers, make sallies and jump-flights and hover (Table 5.11 in Lack 1980; Figure 9B in Zwarts & Bijlsma 2015; Rob Bijlsma unpubl.). However, both species were more, not less, selective in the choice of tree species than the gleaning bird species (Figure 7).

Fourth, bird species feeding in low trees and in shrubs were found in a larger variety of woody plants than species bound to the canopy of large trees (Figure 11). The explanation might be simple: the canopy surface of scrub and low trees is (much) smaller than of trees making it more likely that scrub-foraging birds will constantly move from one woody plant to another, and therefore visit more woody species than bird species feeding in the canopy of tall trees.

More Cashew and Shea trees, fewer birds

Cashew trees are avoided by arboreal birds: the density/ha canopy was a meagre 0.2 migrants and 2.0 residents (1.8 insectivores, 0.2 sunbirds and 0 frugivores; Figure 3). Cashew plantations cover a large part of the hyper-humid zone in West Africa, mainly in Côte d'Ivoire (not visited by us, beside Comoé National Park). In Guinea-Bissau, where we collected data from two grid cells, cashew plantations contributed 44.6% of the woody cover in the northern grid cell (the overall woody cover was 44.3% of which 19.8% cashew) and as much as 51.8% in the southern grid cell (overall cover 57.1% of which cashew 29.6%); see Figure S5 for the cover by cashew and Figure 6B in Zwarts *et al.* 2023a for the total woody cover.

In Guinea-Bissau cashew plantations were very rare in the early 1980s, but cashew planting has soared in later years. According to FAO data, cashew covered already 0.29 million ha of the country in 2020. At the same time, even larger areas were converted into cashew plantation in Côte d'Ivoire (2.03 million ha in 2020) and Benin (0.52 million ha in 2020) and for West Africa as a whole 3.37 million ha (www.fao.org/faostat/en/#data/QCL). Comparisons of high-resolution Google Earth satellite images available since 2004 clearly show that small Cashew trees, spaced at a distance of 5–8 m, had formed a closed canopy within 5 to 10 years after planting. Such plantations were usually without understorey of shrubs or small trees, instead were typified by bare ground with leaf litter (Photo 3).

We found no information if and how bird population changed after woody savannah or agroforestry parkland had been converted into Cashew plantation. But the newly created Cashew plantations in Guinea-Bissau must have had a negative impact on the average bird density: 2–5 birds/ha canopy in Guinea-Bissau compared to 17–43 birds/ ha canopy in the woody savanna in Chad and the Central African Republic in the same rainfall zone (Figure 3A and Figure 8 in Zwarts *et al.* 2023b). The impoverished bird fauna in monotonous Cashew plantations contrasts with the high bird diversity and density in natural woody vegetation of humid woody savanna, where a diversity of woody species attracts birds, especially when flowering (Tamarind *Tamarindus indica*, Kapok Tree *Ceiba pentandra*, Red Kapok Tree *Bombax costatum*, White Thorn *Acacia sieberiana*, Red Acacia *Acacia seyal*, West African Copal *Daniellia oliveri*) or bearing fruit (Candlewood *Zanthoxylum zanthoxyloides*, *Gymnosporia* (=*Maytenus*) *senegalensis*, *Ficus* spp.). Affected birds cover the complete range of residents, insectivores, frugivores and nectarivores, including four migrants: European Pied Flycatcher, Willow, Wood and Melodious Warbler (Figure 5 in Zwarts *et al.* 2023b).

Following conversion of agroforestry parkland into monoculture of Cashew overall woody cover did not decline, and sometimes may even have increased. Global forest maps (Hansen *et al.* 2013) fail to distinguish between tropical forests and plantations of Cashew, or, for that matter, of banana, oil palm or pineapple plantations. The net result is an underestimate of real forest loss (Tropek *et al.* 2014). Cashew plantations are economically profitable (Monteiro *et al.* 2017) and are considered as beneficial afforestation leading to less soil erosion, enhanced soil fertility, a cooler microclimate and rehabilitation of degraded lands (CILSS 2016). The flip side of the coin is: more Cashew equates to far fewer birds

The Shea Tree *Vitellaria paradoxa* (Photo 4) does not attract many birds, although it is not as poor in that respect as Cashew (Table 2 and Figure 3). However, its negative impact on overall bird density is large, since it is a dominant tree in the agricultural zone of Mali, Burkina Faso and Benin where the annual rainfall varies between 700 and 1000 mm (average cover of Shea alone was 2.1%, but for all woody species combined 9.6%; Figure S9 and Figure 5 in Zwarts *et al.* 2023a). The average bird density, calculated for 199 study sites within this region amounted to 5.0 birds/ha canopy, but it was 23.8 and 2.7 birds/ha canopy respectively when the data were split for sites where woody cover of Shea was less or more than half of the total woody cover. A similar large difference is found when the bird density in Mali, Burkina Faso and Benin (on average 17.1% Shea for all woody species combined) is compared to the one measured in Chad (0.4% Shea) within the same rainfall zones: 5 birds/ha canopy in Mali, Burkina Faso and Benin compared to 26.6 birds/ha canopy in Chad (92 sites; see also Figure 3 in Zwarts *et al.* 2023b). Obviously, the expansion of Shea agro-forestry parkland has had a large negative impact on tree-dwelling birds.

How many birds are present in different woody species?

The total woody cover in Africa between 7°N and 22°N amounts to 0.897 million km^2, equivalent to 9% of the total land surface (see Supplementary Material). The contribution of the woody species from the semi-arid zone, among which are several bird-rich trees, declines when correcting for the under-representation of the most arid and most humid region in our study sites.

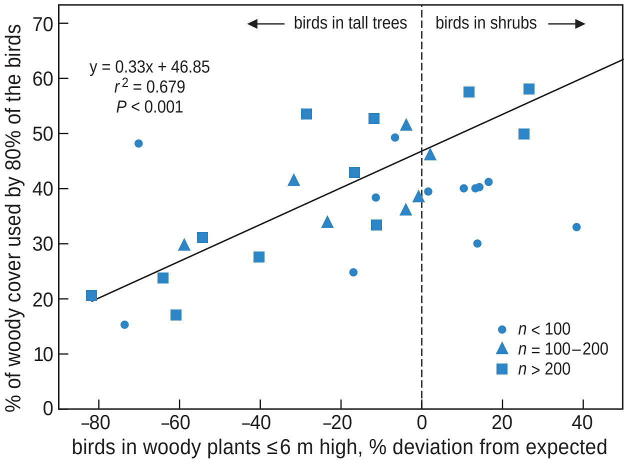


Figure 11. The relationship between degree of tree selection by bird species (% of woody cover utilized by 80% of the birds; same data as in Figure 7) and their habitat association with respect to vegetation height (occurrence of woody plants ≤6 m, given as percent deviation from expected; as in Figure 8). Symbols denote numerical classes for 32 bird species. The regression line refers to the 19 most common species (*n* > 100).

Photo 3. Monoculture of Cashew in Guinea-Bissau at 12.002°N and 14.834°W (500 × 700 m); all woody plants visible on this Google Earth image (28 February 2019) are cashew trees of different ages with the most recent plantation on the left and older ones on the right (see image taken on the spot on 3 February 2014).

The woody cover of *Faidherbia*, for instance, declines from 2.2% in the covered grid cells to 1.21% for the entire region (more details in Supplementary Material). Multiplying the woody cover per woody species with the corresponding bird density/ha canopy gives a total estimate of bird numbers and how they are distributed over the various woody species (Table 3). Most migrants are present in *A. tortilis* – 90 million (split-half: 85–92 million; based on an estimated 37.6 migrants/ha canopy and a total surface of 2.38 million ha canopy (split half: 2.26–2.46). The bird density in *Faidherbia* is higher (49.9 migrants/ha) but the associated surface area is much smaller (1.08 million ha canopy; split-half estimates the same) so that fewer migrants are found in *Faidherbia* – 54 million (Table 3). We estimate that 42 (split-half: 39–45) million migrants are present in *Balanites* because the lower density (16.6 migrant birds/ha) is more than compensated for by the large surface area of the woody cover (2.52 million ha; split half: 2.31–3.71). Two uncommon woody species *Maerua* (0.14 million ha canopy) and *Salvadora* (0.09 million ha) harbour 10.8 and 7.3 million migrants due to their high bird densities (74.6 and 81.4 migrants/ha canopy, respectively). For all woody species together, we arrive at 355 million arboreal migrants for the entire region (Table 3). In total, 186 million of these 355 million migrants (52%) are concentrated in three bird-rich and common trees, i.e. in only 6.7% of the total woody cover (Table 3).

The estimated total of 355 million arboreal migrants in Africa between 7 and 22°N is 0.7% above the estimate of 354 million birds for the same region given in Zwarts *et al.* (2023b). Thus, both estimates do not differ although they were calculated in different ways: directly (Zwarts *et al.* 2023b), based on bird counts in the sites assembled per subregion, or indirectly (this

Photo 4. Shea trees dominate the agro-forestry parkland in southern Mali, Burkina Faso and northern Benin. (Photo: Mali, 12.899°N, 6.813°W, 28 January 2012).

Table 3. The importance of various tree species ranked according to the estimated total number of arboreal migrants they support. Estimated total surface of the canopy (km^2), density (*n*/ha canopy) and number (millions) of arboreal migrants between 7 and 22°N; given separately for 22 woody species being most important for migrants. No more than 12% of the birds were present in 382 other woody species not mentioned, although their total woody cover amounts to 66%. The overall density of arboreal insectivorous birds declined to 4.0/ha canopy when all woody species were taken into account (on average 0.7 birds/ha canopy in trees not mentioned in the table).

Woody species	km^2	*n*/ha	million
Acacia tortilis	23,820	37.6	89.5
Faidherbia albida	10,831	49.9	54.1
Balanites aegyptiaca	25,248	16.6	42.0
Acacia nilotica	9194	20.1	18.5
Acacia seyal	26,546	5.4	14.3
Maerua crassifolia	1452	74.6	10.8
Mangifera indica	13,518	6.6	8.9
Acacia senegal	7227	11.5	8.3
Acacia ehrenbergiana	3441	22.5	7.7
Piliostigma reticulatum	7108	10.4	7.4
Salvadora persica	899	81.5	7.3
Acacia etbaica	1850	39.4	7.3
Acacia sieberiana	13,669	4.1	5.7
Ziziphus mauritiana	3164	16.6	5.2
Anogeissus leiocarpus	63,010	0.6	3.7
Mitragyna inermis	14,853	2.3	3.4
Parkia biglobosa	34,620	1.0	3.3
Tamarindus indica	15,140	2.2	3.3
Combretum glutinosum	21,560	1.4	3.0
Ceiba pentandra	1351	19.5	2.6
Azadirachta indica	4528	5.7	2.6
Ziziphus spina-christi	1450	14.5	2.1
All other species	592,091	0.7	44.0
TOTAL	**896,570**	**4.0**	**355.3**

paper), based on the estimated woody cover and average bird density/ha canopy per woody species.

The most important conclusion is that when 52% of the arboreal migrants are concentrated in 6.7% of the woody cover (Table 3), it is not total woody cover per se that matters for these birds, but the presence of their preferred woody species. For the same reason, global indications of increase or decline of the woody vegetation, although highly relevant in other respects; Brink & Eva 2009, Hansen *et al.* 2013) are not helpful in explaining trends in bird populations. Any explanation of these trends must take into account detailed knowledge about the presence and extent of bird-rich and bird-poor woody species within the wintering regions. Furthermore, Brink & Eva (2009) and Hansen *et al.* (2013) provided the extent of 'forest cover', not of 'woody cover'. In well-wooded regions this may equate the same, but definitely not in the Sahel where low densities of single trees in savannah or farmland cannot be detected with Landsat imagery having a resolution of 30 × 30 m (Figures 6 and 7 in Zwarts *et al.* 2023a), i.e. the data source used in their studies. This potential discrepancy has recently been solved with the advent of high-resolution satellite imagery with which woody cover can be estimated accurately (Brandt *et al.* 2020); even individual *Faidherbia* and other tree species can now be identified (Lelong *et al.* 2020).

Ecological and socio-economic values of woody species

How many arboreal birds may live in the Sahel depends on the woody cover of bird-rich trees and shrubs. If bird-rich trees were to decline or replaced by commercially interesting tree species, bird populations can be expected to suffer. Bird densities in, for example, Shea Tree and Cashew are extremely low, yet these commercially valuable tree species cover large tracts of land in West Africa, usually at the expense of indigenous tree species valuable to birds. Insect supply and richness are still major unknowns for the tree species in the Sahel, but it is obvious that some woody plants have more to offer to birds than others (Greenberg & Bichier 2005, Zwarts *et al.* 2015).

The total woody cover in the study area amounts to only 9%. A tiny fraction of the already scarce woody cover is exploited by arboreal birds. In some bird species more than half of the individuals make use of a single tree species during the dry season, a delicate dependency compared to birds with a wider use of tree species. Dependence on just a few woody species not only holds for several residents but also for many migratory bird species spending the non-breeding season in the Sahel and for migrants wintering farther south which use the Sahel to refuel during autumn migration (Zwarts *et al.* 2023d).

Farmers have some impact on woody cover when savannah is converted into agricultural land (Brandt *et al.* 2018). More important, however, is that people selectively remove specific woody species and guard and plant others and have determined in this way the species composition of the woody vegetation in large parts of the dry belt of the northern tropics (Zwarts *et al.* 2023e). Many woody species are highly valued by local people, not only for firewood, but also as a source

Photo 5. A still small Neem *Azadirachta indica* tree beside the trunk of a Winter Thorn *Faidherbia albida*. The evergreen Neem, native to India, has been planted in tropical Africa alongside roads and in settlements to provide shade. Its leaves are toxic and are used as a biopesticide. Exactly this quality results in a tree with very few insects, except ants (Stoate & Moreby 1995). Neem was largely avoided by birds, except small numbers of Eastern and Western Olivaceous Warblers which were observed preying on ants (own unpubl. data). The picture shows cropland in S Mali (13.049°N and 5.894°W, 2 February 2012), where the farmer has – uncharacteristically – replaced some of his White Thorns by Neem. Were this type of management to become more popular, the negative impact on birds, especially Bonelli's Warbler, would be very large.

for veterinary and human medicine (reviewed by Arbonnier 2019) and many other purposes (Lykke *et al.* 2004, Ouédraogo *et al.* 2017). The future of arboreal birds in the Sahel would be bleak should trees ranking high on socio-economic values be bird-poor. Fortunately, a bird-rich tree as *Faidherbia* ranks high concerning its socio-economic values but, alas, an extremely bird-poor indigenous tree, Shea Tree *Vitellaria paradoxa*, has a large economic value, and this also holds for plantations of exotic tree species virtually devoid of birds (Cashew, Teak *Tectona grandis* and *Eucalyptus* spp.; Figure 3). The impact on arboreal bird species of the conversion of the dry sub-Saharan zone into a semi-natural open farmland with scattered trees in fields and pastures is dealt with separately (Zwarts *et al.* 2023e).

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SAMENVATTING

In de Sahel, hier opgevat als de brede overgangszone tussen Sahara en natte tropische bossen verder naar het zuiden, komen nauwelijks bossen voor. Maar het gebied is bepaald niet arm aan bomen, integendeel. En wat nog opmerkelijker is: het struikgewas en de losstaande bomen zijn opvallend vogelrijk. Voor een groot deel bestaat de lokale vogelbevolking in de winter uit Afro-Palearctische trekvogels, waaronder soorten die in het broedgebied juist in aaneengesloten bossen voorkomen. Dit artikel beschrijft welke bomen en struiken worden geselecteerd door 14 insectivore trekvogels en 18 Afro-tropische vogelsoorten (10 insectivoren, 3 frugivoren en 5 nectarivoren) op basis van een gestratificeerde inventarisatie van de gehele Sahel. In totaal werden 760.000 bomen en struiken op naam gebracht (304 soorten). Van elk boom en struik apart werden hoogte en breedte gemeten. Met die gegevens werd vervolgens het oppervlak van elke boom uitgerekend, de zogenaamde kroonbedekking. Vogels werden afzonderlijk geregistreerd per boom/struik. Van de vogels was 99,5% geconcentreerd in slechts 41 soorten bomen/struiken. Voor 20 van de 32 vogelsoorten was *Faidherbia albida*, een acacia, de meest benutte boomsoort. Twee andere belangrijke bomen waren *Acacia tortilis* en de Woestijndadel *Balanites aegyptiaca*, die het vaakst werden gebruikt door respectievelijk zeven en zes vogelsoorten.

In deze drie boomsoorten, tezamen goed voor slechts 11% van de totale kroonbedekking, werden 89% van de Bergfluiters *Phylloscopus bonelli* waargenomen en 77% van de Baardgrasmussen *Curruca iberiae + subalpina + cantillans*. Vogelsoorten die zich vooral in struiken ophielden werden in grotere diversiteit van bomen en struiken gezien dan soorten die bij voorkeur in (hoge) boomkronen foerageerden. De hoogste vogeldichtheden (80–160 vogels/ha kroon) werden aangetroffen in drie houtige soorten met een beperkte verspreiding in de zuidelijke Sahara en de noordelijke Sahel: de bessendragende Tandenborstelboom *Salvadora persica*, de doornige struik *Capparis decidua* en de kleine boom *Maerua crassifolia*. Andere vogelrijke boomsoorten waren zonder uitzondering doornig (*Balanites aegyptiaca*, diverse soorten acacia's en *Ziziphus*). 27% van de totale kroonbedekking kwam voor rekening van slechts vijf algemene soorten: Cashew *Anacardium occidentale*, *Anogeissus leiocarpus*, *Combretum glutinosum*, *Guiera senegalensis* en Karitéboom *Vitellaria paradoxa*, maar deze boomsoorten werden zelden door foeragerende vogels bezocht. Sterker nog, negen insectenetende soorten werden er nooit in aangetroffen. Honingzuigers waren geconcentreerd in een beperkt aantal bloeiende bomen, fruiteters in een klein aantal vruchtdragende soorten. Insectenetende vogels beperkten zich grotendeels tot doornige boomsoorten, vermoedelijk vanwege de aanwezigheid van rupsen en motten. In de Sahel is niet de totale bosbedekking sec van belang voor vogels, maar de aanwezigheid van specifieke boomsoorten. Deze bevinding heeft belangrijke implicaties voor uitspraken over de geschiktheid van het gebied voor vogels in de winter. Satellietbeelden die een algemene toename of afname van bosvegetatie laten zien, zeggen in dat opzicht niet zo veel. Het gaat namelijk om wélke bomen toe- of afnemen. Het voorkomen van bomen en struiken in de Sahel hangt in sterke mate af van de jaarlijkse regenval, maar wordt mede bepaald door de plaatselijke bevolking die selectief soorten kapt én aanplant. De gevolgen voor vogels zijn enorm. *Faidherbia albida*, de belangrijkste boom voor een aantal trekvogelsoorten in de Sahel, wordt door de plaatselijke bevolking zeer gewaardeerd (en dus aangeplant of gespaard) en staat vrijwel uitsluitend op boerenland. Anderzijds zijn cashewplantages buitengewoon vogelarm en betekent de snelle uitbreiding daarvan sinds 1980 een groot habitatverlies voor trek-, maar vooral voor lokale vogels. Ook de wijdverbreide en door de lokale bevolking gekoesterde Karitéboom heeft een negatieve invloed op het voorkomen van insectenetende trekvogels.

RÉSUMÉ

Le Sahel, vaste zone de transition entre le Sahara et les forêts tropicales humides plus au Sud, n'abrite quasiment pas de forêts. Mais la région n'est pas pauvre en arbres, bien au contraire, et la savane y est remarquablement riche en oiseaux. En hiver, de nombreux migrateurs afro-paléarctiques la fréquentent, y compris des espèces qui se reproduisent dans des habitats purement forestiers. Cet article identifie les espèces ligneuses préférentiellement sélectionnées par 14 espèces d'oiseaux migrateurs insectivores et 18 espèces d'oiseaux afro-tropicaux (10 insectivores, 3 frugivores et 5 nectarivores) sur la base d'un inventaire par échantillonnage stratifié de l'ensemble du Sahel. Au total, 760 000 arbres et arbustes appartenant à 304 espèces ont été inventoriés. Pour chacun, la hauteur et la largeur ont été mesurées, afin de calculer la superficie de houppier, et tous les oiseaux présents y ont été recensés. 99,5% étaient concentrés dans seulement 41 espèces ligneuses. *Faidherbia albida*, un acacia, était l'essence préférentielle de 20 des 32 espèces d'oiseaux étudiées, tandis que l'Acacia faux-gommier *Acacia tortilis* l'était pour sept espèces et le Dattier du désert *Balanites aegyptiaca* pour six. À elles trois, ces essences qui ne représentent que 11 % de la couverture totale de la canopée, accueillaient 89 % des Pouillots de Bonelli *Phylloscopus bonelli* et 77 % des fauvettes du complexe « passerinette » *Curruca iberiae + C. subalpina + C. cantillans*. Les espèces d'oiseaux qui s'alimentent principalement dans les arbustes ont été observées dans une plus grande diversité d'essences que les espèces qui se nourrissent dans la canopée. Les plus fortes densités (80–160 oiseaux/ha de houppier) ont été trouvées dans trois essences à la distribution restreinte au Sud du Sahara et au Nord du Sahel : le Siwak ou « Arbre brosse à dents » *Salvadora persica*, le Karira, un arbuste épineux *Capparis decidua* et l'Agar *Maerua crassifolia*. Les autres espèces d'arbres fréquentées étaient sans exception épineuses (*Balanites aegyptiaca*, diverses espèces d'acacia et de jujubier). Cinq essences communes composent à elles seules 27% de la couverture totale de la canopée – l'Anacardier *Anacardium occidentale*, le Bouleau d'Afrique *Anogeissus leiocarpus*, *Combretum glutinosum*, le Guier du Sénégal *Guiera senegalensis* et le Karité *Vitellaria paradoxa* – mais ces essences d'arbres sont rarement visitées par les oiseaux en quête de nourriture. Neuf espèces insectivores n'y ont même jamais été trouvées. Les souimangas ne fréquentaient quant à eux qu'un nombre limité d'arbres à fleurs et les frugivores uniquement quelques essences fruitières. Les insectivores étaient essentiellement présents dans les essences épineuses, probablement en raison de la présence de chenilles et de papillons de nuit. Au Sahel, ce n'est donc pas la couverture forestière totale mais la composition spécifique des peuplements arborés qui est importante pour les oiseaux. Ces résultats ont des implications importantes pour la conservation des oiseaux hivernants. Les évolutions du couvert forestier visibles par images satellites n'ont qu'un intérêt limité : ce qui compte, c'est de connaître l'évolution de l'abondance des différentes essences. La présence d'arbres et d'arbustes dans le Sahel dépend en grande partie des précipitations annuelles, mais elle est également influencée par l'importance des coupes et des plantations sélectives réalisées par la population locale et donc les conséquences pour les oiseaux sont énormes. *Faidherbia albida*, essence privilégiée par un certain nombre d'espèces migratrices au Sahel, est très appréciée par la population locale (et donc plantée ou préservée) et se rencontre presque exclusivement dans les zones cultivées. A l'opposé, les plantations de cajou sont extrêmement pauvres en oiseaux et leur expansion rapide depuis les années 1980 a entraîné une importante perte d'habitat pour les migrateurs, mais encore plus pour les espèces locales. De même, le Karité, très répandu et apprécié par la population locale, a un impact négatif sur la présence d'oiseaux migrateurs insectivores.

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SUPPLEMENTARY MATERIAL

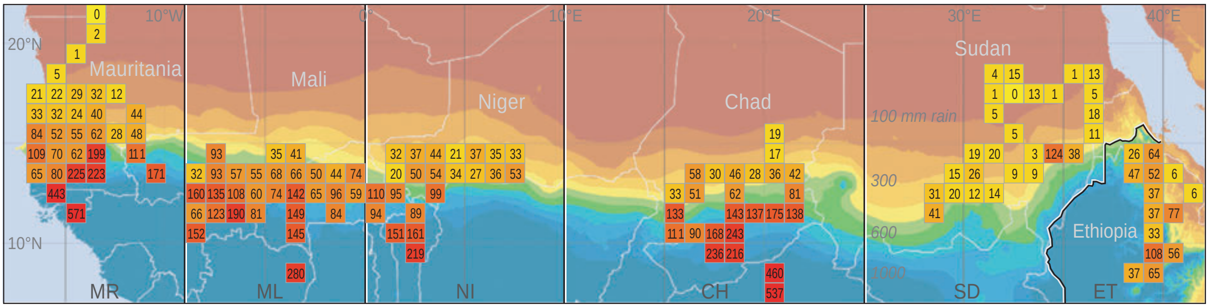
Table 2 gives bird density/ha canopy separately for different woody species as well as for woody cover. The total number of birds present in the different trees may be calculated by multiplying, for each woody species, bird density and woody cover. The numbers generated in this way cannot be used, however, to estimate the total number of birds present in the region between 7 and 22°N because the sites are not entirely representative for this region (too many sites in the western and too few in the eastern Sahel, too few in the most arid and most humid zones). This problem is solved by combining sites into 150 1° × 1° grid cells and using mean densities in grid cells to calculate an overall mean. This procedure has no impact on average woody cover, i.e. 75‰ as grand mean (based on 1901 sites) compared to 75‰ as mean of the means (based on 150 grid cells). Species composition, however, differs, depending on the way it is calculated. The average woody cover of *Faidherbia* in the 1901 sites amounts to 6.0‰ but is reduced to 2.2‰ when calculated over the 150 grid cells (Figure S4). A smaller difference was found in *Balanites* (mean of the sites 6.8‰ and mean of the grid cells 3.5‰; Figure S2) and in *A. tortilis* (2.7‰ for sites and 2.3‰ grid cells; Figure S3). However, even the grid cells are not fully representative of the entire region (see Zwarts *et al.* 2023a), which is why the entire region was divided into eleven rainfall zones and six longitudinal bands. The average woody cover of all species is calculated for 65 subcategories using the surface area of these zones as weighting factor (Figure S1 in Zwarts *et al.* 2023a). The same procedure was used to calculate average woody cover in the entire region; further explanation given in Zwarts *et al.* 2023a.

The next five pages give distribution maps of the total woody cover for eight woody species, three most important for birds (Figures S2–S4) and five of the most common species (Figures S5–S10). The table in the legend to Figures S1–S4 gives the average woody cover (‰) for eleven rainfall zones and six longitudinal bands; interpolated values are marked grey. Figure S1 in Zwarts *et al.* 2023a gives the land surface area of the 65 subregions. These data are available for 53 of the 65 subregions. To estimate the woody cover in the 12 missing subregions, we averaged the densities in two adjacent cells with a similar rainfall. Since the grid cells of South Sudan differ drastically from those in the nearby Ethiopian Highlands, we substituted the adjacent values of Chad and the Central African Republic for missing South Sudan cells. The woody cover between 7 and 22°N is calculated by using the measured or interpolated average woody cover in 65 subareas multiplied with the surface area (Figure S1 in Zwarts *et al.* 2023a). For all woody species combined we arrived at a total woody cover of 0.897 million km^2 or 8.99% of the total land surface (9.974 million km^2). To estimate the reliability of these estimates, we split the sites in two halves (even and odd) and repeated all calculations. The two estimates obtained with the split-half method are given in the legends.

Number of trees

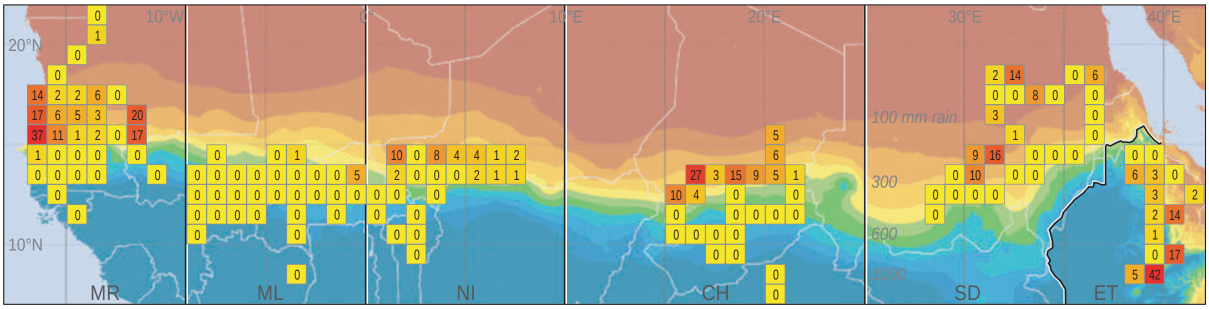
The increase of woody cover with rainfall (Figure S10A) is due mainly to an increase of tree density, from 6 woody plants/ha in the hyper-arid zone (<100 mm) to more than 200 in the hyper-humid zone (Figure S10B). Trees are also taller in the humid zone. The average height increases from 3 m in the hyper-arid to 9 m in the hyper-humid zone (Figure S10C) and the average canopy surface per tree increases from 7 to 20 m^2 (Figure S10D).

The average number of woody plants in the 150 grid cells amounted to 101/ha, but after accounting for sites in the desert that are under-represented, we arrived at an overall average of 86 trees and shrubs per ha, which implies that in the entire region between 7–22°N and 17°W–42°E, 87 billion trees and shrubs may be found (80–94 billion; split half). This estimate may be compared to data collected by Brandt *et al.* (2020) who used satellite imagery with a resolution of 0.5 m to count and measure the crown surface of individual trees in the western Sahel (west of 6°W) in the rainfall zone of 0 to 1000 mm rainfall per year (i.e. between 13 and 22°N), an area of 1.3 million km^2. Within this area, they detected 13.4 trees per ha, in total 1.8 billion trees, with an average crown surface of 12 m^2. When we select the same area, our data suggest a much higher total of 9.4 billion trees. This difference was to be expected, since we counted during our field work all trees of ≥1 m high, being equivalent to woody plants with a crown surface of about ≥0.8 m^2, whereas Brandt *et al.* (2020) took >3 m^2 as their lower limit. In total, 51.4% of our counted trees had a diameter of 1 m (0.8 m^2) and 25.9% a diameter of 2 m (3.1 m^2). Discarding these small woody plants, we arrive for the region surveyed by Brandt *et al.* (2020) at 3.7 billion trees >0.8 m^2 and 2.1 billion trees >3.1 m^2. Our field data underline the conclusion of Brandt *et al.* (2020) that there are many more trees in drylands than assumed so far.



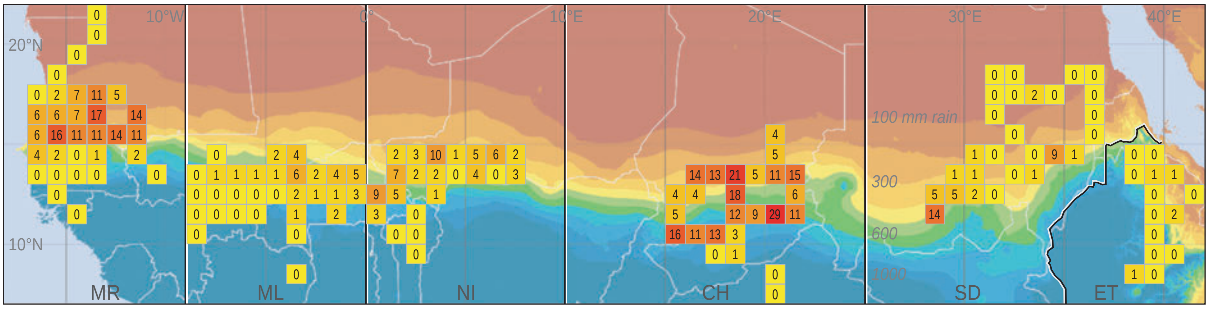
rain (mm)	MR	ML	NI	CH	SD	ET
<100	2	3	4	5	6	
100–200	24	21	19	17	15	3
200–300	29	26	23	23	21	15
300–400	61	45	30	44	14	18
400–500	49	36	30	33	42	18
500–600	112	52	58	97	84	63
600–700	67	66	88	93	93	90
700–800	128	74	97	138	138	18
800–900	251	104	96	165	165	28
900–1000	290	147	109	217	217	58
>1000	497	154	168	387	387	80

Figure S1. Woody cover (‰) of all woody plants together; present in 98% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 75‰ ± 92.
Estimated overall woody cover in Africa in the region shown on the map (10 million km^2; 7–22°N, 17°W–42°E): 90‰, based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 896,550 km^2, of which 118,110, km^2 interpolated; range 883,180–909,930 km^2 (split-half).



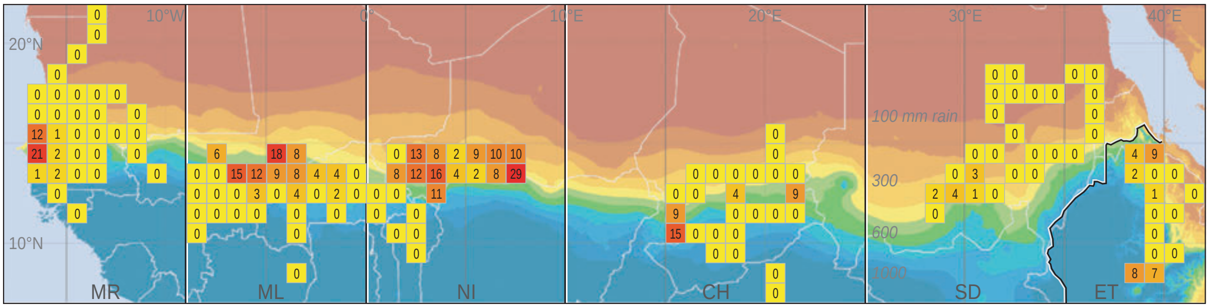
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.29	1.09	1.89	2.69	63.49	
100–200	6.15	5.92	5.68	5.45	4.54	1.41
200–300	7.51	5.46	0.64	6.87	9.35	4.32
300–400	20.26	11.22	2.18	13.68	0.17	1.78
400–500	4.85	3.62	1.37	7.24	0.01	0.55
500–600	0.48	0.17	0.00	0.32	0.11	20.81
600–700	0.01	0.00	0.00	0.00	0.00	8.02
700–800	0.04	0.00	0.00	0.00	0.00	0.63
800–900	0.00	0.00	0.00	0.00	0.00	5.37
900–1000	0.00	0.00	0.00	0.00	0.00	0.25
>1000	0.00	0.00	0.00	0.00	0.00	1.99

Figure S2. Woody cover (‰) of Umbrella Acacia *Acacia tortilis*; present in 49% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 2.7‰ ± 6.1.
Estimated overall woody cover: 2.3‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 23,330 km^2, of which 7520 km^2 interpolated; range: 22,580–24,050 km^2 (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.07	0.16	0.16	0.16	0.25	
100–200	4.74	4.17	4.17	3.61	0.09	0.26
200–300	6.47	4.40	2.32	5.19	0.53	0.12
300–400	10.79	7.09	3.39	10.85	0.73	0.05
400–500	6.50	2.55	1.89	9.73	6.14	1.01
500–600	3.90	2.87	1.07	10.17	10.34	1.01
600–700	1.28	1.76	0.25	11.01	11.01	1.10
700–800	0.14	1.36	7.05	15.84	15.84	0.00
800–900	0.00	0.77	4.08	13.98	13.98	0.22
900–1000	0.00	0.45	0.04	2.64	2.64	0.19
>1000	0.00	0.00	0.04	0.52	0.52	0.23

Figure S3. Woody cover (‰) of *Balanites aegyptiaca*; present in 72% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 3.5‰ ± 5.4.
Estimated overall woody cover: 2.5‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 25,200 km^2, of which 8250 km^2 interpolated; range: 23,110–27230 km^2 (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.00	0.00	0.00	0.00	0.00	
100–200	0.04	0.03	0.02	0.00	0.00	0.00
200–300	0.05	0.60	1.15	0.11	2.58	0.00
300–400	2.59	6.48	10.37	0.02	0.19	0.00
400–500	11.89	14.11	5.76	0.00	1.93	0.00
500–600	17.48	6.84	8.54	10.68	0.00	0.69
600–700	0.96	8.68	9.52	6.32	6.32	3.11
700–800	0.01	2.12	0.00	0.13	0.13	5.67
800–900	0.00	1.26	0.00	0.00	0.00	4.09
900–1000	0.03	0.22	0.00	0.01	0.01	2.64
>1000	0.00	0.01	0.00	0.02	0.02	1.72

Figure S4. Woody cover (‰) of *Faidherbia albida*; present in 41% of the 150 cells. Average woody cover (mean ±SD) in grid cells: 2.2‰ ± 4.3.
Estimated overall woody cover: 1.2‰ based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total woody cover: 11,130 km², of which 1220 km² interpolated, range: 11,110–11,400 km² (split-half).

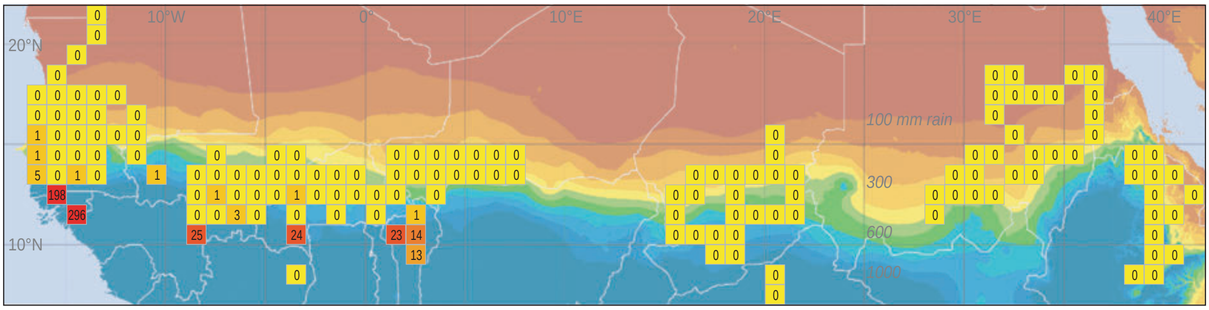


Figure S5. Woody cover (‰) of Cashew *Anacardium occidentale*, mean ± SD: 4.1 ± 29.1; present in 13% of the 150 cells.

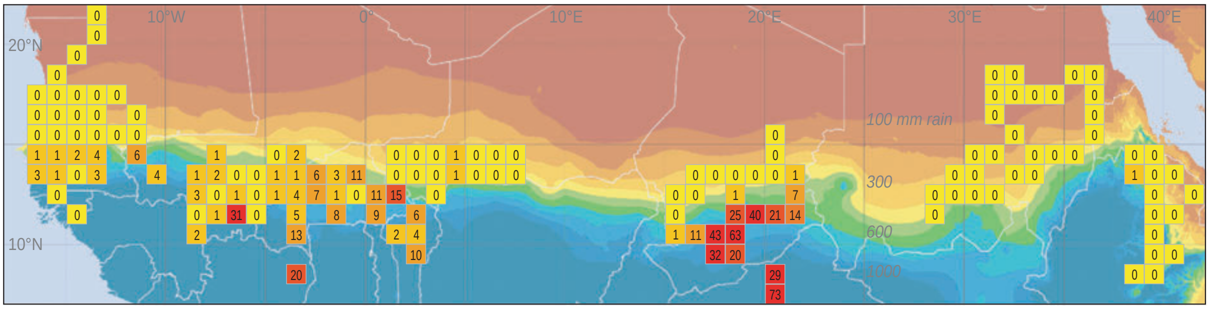


Figure S6. Woody cover (‰) of African Birch *Anogeissus leiocarpus*, mean ± SD: 3.9 ± 10.6; present in 45% of the 150 cells.

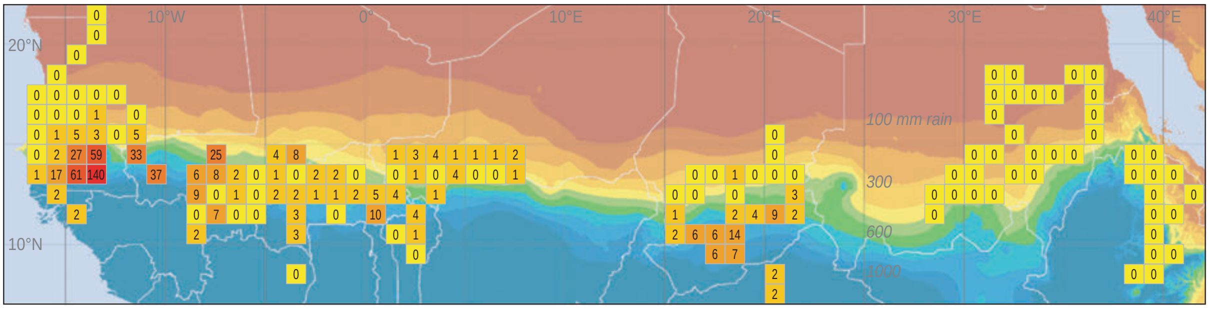


Figure S7. Woody cover (‰) of *Combretum glutinosum*, mean ± SD: 4.0 ± 14.1; present in 59% of the 150 cells.

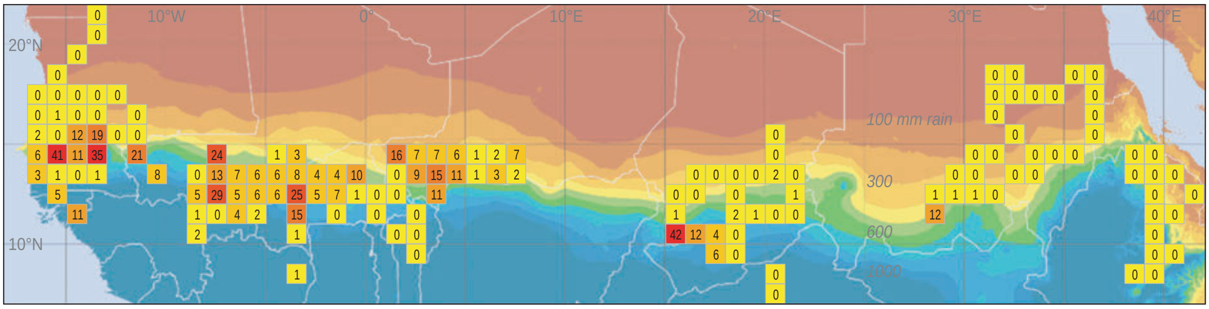


Figure S8. Woody cover (‰) of *Guiera senegalensis*, mean ± SD: 3.8 ± 7.4; present in 53% of the 150 cells.

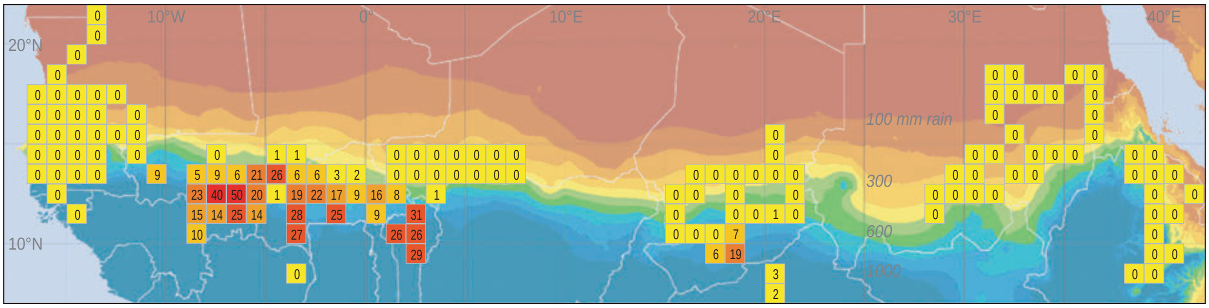


Figure S9. Woody cover (‰) of Shea Tree *Vitellaria paradoxa*, mean ± SD: 4.3 ± 9.2; present in 30% of the 150 cells.

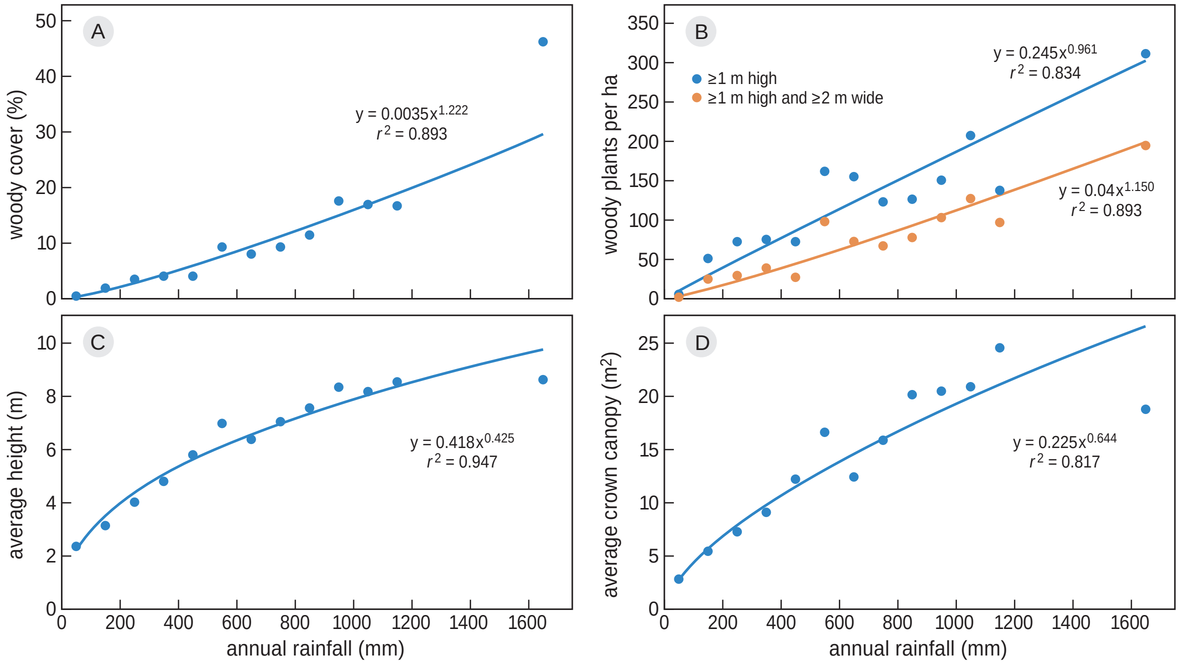
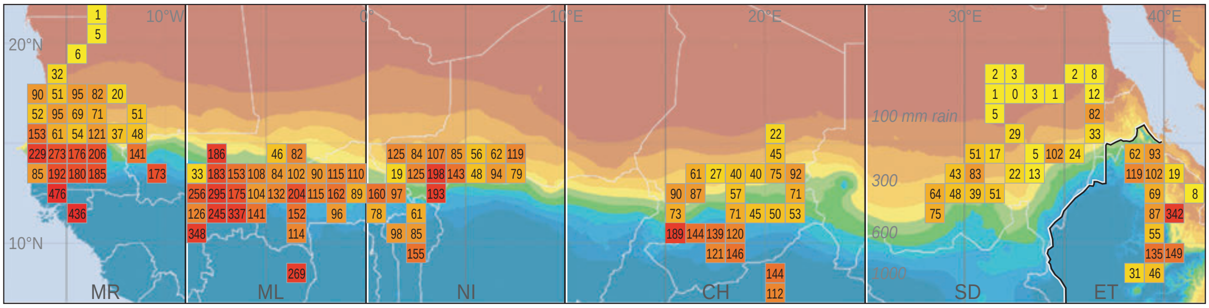


Figure S10. (A) Woody cover (%), (B) number of woody plants (≥1 m high or ≥1 m high and diameter ≥2 m), (C) height (m) and (D) crown canopy (m^2), all averaged per 100 mm rainfall zones, as a function of annual rainfall. All relations are highly significant. Trees from the rainfall zones 1300–2300 mm are taken together, due to the smaller sample size.



rain (mm)	MR	ML	NI	CH	SD	ET
<100	10	8	7	5	3	
100–200	68	53	37	22	45	7
200–300	77	106	135	48	49	13
300–400	112	97	81	62	37	43
400–500	75	55	95	61	58	44
500–600	247	89	192	75	57	109
600–700	168	130	191	59	59	324
700–800	158	135	97	90	90	30
800–900	158	167	97	109	109	71
900–1000	221	182	79	134	134	71
>1000	458	228	101	58	58	133

Figure S11. Density per ha of woody plants ≥1 m high. Average number of woody plants (*n*/ha ±SD) in grid cells: 108 ± 82.
Estimated overall density in Africa in the region shown on the map (10 million km^2; 7–22°N, 17°W–42°E): 87 per ha, based on averages given in the table for 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.
Estimated total number of woody plants in the same region: 87 billion, of which 10 billion is interpolated; range 80–94 billion (split-half).

Frequent agonistic interactions among arboreal birds in savannahs but not in humid forests of Africa

Leo Zwarts[1,*], Rob G. Bijlsma[2] & Jan van der Kamp[1]

Zwarts L., Bijlsma R.G. & van der Kamp J. 2023. Frequent agonistic interactions among arboreal birds in savannahs but not in humid forests of Africa.
Ardea 111: 175–188. doi:10.5253/arde.2022.a30

Arboreal birds in the Sahel are highly selective in their tree choice. Most migrant, but also resident, birds are found in a few tree species and within those species often only in trees with abundant leaves and flowers. For this reason alone, preferred trees were expected to teem with birds. This was not the case. Most bird species were present in trees as singletons, even half of the Senegal Eremomela *Eremomela pusilla* – the most social species of all – were recorded as solitary birds. The probability that two different bird species were in the same tree was also very small, 2.8% on average. Mixed-group foraging flocks of arboreal birds, as so often reported for tropical forests, did not occur in the Sahel. Perhaps birds forage singly because they have no need to fear the raptors that are common in the forests further south. Some species, such as European Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*, defend winter territories, but for other species individual home ranges show overlap. In the humid forests further south, and among resident species in the Sahel, few agonistic interactions were seen, but migratory birds were often agonistic with congeners and even more frequently with birds of other species. Larger bird species usually won agonistic interactions, but Western Olivaceous Warblers *Iduna opaca* chased off birds twice their own body size. Subalpine Warbler *Curruca iberiae* + *subalpina* + *cantillans* and other *Curruca* species, with the exception of Lesser Whitethroat *Curruca curruca*, were also intolerant. Western Bonelli's Warblers *Phylloscopus bonelli*, and during migration also Willow Warblers *Phylloscopus trochilus*, were most often on the receiving end of agonistic interactions. Far fewer agonistic interactions were recorded in the more humid regions to the south of the Sahel. This disparity may hinge on the higher intra- and interspecific encounter rate in the Sahel, where a greater fraction of trees are occupied by birds, than in the humid forests.

Key words: Sahel, interference competition, agonistic behaviour, dominance hierarchy, Sahel, arboreal birds

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The arrival of large numbers of Eurasian migrants in Africa raises the question whether food is a limited resource during the non-breeding season. And if so, do migrants compete for food resources with local residents (Moreau 1972, Leisler 1992, Jones 1998, Salewski & Jones 2006, Wilson & Cresswell 2007, Gbemiga 2014). Interactions, hierarchy dominancy and niche partitioning would be expected between migrants and residents in a region flooded with so many birds from Eurasia. A study on ground-foraging bird species in Kenya indeed suggested this to be the case (Leisler *et al.* 1983), but this study recorded wheatears on burned sites that were a temporary magnet for wheatears and other small ground-foraging passerines and may not have been representative. Eleven species of wheatears in SW Iran largely avoided competition by spatial segregation in geography, altitude and habitat (Cornwallis 1975). Dominance hierarchies were not generally apparent in tree-dwelling species in Kenya, Zimbabwe, Ghana and Ivory Coast (Rabøl 1987, 1990, Salewski *et al.* 2002b, 2003); these birds showed very little if any agonistic behaviour. A lack of agonistic behaviour does not prove a lack of competition, which can be too cryptic to detect, such as subdominant birds performing geographic shifts, or competition occurring at the microhabitat level (e.g. Bijleveld *et al.* 2012, van den Hout *et al.* 2017).

In contrast to wintering Afro-Paleartic migrants, intra- and interspecific interactions between foraging birds during return migration at a stopover site in the Sahara were sufficiently frequent to suggest noncryptic interference competition (Salewski *et al.* 2007). Three possible explanations were provided for why the behaviour of these birds differed so much from those on the wintering grounds: (1) higher encounter rate because the birds were concentrated in a relatively small wadi and reached high densities; (2) relatively high energy demand during fuelling up and therefore more competition; (3) a small food supply. Salewski *et al.* (2007) found that larger birds were dominant over smaller ones, but was unable to test whether residents dominated migrants because there were no residents with a body mass within the range of the body masses of the migrant species at the study site.

Our field study was not designed to address these questions, but the data were systematically collected in a wide range of climate zones south of the Sahara and may be used to reflect on some of the afore-mentioned ideas. We aim to answer five questions: (1) how often do intra- and interspecific interactions occur in arboreal birds? (2) are there more interactions among birds living in the arid than in the humid zone? (3) are there more or fewer interactions among migrating than wintering birds? (4) is the dominance hierarchy, based on the percentage of won and lost interspecific interactions, related to body mass? (5) are, within this dominance hierarchy, migrants subordinate to residents?

METHODS

Fieldwork in the Sahel was restricted to the dry season, between October and March 2007–2019, but mostly to January and February. We disregarded the data collected in 2007–2011, when interactions were not yet systematically noted. We determined bird densities and woody cover within 2144 plots situated between 7 and 22°N and 15°W and 42°E (Zwarts *et al.* 2023a). Within this extensive zone, the Sahara is largely devoid of vegetation except in wadis, it gradually changes into savannah with shrubs and scattered trees, and finally morphs into woody savannah and humid forests some 1000 km south of the edge of the Sahara. Half of the savannah has been converted into agricultural land, though still extensively covered with scattered trees (Photo 1). For each study plot, we determined annual local rainfall for the period 1950–2000 (using Hijmans *et al.* 2005), in order to test whether the occurrence of agonistic behaviour varied per rainfall zone.

The 2144 study plots contained 766,000 individual shrubs and trees, which were identified to species, height and width, and in which 30,903 birds were recorded and assigned to individual trees or shrubs. We restrict the analysis to the 29 most common bird species, in total 11,433 individuals, excluding species using trees for resting or perching only. The average woody cover increased with annual rainfall from 0% in the hyper-arid zone (annual rainfall <100 mm) to 35% in the hyper-humid zone (>1200 mm rainfall/year) which reflects an increase of the average number of trees and shrubs (from 50 per ha in hyper-arid to 250 per ha in the hyper-humid zone) and ditto of tree size (average canopy surface increasing from 3 to 21 m^2).

Typical woodland birds on their Eurasian breeding grounds, inhabiting closed-canopy forest, find themselves in the Sahel foraging in an open landscape where woody cover usually varies between 3 and 15% but where the trees stand apart from each other (Zwarts *et al.* 2019). Our focus is on the agonistic behaviour in tree-dwelling African residents and Eurasian migrants. Since so many trees held no birds at all or just a single specimen, in this paper we pay particular attention to how often birds were single or together with birds of the same or other species in the same tree.

Depending on size and opacity of the canopy, the time spent per tree to detect all birds was systematically noted and varied from some seconds to 45 minutes, but always took more time when one or more birds were present (Figure 4–7 in Zwarts & Bijlsma 2015). The data were collected with a team of three, sometimes four, persons. The basic principle was that we observed a tree simultaneously from various positions until we were convinced that all birds present had been recorded. Quarrels and chases between birds were systematically noted and are used to analyse intra- and interspecific agonistic behaviour. When a tree held more than one bird, we often noticed that birds avoided each other, but this behaviour was difficult to quantify and was not recorded. Other more or less overt forms of agonistic behaviour, such as calling and bill rattles, were omitted in the present analysis, because they were not always systematically recorded and, when more than two birds were present, it often was not clear which bird was threatened.

Species have been categorized as Afro-Palearctic (termed migrants) and Afro-tropical (termed residents, although some perform intra-African movements). The analysis is restricted to 17 migrants and 12 residents, all common tree-dwellers. Rufous-tailed Scrub Robins *Cercotrichas galactotes* are partly migrant, partly resident, and treated here as resident. Spectacled Warblers *Curruca conspicillata* breed in NW Africa of which the majority spends the winter in or south of the Sahara (Thévenot *et al.* 2003), thus should be regarded as migrant, but the birds we recorded in NW Mauritania in late January showed breeding behaviour (full song, display, territorial disputes) and, thus, are considered here as residents (see also Salewski *et al.* 2005). The species is excluded from comparisons between migrants and residents because none of the other species showed courtship behaviour during our observation periods. The Subalpine Warbler *Curruca cantillans* was recently split into three species, but recorded by us as one species. Most were observed in the western, and none in the eastern, Sahel. The characteristic rattle of Moltoni Warbler *C. subalpina* was infrequently heard in the central Sahel. We assume that most of our birds were Western Subalpine Warblers *C. iberiae*. Within the range of Iberian Chiffchaffs *Phylloscopus ibericus* (North of 13°N and West of 4°W), 44% of birds were noted as unspecified Chiffchaffs, but are considered here as Iberian Chiffchaff. We assume that unspecified Olivaceous Warblers (62%) were Western Olivaceous Warbler *Iduna opaca* or Eastern Olivaceous Warbler *Iduna pallida* depending on whether occurring West or East of 3°E, respectively; this classification is not entirely correct because small numbers of Olivaceous Warblers in West Africa are *I. pallida* (*reiseri*) (Salewski & Herremans 2006).

RESULTS

For interactions to occur, more than one bird should be present in a tree. However, most trees in the Sahel are devoid of birds. The presence of arboreal birds largely

Photo 1. A typical view of the Sahel, where foraging arboreal birds have to do with single trees which are widely distributed on savannah and farmland, as shown here on an aerial picture taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) of an intensively cultivated area in West Senegal. Closed-canopy forests are confined to the humid Guinean vegetation zone, hundreds of km south of the Sahel.

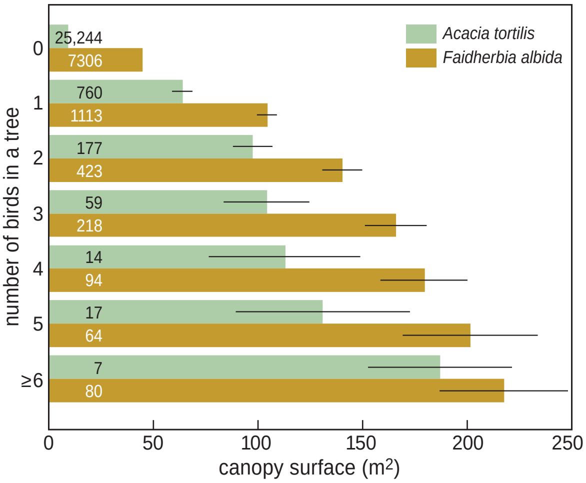

Figure 1. Tree size (canopy surface ± 95% interval of confidence, m^2) of two bird-rich woody species, *Faidherbia albida* and *Acacia tortilis*, in which between 0 and ≥6 arboreal birds were present. Number of trees shown in the bars. ANOVA: *A. tortilis*: $r^2 = 0.20$, $P < 0.0001$ and *Faidherbia*: $r^2 = 0.23$, $P < 0.0001$.

depends on tree species, the birds being highly selective (Zwarts *et al.* 2023c), and on tree size. On average for the entire zone, 51% of the trees and shrubs had a diameter of 1 m and 26% a diameter of 2 m (Zwarts *et al.* 2023c). Most birds were seen, however, in larger trees. Trees or shrubs in which at least one tree-dwelling bird was detected were, on average, 8.3 ± 3.6 m high (±SD) and had a canopy surface of 81.2 ± 83.7 m^2, equivalent to a tree with a canopy width of 10 m. Only large trees may attract more than a single bird (Figure 1).

Among 7034 migrants and 4399 residents recorded in 766,000 trees and shrubs, we noted 202 instances of agonistic behaviour (Table 1), i.e. in 2% of all birds observed. However, agonistic behaviour differed substantially in frequency among species. Intraspecific interaction was observed in 2% of *Curruca* Warblers, but it was completely absent in 12 other species (see Figure 2A). Among migrants, intraspecific agonistic encounters averaged 1.4% compared with 0.1% among residents (excluding Spectacled Warbler; Figure 2A).

Interspecific agonistic behaviour was noted, on average, in 4.7% of the migrants and 1.1% of the residents (Figure 2B). Among migrants, agonistic encoun-

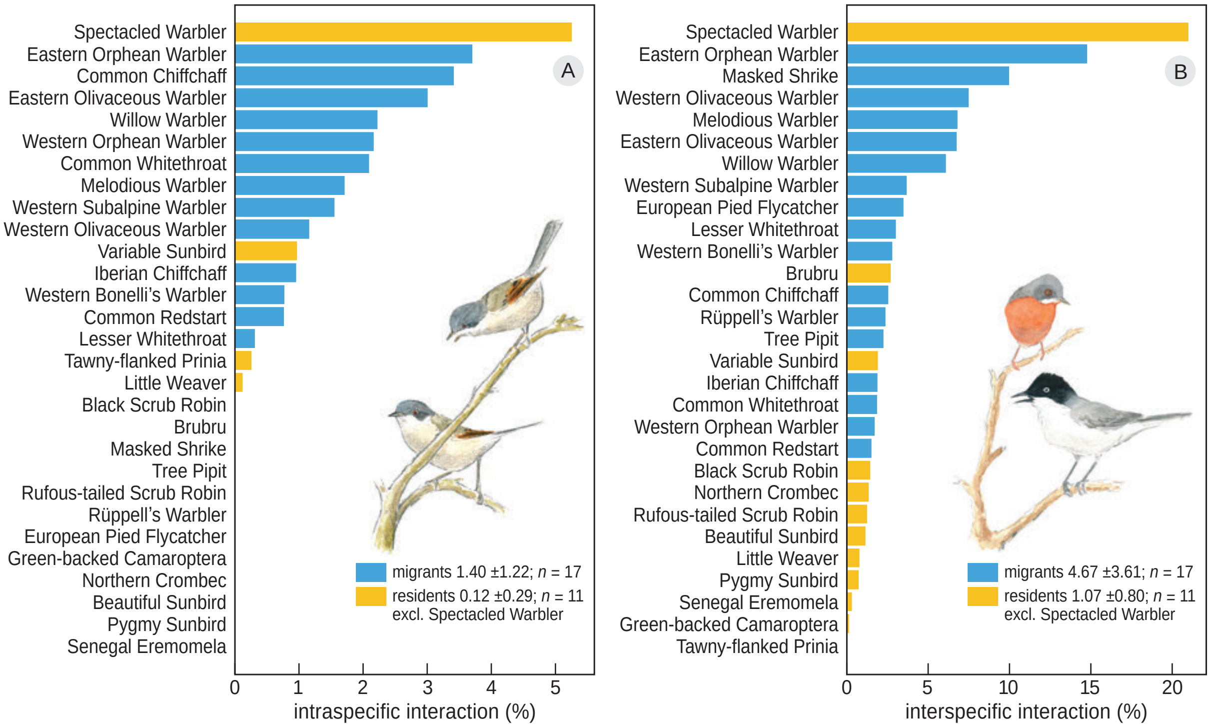

Figure 2. (A) Percentage of (A) intra- and (B) interspecific interactions in tree-dwelling bird species, based on data shown in Table 1. The legends give the average number of interactions (% ± SD) for 17 migrants and 11 residents. Migrants and residents differ significantly (ANOVA): Intraspecific: $r^2 = 0.31$, $P = 0.002$; interspecific: $r^2 = 0.29$, $P = 0.003$, $n = 28$.

ters with other species were recorded 109 times, of which 98 involved other migrants and 11 residents. Three migrant species were more aggressive than all other species, namely Melodious Warbler *Hippolais polyglotta*, Subalpine Warbler and Western Olivaceous Warbler. The latter species, with an average body mass of 10.6 g, was able to successfully chase species twice its body mass, such as Brubru *Nilaus afer* and Tree Pipit *Anthus trivialis*. Normally, when the dominant bird was a migrant, 77% (75/98) of the attacks were directed towards species with a smaller body mass, almost the same as in residents (9 out 13 directed towards a bird with lower body mass).

Agonistic behaviour was understandably rarely recorded because most birds were on their own in single trees. On average, 91% of the migrants and 75% of the residents foraged in a tree without congeners. Some species were nearly always solitary, such as European

Table 1. Number of agonistic interactions between 17 migrant (marked blue) and 12 resident tree-dwelling bird species, ranked according to body mass (column 2; Urban *et al.* 1997, Fry *et al.* 2000 & 2004, Cramp 1992, Cramp & Perrins 1993, Salewski *et al.* 2002c, Cox *et al.* 2011). Upper row: dominant bird species, chasing away other birds (first column), with intraspecific interactions on the diagonal. Average annual rainfall (mm) within their distribution area between late November and early March (from Zwarts *et al.* 2023b) is given in column 3 and number of birds in column 4. The last three columns give percentage of birds engaged in intra- and interspecific interactions and percentage of interspecific interactions won. The birds in the left lower triangle refer to interactions directed towards species with a higher body mass and those in the right upper triangle to species with a lower body mass.

	body mass (g)	avg. annual rainfall	no of birds observed	Variable Sunbird	Pygmy Sunbird	Beautiful Sunbird	Senegal Eremomela	Iberian Chiffchaff	Common Chiffchaff	Willow Warbler	Western Bonelli's Warbler	Northern Crombec	Tawny-flanked Prinia	Eastern Olivaceous Warbler	Subalpine Warbler	Spectacled Warbler	Melodious Warbler	Western Olivaceous Warbler	Green-backed Camaroptera	Lesser Whitethroat	European Pied Flycatcher	Little Weaver	Common Whitethroat	Rüppell's Warbler	Common Redstart	Robin	Eastern Orphean Warbler	Western Orphean Warbler	Tree Pipit	Masked Shrike	Brubru	Black Scrub Robin	% intraspecific	% interspecific	% interspecific wins
Variable Sunbird	6.3	896	109	1																													1.0	1.8	100
Pygmy Sunbird	6.6	699	549								1				1							2											0.0	0.7	0
Beautiful Sunbird	7.0	850	470								2												1										0.0	1.1	40
Senegal Eremomela	7.0	783	321									1																					0.0	0.3	0
Iberian Chiffchaff	7.0	227	504					2							4																		0.9	0.8	0
Common Chiffchaff	7.0	707	141			2			4									1					1										3.4	2.8	0
Willow Warbler	7.9	1129	184							4					2		6					1											2.2	6.0	18
W. Bonelli's Warbler	8.0	450	2083	2						1	13				18		1	15				4						1					0.8	2.3	13
Northern Crombec	8.1	646	233								1							1															0.0	1.3	33
Tawny-flanked Prinia	8.4	725	849										2																				0.3	0.0	
E. Olivaceous Warbler	9.0	416	133											4	2																		3.0	6.8	78
Subalpine Warbler	9.3	368	1581							1	2			1	21		2	10										2					1.6	3.2	64
Spectacled Warbler	10.0	95	19													1							1										5.3	21.1	75
Melodious Warbler	10.3	875	123														2	2															1.7	6.5	75
W. Olivaceous Warbler	10.6	560	655															6															1.2	6.0	100
Green-b. Camaroptera	10.9	752	696																		1												0.0	0.1	0
Lesser Whitethroat	11.4	318	332											4	2					1			2				2						0.3	3.0	0
Eur. Pied Flycatcher	12.9	1124	86																						2								0.0	3.5	33
Little Weaver	13.5	579	902															1				1											0.1	0.8	86
Common Whitethroat	13.5	466	499															4					10										2.1	1.8	56
Rüppell's Warbler	14.4	188	84											2																			0.0	2.4	0
Common Redstart	14.6	608	273															2							2								0.8	1.5	50
Ruf.-tailed Scrub Robin	18.4	553	98																													1	0.0	1.0	0
E. Orphean Warbler	19.8	247	27																								1						3.7	14.8	100
W. Orphean Warbler	20.2	287	249															1										5					2.2	1.6	75
Tree Pipit	21.3	926	58															1															0.0	1.7	0
Masked Shrike	22.0	485	22																								2						0.0	9.1	0
Brubru	23.0	699	45															1															0.0	2.2	0
Black Scrub Robin	25.4	428	108																														0.0	0.9	100

Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*. Senegal Eremomela *Eremomela pusilla* was the most social bird, but even in this species half of the individuals were recorded as a solitary bird in a tree (Figure 3). The average number of individuals in a tree varied between 1.0 for the Pied Flycatcher and 1.8 for the Senegal Eremomela. In 7 of the 29 species, we never saw more than 2 birds of the same species in a single tree, in 16 and 21 of the 29 species never more than 3 or 4 birds, respectively. Bird concentrations in a tree were always associated with very large trees (Figure 1), usually *Faidherbia* which can be 20 m high with a canopy surface of up to 700 m^2.

The probability that two different species from the 29 selected for this study met each other in the same tree was 2.8% on average, and higher for common (e.g. W. Bonelli's Warbler 15.3%, Subalpine Warbler 7.5% and Common Whitethroat 6.9%) than for less common species (varying between 0.1 and 4.6%). The encounter rates, shown for six common bird species in Table 2, were used to calculate how often birds had interspecific agonistic interactions when in the same tree.

Table 2. The probability (%) in six common bird species that a bird (mentioned in the first row) encounters a congener or another species (mentioned in the first column). Species are ranked according to the relative frequency at which they encounter birds of other species; migrants marked blue.

	Tawny-flanked Prinia	Little Weaver	W. Bonelli's Warbler	Subalpine Warbler	Common Whitethroat	W. Olivaceous Warbler
Tawny-flanked Prinia	46.5	4.2	1.7	1.9	4.5	1.5
Little Weaver	10.3	56.7	8.2	3.3	9.9	8.1
W. Bonelli's Warbler	5.3	15.9	43.1	22.5	20.4	34.0
Subalpine Warbler	2.9	3.9	12.3	10.3	9.6	27.4
Common Whitethroat	2.2	2.1	2.6	2.7	9.0	2.9
W. Olivaceous Warbler	1.3	2.9	7.9	11.1	5.1	10.9
Total 5 other species	22.0	29.0	32.7	41.6	49.4	73.9
Total number of birds	849	902	2083	1581	499	504

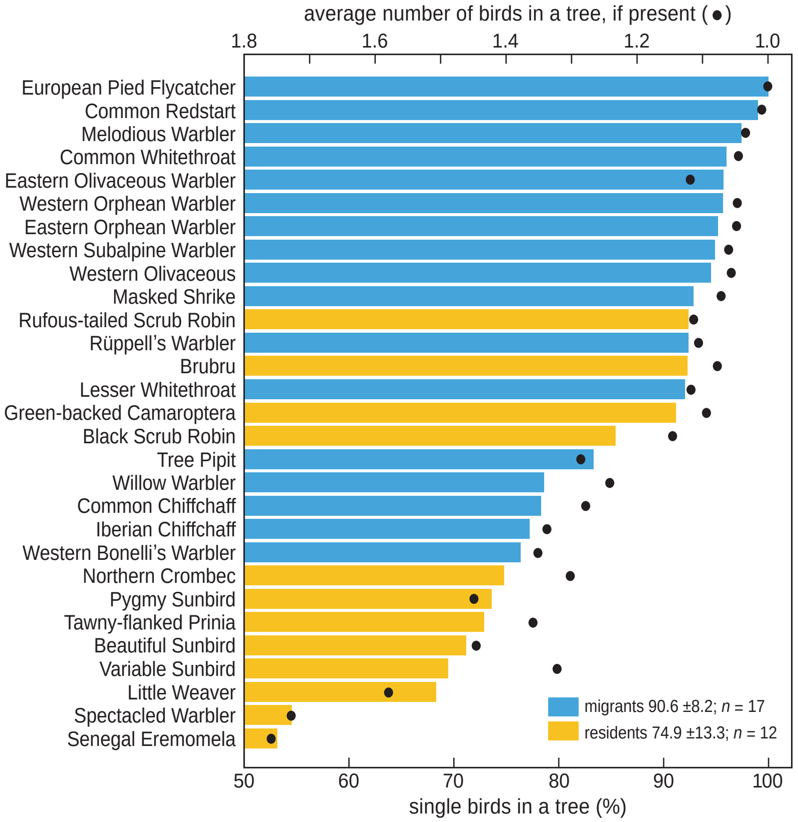

Figure 3. Average number of congeners present in a tree or shrub (upper horizontal axis) and percentage of birds recorded as single (i.e. without congener) in a tree or shrub (lower horizontal axis). For number of observed birds, see Table 1. Migrants and residents differ significantly (ANOVA): % single birds: $r^2 = 0.36$, $P = 0.001$; average number of birds in a tree: $r^2 = 0.41$, $P = <0.001$, $n = 28$.

The Western Olivaceous Warbler was dominant over all other species (Table 1) and always intolerant to congeners. This species shared a tree with other birds in 28 out of 655 cases; all 6 encounters with a congener resulted in a chase. Western Bonelli's Warbler were often on the receiving end of agonistic behaviour when sharing a tree with other, usually dominant species (Table 1). Bonelli's Warbler was chased in 11% and 9% of the cases when it shared a tree with respectively Western Olivaceous Warbler or Subalpine Warbler (Table 4). Willow Warbler *Phylloscopus trochilus* was subordinate to Melodious Warbler (32%; 6/19) and Subalpine Warbler (12%; 2/17). Lesser Whitethroat *Curruca curruca* was subordinate to Eastern Orphean Warbler *Curruca crassirostris* (40%; 2/5), Subalpine Warbler (40%; 2/5), Common Whitethroat (17%; 2/12) and Eastern Olivaceous Warbler (17%, 4/24). Migrants, and particularly Western Olivaceous Warbler and several *Curruca* species, except Lesser Whitethroat, were more often involved in agonistic behaviour than residents, against congeners as well as other species.

Table 3. The number of times that Western Olivaceous Warblers (655 birds in total) shared a tree with another bird ('total') and how often agonistic behaviour ('agon') was then noted. The species are ranked according to the relative frequency of agonistic behaviour; migrants marked blue.

	Number		%
Recipient	Total	agon.	agon.
Common Whitethroat	15	4	27
W. Olivaceous Warbler	**28**	**6**	**21**
Melodious Warbler	11	2	18
Common Redstart	23	2	9
W. Bonelli's Warbler	177	15	8
Subalpine Warbler	142	10	7
W. Orphean Warbler	15	1	7
Little Weaver	42	1	2
Sunbird spp.	61	0	0
Iberian Chiffchaff	42	0	0
Willow Warbler	21	0	0
Green-backed Camaroptera	11	0	0

Table 4. The number of times that Western Bonelli's Warbler shared a tree with another bird ('total') and how often agonistic behaviour ('agon.') was recorded. The species are ranked according to the relative frequency of agonistic behaviour; migrants marked blue.

	Number		%
Agressor	Total	agon.	agon.
W. Olivaceous Warbler	131	15	11
Subalpine Warbler	205	18	9
Willow Warbler	20	1	5
Melodious Warbler	26	1	4
Little Weaver	136	4	3
W. Orphean Warbler	47	1	2
W. Bonelli's Warbler	**717**	**13**	**2**
Sunbird spp.	149	2	1
Senegal Eremomela	33	0	0
Iberian Chiffchaff	54	0	0
Northern Crombec	22	0	0
Tawny-flanked Prinia	33	0	0
Green-backed Camaroptera	26	0	0
Common Whitethroat	44	0	0
Common Redstart	36	0	0

To investigate whether the relative frequency of agonistic encounters varied per rainfall zone, we compared the relative occurrence per rainfall zone for residents and migrants as a group, and separately for the five most common migrants. In none of seven analyses significant differences were apparent in χ^2-tests. However, Willow Warblers were encountered in the semi-arid climate zones exclusively during migration (i.e. before 15 November) and later on exclusively in their wintering grounds (after 15 November). The 143 Willow Warblers observed in the Sahel before mid-November shared their trees with 108 other migrants with a similar or higher body mass. Within these loose associations 12 interactions were recorded, with Willow Warblers being twice dominant and ten times subordinate to other migrants (Table 5). In the hyper-humid vegetation zone, where they are present from mid-November onwards, no agonistic interactions were recorded between Willow Warblers and other migrants (of which very few were present anyway).

DISCUSSION

Arboreal birds in the Sahel are on their own

An estimated 87 billion trees are available for 1,3 billion arboreal birds in Africa in the zone between 7 and 22°N, but the majority of bird species are concentrated in just three tree species representing 11% of the total woody cover (Zwarts *et al.* 2023c). For this reason alone, we expect birds in the Sahel to have a fair chance of co-occurrence, either opportunistically or whilst feeding in ephemeral mixed-species flocks. Large White Thorn *Faidherbia albida* or Umbrella Acacia *Acacia tortilis*, provided that they are densely leafed or in full bloom, indeed occasionally attracted up to 6 insectivorous species and up to 14 birds in a single tree. However, this was truly exceptional, given the fact that altogether we recorded more than 5 or 10 birds in respectively 1.4% or 0.07% of the individual trees in which birds resided anyway.

Within our study area, arboreal birds were typically not feeding in flocks (Figure 3). Tree-dwelling bird species in the Sahel not mentioned in this paper were also usually scattered as solitary birds across trees, except the fruit-eating Blue-naped Mousebird *Urocolius macrourus* which visited fruiting *Ficus* and Desert Date *Balanites aegyptiaca* in flocks of occasionally ten or more birds. Our surveys showed that only Senegal Eremomela was sometimes recorded in small itinerant flocks, and then mostly in the humid forests in the south. This contrasts sharply with non-breeding birds in temperate and tropical forests, including Africa, where flock-feeding is widespread among arboreal insectivores, frugivores and nectarivores which often join in mixed-species flocks (Craig 2022). The scarcity of conspecific- and mixed-species flocks in our region is all the more surprising because flock-feeding is supposed to be most common among bird species that are (1) small, (2) feed on insects and (3) live in woody vegetation (Sridhar *et al.* 2009, Craig 2022), traits that apply to the 29 species of the present study. Furthermore, several of the 29 species studied in this paper, or closely related species, were observed to join flocks in forests and woodlands elsewhere in Africa (Winterbottom 1949, Greig-Smith 1978, Sinclair 1978, Salewski *et al.* 2003, Thompson & Ferguson 2007, Craig 2022).

Table 5. Number of Willow Warblers observed before and after 15 November, with average latitude and associated average rainfall. In the same trees where Willow Warblers were seen, five other migrant species were recorded: n = number of birds, D and S are the number interactions where the Willow Warbler was dominant (D) or subordinate (S). In addition, two intraspecific interactions of Willow Warblers were noted before 15 November and none after 15 November.

Season	<15 Nov.			>15 Nov.		
Avg. rainfall (mm/year)	502			1241		
Latitude (°N)	14.57			11.69		
Willow Warbler (*n*)	143			41		
	n	D	S	*n*	D	S
W. Bonelli's Warbler	29	1	1	0	0	0
W. Subalpine Warbler	22	1	2	1	0	0
Melodious Warbler	12	0	6	10	0	0
W. Olivaceous Warbler	17	0	0	1	0	0
Little Weaver	28	0	1	1	0	0

Feeding in flocks may enable birds to forage in habitats that would be too risky to exploit as a solitary bird, and is supposed to reduce predation risk anyway (e.g. Thiollay 2003, van den Hout *et al.* 2017). Bird-hunting raptors form a diverse guild and are omnipresent in the humid zone south of the Sahel, but decidedly scarce in species and numbers in the Sahel during the dry season (Thiollay 1978, Anadón *et al.* 2010, Zwarts *et al.* 2019). The raptors in the Sahel mainly feed on lizards, insects and ground-foraging birds; arboreal birds are probably difficult to ambush in the open landscape with scattered trees (Buij 2012, Zwarts *et al.* 2019). A low predation risk for arboreal birds may be conducive to exploitation of food resources as single birds, especially when flock-feeding would be counter-productive in solitary trees with limited food supply and higher chances of kleptoparasitism. This has not yet been studied for the bird species concerned.

Is the single-bird-per-tree distribution of Eurasian migrants in the Sahel perhaps the result of territorial behaviour? Several studies found that migrants in West African wintering areas were solitary, sedentary and territorial, e.g. in Western Olivaceous Warbler, Melodious Warbler, Common Whitethroat, Subalpine Warbler, Common Redstart and European Pied Flycatcher, in contrast to Willow Warbler and Common Chiffchaff which were recorded to be itinerant (Skilleter 1995, Sauvage *et al.* 1998, King & Hutchinson 2001, Salewski *et al.* 2002a, Willemoes *et al.* 2018, Thorup *et al.* 2019, Mostafa *et al.* 2021, Tapia-Harris & Cresswell 2022). Territorial birds can be expected to engage more often in intraspecific agonistic encounters, especially when suitable habitat is scarce or food resources are in short supply, and in interspecific competition when foraging habitat and behaviour show overlap with those of ecologically closely related species (Brown 1964, Wilson & Cresswell 2007). The few available data indeed suggest such an overlap in arboreal birds: most species preferred the same tree species (*Faidherbia*, acacias) and many fed on the same prey, the caterpillar/moth *Crypsotidia conifera* (Zwarts *et al.* 2022c). Our data are unsuitable to rank species as more or less territorial than others. The proportion of birds feeding alone in a tree may instead be used as a proxy of territoriality, under the assumption that bird species most often recorded as a single bird are the most territorial. In our dataset, Common Redstart and European Pied Flycatcher were always (or nearly so) single. Both species have been identified as territorial in their wintering quarters (Salewski *et al.* 2002a, Thorup *et al.* 2019). Senegal Eremomela, with half of the birds recorded as single, represents the other end of the spectrum. The proportion of birds engaged in intra- and interspecific agonistic interactions (Table 1; second last and last but one column) increased in species that were more often single (Figure 3), but non-significantly. The species most often associated with congeners or other species showed the least agonistic behaviour. Essentially solitary species were either aggressive when encountering other birds (Olivaceous Warbler), or rarely so (Common Redstart and European Pied Flycatcher). The latter two species have well-defined territories in winter and border disputes are typically confined to the time of arrival on the wintering grounds when forming discrete territories (Salewski *et al.* 2002a, Willemoes *et al.* 2018, Thorup *et al.* 2019). Western Olivaceous Warbler and the *Curruca* species were intolerant of conspecifics and frequently of other species as well, but it is still unknown whether they defend territories over longer time periods. Playback experiments in Senegal between 21 February and 19 March 2017 suggest that Subalpine Warblers were territorial, with 64% responding vocally to playback and 39% resorting to chases when conspecifics showed up (Mostafa *et al.* 2021).

Agonistic behaviour of birds: common in savannah trees but rare in forests

Between-species interactions were more common than within-species agonistics, both in migrants (3 times more often; Figure 2B) and in residents (9 times, Figure 2A). Agonistic behaviour was in general directed towards birds with a lower body mass (the typical outcome in birds, with 87% of aggressive interactions being in favour of the larger species; Martin *et al.* 2017), except in Western Olivaceous Warbler which also chased larger bird species out of a tree and was always the dominant species during attacks. The dominance hierarchy, such as determined by Salewski *et al.* (2007), closely resembled our findings in the Sahel. Western Olivaceous Warbler chased most other bird species in its tree of choice, *Phylloscopus*-species were at the bottom of the pecking order and *Hippolais*- and *Curruca*-species were in between (Figure 5). The position of residents within the hierarchy was difficult to assess because they displayed few interactions with other birds; no attempts to dominate other bird species were recorded.

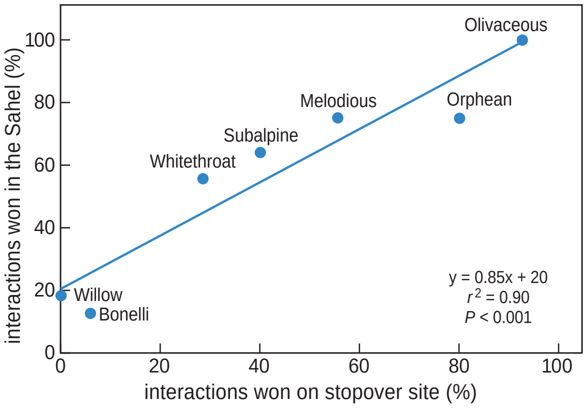

Figure 4. Percent interspecific interactions won in seven migrant warblers, such as determined on a stopover site in the Sahara in March–May 2003 and 2004 by Salewski *et al.* (2007; their Table 1) and in the Sahel in 2011–2019 (last column in Table 1).

On average, 6.1% of the migrants showed intra- or interspecific interactions, and just 1% of the residents (excluding Spectacled Warbler; Figure 2). These data refer to birds observed while we determined bird numbers in a tree. The frequency of agonistic interactions was inferred from the observation time per tree, which increased with canopy size and number of birds present (Zwarts & Bijlsma 2015). A Common Redstart (2.3% interactions) was thus calculated to have one interaction per 280 min, but a Western Olivaceous Warbler (9.8% interactions) once per 66 min. Agonistic behaviour must have occurred at a higher frequency than noted, because our methodology of observing birds in trees was specifically targeted at finding all birds within individual trees. This had the side-effect that birds already noted were only peripherally kept track of to prevent double-counting. Indeed, systematic notes on foraging behaviour of random individuals revealed much higher frequencies of agonistic behaviour for several species, especially in Western Olivaceous Warbler and *Curruca*-species (see Supplementary Material).

Salewski *et al.* (2007), studying foraging birds on stopovers in Mauritania in March–May, found that intraspecific interactions were most common in Subalpine Warblers: once per 15 min and even once per 5 min if a congener was within 5 m. Western Orphean Warbler and Olivaceous Warblers were less aggressive against congeners while Willow Warblers had no intraspecific interactions. In contrast, in most interspecific encounters Willow Warblers were involved, and always on the receiving end. The most aggressive bird in their study was Olivaceous Warbler which interrupted foraging by intraspecific aggression every 23 min, and even every 12 min when an individual of another species was nearby. The observed aggression among Eurasian migrants on the Mauritanian stopover site and in the Sahel fit well: the dominance hierarchy and the frequency of interactions are about the same (Figure 5). Birds may show their dominance by performing overt, agonistic behaviour, as registered by Salewski *et al.* and in our study, but also by other non-registered, equally effective ways to display their dominance, e.g. calling and bill rattles. Thus, the frequency of agonistic behaviour must be higher than shown in Table 6.

The frequency of agonistic behaviour in migrant species did not differ per rainfall zone. This does not necessarily imply that the impact of interactions on feeding success and food intake is the same across rainfall zones. In the humid forests, contrary to birds residing in arid and semi-arid zones, we recorded subtle forms of interaction, for instance between foraging sunbirds and Willow Warblers. The latter took such interactions in their stride without interrupting feeding. The difference in agonistic behaviour in the Sahel could not be larger. Eight Sahel-dwelling species (*Hippolais*, *Iduna*, *Curruca* warblers) usually chased other birds out of a tree. Arboreal birds in the Sahel are feeding in a landscape with widely scattered trees, which complicates the defence of a set of trees against intruders but offers subordinates a wider range of feeding opportunities (Zwarts *et al.* 2019, see Photo 1). However, agonistic behaviour must be costly to the aggressor in terms of lost feeding time, but must have an even larger impact on *Phylloscopus* species which were evicted from their feeding site and had to search for another suitable tree.

Salewski *et al.* (2007) suggested several explanations for the frequent aggressive interactions among birds on a Mauritanian stopover site compared to the lack of this behaviour in their tropical wintering area:

(1) Bird density in their Saharan wadi was much higher (13 migrants/ha) than on the tropical wintering grounds. Woody cover in the wadi varied between 10 and 40% (excluding *Leptadenia pyrotechnica* shrubs; estimate based on Google Earth image; for landscape photo of the site, see Salewski *et al.* 2006). Density converted into birds per ha of canopy is then 30 to 130. For our study plots in the arid Sahel, bird densities ranged from 29 per ha of canopy (for *Acacia ehrenbergiana*), to 35 (*Balanites aegyptiaca*), 52 (*Acacia tortilis*) and 128 (*Maerua crassifolia*). Indeed, bird density of arboreal migrants (also when including residents) in arid and semi-arid regions are much higher than in the humid zone (2–8/ha canopy; Figure 5).

(2) Birds at stopover sites may be more aggressive due to their higher required food intake rate. However, a similar aggression rate was found in the Sahel during the wintering period, which shows that agonistic behaviour is not limited to the premigration period in March–April.

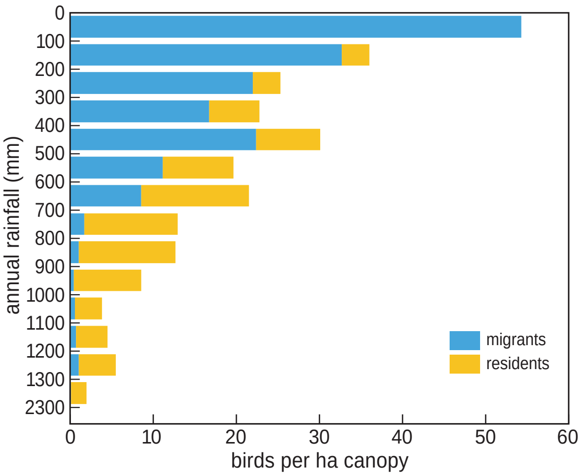

Figure 5. Density of arboreal birds in woody vegetation (*n*/ha canopy; data from Zwarts *et al.* 2023b).

(3) Heavy insect predation and a high density of arboreal birds must result in a declining food supply in the course of the dry period, with a concomitant higher incentive for aggression. This might be true, were it not for the fact that feeding circumstances for arboreal birds in the northern Sahel improve during the dry season, because many trees and scrubs carry flowers and berries in the second half of the dry season. The switch of *Curruca* species from semi-arid to arid zones during their stay in the Sahel suggests that migrant birds exploit waves of food abundance (Salewski *et al.* 2006, Zwarts *et al.* 2023d).

The much lower frequency of agonistic encounters among migrants in the hyper-humid zone first and foremost harks back to the absence of the aggressive migrant species that are dominant in the Sahel. Eurasian migrants are thinner on the ground in humid

Table 6. Frequency of intra- or interspecific agonistic behaviour (given as minutes between interactions) in four bird species, split up for situations when within 5 m other birds were absent ('single') or present ('<5 m'). Data from: Salewski *et al.* (2007) on a stopover site in Mauritania in March to May 2004. *Willow Warblers had 7 intraspecific interactions (time not specified) in March–May 2003.

	Intraspecific		Interspecific	
	single	<5 m	single	<5 m
W. Subalpine Warbler	15	5	115	39
W. Orphean Warbler	36	30	54	28
Olivaceous Warbler	84	10	23	12
Willow Warbler	0*	0	15	10

vegetation zones anyway (Figure 5), with less scope for interspecific interactions, on top of several being territorial and occupying species-specific niches (notably Pied Flycatcher and Melodious Warbler). Furthermore, Willow Warblers lead an itinerant life in the humid zone without the simultaneous presence of aggressive Palearctic migrants in their foraging niches. Co-existence with resident bird species on the wintering grounds also appears to be largely without much conflict (Rabøl 1987, 1990, Salewski *et al.* 2002a, 2003, Gbemiga 2014). A big difference between arid and humid zones refers to the configuration of trees, namely either scattered and solitary or forming closed-canopy forests, and the species composition of trees, namely tens of species compared to hundreds of species. This may have a far-reaching impact on food availability, e.g. patchy or widely dispersed, and hence on agonistic behaviour of insectivorous birds exploiting either habitat (see experiment of Zahavi 1971). However, none of this has been tested in a setting of the Sahel or in humid zones in sub-Saharan Africa.

No matter how haphazard the information on intra- and interspecific behaviour of migrants and residents in Africa, the evidence so far agrees with the conclusion of Rappole & Jones (2002), namely migrants are no 'wandering interlopers, subordinate to Tropical residents, forced to subsist on temporary resource concentrations in marginal habitats'. In fact, considering migrants and residents as separate categories ranking differently in the dominance hierarchy is a construct that belies the fact that Eurasian migrants have two homes, one of which is in Africa.

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SAMENVATTING

In de Sahel zijn vogels die in bomen en struiken foerageren, uiterst selectief. De meeste trekvogels, maar ook lokale vogels, zijn geconcentreerd in een paar boomsoorten en binnen die soorten vaak in grote bomen die volop in blad staan en rijk bloeien. Om die reden alleen al is te verwachten dat in voorkeursbomen vaak meerdere vogels aanwezig zullen zijn. Dat bleek allerminst het geval. Bij sommige vogelsoorten werden zelden of nooit meer dan één individu in een boom gezien en zelfs van de Senegal Eremomela *Eremomela pusilla* – de meest sociale soort – zat de helft van de vogels in hun eentje in een boom. Groepsgewijs rondtrekken, zoals in tropische bossen vaak wordt gezien, komt in de Sahel bij vogels die in bomen foerageren niet of nauwelijks voor. Waarschijnlijk kunnen vogels in de Sahel het zich permitteren om in hun eentje te foerageren, omdat ze niet bang hoeven te zijn gegrepen te worden door een roofvogel, – een kans die een stuk reëler is in de natte bossen in het zuiden. Sommige soorten, zoals de Bonte Vliegenvanger *Ficedula hypoleuca* en Gekraagde Roodstaart *Phoenicurus phoenicurus*, houden er een winterterritorium op na, maar bij andere soorten is er overlap in het gebied waarbinnen individuele vogels voedsel zoeken. In de vochtige bossen verder naar het zuiden, en ook onder lokale vogels die in de Sahel voorkomen, is er weinig onderlinge agressie. Trekvogels hebben vaker ruzie met soortgenoten, maar nog vaker met vogels van een andere soort. Grotere vogels winnen meestal van kleinere vogels, maar Vale Spotvogels *Iduna opaca* jagen ook vogels weg die twee keer zo zwaar zijn als zijzelf. Ook Baardgrasmussen *Curruca iberiae + subalpina + cantillans*, en in mindere mate andere grasmussoorten uitgezonderd Braamsluiper *Curruca curruca*, zijn onverdraagzaam. Bergfluiters *Phylloscopus bonelli* zijn het vaakst slachtoffer van onverdraagzaam gedrag; ze werden zo vaak uit een boom verjaagd dat het wel een effect moet hebben op hun boomkeuze. In de trekperioden is dat ook het geval met Fitissen *Phylloscopus trochilus* die de Sahel passeren. Op hun uiteindelijke overwinteringsplek, minstens enkele honderden km zuidelijker in de humide tropische bossen, leken ze echter gevrijwaard te zijn van agonistisch gedrag van andere zangvogelsoorten. De grote vraag is nu waarom er onderlinge agressie is tussen trekvogels in de droge wereld ten zuiden van de Sahara en nauwelijks in de vochtige bossen nog verder naar het zuiden. Een verklaring zou kunnen zijn dat zangvogels in de Sahel een handjevol boomsoorten benutten en daar dicht op elkaar zitten (in de uitgestrekte zuidelijke bossen is de trefkans behoorlijk wat kleiner). Of dat die bomen in de Sahel los van elkaar als solitaire bomen voorkomen, in tegenstelling tot de meer aaneengesloten vochtige bossen in de Guinea-vegetatiezone. Of is het gewoon toeval dat een aantal intolerante trekvogels in de Sahel overwinteren en zouden ze hetzelfde gedrag vertonen in humide bossen (als ze daar zouden voorkomen, wat niet het geval is)?

RÉSUMÉ

Au Sahel, les oiseaux qui se nourrissent dans les arbres et les arbustes sont très sélectifs. La plupart des espèces migratrices, mais aussi locales, privilégient une faible diversité d'essences. Parmi celles-ci, elles se concentrent principalement sur les arbres au feuillage développé et en pleine floraison. Il serait donc logique de trouver des concentrations de plusieurs individus de la même espèce dans ces arbres. Mais cela s'est avéré être loin d'être le cas lors de nos prospections. Chez certaines espèces, nous n'avons que rarement voire jamais vu plus d'un individu par arbre. Même chez l'Érémomèle à dos vert *Eremomela pusilla* – l'espèce la plus sociable – la moitié des oiseaux se trouvaient seuls dans un arbre. La probabilité de rencontrer deux espèces d'oiseaux dans un même arbre est également très faible : 2,8 %. La formation de rondes, où plusieurs espèces se regroupent à la recherche de nourriture, est souvent observée dans les forêts tropicales, mais il s'agit d'un phénomène rare ou inexistant chez les oiseaux arboricoles au Sahel. Il est possible que dans cette zone, les oiseaux puissent se permettre de chercher leur nourriture seuls car ils n'ont pas à craindre d'être capturés par un rapace, alors que le risque est bien plus élevé dans les forêts humides plus au Sud. Certaines espèces, telles que le Gobemouche noir *Ficedula hypoleuca* et le Rougequeue à front blanc *Phoenicurus phoenicurus*, défendent un territoire hivernal, mais pour d'autres, les zones d'alimentation des individus se chevauchent. Dans les forêts humides, mais également au Sahel entre espèces sédentaires, les comportements antagonistes sont rares. En revanche, les migrateurs se querellent régulièrement avec leurs congénères et encore plus fréquemment avec des individus d'autres espèces. Les espèces les plus grandes dominent généralement les plus petites, mais l'Hypolaïs obscure *Iduna opaca* est capable de chasser des oiseaux pesant jusqu'au double de son poids. Les Fauvettes du groupe passerinette *Curruca iberiae + subalpina + cantillans* et, dans une moindre mesure, les autres espèces de fauvettes, à l'exception de la Fauvette babillarde *Curruca curruca*, sont également agressives. Les Pouillots de Bonelli *Phylloscopus bonelli* sont les victimes les plus fréquentes de ces comportements, à tel point qu'ils sont si fréquemment pourchassés que leur choix de site d'alimentation en est probablement affecté. Il en est de même en période de migration pour les Pouillots fitis *Phylloscopus trochilus* qui traversent le Sahel. Cependant, sur son site d'hivernage final, à plusieurs centaines de kilomètres au Sud dans des forêts tropicales humides, cette espèce est à l'abri de tels comportements. Pourquoi les passereaux migrateurs s'agressent-ils mutuellement dans les zones arides du Sahel alors qu'ils ne le font pratiquement pas dans les forêts humides plus au Sud ? Il est possible que la concentration dans certaines essences d'arbres induise un taux d'interaction entre individus bien plus élevé. Ou que la dispersion des arbres au Sahel induise des comportements plus territoriaux que dans les forêts continues de la zone de végétation guinéenne. Il se pourrait aussi qu'il ne s'agisse que d'une coïncidence liée au fait qu'un certain nombre d'espèces migratrices agressives hivernent au Sahel et pas dans les forêts humides où elles auraient fait preuve du même comportement.

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SUPPLEMENTARY MATERIAL: frequency of agonistic behaviour

One of us (RGB) made, in between the bird counts, systematic notes on the feeding behaviour and agonistic encounters of random individual birds. Individual European Flycatchers were followed in total 306 min, during which there was once an interaction with a congener and once an attack of an African Paradise-Flycatcher *Terpsiphone viridis*. Common Redstarts, followed for 124 min, had once a border dispute with a congener and once attacked a Speckle-fronted Weaver *Sporopipes frontalis*. Western Olivaceous Warblers (62 min) had one intraspecific interaction and chased one Western Bonelli's Warbler and one Common Whitethroat. Many encounters were noted in three *Curruca* species: Subalpine Warblers (49 min) had one intraspecific interaction and chased one Wood Warbler *Phylloscopus sibilatrix*, Common Whitethroat (36 min) was chased once by a Western Olivaceous Warbler and Western Orphean Warblers (22 min) had two intraspecific interactions. Hardly any aggression was seen in the *Phylloscopus* species, two in 143 min: Common Chiffchaff (just 1 min) one intraspecific interaction, and Western Bonelli's Warbler (101 min) attempted to steal a prey from a Northern Crombec *Sylvietta brachyura*. No interactions were observed in Eastern Bonelli's Warbler *Phylloscopus orientalis* (7 min), Willow Warbler (8 min), Wood Warbler (19 min) and Iberian Chiffchaff (7 min), neither in 11 arboreal resident species followed for a total of 69 min. Taking this information together, interactions varied between one per 16, 18 or 25 min in the *Curruca* species, once per 28 min in Western Olivaceous Warbler, once per 70 min in *Phylloscopus* species and still longer in Redstart and Pied Flycatcher. These data suggest that the estimated frequency of interactions, as derived from our observation time per tree, may have been more than twice too low.

Savannah trees attract more migratory bird species than residents, but why?

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Arboreal bird species occurring in the wide transient zone between Sahara and tropical rain forest are unequally distributed across the rainfall zones. As this also holds for the woody plant species which they select for foraging, it is possible that birds are bound to specific rainfall zones because their preferred woody species are common there. But it may also be the other way around, i.e. that the distribution of birds is primarily determined by their selection of a specific rainfall zone, with the choice of particular woody plants being collateral. We made maps of the predicted distribution of birds based on their occurrence in different woody species (such as measured from field study sites) multiplied by the average density at which bird species forage in those woody plant species. We then compared these maps with the observed distribution of 13 bird species (7 Afro-Palearctic migrants and 6 Afro-tropical residents). This comparison shows that the distribution of birds is largely determined by the distribution of their preferred woody species rather than rainfall. However, there are small, but systematic differences between observed and predicted bird densities in the most arid and most humid parts of their distributions. Most migrants are commoner than predicted in the semi-arid and arid zone (100–600 mm rainfall/year) and most residents commoner in the humid zone. This was confirmed in a separate analysis of the densities at which these bird species forage in five common and bird-rich tree species occurring over a wide range of rainfall zones. There are no empirical data to support the idea that migrants and residents are spatially separated to avoid interspecific competition, so the question remains what migrants gain by their preference for trees from the (semi)arid zone. In the (semi)arid zones, preferred trees are as fully leafed in the dry season as the same trees farther south, but insectivorous birds in the arid zone had a higher capture rate in those trees, suggesting a larger supply of insect prey. In addition, the driest zones held far fewer avian predators than any other vegetation zone in the sub-Sahara, indicating a lower predation risk. We suggest that arboreal birds find better living conditions in the dry zones than in the more humid zones. But there is a trade-off: arid regions have a higher overall probability of very low rainfall years when trees lose their leaves or even die, than do the more humid regions. In those years, mortality among birds in the arid zones will be disproportionally high.

Key words: Sahel, arboreal birds, Afro-Palearctic migratory birds, Afro-tropical birds, savannah, tree preference

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The distribution of birds, be they Afro-Palearctic (migrants) or Afro-tropical species (residents), in the transient zone between Sahara and humid forests is far from random. Midwinter/dry season distribution of birds species was found to be strongly associated with rainfall gradient and woody cover (Zwarts *et al.* 2023b,c). This paper attempts to answer the question of whether the distribution of arboreal birds is primarily determined by the selection of a specific rainfall zone or by the distribution of preferred woody species. First, we show how bird species are distributed across the various rainfall zones. Second, we use the average bird density per woody species and the percent woody cover of the selected woody species to calculate the predicted distribution of all bird species assuming species-specific densities in the woody species are uniform. Comparing the observed distribution to the modelled distribution may show to what degree bird species select specific rainfall zones, independent of tree selection. Third, we investigate in five bird-rich and common woody species with a wide distribution whether the density of different bird species in these tree species varies with rainfall. Fourth, we explore whether (a proxy of) food supply for insectivorous birds varies per rainfall zone.

METHODS

The methods, and their pitfalls, for counting birds and woody plants are extensively described by Zwarts & Bijlsma (2015) and briefly again in Zwarts *et al.* (2023a,b). In short, between 2011 and 2019 birds were counted in 1901 randomly selected study sites (each 4.5 ha) between 7° and 22°N and between 17°W and 42°E (in total 10 million km^2; Figure 3 in Zwarts *et al.* 2023a) during the dry season (20 November – 10 March). All woody plants were registered separately (species, height, width of canopy) within the study sites. We also noted for every arboreal bird the individual woody plant in which it was detected. This allowed us to convert bird counts in the study sites into bird densities per ha, but also to calculate bird density per ha canopy, separately per woody species. We used a five-point scale to score the opacity of the canopy. The data were collected in random sites, but the analysis of the distribution of birds present in five bird-rich trees in relation to average annual rainfall necessarily also includes some data from non-random sites, because we actively searched for specific trees beyond their normal climate range, thus in relatively dry and humid habitats.

Two potential problems arise when attempting to interpret the distribution of birds in relation to rainfall independent of tree selection. First, woody cover increases with rainfall from few and scattered trees in the arid zone to a denser woody cover in more humid zones. If birds avoid scattered, isolated trees, one may expect, on average, fewer birds in woody plants in the arid zone. Similarly, when the presence of a bird in a tree is affected by other trees in its direct surroundings, it might bias our analysis. No evidence was found, however, that isolated trees were visited less often by woodland birds, nor that the presence of (preferred or non-preferred) woody plants in the vicinity had an impact on bird density in specific woody plants (Zwarts *et al.* 2018). We therefore disregard woody cover and nearby presence of other tree species in our analysis. Second, bird density in woody plants is defined as birds per ha canopy (measured in a horizontal plane), lumped for all woody plants irrespective of size. This potentially complicates our analysis because woody plants are smaller in the arid zone, not only between, but also within woody species. Thus, when bird density in woody plants increases with height and width, we may expect systematically higher bird densities per woody species in the more humid zone. Hence, we did a separate analysis of bird density in relation to tree height (Supplementary Material 1) with which the impact of the height of woody plants on the bird density could be integrated in the modelled bird distribution.

We made a prediction of bird distribution assuming that their preference for specific woody species would be the same across the entire distributional range, multiplied by tree density to arrive at a density estimate. This was compared to the overall density actually mapped. If bird density in an area is determined by tree availability alone, the estimates should match. Any discrepancies might then be due to other important factors, especially rainfall. The predicted bird distribution was calculated as follows:

(1) The distribution area of the bird species was defined as the summation of grid cells of 1° latitude × 1° longitude where a species was observed; maps are given in Supplementary Material of Zwarts *et al.* (2023b).

(2) The relative woody cover (% of total surface) per woody species of all study sites within the distribution areas of the bird species was calculated separately for each bird species. Zwarts *et al.* (2023c) give maps of the most important woody species and show how the percent woody cover of three bird-rich woody species varied within the distribution areas of the different bird species (Figure 2 in Zwarts *et al.* 2023c).

(3) The woody cover for the common and bird-rich woody species was calculated separately for height categories.

(4) For each bird species its average density per ha canopy was determined separately per woody species and height category; Table 2 in Zwarts *et al.* (2023c) gives average densities per bird species in the 29 most common and 13 most bird-rich woody species.

(5) The average bird density for all these categories were multiplied for each study site with the observed woody cover of the same height categories. The sum equals the predicted bird density per study site.

(6) The predicted bird densities in study sites were averaged per grid cell. Maps are given to show the predicted and observed distribution of the bird species.

To investigate whether bird densities vary per rainfall zone we selected five common woody species rich in birds and present in a variety of rainfall zones from semi-arid (400–600 mm rain/year) to humid (800–1200 mm rain/year). These five are Umbrella Thorn *Acacia tortilis*, Egyptian Acacia *A. nilotica*, Red Acacia *A. seyal*, Winter Thorn *Faidherbia albida* and Desert Date *Balanites aegyptiaca*. Since bird density differed for the western and eastern Sahel, we selected trees from a limited region where most data had been collected, i.e. the area between 1°W and 17°W. To reduce the impact of tree size, we excluded woody plants <6 m high in *Faidherbia* and <4 m high in other acacias and *Balanites* (Figure S4 in Supplementary Material 1). *Faidherbia* is a widely distributed tree species across many climate zones. The most northerly were recorded in desert villages in Sudan and Mauritania (17°N, 150–200 mm rain per year), the most southerly in Ethiopia and in a village in the Central African Republic (8°N; Photo 1). *Faidherbia* was as common in the coastal rice fields at sea-level in Guinea-Bissau (12°N and 1750 mm rain) as in the Ethiopian Highlands (up to 2300 m above sea level).

We did not attempt to quantify the food supply in trees but used an indirect measure to estimate the abundance of the moth *Crypsotidia conifera*, an important prey for birds present in *Faidherbia*. During daytime, the moths were hidden in cracks in the bark. We counted the number of flushed moths after striking the bark three times at breast level (see Figure 16 in Zwarts & Bijlsma 2015), thus providing the fraction of *Faidherbia* with moths per rainfall zone. In addition, we noted systematically if and when birds recorded during the standard counts were handling a large, easily visible prey, usually a caterpillar or moth. The fraction of birds with large prey was used to show variation in food abundance per rainfall zone.

RESULTS

Observed and predicted distribution of birds

Assuming that during the dry season bird densities vary between woody species (see Table 2 in Zwarts *et al.* 2023c) but do not vary geographically, we compared observed densities per grid cell (using data from Zwarts *et al.* 2023b) with predicted distributions of three migratory species (Figure 1). The total number of Western Bonelli's Warblers *Phylloscopus bonelli* (Figure 1A) observed in the different study sites per 100 mm rainfall zone closely resembled the predicted number

Photo 1. Winter Thorn *Faidherbia albida* has a wide distribution in arid, semi-arid and humid zones, the extremes here exemplified by a desert village in Sudan (164 mm rainfall/year, on average; 26 January 2018; left) and a coastal rice field in Guinea-Bissau (1758 mm rainfall/year; 28 November 2014).

($r = +0.91$, $P < 0.001$). Within the range of Bonelli's Warbler, density apparently depended on the distribution of their preferred tree species. The correlation between observed and predicted number is even higher in the Subalpine Warbler *Curruca iberiae* + *subalpina* + *cantillans* ($r = +0.94$), but we noted that observed numbers were slightly higher than predicted when the average annual rainfall was <300 mm, and lower when rainfall was >300 mm (Figure 1B). Thus, as in Bonelli's Warbler, trees determined the distribution of Subalpine Warbler, apart from a preference for drier habitats in the latter. The same applied for Western Orphean Warbler *Curruca hortensis* (Figure 1C) which showed an even stronger preference for drier habitats (but correlation between observed and expected was rather small; $r = +0.67$, $P = 0.03$). Maps as in Figure 1 were also made for a selection of 5 other migrants and for 5 residents, all species occurring in a wide range of rainfall zones (Supplementary Material 2).

When plotting the ratio between observed and predicted bird numbers against annual rainfall, migrants were more common than expected in the rainfall zone <100 and 100–200 mm, but less common when rainfall exceeded 300 mm (Figure 2). The difference between expected and observed was particularly pronounced in Western Orphean Warbler and Lesser Whitethroat *Curruca curruca*, less so (although significant) in Subalpine Warbler and Western Bonelli's Warbler and still less, and non-significant, in three other migrants (Common Whitethroat *Sylvia communis*, Common Redstart *Phoenicurus phoenicurus*, Western Olivaceous Warbler *Iduna opaca*). In four resident species (Senegal Eremomela *Eremomela pusilla*, Tawny-Flanked Prinia *Prinia subflava*, Little Weaver *Ploceus*

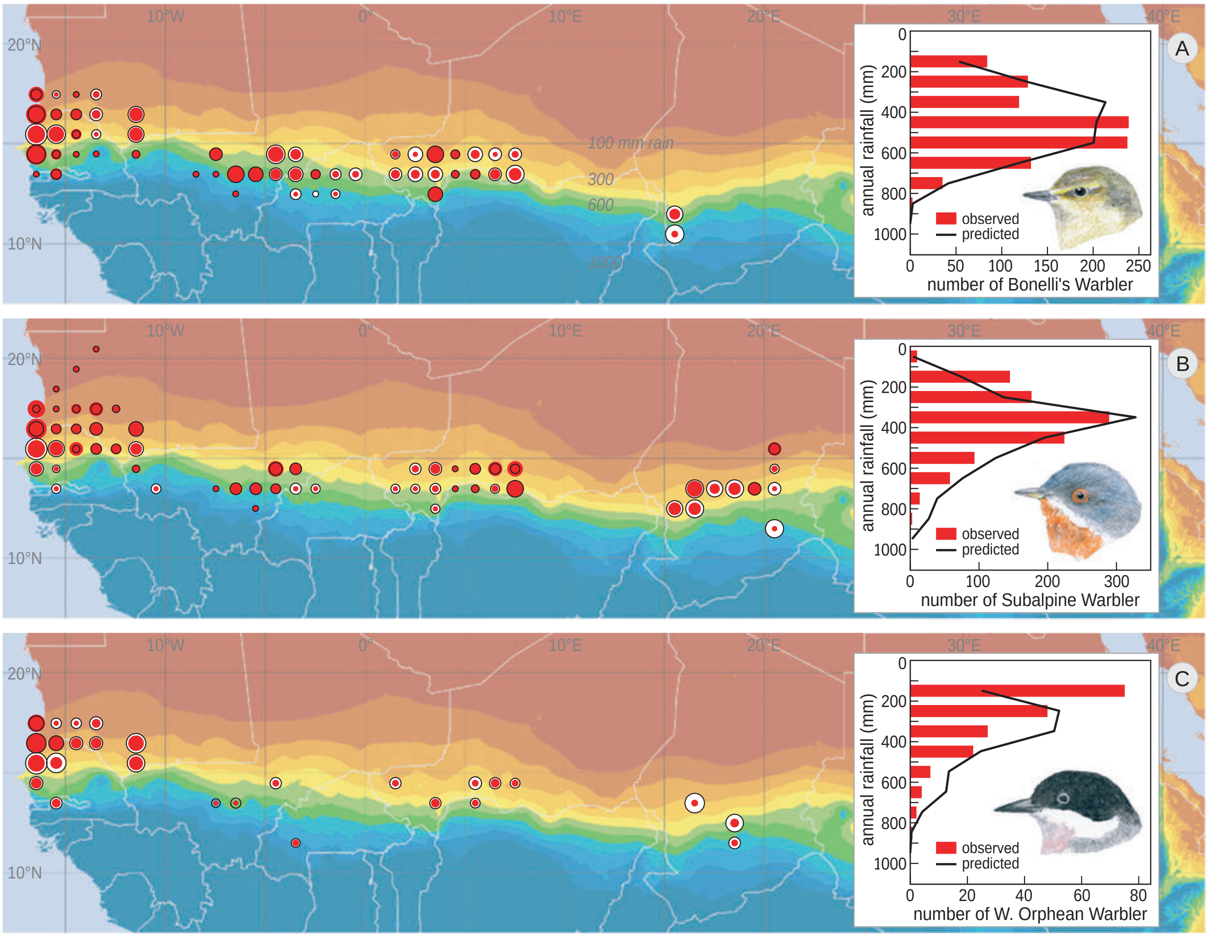

Figure 1. Predicted (○) and observed distribution (●) of (A) Western Bonelli's Warbler, (B) Subalpine Warbler and (C) Western Orphean Warbler in the Sahel in winter (20 November – 10 March); same data as in Supplementary Material of Zwarts *et al.* (2022b): (Figure S10, S24 and S21, respectively). The graph shows observed and predicted total number of birds in all study sites for eleven rainfall zones.

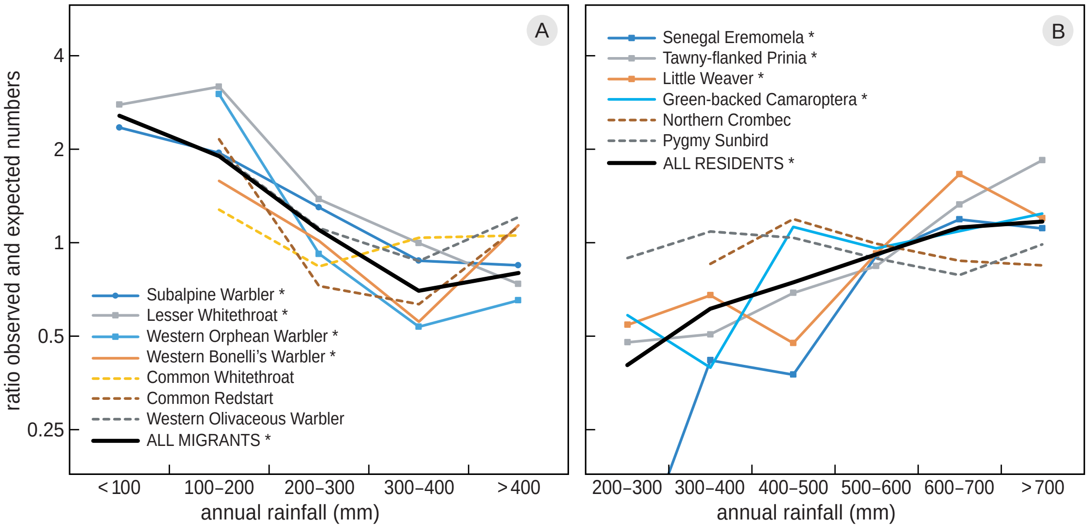

Figure 2. The ratio of observed and expected numbers of birds as a function of annual rainfall in (A) seven migrants and (B) six residents; original data are given in Figure 1 and in Supplementary Material 2 (Figure S5–S14). The observed numbers deviate significantly from expected in 8 of the 13 bird species and when migrants and residents are taken together (marked *: $P < 0.001$, using χ^2 tests).

luteolus, Green-backed Camaroptera *Camaroptera brachyura*) the trend was opposite to those of the migrants, with more birds than predicted in the zone with a higher annual rainfall. No significant difference was found in Northern Crombec *Sylvietta brachyura* and Pygmy Sunbird *Hedydipna platura*.

Distribution of birds in preferred trees

The previous section showed that the distribution of birds and their preferred trees were correlated, but also that bird species differed in their preference for drier (most migrants) or more humid (most residents) zones. When bird species are more abundant in the arid (or humid) zone than expected given the distribution of their preferred trees, a rainfall-related shift in density in those trees might underly the observed pattern. The analysis of whether bird density (per ha canopy) was related to rainfall was done in five tree species rich in birds and found over a wide range of rainfall zones (Photo 1), unlike most other woody species that were either avoided by birds or occurred within a relatively narrow climate zone.

Faidherbia attracted 60–100 migrants per ha canopy in rainfall zones with <1000 mm per year, declining to 25–31 migrants/ha in more humid regions. Insectivorous residents were much less common in *Faidherbia* but showed a similar decline with rainfall as the migrants (from 20 to 6/ha). In all bird species, except two insectivorous residents, the density was significantly related to rainfall (Table S1). However, the trends differed per bird species. In migrants, density declined with rainfall in Subalpine Warbler (from 29 to 0/ha canopy) and in other *Curruca* species, but peaked in Western Bonelli's Warbler at 800–1000 mm rainfall (with lower numbers in drier and more humid zones). Melodious Warbler *Hippolais polyglotta*, and especially Willow Warbler *Phylloscopus trochilus*, were restricted to the most humid zone. Little Weaver was restricted to the drier zones and the only insectivorous resident that was abundant in *Faidherbia*. The few Pygmy Sunbirds in *Faidherbia* trees were exclusively observed in the dry zone, the much more numerous Beautiful Sunbird *Cinnyris pulchellus* only in the humid zones.

In four other tree species, each with a more restricted distribution than *Faidherbia*, Iberian Chiffchaff, Subalpine Warbler and Western Orphean Warbler reached their highest densities in the driest zones. Opposite trends were found in Western Bonelli's Warbler and Common Whitethroat: increasing densities with rainfall in *Balanites*, declining densities in *Acacia seyal* and *A. nilotica*, and no trend in *A. tortilis*. Common Redstart and insectivorous residents were not recorded in the arid zone.

Within their preferred tree species Iberian Chiffchaff, Western Orphean and Subalpine Warbler consistently occurred in higher densities than expected in dry habitats, and two other migrants (Willow and Melodious Warbler) in higher-than-expected densities in humid habitats. No such effect was found in the remaining migrants, nor in residents.

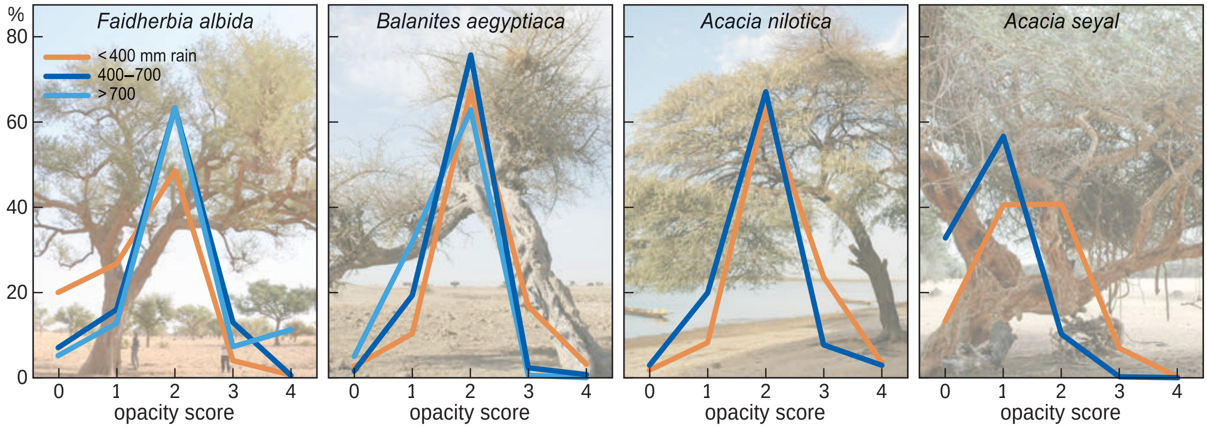

Figure 3. The frequency distribution of the opacity score (0 = bare tree to 4 = dense canopy) in *Faidherbia* (n = 2237), *Balanites* (n = 997), *Acacia nilotica* (n = 311) and *A. seyal* (n = 1627), separately for three rainfall zones. Selection made of trees ≥6 m high in *Faidherbia* and ≥4 m in other three species, from December–February.

Suitability of woody plants from the arid zone for birds

Previous work showed that *Faidherbia* and *Acacia seyal* host many insectivorous birds unless without leaves or thinly leafed (Zwarts & Bijlsma 2015). Consequently, the average number of birds per rainfall zone present in these tree species would be affected by the fraction of leafless trees. We investigated whether the opacity score (from 0 = bare to 4 = dense canopy; see Figure 3 in Zwarts & Bijlsma 2015) differed per rainfall zone for common and bird-rich tree species. In *Faidherbia*, we recorded more bare and sparsely leafed trees in the dry zone (<400 mm rain/year; Figure 4), but the opposite in *Balanites*, *A. nilotica* and *A. seyal*. A similar comparison could not be made for *A. tortilis* due to lack of trees in the zone with >400 mm rain, but opacity of *A. tortilis* did not differ in the four driest rainfall zones (<100 mm to 300–400 mm). With the exception of *Faidherbia*, we found no evidence that, during the dry season, in arid conditions (<400 mm rain/year) bird-rich trees were more often bare (Figure 3) and for that reason less attractive to insectivorous birds than in the more humid zone.

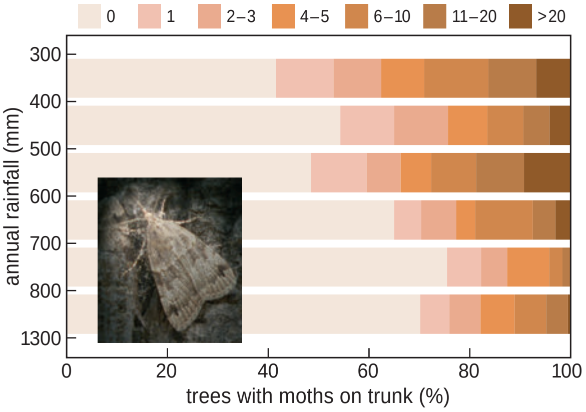

Figure 4. Average number of moths flushed from the trunk of *Faidherbia* after three strikes, shown for six rainfall zones. The number of *Faidherbia* trees (≥6 m high) varied for the six categories between 192 and 631. The presence of moths differed significantly per rainfall zone ($\chi^2 = 63.6$, $n = 6$, $P < 0.001$); the percentage of trees without moths increases with rainfall (linear regression analysis: $r = +0.91$, $P < 0.01$).

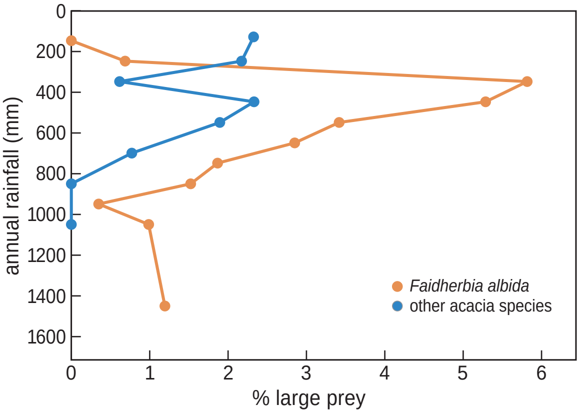

Figure 5. Percent of observed birds during standard counts eating a large prey as a function of annual rainfall. Number of observed birds varies per category between 78 and 925 for *Faidherbia* and between 100 and 804 for other acacias (excluding species restricted to floodplains: *A. kirkii*, *A. seyal* and *A. nilotica*). The relative frequency at which large prey were taken differs significantly per rainfall zone for *Faidherbia* ($\chi^2 = 44.3$, $n = 11$, $P < 0.001$), but not for the other acacias ($\chi^2 = 13.2$, $n = 8$, $P = 0.07$).

Using moths flushed from the bole as an indicator of food supply for insectivorous birds, 60% of the

Faidherbia trees were found to have moths when the annual rainfall was <400 mm; this gradually declined to 25–30% at rainfall >700 mm. Trees with more than 20 moths (maximum 120) flushed were only recorded in areas where rainfall was <700 mm/year. In general, *Faidherbia* in humid zones carried fewer moths than in drier zones (Figure 4).

While searching for birds in random sites, 3% of the insectivorous birds observed in *Faidherbia* and 2% of birds in other acacias were recorded as handling a large prey, usually a moth or caterpillar (Figure 9 in Zwarts *et al.* 2023c). Handling large prey was less often recorded in the more humid zone, in *Faidherbia* also less often in the most arid part of its distribution area (Figure 5).

Photo 2. Moths *Crypsotidia conifera*, hiding in the cracks of the trunk of *Faidherbia albida*, are flushed to be counted. The caterpillars of *C. conifera* were locally so abundant that they completely defoliated mature trees, as described by Dunham (1991) for *Faidherbia* along the Zambesi River. Photos were taken in agroforestry parklands near Djenné, Mali, on 26 January 2016, where all *Faidherbia* trees were defoliated over an area of at least dozens of km^2. Western Bonelli's Warbler, and in October–November also Wood Warbler *Phylloscopus sibilatrix* and Willow Warbler, captured moths from the trunk and from branches in the canopy of *Faidherbia* by hovering and making sallies.

DISCUSSION

Our data suggest that tree preferences largely explain the distribution of birds within their own distribution range. Take, for instance, the Western Bonelli's Warbler of which 56% of the birds were found in *Faidherbia*, a tree species common in the semi-arid zone (annual rainfall 400–600 mm), and another 27% in *Acacia tortilis* (300–400 mm rainfall/year) in which they reached a high density (Table 1 & 2 in Zwarts *et al.* 2023c). Not surprisingly, most birds were found in the rainfall zones where their preferred tree species were most common (Figure 1A). The density of Western Bonelli's Warbler in the grid cells was highly correlated with the combined woody cover of these two preferred tree species:

$$\text{number/km}^2 = 2.29 + 2.017 \times \text{woody cover(\%)} \quad (1)$$

(linear regression: $r^2 = 0.61$, $n = 84$, $P < 0.0001$; raw data in Figure S10 in Zwarts *et al.* 2023b (bird density) and Figure S2 and S4 in Zwarts *et al.* 2023c (woody cover of *Faidherbia* and *Acacia tortilis*); selection made for all grid cells west of 8°E).

In a multiple regression with woody cover, rainfall and rainfall^2 using the same data, rainfall and rainfall^2 appeared to be far from significant ($P = 0.519$ and $P = 0.398$, respectively); the total explained variance ($r^2 = 0.61$) was the same as in the simple regression (equation 1). In the humid zone (800–1200 mm rainfall/year) *Faidherbia* was rare and Bonelli's Warblers were absent in our random study sites (Figure 1A). However, since we searched systematically for *Faidherbia* trees in the humid zone, we found that in those rare trees Bonelli's were even twice as abundant as in the sub-humid zone (Table S1). The density of Bonelli's Warbler, however, declined in *Faidherbia* trees in the hyper-humid zone (>1200 mm rainfall/year; Table S1). This suggests that the distribution of the Western Bonelli's Warbler is largely determined by the availability of their preferred tree species, but only to a certain extent given their absence from *Faidherbia* in the hyper-humid zone.

Willow Warblers and Melodious Warblers showed the opposite trend in *Faidherbia* (Table S1). These two species were not or rarely recorded in *Faidherbia* outside the hyper-humid zone where they spend the northern winter. Their distribution was predominantly determined by rainfall and not by the availability of *Faidherbia*, although this tree species was commonly used in the humid zone, a few hundred km to the north, during migration in October and November (Zwarts *et al.* 2023c).

The presence of Western Bonelli's Warbler in *Faidherbia* outside their normal distribution area raises the question of whether other migrants concentrated in acacias and other thorny species in the Sahel would extend their distribution area farther south into the humid zone if their preferred trees were available. The small numbers of Sahelian migrants observed in Ghana, Togo and Benin were indeed recorded in the few available Sahelian trees (Dowsett-Lemaire & Dowsett 2014, 2019). An *Acacia nilotica* plantation in southern Mali (average annual rainfall 1073 mm, i.e. far beyond the normal climate range of 200–800 mm

Photo 3. Willow Warblers and Pied Flycatchers spend the northern winter in a region that receives 1000–1500 mm rain/year, but there is no escaping from the dry season (November–May) with its withered vegetation and leafless trees, as shown for the same spot in southern Senegal (14.16°W, 12.74°N; average annual rainfall 1160 mm) in the middle of the rainy season (August 1993) and at the end of the dry season (May 1984; photos: G. Gray Tappan, U.S. Geological Survey, EROS Center, USA).

rainfall for this tree species) was found to attract many Sahelian migrants, albeit in lower densities than in their normal distribution range (Zwarts *et al.* 2023c). Of the bird species investigated, *Curruca* warblers showed, within their range of occurrence, the most pronounced preference for trees of the semi-arid and arid zone (100–600 mm rain/year; Figure 2A).

The distribution of the investigated bird species is determined by the availability of their preferred tree species, with a subsidiary role of rainfall of which the importance differs per bird species. These preferences do not explain why some migratory arboreal bird species spend the northern winter in arid zones when most residents and many migrants are exclusively found in more humid zones (Figures 1 and 2). Several alternative explanations, not necessarily mutually exclusive, can be formulated:

Avoidance of competition has been suggested as the explanatory variable (Rabøl 1987, Leisler 1992), but field data – even when collected on a large-scale – without experiments and without detailed information on habitat choice, food availability and use of seasonal food resources are not suitable to test this hypothesis (review by Salewski & Jones 2006, but see Powell *et al.* 2021). Nonetheless, interference competition is likely to occur in the Sahel because agonistic interactions are common. Olivaceous Warblers and *Curruca* species, mostly confined to the semi-arid and arid zone, are the most intolerant species and chase all other bird species. Such aggressive behaviour is rare among residents (Salewski *et al.* 2007; Zwarts *et al.* 2023d). The selection of humid habitats by residents may have to do with the presence of aggressive migrants in the arid zone, but apart from circumstantial evidence this is uncertain.

Avoiding parasites: For migrants it might be important to avoid the tropical humid zone and its associated high risk of exposure to avian parasites and their insect vectors (Waldenström *et al.* 2002, Piersma & van der Velde 2012). In fact, tropical rainforest is largely devoid of Palearctic migrants (Newton 1996).

Lower predation risk: Arboreal birds in arid zones face very few – and mostly aerial at that – avian predators, whereas the raptor guild in the humid, wooded zone is more varied with a higher density; predation risk must vary accordingly from almost nil to substantial (Thiollay 1998, Bijlsma 2001, Figure 4 in Zwarts *et al.* 2018).

Cover from, and insects in, foliage: In four of the five bird-rich tree species, trees are not better leafed in the humid zone than the same trees in the arid zones (Figure 3). In fact, many trees in the humid zone – just like the ones in the semi-arid and arid zone except *Faidherbia* – shed their leaves in the dry season (Photo 3), and have a near-similar phenology of flowering and fruiting (Mahamane *et al.* 2007).

Food abundance: In the most important woody species, *Faidherbia*, moths (Figure 4), and by default caterpillars, can be abundant. Thorny trees in general – the dominant woody plants in the Sahel – are richer in herbivorous insects than non-thorny trees, the latter in the humid zones replacing thorny trees (Colgan *et al.* 2015, Zwarts *et al.* 2015).

Prey size: Birds residing in *Faidherbia* and other acacias in the arid zone more often take large prey (Figure 5), conducive to a high food intake rate.

Wintering in an arid environment has advantages for arboreal migrant birds, but it is also a risky strategy because the annual rainfall in the drier zone is more erratic, and thus less predictable, than in the humid zones (Hiernaux & Le Houérou 2006; Figure 8 and 11 in Zwarts *et al.* 2009). As a consequence, herbivorous insects may be unreliable as a food resource because in dry years woody plants shed their leaves earlier or – when retaining foliage in the dry season – have fewer leaves during droughts (Bille 1974, Poupon 1980). Many woody plant species in semi-arid and arid climate zones drop their leaves in the dry season anyway. Even if the *average* food supply in the arid zone is higher than farther south, the mortality risk of birds, averaged over a series of years, would be higher during prolonged droughts, such as between 1969 and 1992. Many migratory birds are not restricted to the arid zone, however. Several species (e.g. Willow and Wood Warbler, Spotted Flycatcher *Muscicapa striata* and European Pied Flycatcher *Ficedula hypoleuca*) are common in the Sahel during passage in the early dry season (October–November) but spend the rest of their wintering period farther south (Zwarts *et al.* 2023e). They may profit from the high food supply in savannah trees for some weeks during migration periods without having to cope with the harsh conditions there during the dry season in drought years. However, adverse effects of droughts spill over into vegetation zones south of the Sahel. Leaving the Sahel in late autumn does not equate with escaping from severe drought (Photo 3, see also Figure 11 in Zwarts *et al.* 2009, Nicholson *et al.* 2018), even when considering the likelihood that adverse effects of droughts are less spectacular for birds wintering in humid zones compared to those staying semi-arid and arid zones.

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SAMENVATTING

In de noordelijke helft van Afrika bezuiden de Sahara komen overal in bomen foeragerende vogels voor, zelfs in de woestijn. Tussen de Sahara en de bossen van de Guinea-vegetatiezone varieert de jaarlijkse regenval van minder dan 100 mm tot meer dan 1200 mm. Maar niet alle vogelsoorten komen overal voor. De meeste soorten beperken zich tot specifieke neerslagzones en dat geldt ook voor de bomen en struiken waarin ze foerageren. De vraag is of deze vogelsoorten in bepaalde regenvalzones voorkomen omdat daar hun voorkeursbomen staan of dat het andersom is: kiezen vogels primair voor bepaalde regenvalzones en concentreren ze zich daar in bepaalde boomsoorten? In dit onderzoek is tussen 2011 en 2019 in 1901 willekeurige telvakken, verspreid over de hele Sahel, elke boom en struik op naam gebracht en opgemeten. Voor elke vogel apart is genoteerd in welke individuele boom die werd gezien. Aan de hand van deze gegevens zijn voor zeven trekvogelsoorten en zes lokale soorten kaarten gemaakt van de waargenomen en de voorspelde verspreiding van vogels op basis van de dichtheid waarin ze in verschillende boomsoorten voorkomen. Uit deze vergelijking bleek dat de verspreiding van vogels voor een groot deel wordt bepaald door de verspreiding van hun voorkeursbomen en niet zozeer door de regenval. Er zijn echter kleine, maar systematische, verschillen tussen de waargenomen en voorspelde vogeldichtheden in de meest droge en de meest natte delen van hun verspreidingsgebied. De meeste trekvogels, met name in de grasmussenfamilie, komen vaker dan voorspeld voor in de semi-aride en aride zone (100–600 mm regen/jaar), maar de meeste Afrikaanse vogels juist vaker in de semi-humide en humide zone (600–1200 mm regen/jaar). Dit werd bevestigd in een afzonderlijke analyse van de dichtheden waarin deze vogelsoorten foerageerden in vijf vogelrijke boomsoorten die in een breed scala van neerslagzones voorkomen. Daarmee is niet gezegd dat regenval geen rol speelt in de verspreiding van deze vogels. Bergfluiters *Phylloscopus bonelli*, bijvoorbeeld, zijn heel algemeen in *Faidherbia*, maar als die boomsoort in regenrijke zones staat, ontbreken Bergfluiters. Bij Fitis *Phylloscopus trochilus* en Orpheusspotvogel *Hippolais polyglotta* is het net andersom, want die zijn – binnen de Sahel – gedurende het droge seizoen vooral te vinden in *Faidherbia* in de meer humide zone. Hoewel empirische gegevens ontbreken ter ondersteuning van het idee dat trekvogels en lokale vogels ruimtelijk gescheiden zijn om onderlinge concurrentie te vermijden, lijkt het er niet op dat trekkers door competitie met Afrikaanse soorten naar de drogere zone worden verdrongen en daar dan in het nadeel zijn. Bomen in de droge zone hebben gemiddeld evenveel blad als diezelfde bomen in de meer humide zone (voor zover ze daar voorkomen), maar zijn wel voedselrijker. Dat laatste weten we niet zeker, maar een aanwijzing ervoor vonden we in een voor vogels belangrijke boom *Faidherbia albida*, die in de droge zone meer motjes te zien gaf dan *Faidherbia* in de humide zone. Een ander voordeel van verblijf in de droge zone kan zijn gelegen in een lager predatierisico, omdat er veel minder vogeljagende roofvogels voorkomen dan in de natte zone. Maar de droge zone heeft niet alleen maar voordelen voor trekvogels. In een extreem droog jaar lopen overwinterende vogels er een groter sterfterisico dan vogels in meer humide zones zuidelijker. In de Sahel in brede zin is de jaarlijkse regenval variabel en die variatie is groter in gebieden met minder regen. Droge jaren zijn er rampjaren, omdat bomen hun blad verliezen of doodgaan; voor vogels die specifiek in de droge zone overwinteren betekent dat forse sterfte.

RÉSUMÉ

Dans la zone subsaharienne de la moitié nord de l’Afrique, les oiseaux arboricoles sont omniprésents, même dans le désert. Mais tous ne s’y rencontrent pas partout. Entre le Sahara et les forêts de la zone de végétation soudano-guinéenne, les précipitations annuelles varient de moins de 100 mm à plus de 1200 mm, voire plus de 3000 mm par endroits. La plupart des espèces sont limitées à des régions pluviométriques spécifiques, comme les arbres et arbustes dont elles dépendent pour leur alimentation. Nous avons cherché à comprendre si ces espèces sont inféodées aux zones qui abritent leurs arbres préférés, ou si à l’inverse, elles sélectionnent des régions pluviométriques spécifiques et s’y concentrent dans les essences d’arbres les plus favorables. Nous avons identifié et mesuré tous les arbres dans 1901 carrés de comptage choisis au hasard dans tout le Sahel et nous avons noté l’arbre fréquenté par chaque oiseau observé. À l’aide de ces données, nous avons comparé les distributions observées et celles prédites en fonction des densités de chaque espèce par essence d’arbre. Cette comparaison montre que la répartition des oiseaux est principalement déterminée par celle de leurs essences d’arbres favorites plutôt que par les précipitations. Cependant, il existe des écarts faibles, mais systématiques, entre les densités d’oiseaux observées et prédites dans les zones les plus sèches et les plus humides de leurs aires de répartition. La plupart des oiseaux migrateurs, notamment la famille des fauvettes, sont plus fréquents qu’attendu dans la zone à dominante aride, alors que la plupart des oiseaux africains le sont dans la zone à dominante humide. Ce résultat a été confirmé par l’analyse séparée des densités d’occurrence de ces espèces dans cinq essences d’arbres riches en oiseaux et présentes dans une large gamme de régions pluviométriques. Pour autant, le rôle des précipitations dans la répartition de ces espèces n’est pas négligeable. Le Pouillot de Bonelli *Phylloscopus bonelli*, par exemple, est très commun dans les *Faidherbia*, mais uniquement dans les zones de faible pluviométrie. Pour le Pouillot fitis *Phylloscopus trochilus* et l’Hypolaïs polyglotte *Hippolais polyglotta*, c’est l’inverse, puisqu’ils se rencontrent principalement dans les *Faidherbia* des zones les plus humides. Bien que l’on manque de données empiriques pour soutenir l’idée que les oiseaux migrateurs et les oiseaux locaux sont séparés spatialement pour éviter la compétition, les migrateurs semblent tirer profit de leur préférence pour les arbres des zones les plus arides. Ce choix pourrait s’expliquer par une plus grande richesse en proies dans le feuillage des arbres de ces zones à superficie de canopée équivalente. Cette hypothèse est suggérée par le fait que les *Faidherbia* des zones sèches sont plus riches en papillons que ceux des zones humides. La faible abondance de rapaces ornithophages dans la zone sèche peut également constituer un avantage. Mais cette zone ne présente pas que des avantages pour les oiseaux migrateurs. En effet, dans le Sahel, les précipitations annuelles sont variables et cette variation est plus importante dans les zones les moins arrosées. En cas d’année extrêmement sèche, les arbres peuvent y perdre leurs feuilles et mourir, ce qui entraîne une mortalité élevée pour les oiseaux qui y hivernent préférentiellement.

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SUPPLEMENTARY MATERIAL 1: Tree dimensions and bird density

Between woody species

The average bird density per ha canopy is given for 32 bird species in 42 woody species (Table 2 in Zwarts *et al.* 2023c) and for migrants and residents combined in 112 woody species (Figure 3 in Zwarts *et al.* 2023c). Bird density is defined as the number of birds per ha canopy surface measured in a horizontal plane. We had expected that the number of birds foraging in a tree is not a function of canopy surface, but rather a function of canopy volume. If so, bird density per ha canopy should be higher in tall tree species than in shrubs. This trend was not found when woody species were compared. We plotted per tree species average bird density per ha canopy (raw data given in Table 2 of Zwarts *et al.* 2023c) against average height of woody species (per bird species separately calculated for trees occurring within their distribution area). In 23 of 32 bird species, the correlation was, contrary to expectation, not positive but negative (of which 20 were non-significant; a weak significance was found in Common Whitethroat ($P = 0.03$) and Common Redstart ($P = 0.02$) and a high significance in Green-backed Camaroptera ($P = 0.002$)). Thus, most bird species reached higher densities in shrubs and low trees. In nine species the correlation between bird density and average height of the woody species was positive of which four were weakly significant: African Yellow White-eye *Zosterops senegalensis* ($P = 0.04$), Vieillot's Barbet *Lybius vieilloti* ($P = 0.02$), Green Woodhoopoe *Phoeniculus purpureus* ($P = 0.02$) and Common Bulbul *Pycnonotus barbatus* ($P = 0.04$). These species were more abundant in tall trees. On average, however, there are not more birds per surface unit in tall tree species than in small tree and shrub species.

Within woody species

Is bird density in a tree species related to tree height independent of canopy surface? In five bird-rich and common tree species, trees of 1 m high have a canopy surface of 0.7–0.8 m^2 but the average canopy surface of trees of 10 m high is 100 times larger (Figure S1). There are, on average, 1.375 migrants in a tree of 10–14 m high, but only 0.00038 migrants in a tree of 1 m high. The number of migratory birds in an individual tree is exponential to the height of the tree (Figure S2). The exponents are close to three, which suggests that bird numbers are a function of (foliage) volume. However, when the smallest trees are left out, the exponent is reduced in all five tree species. Selecting trees ≥5m high, the function changes into $0.0045x^{2.076}$ in *A. tortilis* ($r^2 = 0.939$) and into $0.0039x^{2.038}$ for *Faidherbia* ($r^2 = 0.989$), where x is tree height (m). Excluding the smallest trees, the number of birds in a tree is a function of canopy surface.

The average density of migrants in a tree is a function of canopy surface, independent of tree height, but the smallest trees are visited less often than random use with availability would predict (Figure S3). In *Balanites*, on average, 44% of trees were 1 m high, but this proportion in *Acacia seyal* was only 15% (Figure S3). In

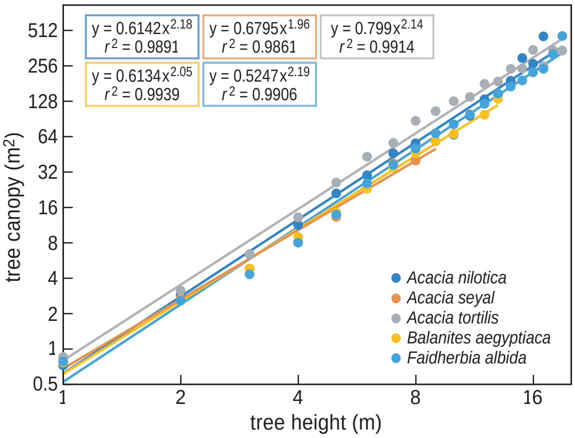

Figure S1. The average canopy (m^2 surface) as a function of tree height in five tree species; same data as Figure S2. Averaged for all measured trees, the surface of tree canopy is a quadratic function of its height.

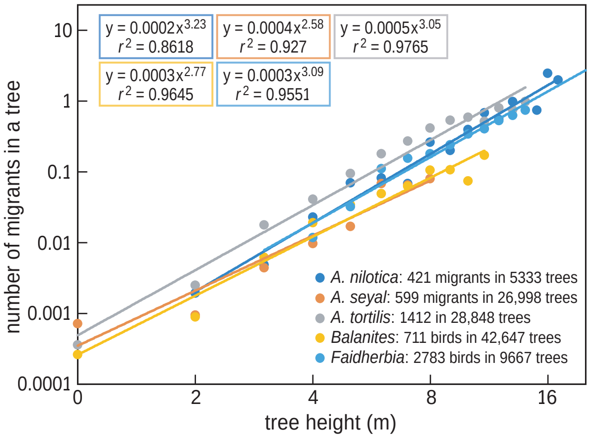

Figure S2. The average number of migratory birds in a tree as a function of its height, given for five woody species. The total number of migrants and trees is indicated. Regression lines are based on the average values.

regions with many small trees, their contribution to the total canopy was still minor. 44% of *Balanites* of 1 m high contributed only 3.9% to total woody cover of this species. In four other tree species, the total canopy surface of small trees is even less (Figure S3). The contribution of small trees in the calculation of the average bird density per woody species was insignificant.

Common Whitethroat and Common Redstart are the only migratory bird species in the Sahel in which densities were independent of tree height (Figure S4). The other common migratory species showed higher densities in taller trees, with some species-specific variation: Western Olivaceous Warbler only used trees ≥6 m high but Subalpine Warbler was also found in smaller trees. In all bird species, the increase of bird density with tree height levelled off, or even decreased in larger trees for Subalpine Warbler. Tall trees held fewer birds per canopy surface than medium-sized trees. This was not an artefact of having overlooked birds in larger trees, because our labour-intensive methodology was specifically developed – and found to be accurate – to detect all birds during our stratified random surveys (Zwarts & Bijlsma 2015).

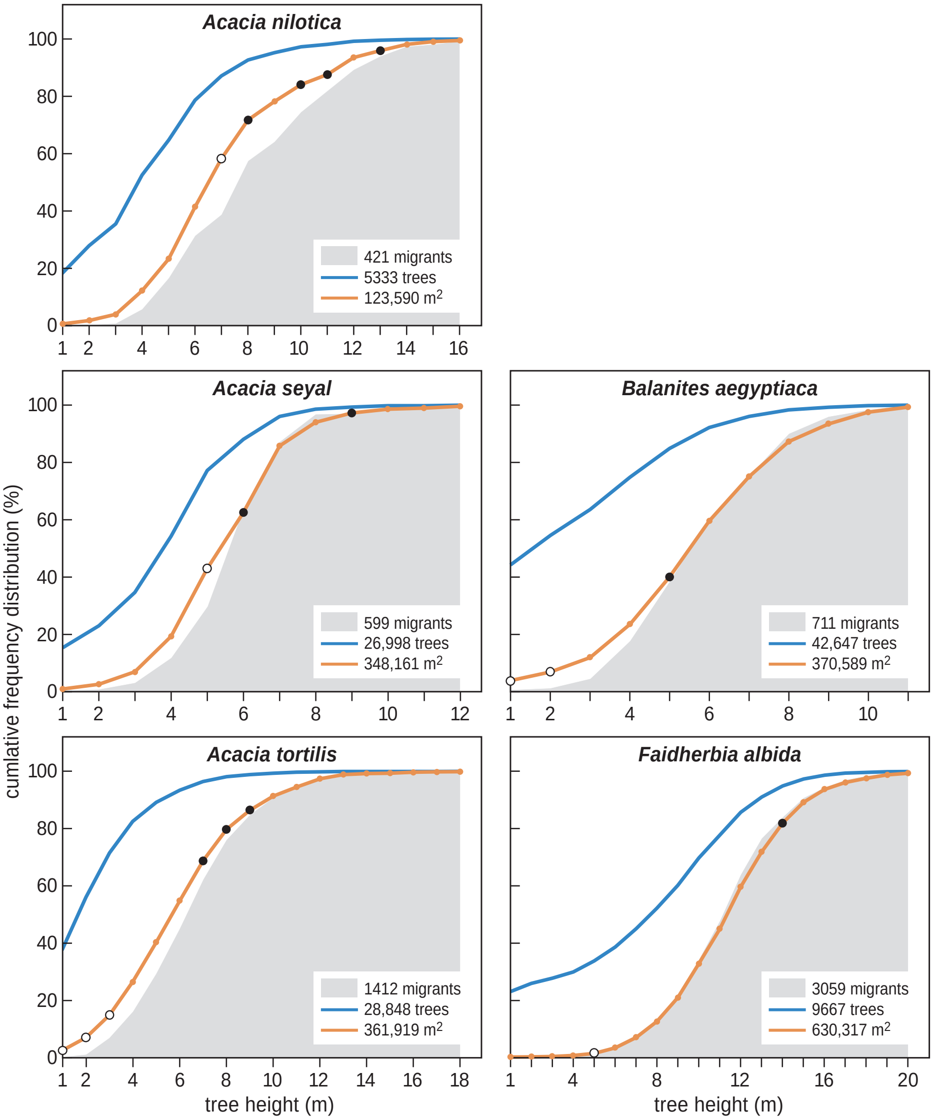

Figure S3. Cumulative frequency distribution (%) of the number of trees, the total canopy surface (m^2) and the number of migratory birds as a function of tree height. The observed number of birds in 77 height categories did not deviate 60 times significantly from the expected number given the surface of its canopy, was seven times lower than expected (○; mainly in small trees) and ten times higher (●; mainly in tall trees); χ^2-tests, $P < 0.01$.

	A. tortilis		*Balanites*		*Faidherbia*	
	n	*P*	*n*	*P*	*n*	*P*
🟩 W. Orphean Warbler	52		20	***	37	
⬜ W. Olivaceous Warbler	16	**	9	*	130	
🟦 W. Bonelli's Warbler	219	***	58	***	587	
🟦 Common Redstart	13		6		43	
🟧 Subalpine Warbler	111	*	184		280	
🟨 Common Whitethroat	13		21		66	

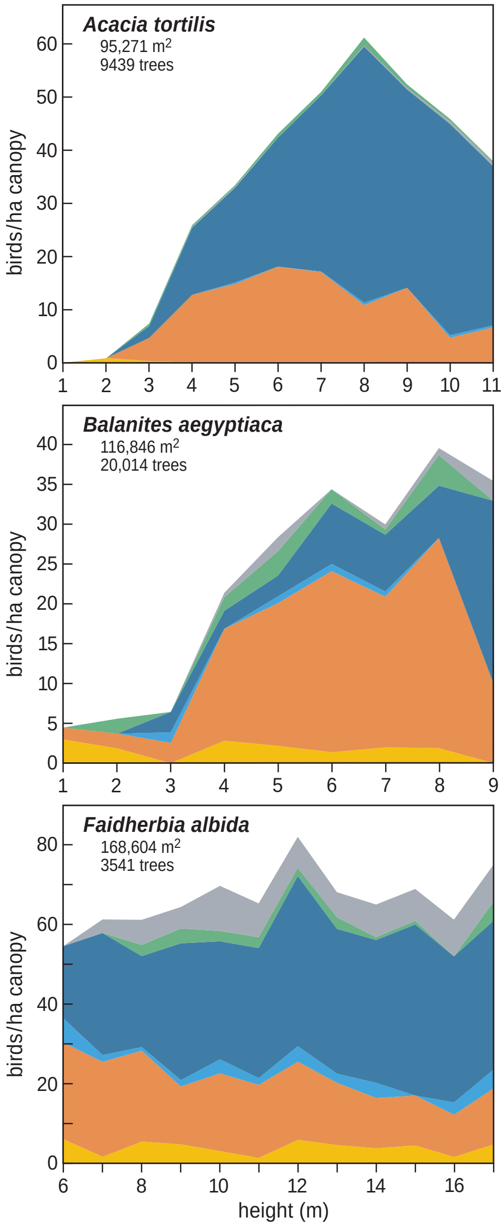

Figure S3. Bird density (*n*/ha canopy) of the six most common arboreal migrants as a function of tree height in three bird-rich tree species; same data as Figure S1–S3, but selection made for sites with an annual rainfall between 200 and 700 mm in the Western Sahel (Mauritania, Senegal and Mali) and between 20 November and 10 March. Canopy surface and number of trees shown in the panels. The table gives the number of birds (*n*) and whether the number of birds per height category deviates from expected given the surface area of the canopy; χ^2-tests: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Note that small *Faidherbia* trees (<6 m high) were too rare to be included in the analysis.

SUPPLEMENTARY MATERIAL 2: Predicted and actual bird distributions

Table S1. Bird density per ha canopy in five bird-rich tree species as a function of annual rainfall, shown for 10 common migrants and 11 common residents (6 insectivores and 5 sunbirds). All data refer to West Africa (1–17°W), the dry season (20 November – 10 March) and large trees (≥6 m high in *Faidherbia* and ≥4 m in other species). The data were collated per rainfall class, based on, in total, 69.89 ha canopy. To test whether density varied with rainfall, the observed number of birds per rainfall class was compared to the expected number, assuming an equal distribution over rainfall classes. The significance level of the χ^2-test is indicated with different colours ($P < 0.05$, $P < 0.01$, $P < 0.001$).

	insectivorous migrants											insectivorous residents							sunbirds					
annual rainfall	W. Bonelli's Warbler	Willow Warbler	Common Chiffchaff	Iberian Chiffchaff	W. Olivaceous Warbler	Melodious Warbler	W. Orphean Warbler	Subalpine Warbler	Common Whitethroat	Common Redstart	**Total migrants**	Afr. Grey Woodpecker	Northern Crombec	Tawny-flanked Prinia	Gr.-backed Camaroptera	Senegal Eremomela	Little Weaver	**Total ins. residents**	Pygmy Sunbird	Scarlet-chested Sunbird	Beautiful Sunbird	Splendid Sunbird	Variable Sunbird	**Total sunbirds**
Unbrella Thorn *Acacia tortilis*																								
0–200	26	0	0	6	3	0	18	31	2	0	90	1	1	0	1	1	1	4	1	0	0	0	0	1
200–400	25	0	0	1	2	0	5	12	1	1	49	0	1	0	0	0	2	6	0	0	0	0	0	0
400–600	28	0	0	0	1	0	6	14	1	5	55	2	1	0	0	1	5	10	0	0	0	0	0	0
Desert Date *Balanites aegyptiaca*																								
0–200	1	0	0	3	1	0	4	27	1	1	36	0	0	0	0	0	0	0	1	0	0	0	0	1
200–400	3	0	0	1	1	0	2	18	1	0	26	0	1	0	0	0	1	5	1	0	0	0	0	1
400–600	10	0	0	0	2	0	1	16	3	1	35	1	1	9	3	3	3	22	1	0	0	0	0	1
600–800	0	0	0	0	1	1	0	9	9	3	24	0	0	3	8	5	0	18	0	0	0	0	0	0
Egyptian Acacia *Acacia nilotica*																								
200–400	11	0	0	21	11	0	1	32	1	1	77	0	3	0	0	0	1	4	0	0	0	0	0	0
400–600	9	0	0	8	2	0	1	3	2	6	30	0	0	0	2	0	0	2	0	0	0	0	0	2
Red Acacia *Acacia seyal*																								
200–400	34	0	0	12	2	0	2	19	5	1	75	0	2	0	0	0	0	2	0	0	0	0	0	0
400–600	3	0	0	0	1	0	0	0	2	2	8	0	1	1	1	2	0	5	0	0	0	0	0	0
600–800	7	0	0	0	7	1	0	0	2	2	21	0	5	4	1	1	2	13	1	1	0	0	4	5
Winter Thorn *Faidherbia albida*																								
200–400	24	0	0	6	16	0	7	29	3	0	85	4	3	1	2	3	6	20	5	0	3	0	1	9
400–600	34	0	0	1	7	0	2	16	4	2	67	1	1	2	1	1	11	18	2	0	0	0	0	3
600–800	34	0	0	2	9	0	0	12	1	5	63	1	0	3	1	3	4	13	3	1	0	0	0	6
800–1000	64	0	2	0	17	3	0	10	1	0	98	2	1	3	1	0	0	8	1	1	25	2	7	37
1000–1200	40	0	1	0	10	2	0	6	0	0	60	1	1	1	0	2	1	6	0	0	15	1	2	18
1200–1500	6	2	1	0	1	16	0	0	0	0	25	0	0	5	0	2	1	9	0	0	16	0	2	24
1500–1800	1	18	0	0	0	11	0	0	0	0	31	1	0	0	0	4	0	6	0	0	10	0	1	13

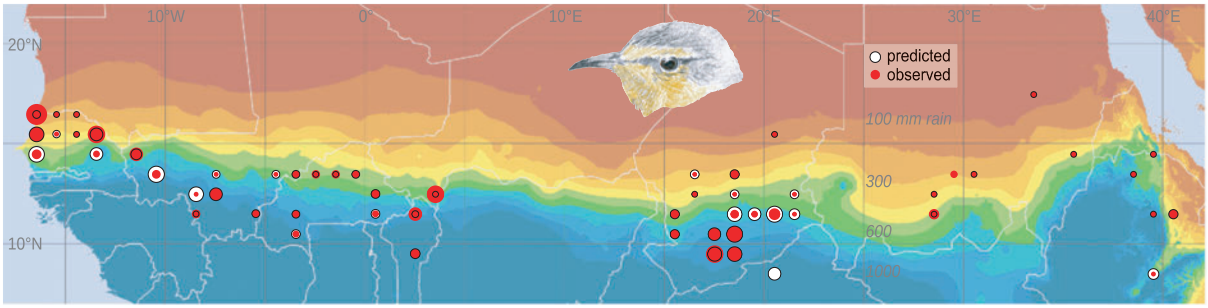

Figure S5. Northern Crombec. Predicted and observed distribution; same data as in Figure S10 in Zwarts *et al.* (2023b).

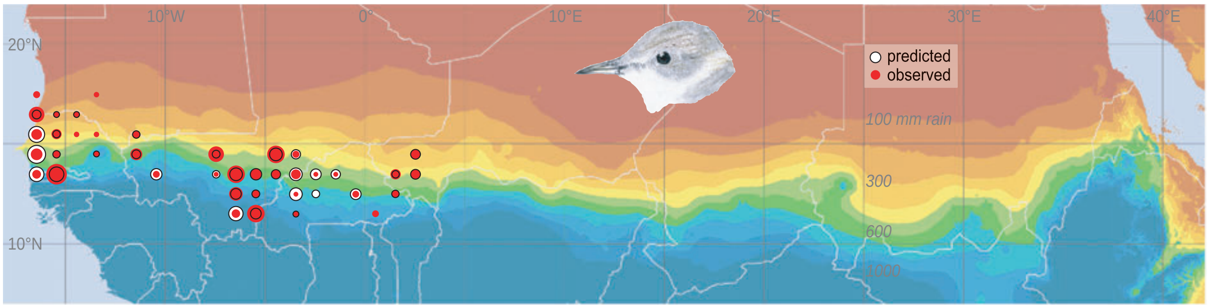

Figure S6. Western Olivaceous Warbler. Predicted and actual distribution; same data as in Figure S15 in Zwarts *et al.* (2022b).

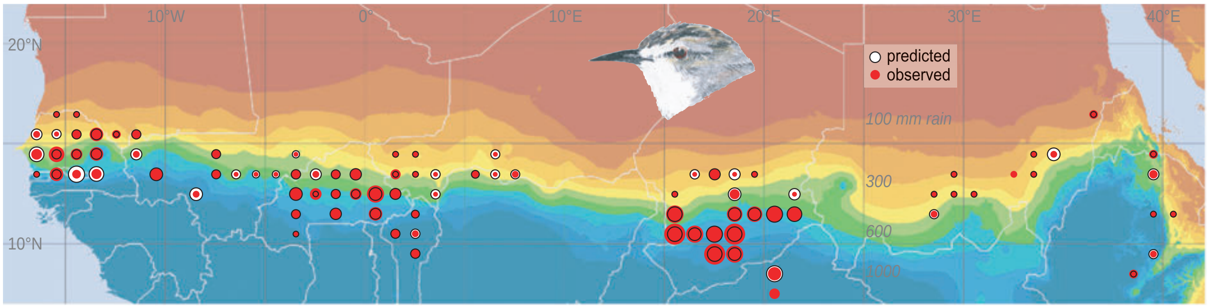

Figure S7. Tawny-flanked Prinia. Predicted and actual distribution; same data as in Figure S16 in Zwarts *et al.* (2022b).

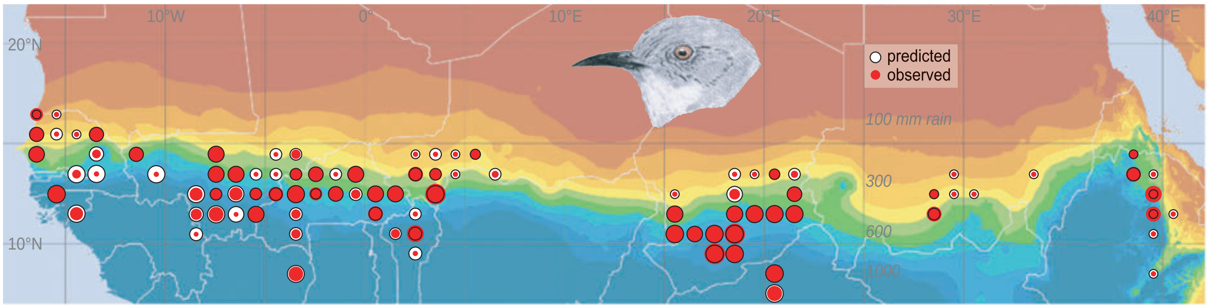

Figure S8. Green-backed Camaroptera. Predicted and actual distributio; same data as in Figure S17 in Zwarts *et al.* (2022b).

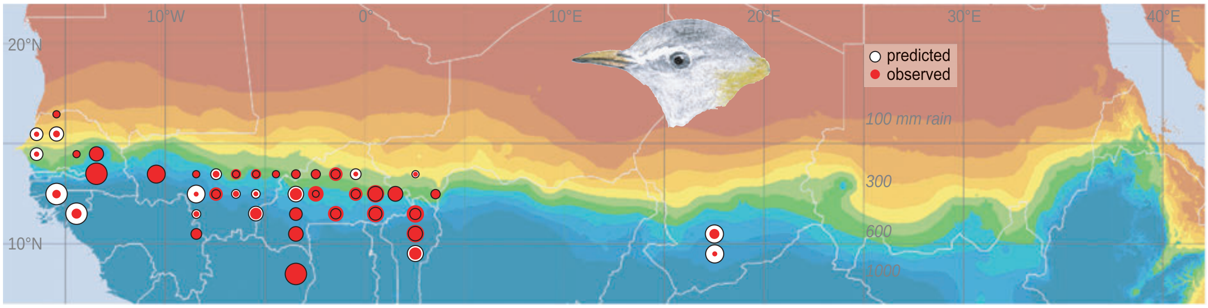

Figure S9. Senegal Eremomela. Predicted and actual distribution; same data as in Figure S19 in Zwarts *et al.* (2022b).

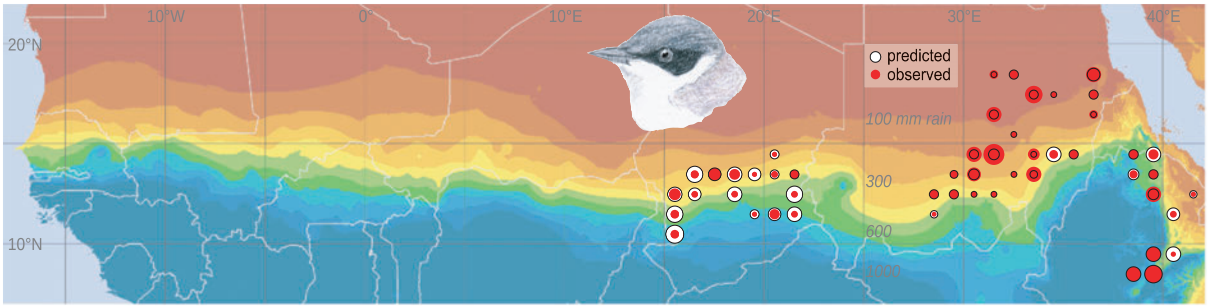

Figure S10. Lesser Whitethroat. Predicted and actual distribution; same data as in Figure S20 in Zwarts *et al.* (2022b).

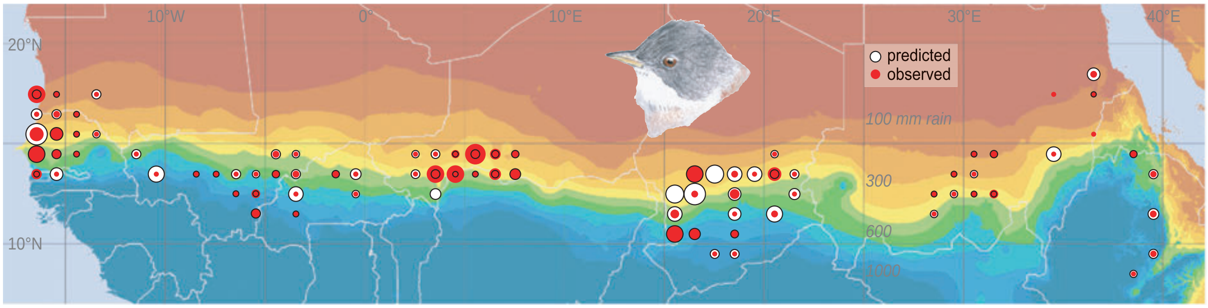

Figure S11. Common Whitethroat. Predicted and actual distribution; same data as in Figure S25 in Zwarts *et al.* (2022b).

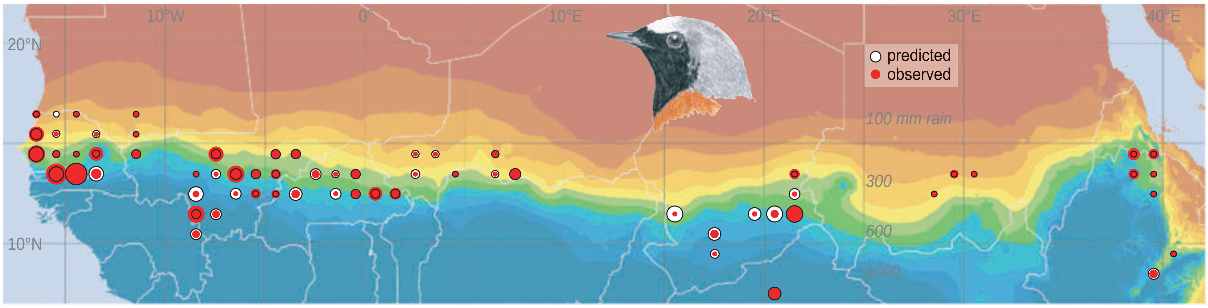

Figure S12. Common Redstart. Predicted and actual distribution; same data as in Figure S28 in Zwarts *et al.* (2022b).

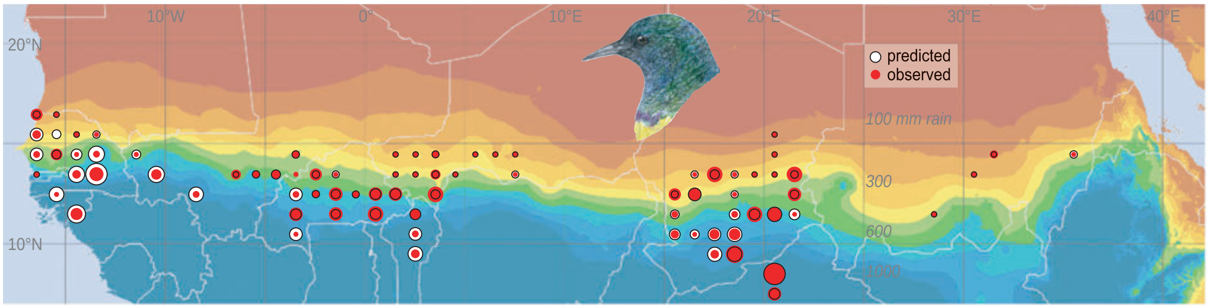

Figure S13. Pygmy Sunbird. Predicted and actual distributio; same data as in Figure S29 in Zwarts *et al.* (2022b).

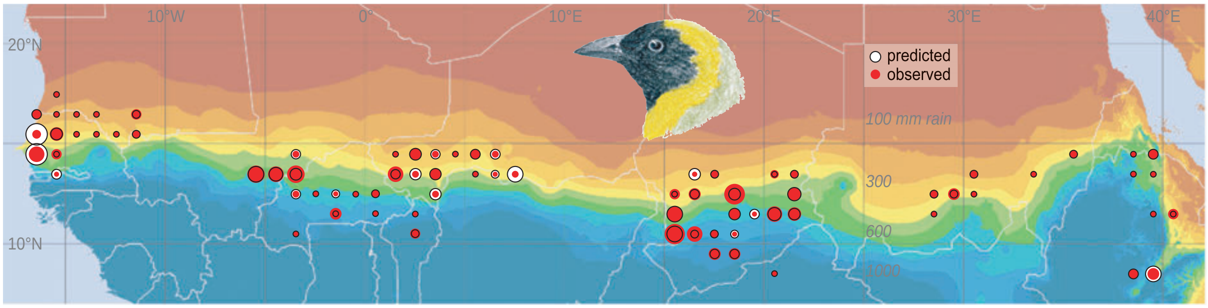

Figure S14. Little Weaver. Predicted and actual distribution; same data as in Figure S34 in Zwarts *et al.* (2022b).

OPEN ACCESS

The Gap of Chad, a dearth of migratory birds in the central Sahel

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Many migratory bird species cross the Mediterranean during autumn migration, but most do so either at the western or eastern ends where they can avoid, or minimise, sea crossings. The intervening 3500 km has long sea crossings, probably adding to the barrier imposed by the Sahara. If this were the general migration pattern, it would result in high concentrations of Afro-Palearctic migrants in West and East Africa and fewer in the central sub-Saharan zones. Unless migrants reorientate upon reaching the sub-Sahara, densities of migratory birds in the central Sahel should be much lower than at either end of the African savannah range. The available studies of birds equipped with GPS or geolocators show that south of the Sahara at least some species perform lateral movements to some extent. However, many remain either in the Sahel's western or eastern parts or continue moving southwards along the same longitudinal axis. We use density counts of arboreal birds from across the full width of the Sahel to explore the extent to which the central Sahel zone is underused by migratory birds. Eleven out of twelve common migratory arboreal species occurred at lower densities in the central Sahel than could be explained by tree-related variables. Western Bonelli's Warbler *Phylloscopus bonelli*, Western Orphean Warbler *Curruca hortensis* and Subalpine Warbler *Curruca cantillans* were most common in the western and (much) less common in the central Sahel, whereas Eastern Olivaceous Warbler *Iduna pallida*, Eastern Orphean Warbler *Curruca crassirostris*, Lesser Whitethroat *Curruca curruca* and Rüppell's Warbler *Curruca ruppeli* were most common in eastern, but less so in the central Sahel. Woodchat Shrike *Lanius senator* and Common Redstart *Phoenicurus phoenicurus* were more common in the western and eastern parts than in the central Sahel. No longitudinal variation was found for Common Whitethroat *Curruca communis*, which is consistent with the knowledge that many cross the Mediterranean waters upon encountering them. The conclusion is justified that the central Sahel is underused by migratory birds and by consequence, as far as these birds are concerned, not 'saturated'. The question arises whether in the past, when the number of migratory birds was much greater than today, there might not have been a Gap of Chad.

Key words: bird migration, migratory divide, ecological barrier, Sahel, Sahara, Mediterranean Sea

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Annually, a multi-million bird wave heads from breeding areas in Eurasia to their second home in Africa. On radar images, a seemingly amorphous mass of winged creatures amasses along the shores of the Mediterranean and can be seen to depart from mainland Europe at nightfall, as if the shoreline suddenly broadens into the sea. In the early 1960s, radar studies suggested a passerine migration along the whole length of the Mediterranean Sea at almost uniform density except the Ionian Sea where it was greatly reduced

(Casement 1966). However, non-passerines are known mostly to align with another strategy that largely avoids open sea-crossings by following land-based routes at either end of the Mediterranean. This pincer movement gave birth to the term 'Zugscheide' (migratory divide), based on the dichotomous flyways of White Storks *Ciconia ciconia* breeding in Europe (Schüz 1953). It is a standard textbook example: White Storks from the western population migrate through Spain and Morocco to spend the northern winter in West Africa, and the eastern population transits Turkey, Israel and Egypt en route to eastern and southern Africa. Clearly, White Storks avoid open water. Detours via west or east, especially by migrants using soaring flight, as well as migratory divides have been confirmed with a plethora of studies (Panuccio *et al.* 2021), although (facultatively) soaring species like Osprey *Pandion haliaetus* and European Honey Buzzard *Pernis apivorus* can use the uplift potential of the seascape to successfully cross the central Mediterranean Sea (Nourani *et al.* 2020). For most obligate soaring migrants, though, the thermals over open water are probably too weak to use effectively (Duriez *et al.* 2018), hence the detours over land and via bottlenecks. For birds using active flight, crossing the Mediterranean directly would be less of a problem. Nonetheless, major studies have proved that many migrant species that employ flapping flight also avoid crossing the 500–700 km of open water and detour around one end or other of the Mediterranean (e.g. Pilastro *et al.* 1998, Gargallo *et al.* 2011). For some species this strategy coincides with a distinct longitudinal migratory divide across Europe conducive to western and eastern flyways, for example for Spotted Flycatcher *Muscicapa striata*, Sedge Warbler *Acrocephalus schoenobaenus*, Common Reed Warbler *Acrocephalus scirpaceus*, Common Whitethroat *Curruca communis* and Eurasian Blackcap *Sylvia atricapilla* (Zink 1973, 1985). Most passerine species from western Europe use the western flyway and those from eastern Europe the eastern flyway, with notable exceptions such as Lesser Whitethroat *Curruca curruca*, Marsh Warbler *Acrocephalus palustris* and Red-backed Shrike *Lanius collurio* from western Europe taking the eastern flyway and Aquatic Warbler *Acrocephalus paludicola* and European Pied Flycatcher *Ficedula hypoleuca* from eastern Europe and Asia the western (Zink 1973, Gargallo *et al.* 2011, Salewski *et al.* 2019).

Using radar tracking, infrared and moon-watch data, Bruderer *et al.* (1999) and Bruderer (2001) concluded – in contrast to Casement's earlier findings – that many more migratory landbirds migrate around the western or eastern ends of the Mediterranean than cross it. Systematic field work on island and coastal stations in the western Mediterranean and NW Morocco (Pilastro *et al.* 1998, Gargallo *et al.* 2011), however, revealed species-specific variations in the tendency to cross the western Mediterranean in a broad front or not. Common Whitethroat, Common Redstart *Phoenicurus phoenicurus* and Woodchat Shrike *Lanius senator* actually do, whereas Melodious Warbler *Hippolais polyglotta* and Western Bonelli's Warbler *Phylloscopus bonelli* seem to prefer the shortest possible sea crossing. Geolocator studies complemented and augmented earlier field work and ring recoveries, adding surprising details to complicated migration patterns. Red-backed Shrikes *Lanius collurio* from Spain, for example, make a large detour around the northern Mediterranean across southern Europe and the Middle East to and from wintering grounds in southern Africa (Tøttrup *et al.* 2017).

Would birds migrating into Africa via Spain or the Middle East, points of entry separated by 3500 km, ever meet each other in sub-Saharan Africa? In other words: can redistribution upon crossing the Sahara lead to occupation/saturation of suitable habitat across the full width of the Sudano-Sahelian vegetation zones? It would seem, from tracking studies in storks, that such a scenario is realistic, though to a limited extent (Figure 1). The winter distributions of the two populations of Black Stork *Ciconia nigra* show some overlap in the central Sahel, with an eastern bird showing up in Nigeria (9°E) and a western bird in Chad (18°E). However, apparently only a minority spends the winter in Africa between 0 and 20°E. The question remains whether this gap is exclusively due to the detours made to reach their African wintering areas, and a subsequent failure to move towards the central Sahel. Alternatively, if there were a lack of suitable habitat, such as water bodies in the process of drying out (Chevalier *et al.* 2010b) between 0 and 20°E, this may prevent Black Storks from using the central section of the sub-Sahara. This is clearly not the case, with the presence of large wetlands such as Lake Chad, Lake Fitri and the Waza-Logone and Hadejia-Nguru floodplains between 10 and 18°E, not to mention the thousands of smaller temporary and (semi-)permanent wetlands across the region (Brouwer *et al.* 2003).

Easterly and westerly movements south of the Sahara, as shown by some tagged Black Storks (Figure 1), have been extensively recorded in the much larger samples of GPS-tagged White Storks. Individuals from the western flyway moved as far east as Niger (12°E; Flack *et al.* 2016, Soriano-Redondo *et al.* 2020) and birds of the eastern flyway as far west as Chad (14°E; Rotics *et al.* 2016, 2017). Even so, without the North African breeding population of White Storks, wintering mostly in Niger and Chad (Flack *et al.* 2016), there would be relatively few White Storks in the Sahel between 11 and 15°E.

Approximately the same pattern as in storks has been found for several raptor species. Egyptian Vultures *Neophron percnopterus* using the western route stay in West Africa, mostly between 17°W and 5°E, whereas birds from the eastern flyway overwinter between 15 and 42°E (Phipps *et al.* 2019), leaving a 1000 km-wide gap between birds of the two flyways. The same holds for Black Kites *Milvus migrans*. Birds from Spain enter Africa via Gibraltar and fly SSW across the Sahara. Upon arrival in the Sahel, they remain concentrated in the westernmost 20% of the Sahel, between 17°and 5°W (Sergio *et al.* 2014). Black Kites from central Europe scatter across a larger wintering area in sub-Saharan Africa: birds passing through Spain overwinter west of 5°W, but those transiting Turkey overwinter in Sudan and Ethiopia (30–35°E). The few birds crossing the Mediterranean spend the winter between 5°W and 25°E (Ovčiariková *et al.* 2020).

Like some White and Black Storks (Figure 1), several passerines are known to partake in east-west movements south of the Sahara. Liechti *et al.* (2012), using radar data, showed that Garden Warblers *Sylvia borin* and European Pied Flycatchers, after crossing the western Sahara, shifted their direction abruptly from south-southwest to south and east. Similarly, tagged Aquatic Warblers moved 700–900 km to the east or southeast (Salewski *et al.* 2019), Common Redstarts about 1000 km to the east (Kristensen *et al.* 2013) and Willow Warblers *Phylloscopus trochilus* up to 3000 km (Lerche-Jørgenson *et al.* 2017). An opposite shift in flight direction was shown for a Wood Warbler *Phylloscopus sibilatrix* that moved 3400 km from Sudan to Ivory Coast (Tøttrup *et al.* 2018; Figure 2).

The above examples are tantalizing titbits of factual information on the presence and density of Eurasian migrants in the central sub-Sahara. Most migrants enter Africa in the east and west and largely remain there (with the eastern birds extending into southern Africa, an option rarely exercised by those in the west but – in the future – may become more viable following the break-up of the massive tropical rainforest barrier in the Congo Basin of Central Africa; Hansen *et al.* 2020, Shapiro *et al.* 2021). Or – using the same migration routes – redistribute themselves west- and eastwards upon reaching the sub-Sahara, resulting in a more even distribution along the whole length of the

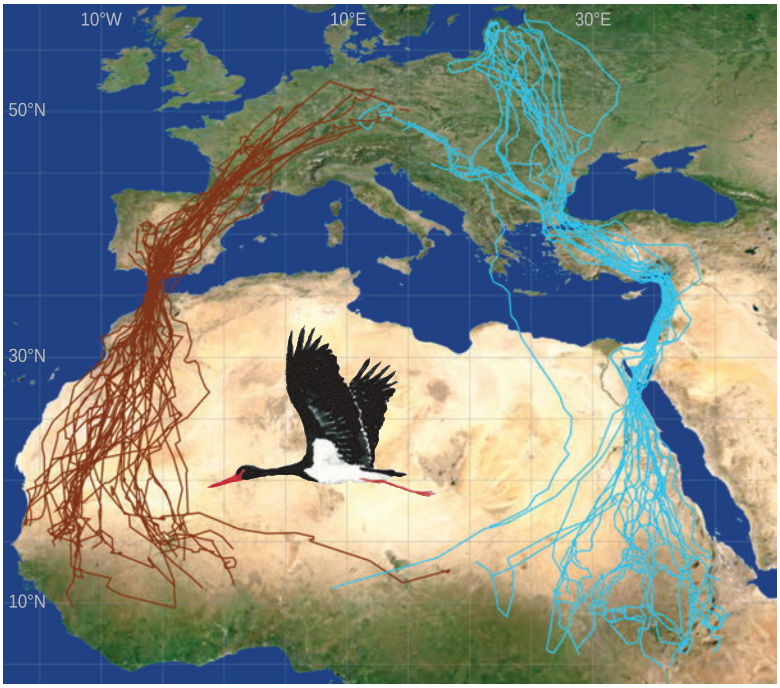

Figure 1. Autumn and spring migration routes of GPS-tagged Black Storks from breeding areas in Spain, France, Czech Republic and Latvia to their African wintering haunts. Birds make a detour around the Mediterranean to the west (brown) or the east (blue). Sources : Bobek *et al.* (2008), Chevallier *et al.* (2010a), Cano & Tellería (2013), Strazds (2021). Base Map: Earthstar Geographics.

Sahel. In the latter case, we would expect passerine densities in Chad – situated in the central sub-Sahara – to be the same as found in similar habitats in the eastern and western parts of the same vegetation zones (as suggested by Finch *et al.* 2017). If not, we should find a 'Gap of Chad' in the distribution and numbers of Eurasian passerines. We tried to solve this enigma with systematic density counts across the entire width of the Sahel to quantify spatial variations in density within and between arboreal bird species (Zwarts *et al.* 2023b; see Supplementary Material for some other migratory bird species).

There are six predictions. (1) The Gap of Chad really exists, with lower densities of Eurasian migrants compared to West and East Africa, especially in species which make a detour (Western Bonelli's Warbler; Cramp 1992, Cramp & Perrins 1993, Pilastro *et al.* 1998, Gargallo *et al.* 2011), but (2) the Gap of Chad will be less striking for species which cross the Mediterranean in broad front, such as Common Whitethroat (Tapia-Harris *et al.* 2022), Common Redstart and Woodchat Shrike, if existing at all.

(3) Subalpine Warbler *Curruca cantillans* has recently been split in three species (Zuccon *et al.* 2020). Moltoni's Warbler *C. subalpina* (breeding in Italy) is thought to spend the winter in the central Sahel and cross the Mediterranean between Tunisia and Italy (Pilot & Blanc 2017), perhaps compensating for a smaller influx of birds from eastern and western populations (we lumped the three species of the *Curruca cantillans* complex into Subalpine Warbler *sensu lato*), although the impact may be small given the tiny population of Moltoni's Warbler (BirdLife International 2021).

(4) Several species wintering in the Sahel have a western Palearctic breeding distribution that includes North Africa, i.e. Woodchat Shrike, Western and Eastern Olivaceous Warbler *Iduna pallida*, Western Bonelli's Warbler, Subalpine Warbler, Common Whitethroat and Western Orphean Warbler *Curruca hortensis*. The migration routes of these North African breeding birds have not been studied to any extent, but they probably move – partly or completely – southward across the Sahara in a broad front. Population estimates for these species in central northern Africa are not available (Isenmann *et al.* 2016). Western Olivaceous Warbler and Western Orphean Warbler were identified as common in North Africa (Cramp 1992, Isenmann & Moali 2000: 256), which may to some extent fill the Gap of Chad.

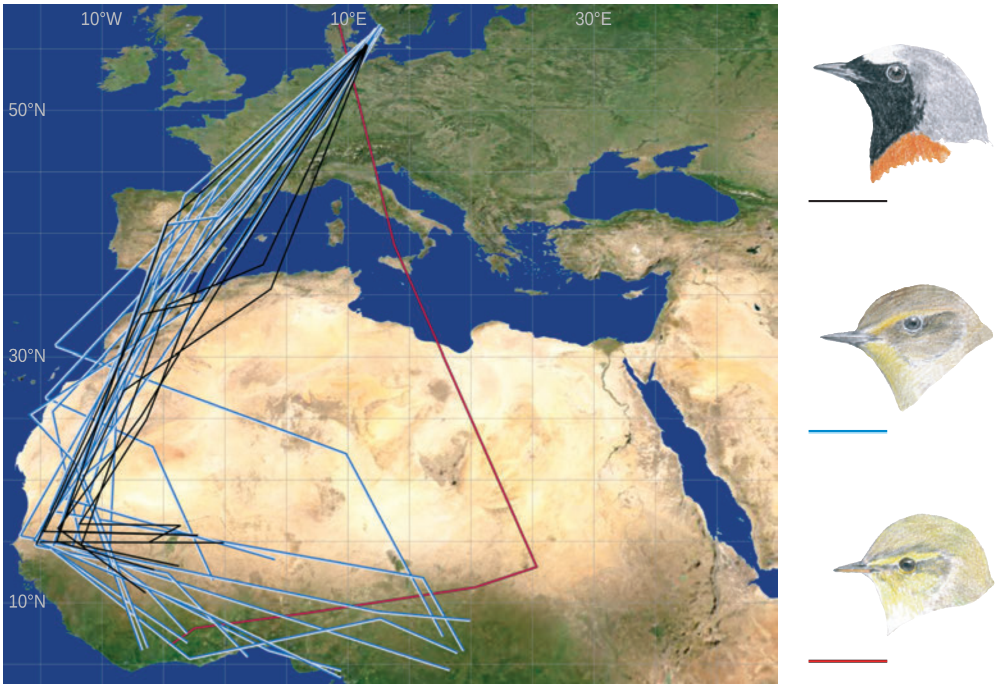

Figure 2. Autumn migration routes of seven Common Redstarts (black lines; Kristensen *et al.* 2013), 14 Willow Warblers (blue lines; Lerche-Jørgenson *et al.* 2017) and one Wood Warbler (red line; Tøttrup *et al.* 2018) equipped with geolocators. Lines connect stopover sites between breeding and final wintering sites and do not necessarily represent routes followed. Base Map: Earthstar Geographics.

(5) Species that enter Africa either in the East or West, and that gradually work their way towards the central Sahel along the same latitude (Figure 2), should gradually reach higher densities in the Gap of Chad during the course of the northern winter. How many bird species use this strategy, and what fraction of the wintering population is involved in each species, is unknown. Such a strategy is less likely to apply to species that exhibit long-lasting site fidelity during their stay on their wintering quarters. In the Sahel, site fidelity over a long period has been found for Western Olivaceous Warbler, Common Whitethroat, Subalpine Warbler, Common Redstart and European Pied Flycatcher, but not for Willow Warbler or Common Chiffchaff *Phylloscopus collybita* (Skilleter 1995, Sauvage *et al.* 1998, King & Hutchinson 2001, Salewski *et al.* 2002, Gersten & Hahn 2016, Thorup *et al.* 2019, Mostafa *et al.* 2021).

(6) In contrast to migrants, we expect no Gap of Chad for residents, but rather densities in line with available habitat.

METHODS

Field methods are described in detail in Zwarts & Bijlsma (2015) and the data set used in this paper is from Zwarts *et al.* (2023a, b). In summary, birds were counted between 2011 and 2019 in 1901 randomly selected study sites (each 4.5 ha) between 7°N and 22°N and between 17°W and 42°E during the dry season (20 November – 10 March; Figure 3). The Sahel is usually defined as the zone where the annual rainfall amounts to 100–600 mm, but we use the term more loosely, to encompass the entire transient zone between the Sahara in the north and the humid forests in the south. To analyse longitudinal variations in bird densities, we selected two rainfall zones (400–500 and 500–600 mm/year) with sufficient data across the full width of the Sahel. All trees and shrubs ≥1 m high within the study sites were registered separately (species, height and width). We also noted the individual tree or shrub for every arboreal bird present. This allowed us to convert bird counts in the study sites into bird densities per ha, but also to calculate bird density per ha of canopy, separately per tree and shrub species. We used the distribution of different woody species (Zwarts *et al.* 2023d) to formulate a prediction of bird distribution on the assumption that their density per ha of canopy in different woody species would be the same across their entire distribution areas and used the deviation of the observed from the predicted distribution to test whether the density of bird species varies per longitude; see Zwarts *et al.* (2023f) for details.

The spatial comparison revolves around 12 arboreal migratory species spending the northern winter in the Sahel: Woodchat Shrike, Eastern Olivaceous Warbler, Western Olivaceous Warbler, Western Bonelli's Warbler, Common Chiffchaff, Western Orphean Warbler, Eastern Orphean Warbler *Curruca crassirostris*, Lesser Whitethroat, Subalpine Warbler, Rüppell's Warbler *Curruca ruppeli*, Common Whitethroat and Common Redstart. We compared the longitudinal trend in density of migratory species with those of the four most common residents occurring over all longitudes, namely a group of birds for which a migratory divide obviously does not apply: Northern Crombec *Sylvietta brachyura*, Green-backed Camaroptera *Camaroptera brachyura*, Tawny-flanked Prinia *Prinia subflava* and Little Weaver *Ploceus luteolus*. We made the same longitudinal comparison between observed and predicted bird densities separately for three common and bird-rich tree species (Umbrella Thorn *Acacia tortilis*, Desert Date *Balanites aegyptiaca* and Winter Thorn *Faidherbia albida*). To account for rainfall in the longitudinal variation in bird density, we selected trees from the rainfall zone where the three woody species were most common: 200–600 mm/year in *A. tortilis* and 300–700 mm/year in *Balanites* and *Faidherbia*. The bird densities for Sudan and Ethiopia were, however, less reliable because the

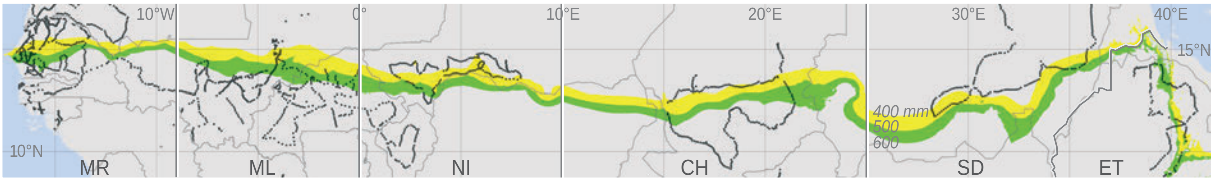

Figure 3. The distribution of study sites in the Sahel (●); yellow and green bands indicate the sites where the average annual rainfall amounts to 400–500 and 500–600 mm, respectively.

three tree species were not well represented in our sites. To decide whether food supply in the Sahel varies longitudinally, we estimated the abundance of a moth *Crypsotidia conifera*, an important prey for birds that frequent *Faidherbia albida* trees. We noted systematically when and if birds recorded during the standard counts were handling large prey, usually a caterpillar (Zwarts & Bijlsma 2015); this paper analyses whether the two vary longitudinally.

RESULTS

Longitudinal variation in density of arboreal birds

The bird species occurring in the wide transient zone south of the Sahara are tied to specific rainfall zones (Zwarts *et al.* 2023b). Within the rainfall zones some species occurred over the full width of 6000 km between the Atlantic Ocean and the Red Sea, among which common residents as Northern Crombec, Tawny-flanked Prinia and Green-backed Camaroptera (Figures S09, S16 and S17 in Zwarts *et al.* 2023b). Only a few migrants covered the same width, notably Common Whitethroat and Common Redstart (Figures S25 and S28 in Zwarts *et al.* 2023b) and to a lesser degree Woodchat Shrike (Figure S13 in Zwarts *et al.* 2023a). The most common migrants in our study area, Western Bonelli's Warbler and Subalpine Warbler were recorded exclusively in the western Sahel (Figure S10, S24 in Zwarts *et al.* 2023b) and Lesser Whitethroat was recorded exclusively in the eastern Sahel (Figure S20 in Zwarts *et al.* 2023b). Closely related species-pairs occupied the Sahel in distinct, near-exclusive distributions, either in the west or the east: Western Bonelli's Warbler and Eastern Bonelli's Warbler *Phylloscopus orientalis*; Western Orphean Warbler and Eastern Orphean Warbler, Western Olivaceous Warbler and Eastern Olivaceous Warbler (Figures S10, S11, S14, S15, S21 and S22 in Zwarts *et al.* 2023b).

Migrants were particularly common in the western Sahel and showed declining densities towards the more easterly regions in both rainfall zones (Table 1). The decline was pronounced in Subalpine Warbler and even larger in Western Bonelli's Warbler, but less so in Common Whitethroat. The migratory species limited to the eastern part of Africa were relatively more common in Sudan than in Chad. Such differences were not found in residents (Table 1).

The longitudinal variation in density of arboreal birds might be due to the declining (from west to east) extent of woody cover in the rainfall zones of 400–500 mm and 500–600 mm, especially in the rainfall zone 400–500 mm (Table 1). The bird density per longitude appeared to be related to total woody cover, but when a selection was made for only bird-rich tree species (>80 birds/ha canopy), the density of Western Bonelli's Warbler became highly correlated with woody cover in the 400–500 mm rainfall zone (increasing from $r = +0.65$ to $r = +0.87$ for total and bird-rich woody cover, respectively) and the difference was still larger in Subalpine Warbler (increasing from $r = +0.60$ to $r = +0.96$). There were no such clear relationships in the rainfall zone 500–600 mm.

Observed and predicted density of arboreal birds

To rule out longitudinal variation in woody cover as a possible confounding variable (Table 1), we determined per longitude the expected bird numbers based on the percentage of woody cover of shrub and tree species across the Sahel, assuming that the bird density per ha of canopy in the different woody species (Zwarts *et al.* 2023d) would be the same everywhere. We then compared this to the numbers actually counted within the six longitudinal bands. Although the occurrence of selected woody species within the same rainfall zone explained part of the longitudinal variation in bird density, systematic differences between observed and predicted numbers were apparent, independent of the occurrence of the selected woody species (Figure 4). When plotting the ratio of observed and predicted numbers for the six longitudinal zones, five trends emerged:

(1) a decline from west to east of migrants in the western Sahel, the birds being 2–8 times more common in Senegal than in Chad; Western Olivaceous Warbler was absent in Chad (Figure 4A),

(2) 4 to 6 times more migrants in Sudan than in Chad; Eastern Orphean Warbler was not recorded in Chad (Figure 4B),

(3) 2 to 3 times more migrants in the west and the east than in Chad in species distributed across the full range, with Common Whitethroat as exception (Figure 4C),

(4) 2 to 4 times more migrants in Sudan than in Ethiopia in 4 species, but equal densities in 2 migrants, and Common Chiffchaff only occurring in Ethiopia (Figure 4B and 4C),

(5) on average, an increase from west to east in residents (Figure 4D); none of the four residents had a lower density in Chad, contrasting with 11 of the 12 migrants.

Most migrants were concentrated in three woody species: Desert Date, Umbrella Thorn and Winter Thorn (Zwarts *et al.* 2023d). Migratory species found in these trees in the western Sahel reached their highest densities in Senegal, sometimes in Mali, and typically declined further east (Table 2). They are partly replaced by other bird species in Chad and further east.

Confounding factors potentially impacting bird densities across the Sahel

The longitudinal variation in bird densities, as shown in Figure 5, might be related to systematic differences in the food supply within the region. For the moth *Crypsotidia conifera*, an important prey for birds (Figure 5), we indeed recorded a distinct zonal variation in the percentage of *Faidherbia* trees afflicted with moths, being highest in the three western longitudinal zones and lowest in the three eastern zones (Figure 5). The fraction of *Faidherbia* trees with a high density of >20 moths flushed per tree was largest in Niger, where we also saw the highest fraction of birds with large prey (moth or caterpillar). In *A. tortilis*, we did not find substantial longitudinal variation in the percentage of large prey taken by birds: 1.5% in Senegal and 2.0% in the five other zones.

Table 1. Bird density (n/km^2) in six longitudinal bands (see Figure 3) given separately for two rainfall zones. The average woody cover (%) is given for all trees and shrub species, but also for a selection of woody species where the average bird density is higher than 5, 10, 20, 40 or 80 birds per ha canopy (data from Zwarts *et al.* 2023d). Results of one-way ANOVA: explained variance (r^2) and level of significance ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

	Annual rainfall: 400–500 mm								Annual rainfall: 500–600 mm							
	MR	ML	NI	CH	SD	ET	r^2	P	MR	ML	NI	CH	SD	ET	r^2	P
Woodchat Shrike	16	4	2	2	3	0	0.16	***	10	4	0	4	4	0	0.04	NS
W. Bonelli's Warbler	66	38	14	0	0	0	0.19	***	76	16	20	8	0	0	0.14	***
Common Chiffchaff	0	0	0	0	0	10	0.17	***	0	0	0	0	0	25	0.17	***
E. Olivaceous Warbler	0	0	7	1	6	2	0.07	**	0	0	0	11	9	1	0.13	***
W. Olivaceous Warbler	8	19	1	0	0	0	0.13	***	9	6	0	0	0	0	0.03	NS
Lesser Whitethroat	0	0	0	8	10	2	0.18	***	0	0	0	11	16	3	0.21	***
W. Orphean Warbler	8	1	1	0	0	0	0.12	***	5	0	0	0	0	0	0.03	**
E. Orphean Warbler	0	0	0	0	0	15	0.11	***	0	0	0	0	4	0	0.10	**
Rüppell's Warbler	0	0	0	1	0	0	0.03	NS	0	0	0	1	7	0	0.16	**
Subalpine Warbler	52	40	21	14	0	0	0.18	***	23	11	7	0	0	0	0.04	NS
Common Whitethroat	10	3	21	7	3	0	0.13	***	24	6	18	7	0	2	0.09	**
Common Redstart	2	7	3	0	1	0	0.07	*	16	6	0	5	0	2	0.03	NS
All migrants	163	118	70	33	27	30	0.16	***	165	53	44	47	40	33	0.12	***
Northern Crombec	9	0	0	0	3	0	0.13	***	8	2	0	6	2	6	0.02	NS
Tawny-flanked Prinia	24	0	3	3	6	0	0.22	***	20	9	7	12	7	8	0.04	NS
G.-backed Camaroptera	7	8	8	7	8	0	0.01	NS	22	13	20	18	0	1	0.03	NS
Little Weaver	5	0	9	4	6	0	0.02	NS	41	5	13	22	9	5	0.08	*
other insectivores	19	10	4	11	4	0			14	18	4	7	0	73		
Frugivores	6	0	7	1	10	5	0.01	NS	10	0	0	3	0	39	0.09	**
Nectarivores	12	0	8	2	2	32	0.08	*	8	8	33	28	4	58	0.13	***
All residents	42	10	28	18	22	37	0.07	*	73	31	50	60	13	175	0.09	**
Total woody cover, %	4.9	3.6	3.0	3.3	4.2	1.8			11.2	5.2	5.8	9.7	8.4	6.3		
>5 birds/ha canopy	4.8	3.6	3.0	3.2	4.1	1.6			11.2	5.2	5.8	9.6	8.4	6.1		
>10 birds/ha canopy	3.5	3.2	2.4	2.9	3.8	1.6			9.4	4.0	4.0	5.8	8.4	5.4		
>20 birds/ha canopy	3.0	3.0	2.3	2.5	3.4	0.7			9.4	3.1	3.6	5.3	8.3	5.1		
>40 birds/ha canopy	2.5	2.4	1.7	2.4	1.3	0.5			3.0	1.7	1.3	3.8	4.2	4.3		
>80 birds/ha canopy	1.7	1.8	0.7	0.8	0.2	0.1			2.0	0.8	0.9	1.3	0.0	2.3		
Number of sites	53	21	67	26	40	9	216		77	62	10	15	10	31	205	

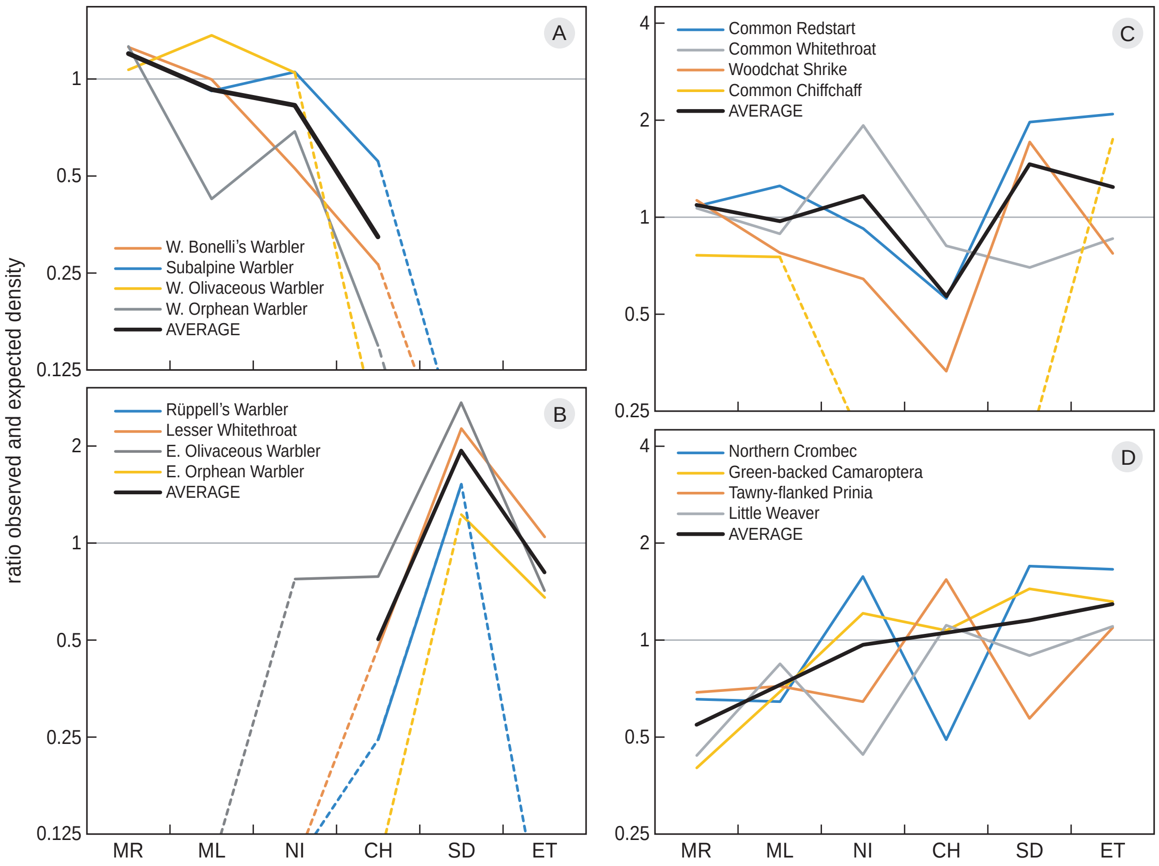

Figure 4. Ratio of observed and expected number of birds as a function of longitude (see Figure 3) in (A) migrants wintering in the western Sahel, (B) migrants wintering in the eastern Sahel, (C) migrants wintering across the Sahel, (D) residents present across the Sahel. Note log-scale on vertical axis. The lines are dashed when connected to a longitudinal zone where birds were expected but not observed (thus ratio = 0). Observed bird densities are given in Supplementary Material of Zwarts *et al.* (2023b) and observed and predicted densities in Figure 3 and Figures S5–S14 in Zwarts *et al.* (2023f). χ^2-tests show that longitudinal variation was in all cases significant ($P < 0.001$).

Figure 5. Average number of moths flushed from *Faidherbia* trunks, shown for six longitudinal zones between Senegal (SN) and Ethiopia (ET). The number of *Faidherbia* trees varied for the six zones between 80 (Chad) and 841 (Niger), the number of observed birds between 105 (Sudan) and 2467 (Senegal). The presence of moths differed significantly per zone ($\chi^2_5 = 128.9$, $P < 0.001$). The black line shows the average percent of observed birds eating large prey in *Faidherbia* during standard counts. The relative frequency at which large prey were taken in *Faidherbia* differs significantly per zone ($\chi^2_5 = 45.4$, $P < 0.001$).

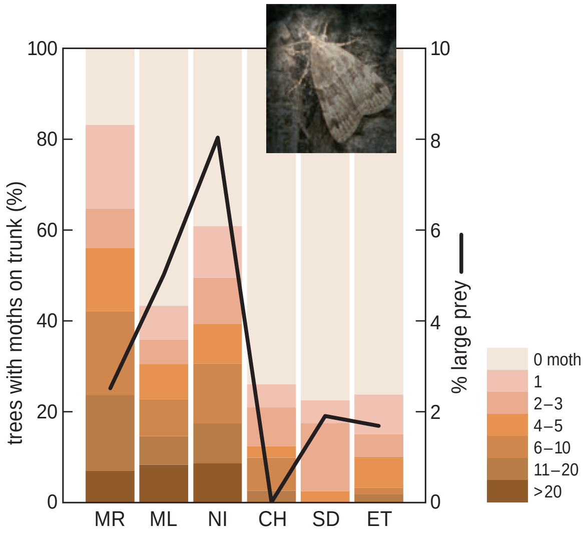

Table 2. Density per ha of canopy for 13 migrants during the dry season (20 November – 10 March) as a function of longitude (six zones as in Figure 3) in three woody species. Five bird species occurring in the western and six in the eastern Sahel are indicated. Average densities were determined for large trees (≥6 m high in *Faidherbia* and ≥4 m the other two species) from the 200–600 mm/year rainfall zone (*A. tortilis*) or 300– 700 mm (both other species), in total 3752 trees and 297,006 m^2 canopy in *Balanites*, 2569 trees and 156,962 m^2 in *A. tortilis* and 3352 trees and 173,263 m^2 in *Faidherbia*.

Balanites aegyptiaca	**SN**	**ML**	**NI**	**CH**	**SD**	**ET**
Woodchat Shrike	4.0	0.7	0.8	0.4	0.6	0.0
W. Bonelli's Warbler	6.7	0.0	2.7	0.0	0.0	0.0
W. Olivaceous Warbler	0.8	0.7	0.0	0.0	0.0	0.0
E. Olivaceous Warbler	0.0	0.0	0.4	0.2	2.4	0.0
Lesser Whitethroat	0.0	0.0	0.0	4.7	3.7	0.0
W. Orphean Warbler	1.4	0.0	0.4	0.0	0.0	0.0
E. Orphean Warbler	0.0	0.0	0.0	0.0	0.6	0.0
Rüppell's Warbler	0.0	0.0	0.0	0.4	0.0	0.0
Subalpine Warbler	14.7	17.9	11.4	6.8	0.0	0.0
Common Whitethroat	2.3	3.0	2.4	2.3	1.2	0.0
Common Redstart	0.9	0.0	0.8	0.2	0.0	0.0
Other migrants	0.8	1.5	0.0	0.0	1.8	0.0
All migrants	31.5	23.9	18.8	15.1	10.3	0.0
Canopy × 100 m^2	654	134	255	511	164	13

Acacia tortilis	**SN**	**ML**	**NI**	**CH**	**SD**	**ET**
Woodchat Shrike	4.6	1.2	0.6	0.3	0.0	0.0
W. Bonelli's Warbler	26.3	15.8	11.2	0.0	0.0	0.0
W. Olivaceous Warbler	2.0	1.2	0.0	0.0	0.0	0.0
E. Olivaceous Warbler	0.0	0.0	0.6	0.0	16.4	0.0
Lesser Whitethroat	0.0	0.0	0.0	2.5	11.7	3.2
W. Orphean Warbler	6.0	0.0	0.6	0.3	0.0	0.0
E. Orphean Warbler	0.0	0.0	0.0	0.0	2.3	0.8
Rüppell's Warbler	0.0	0.0	0.0	0.0	23.5	0.0
Subalpine Warbler	11.8	20.7	7.4	7.9	0.0	0.0
Common Whitethroat	1.2	0.0	6.8	4.5	2.3	0.8
Common Redstart	1.6	7.3	0.6	0.0	0.0	0.0
Other migrants	1.0	7.3	0.0	0.0	0.0	0.0
All migrants	54.5	53.6	27.9	15.6	56.4	4.8
Canopy × 100 m^2	805	82	161	354	43	125

Faidherbia albida	**SN**	**ML**	**NI**	**CH**	**SD**	**ET**
Woodchat Shrike	4.0	0.7	0.8	0.4	0.6	0.0
W. Bonelli's Warbler	39.6	24.4	8.9	6.4	0.0	0.0
E. Bonelli's Warbler	0.0	0.0	0.0	1.2	6.8	0.0
Common Chiffchaff	0.0	0.3	0.0	0.0	0.0	36.7
Iberian Chiffchaff	0.5	1.6	0.0	0.0	0.0	0.0
W. Olivaceous Warbler	6.2	11.4	1.5	4.1	0.0	0.0
E. Olivaceous Warbler	0.2	0.1	1.5	7.0	17.8	0.0
Lesser Whitethroat	0.0	0.0	0.0	5.3	17.8	12.2
W. Orphean Warbler	2.6	0.5	0.4	1.2	0.0	0.0
Subalpine Warbler	16.1	17.1	9.0	0.0	0.0	0.0
Common Whitethroat	4.9	1.5	2.2	0.0	2.7	0.0
Common Redstart	1.4	4.1	0.5	0.6	1.4	3.1
Other migrants	0.3	0.8	0.4	0.0	1.4	0.0
All migrants	75.7	62.5	25.2	26.1	48.4	52.0
Canopy × 100 m^2	113	790	777	171	73	33

As bird density in individual trees varied with the transparency of tree crowns (quantified as opacity score; see Figure 15 in Zwarts & Bijlsma 2015), a lower density of migrant birds in Chad might be related to the trees' transparency of the foliage (more thinly leafed). The opacity score was found to vary per rainfall zone (see Figure 6 in Zwarts *et al.* 2023d) but without a longitudinal trend (L. Zwarts unpubl.) and therefore considered irrelevant to east-west differences in bird density.

Another factor impacting bird numbers is particularly relevant in the case of *Faidherbia albida*, one of the very few tree species that produces leaves and flowers in the dry season and is strongly favoured by migrant birds. And not just birds, pastoralists cut branches to provide food for their livestock. Cutting twigs and branches is in many parts of the Sahel common practice among herders in the dry season (see Figure 19 in Zwarts & Bijlsma 2015). Pruning negatively affected flowering and fruiting in the following year. Large (>10 m high) *Faidherbia* trees without fruit in January–March amounted to 29% in Senegal, 31% in Mali, 4.5% in Chad and 0% in Sudan. Of the *Faidherbia* trees in Senegal, 2% were heavily pruned in January–February, but the practice of pruning declined further east, to 1.3% in Mali, 0.3% in Chad and Sudan and 0.7% in Ethiopia. In Chad nearly all *Faidherbia* remained untouched, in stark contrast with *Faidherbia* in Senegal and Mali. Pruned *Faidherbia* trees attracted fewer migratory birds (Zwarts & Bijlsma 2015), and the almost pristine *Faidherbia* in Chad should therefore offer much better conditions for birds than available in the severely damaged *Faidherbia* in the western Sahel. Instead, we found fewer – not more – migratory birds in *Faidherbia* in the central Sahel (Table 2).

Taking the information together, we tentatively conclude that the observed longitudinal differences in bird density cannot be attributed to tree-related variables.

DISCUSSION

The extent of decline in bird density towards the central Sahel varied between migrants and residents (Figure 3–4; Table 2). The overall picture confirmed the existence of a ‘Gap of Chad’ for migratory passerines (but not for residents). We started the paper with five predictions regarding the Gap of Chad, with the following outcome:

(1) A decline in density in the central Sahel would be least in migrant species known to cross the Mediterranean in a broad front, i.e. Common Whitethroat, Common Redstart and Woodchat Shrike. This was confirmed for Common Whitethroat, but not found in both other species.

(2) We expected the central southern European population of the Subalpine Warbler complex (referring to Moltoni’s Warbler) to cross the central Mediterranean Sea and to show up in the central Sahel. If so, the numbers involved were too small to noticeably reduce the Gap of Chad in Subalpine Warblers. The size of the breeding population of Moltoni’s Warbler is unknown but not likely to number millions of birds (Keller *et al.* 2020, BirdLife International 2021), and the population of Eastern Subalpine Warbler is even smaller (as evident from the absence of Subalpine Warblers in our surveys in Sudan and Ethiopia).

(3) Larger numbers of migratory birds finding their way to the central Sahel were expected from Western Olivaceous Warblers and Western Orphean Warblers, which are common breeding birds in southern Europe as well as locally common in Morocco and Algeria (Bergier *et al.* 2022, Isenmann & Moali 2000). Both species were abundant in the western Sahel but absent or sparsely recorded in Chad (Table 1 & 2, Figure 4), suggesting that the birds from northern Africa spend the northern winter south of the Sahara within the same longitudinal range as their breeding grounds, i.e. to the west of the central Sahel and unlikely to show up in Chad.

(4) For species known for their itinerant behaviour, more birds would be expected to stray into the Gap of Chad (as Willow Warbler, unlike species showing winter site fidelity (e.g. Common Redstart, Subalpine Warbler). The data supported a wider Gap of Chad for Common Redstart and Subalpine Warbler, and the lack of a Gap in Willow Warbler (see below).

(5) No Gap of Chad was expected for resident species. The evidence supported the expectation.

The Gap of Chad is real but species-specific

Our bird counts show a longitudinal variation in the density of migratory species (a trend absent in four common residents), to the effect that the central Sahel (mainly Chad) held much lower densities of migratory birds than either the western or eastern Sahel. This so-called Gap of Chad was substantiated by three lines of evidence, viz. (1) the average density per ha of migratory birds (Table 1), (2) the deviation of observed from predicted bird density as derived from the distribution of their selected woody species (Figure 4), and (3) the bird density per ha of canopy as measured in three common woody species that are attractive to birds (Table 2). Bird species concentrated in the western Sahel (e.g. Western Bonelli’s, Western Orphean and Subalpine Warbler) were most common in the westernmost part of their distribution area (Senegal). The density of these species declined to the east (Mali–Niger–Chad). The same trend, but then declining from east to west, was found in common species restricted to the eastern Sahel (Lesser Whitethroat, Rüppell’s and Eastern Olivaceous Warbler), which had higher densities in Sudan than in Chad. Of the four migrants wintering across the entire Sahel, Common Redstart, Woodchat Shrike, Common Chiffchaff and Common Whitethroat, the first two showed a noticeably lower density in Chad, whereas the Common Chiffchaff was observed only in the westernmost and easternmost parts of the region.

Is the Gap of Chad the logical outcome of the migration strategy of Eurasian songbirds that circumvent the Mediterranean via Iberia or the Middle East and mostly end up in the western and eastern Sahel, the latter with an extension into southern Africa? Or is the large longitudinal variation in bird densities (Figures 3 and 4, Tables 1 and 2) a function of ecological variables in the Sahel associated with longitude? Regarding the latter, we found no evidence that tree-related variables could explain the longitudinal trends in the density of arboreal birds. Annual variation in rainfall might be a confounding variable, since it has a large impact on the distribution of birds (Zwarts *et al.* 2023g). It took nine years to collect the data (2011–2019), with countries in the western Sahel visited during at least three years, but Niger and all countries further east just once, in 2017/18 or in 2018/19. When annual rainfall had differed a lot between the nine years of data collection, a single year's visit might have hit upon an outlier in terms of rainfall (either very dry or extremely wet). A separate analysis (Supplementary Material 4 in Zwarts *et al.* 2023a) revealed that the annual variation of rainfall during the fieldwork period was small with slightly more rainfall than average in the years of fieldwork in Niger and Chad. As the density of arboreal birds during the dry season is lower after poor rainfall in the preceding rainy season (probably due to higher mortality; Zwarts *et al.* 2023g), the shortfall of arboreal birds in Chad cannot be attributed to the confounding impact of annual rainfall. In fact, numbers might have been even lower had rainfall in the year of our visit in the central Sahel not been above average.

If the Gap of Chad in terms of wintering arboreal birds cannot be attributed to rainfall, how then to explain that bird species common in the western Sahel declined from west to east and were only partly replaced by bird species restricted to the eastern Sahel (Table 1 and 2)? The Gap of Chad was evident in birds present in *Faidherbia*, but not found in two other bird-rich trees (*Balanites* and *Acacia tortilis*) in which bird density per ha canopy declined without distinct gaps

Photo 1. In Niger and Chad, we came to doubt ourselves as we were often unable to discover any birds, or very few, in majestic White Thorn *Faidherbia* trees (densely leaved and adorned with many flowers), especially in the light of our experience with similar trees in the western Sahel. It slowly dawned that migratory bird species in Niger and especially in Chad were relatively scarce. This large *Faidherbia* in Niger on 23 December 2017, for example, of 16 m high and 30 m wide had a canopy surface of 700 m^2 but held only a single Western Bonelli's Warbler. A tree of similar size in the western Sahel would have housed, on average, five migrants (Figure 5 in Zwarts *et al.* 2023d). It shows that uneducated extrapolation of density figures derived from restricted geographical areas (even when chosen randomly) may bring wrong results.

from west to east (although sample size for the eastern Sahel is small; Table 2). Probably fewer birds used *Balanites* and *A. tortilis* in the eastern Sahel because they had switched to tree and shrub species which were more attractive and common in the eastern Sahel: the Toothbrush Tree *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua*, the low tree *Maerua crassifolia* and several acacia species restricted to Sudan or Ethiopia (Zwarts *et al.* 2023d).

How widespread is the Gap of Chad among migrant bird species in general?

There is no reason to expect a Gap of Chad in bird species with wide breeding distributions in Eurasia that migrate in a broad front along more or less the same longitudes as their breeding location. Migratory connectivity is a widespread phenomenon among raptor species wintering in sub-Saharan Africa (Panuccio *et al.* 2021), as well as among passerines (e.g. Common Nightingale *Luscinia megarhynchos* and Barn Swallow *Hirundo rustica* wintering to the south of the wider Sahel region; Hahn *et al.* 2014, Rönn *et al.* 2020).

Migrants with an itinerant lifestyle are also unlikely to create a shortfall of wintering birds in the central Sahel, even when the general migration routes from Europe to Africa follow the longitudinal distribution of the breeding quarters (Figure 6A). For example, more than 80% of the Willow Warblers recovered along the Atlantic coast of Mauritania and Senegal (15–20°W) came from Europe west of Greenwich, but birds recovered during migration between Libya and Saudi Arabia and during the northern winter in Chad, Sudan and the Central African Republic (>20°E) mostly originated from (north-) eastern Europe (>15°E; Figure 6B). The majority of British and Irish Willow Warblers recoveries in Africa came from the far west of Africa, although some were found as far east as 500 km inland (Figure 6C). Swedish birds mostly took the eastern flyway and during the early winter stayed some 2000 km farther east in Africa than their British congeners. Swedish Willow Warblers were recovered up to 1500 km to the west later during the northern winter, to such an extent that winter distributions of Swedish and British Willow Warblers partly overlapped at the end of the wintering period (Figure 6C). A similar shift was detected in the ring recoveries of Willow Warblers from the rest of Europe (Figure 6C). The seasonal shift to the west is significant for continental Willow Warblers (one-way ANOVA: $r^2 = 0.27$, $n = 29$, $P = 0.04$), but is absent in British birds ($n = 20$, $P = 0.82$). Willow Warblers of the subspecies *acredula* breeding in Northern Scandinavia spend the northern winter in central and southern

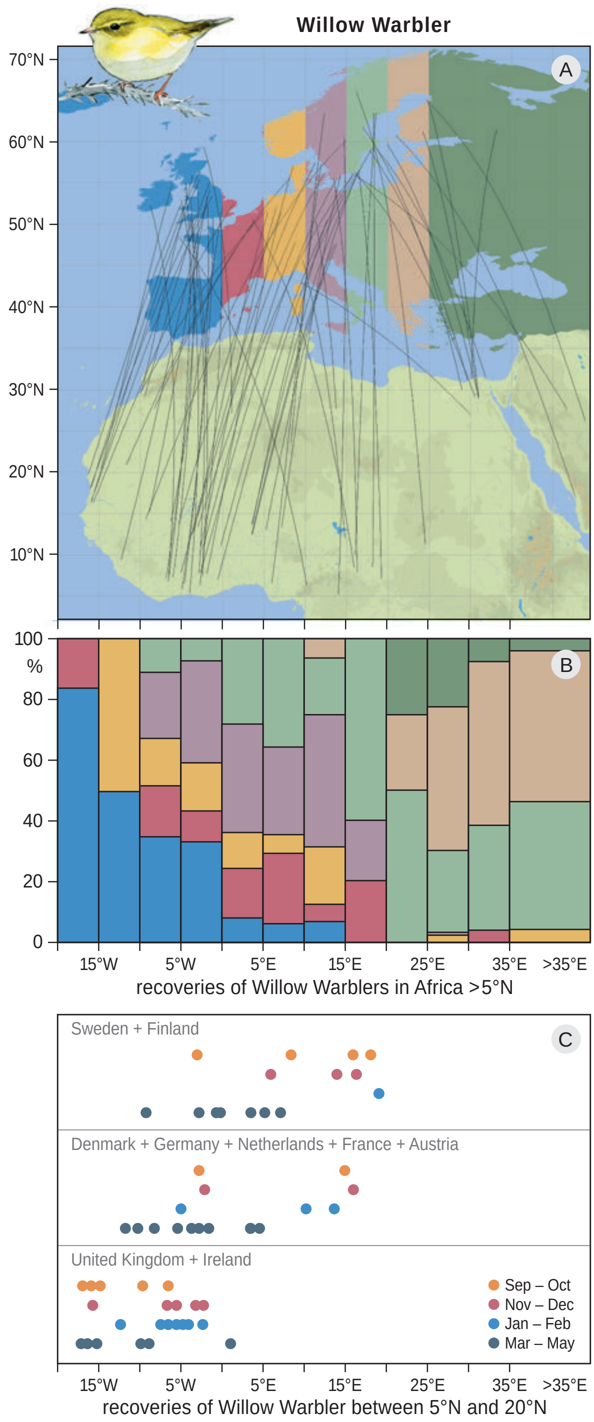

Figure 6. (A) Longitudinal split of Willow Warblers as reflected in ringing recoveries from Africa (and Saudi-Arabia) north of 5°N. Lines connect ringing and recovery site for 61 birds and do not necessarily represent routes followed. In order not to clutter the figure, no lines are shown on the map for 301 African recoveries north of 30°N. (B) Stacked bar chart based on all 362 recoveries shown in (A). (C) Seasonal longitudinal shifts south of the Sahara Desert shown separately for birds originating from three regions in Europe. Based on EURING data (Figure 106 in Zwarts *et al.* 2009).

Africa (Bensch *et al.* 2006); none of the ringing recoveries shown in Figure 6C refer to birds originating from northern Scandinavia. The itinerant behaviour of Willow Warblers in its wintering quarters (Figure 6C; Lerche-Jørgenson *et al.* 2017) is not conducive to a Gap of Chad. The same may apply to Wood Warbler, given the individual that moved up to 3400 km from east to west, partly within the same vegetation zone (Tøttrup *et al.* 2018; see also Figure 2).

The Gap of Chad is less likely in migrants opting for a sedentary life, thus showing prolonged site fidelity during their stay in Africa. Colour-ringed Northern Wheatears *Oenanthe oenanthe* in northern Nigeria occupied, at least during the first half of the northern winter, home ranges with an average diameter of 69 m (Blackburn & Cresswell 2016b). Common Redstarts, Whinchats and European Pied Flycatchers showed site fidelity throughout their non-breeding stay (Skilleter 1995, Salewski *et al.* 2002, Kristensen *et al.* 2013, Ouwehand *et al.* 2015, Blackburn & Cresswell 2016a, Thorup *et al.* 2019). Many other migratory species in Africa, however, use a series of different sites during their wintering period, depending on regional variation in seasonal rainfall, vegetation and food supply (Sinclair 1978, Lack 1983, 1986; Jones 1998). Itinerancy has been suspected of several migratory passerines (Moreau 1972, Pearson & Backhurst 1976, Hedenström *et al.* 1993). Many geolocator studies show that bird species which winter north of the equator sometimes move 300–700 km southward during the gradual desiccation of this zone; several species that winter in tropical or southern Africa use the Sahel as a stopover site during their southbound migration (Supplementary Material).

The Gap of Chad in past and present

The relative scarcity of migrants in the central Sahel may be the result of the pathways used by most migratory birds from Eurasia to enter Africa on either side of the continent, a hard-wired system that evolved over eons but can be altered under the influence of selection when conditions change (Newton 2008: 617). In the Palearctic-African migration system a step change has been the overwhelming decline of migratory birds from the Eurasian hinterland, especially in the past half century. In the European Union alone, the loss of birds was estimated at 560–620 million for just 1980–2017, mostly seedeaters and long-distance migrants, or minus 17% of the total bird population (Burns *et al.* 2021); the decline in North America over a slightly longer time interval (1970–2017) amounted to a net loss of 2.9 billion birds, or 29% of the total population (Rosenberg *et al.* 2019), probably not that much different from Europe at large for the same time period. The plenitude of migrants of >50 years ago may have been more evenly distributed across the Sahel (in the wake of higher competition or spillover into less crowded wintering grounds; see Gill *et al.* 2001), even taking into account that the main wintering grounds in the 1960s were much less degraded than nowadays and therefore able to hold higher numbers of migratory birds (as exemplified for N Senegal; Zwarts *et al.* 2018).

There are several explanations possible why the central Sahel is more thinly occupied by wintering migrants than either East or West Africa.

(1) The central Sahel might offer less food compared to the western and eastern Sahel. Our data suggest the opposite for arboreal birds, as illustrated by the larger fraction of flowering and unpruned *Faidherbia* trees than in West Africa.

(2) The central Sahel might be less attractive for migrants should insectivorous arboreal residents occur in higher densities than in western or eastern Sahel, potentially competing for the same food resources. However, the density of insectivorous arboreal residents is not higher in the central Sahel than elsewhere in the Sahel (Table 1), and migrants in the Sahel are dominant over residents anyway (Zwarts *et al.* 2023e).

(3) Food supply is poor in a dry year and many birds do not survive (Boddy 1993, 1994, Zwarts *et al.* 2023g). It is conceivable that dry conditions force migrants into a more itinerant behaviour, with a subsequent influx in the central Sahel. Available counts suggest a large decline of wintering numbers of arboreal birds during a dry year in Senegal (Zwarts *et al.* 2023g), but to what degree this is due to higher mortality or to movements to the south (Pearson & Backhurst 1976, Pearson *et al.* 2014) or to the central Sahel is unknown.

(4) The substantial decline of populations of migratory birds in recent decades may have reduced competition for resources in the western or eastern Sahel, with a subsequent reduction of dispersive movements towards the central Sahel (or in the East: towards southern Africa). However, quantitative data to substantiate a shift in movement patterns are lacking (but see Howes *et al.* 2019, 2020, for wintering European Honey Buzzard *Pernis apivorus*, showing an apparent southward shift in E Africa associated with habitat fragmentation). When competition plays a role in the choice of consecutive wintering sites, we might assume that subordinate birds will redistribute across the central Sahel under the presumption that juveniles and

females are outcompeted by the heavier adults and males (e.g. Enoksson 1988, Marra 2000, Catry *et al.* 2004). Our data are insufficient to assess geographical variation in the proportions of sexes and ages among migrant birds.

(5) Unlike migratory birds wintering in the western Sahel, which face the barrier of the Atlantic Ocean to the south, those in the eastern Sahel have the option – when conditions deteriorate during droughts – of continuing to migrate southwards via the north-south running Rift Valley, where the varied topography and twin rains produce a mixture of vegetation zones including semi-arid savannah (Newton 2008: 704, Pearson *et al.* 2014). This difference may contribute to smaller numbers of migrants entering the central Sahel from the East than from the West.

When birds, after arrival in the western or eastern Sahel, partly move on towards the centre, a decline in numbers in the westernmost and easternmost Sahel should ensue between September and November with a corresponding gradual increase of numbers in the central Sahel. Subalpine Warbler and Common Whitethroat arrive in N Senegal from mid-August onwards and are present in large numbers throughout September and later on (Morel & Roux 1966). In N Nigeria, both species are rarely present before mid-October, after which the numbers gradually increase until January (Wilson & Cresswell 2010). Some Palearctic migrants in Nigeria, like Subalpine Warbler and Woodchat Shrike, move south in the course of the dry season (Cresswell *et al.* 2009), and such a movement is also recorded in Northern Wheatear and other species (see Supplementary Material). It is likely that an increase in numbers is then largely the result of birds moving from the northern to the southern Sahel, rather than moving west or east (Elgood *et al.* 1973). Moreover, our bird counts between September and February in Senegal did not reveal the expected decline of migrant numbers after September or October, except for Common Redstart (Figures 1 and 2 in Zwarts *et al.* 2023g). Since field data are decidedly scarce, and other data (geolocators, senders) are based on tiny samples of mostly non-passerines originating from affluent countries in Europe (see for example Table S1 in Finch *et al.* 2017), the generality of latitudinal movements as partly shown for Willow and (a single) Wood Warbler is impossible to assess. In any case, present numbers of Palearctic migrants are probably too small to fill the Gap of Chad, but that may have been different in the past when Palearctic migrants were much more common than today.

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SAMENVATTING

Vogels die in Europa broeden en in Afrika overwinteren, steken in een breed front de Middellandse Zee over. Soorten die tijdens de trek van thermiek gebruikmaken (zoals ooievaars en diverse soorten roofvogels), vermijden open water en omzeilen de Middellandse Zee via de west- en oostzijde. Inmiddels is bekend geworden dat ook veel zangvogels voor een trekroute door Spanje of via het Midden-Oosten kiezen. Als gevolg daarvan komen grote aantallen vogels tijdens de herfsttrek terecht in Marokko, in het westen van Afrika, of anders wel 3500 km oostelijker, in Egypte. Daarna moeten ze nog de Sahara oversteken. Als ze dat zouden doen over de kortste afstand, dus van noord naar zuid, zouden verhoudingsgewijs maar weinig trekvogels in het centrale deel van de Sahel terecht komen. Uit de beschikbare studies van vogels die waren uitgerust met een GPS zender of een geolocator blijkt dat veel, maar niet alle, soorten in het westelijke of in het oostelijke deel van Afrika blijven, ofwel in gebieden die in het verlengde liggen van de overheersende zuidelijke trekrichting. Het centrale deel van de sub-Sahara zou dan relatief arm aan trekvogels moeten zijn. Hoe suggestief deze kennelijke concentratie van trekvogels aan weerszijden van Afrika ook is, metingen ter plekke zijn gewenst om te zien of de centrale Sahel (in ruime zin) daadwerkelijk armer is aan Europese trekvogels. Aan de hand van dichtheidstellingen van vogels over de hele breedte van de Sahel is onderzocht of, en zo ja, in hoeverre de centrale Sahel door trekvogels onderbenut wordt. Voor deze analyse werd alleen gekeken naar vogels die zich ophouden in bomen en struiken. Hierbij is het wel nodig de verwachte hoeveelheid vogels, gegeven de verspreiding van hun voorkeursbomen, te bepalen en vervolgens de afwijking tussen verwachte en gevonden verspreiding uit te rekenen. Omdat de getelde vogels per boom apart werden genoteerd, kon per boomsoort worden nagegaan of het kwantitatieve voorkomen van vogels in het centrale deel van de Sahel ijler is dan in het oosten of westen, gecorrigeerd voor de dichtheid van voorkeursbomen. Aan de hand van 12 trekvogelsoorten die foerageren in struiken en bomen, is deze hypothese onderzocht, met vier talrijke en wijdverspreide lokale soorten als controlegroep waarvoor een 'Gat van Tsjaad' niet was te verwachten. Elf van de twaalf soorten trekvogels hadden in de centrale Sahel daadwerkelijk een geringere dichtheid. Bij geen van de lokale soorten was dat het geval. Bergfluiter *Phylloscopus bonelli*, Westelijke Orpheusgrasmus *Curruca hortensis* en Westelijke Baardgrasmus *Curruca iberiae* kwamen het meest voor in het westelijke en (veel) minder in het centrale deel van de Sahel, terwijl de Oostelijke Vale Spotvogel *Iduna pallida*, Oostelijke Orpheusgrasmus *Curruca crassirostris*, Braamsluiper *Curruca curruca* en Rüppells Grasmus *Curruca ruppeli* het meest algemeen waren in de oostelijke, maar minder in de centrale Sahel. Roodkopklauwier *Lanius senator* en Gekraagde Roodstaart *Phoenicurus phoenicurus* waren algemener in het westelijke en oostelijke deel dan in de centrale Sahel. Alleen bij de Grasmus *Curruca communis* werd geen oost-west verschil gevonden in de dichtheid, in overeenstemming met waarnemingen dat Grasmussen, in tegenstelling tot de meeste andere onderzochte soorten, de Middellandse Zee over de volle breedte oversteken. De foerageeromstandigheden in de centrale Sahel – gegeven het voorkomen en de status van preferente boomsoorten – lijken niet slechter te zijn dan in het westen of oosten. De conclusie is gerechtvaardigd dat de centrale Sahel wordt onderbenut door trekvogels. En in het verlengde daarvan dat de Sahel, wat betreft deze vogels, niet 'vol' is. De vraag dringt zich op of er vroeger, toen het aantal trekvogels veel groter was dan nu, misschien geen Gat van Tsjaad is geweest.

RÉSUMÉ

Les oiseaux qui se reproduisent en Europe et hivernent en Afrique traversent la mer Méditerranée sur un large front. Les espèces qui utilisent les ascendances thermiques pendant leur migration, telles les cigognes et de nombreuses espèces de rapaces, évitent les longues traversées maritimes et contournent la Mer Méditerranée par l'Ouest et l'Est. De la même façon, de nombreuses espèces de passereaux choisissent une voie de migration passant par l'Espagne ou par le Moyen-Orient et se retrouvent ainsi à l'automne au Maroc sur la voie occidentale ou

3500 km plus à l'Est, en Égypte, sur la voie orientale. De là, ils doivent traverser le Sahara. S'ils le font selon l'axe Nord-Sud, qui minimise la distance à parcourir, alors peu d'entre eux doivent aboutir dans la partie centrale du Sahel, sauf s'ils se réorientent une fois arrivés. Les études menées sur des oiseaux équipés d'un émetteur GPS ou d'un géolocalisateur montrent que certaines espèces réalisent des mouvements longitudinaux au Sahel, mais que la plupart restent soit dans la partie occidentale, soit dans la partie orientale. D'autres poursuivent leur trajet vers le Sud selon le même axe qu'utilisé lors de la traversée du Sahara. Des inventaires étaient toutefois nécessaires pour confirmer la plus faible abondance de migrateurs européens dans le Sahel central par rapport à ses extrémités ouest et est. Grâce à des comptages systématiques réalisés sur toute la longueur du Sahel, nous avons cherché à vérifier si le Sahel central est sous-utilisé par les migrateurs, et dans quelle mesure. Nous avons déterminé l'abondance des oiseaux arboricoles dans les différentes essences d'arbres et arbustes favorables au Sahel central, puis l'avons comparée avec celle des parties occidentale et orientale. Douze espèces migratrices s'alimentant dans les arbustes et les arbres ont été étudiées, ainsi que quatre espèces africaines témoins, communes et largement répandues pour lesquelles aucune variation d'abondance n'était attendue du fait des axes migratoires. Onze des douze espèces d'oiseaux migrateurs présentaient effectivement des densités plus faibles dans le Sahel central, alors que ce n'était le cas d'aucune des espèces locales. Le Pouillot de Bonelli *Phylloscopus bonelli*, la Fauvette orphée *Curruca hortensis* et les Fauvettes du complexe « passerinette » *Curruca iberiae + subalpina + cantillans* étaient beaucoup plus abondantes dans la partie occidentale que dans la partie centrale, tandis que la Hypolaïs pâle *Iduna pallida*, la Fauvette orphéane *Curruca crassirostris*, la Fauvette babillarde *Curruca curruca* et la Fauvette de Rüppell *Curruca ruppeli* étaient plus communes dans l'Est, que dans la partie centrale. La Pie-grièche à tête rousse *Lanius senator* et le Rougequeue à front blanc *Phoenicurus phoenicurus* étaient plus communs à l'Est et à l'Ouest que dans le Sahel central. Seule la Fauvette grisette Curruca communis présentait une densité sans variation Est-Ouest notable, ce qui est cohérent avec les observations en migration qui montrent que, contrairement à la plupart des autres espèces étudiées, cette espèce traverse la mer Méditerranée sur toute sa longueur. Les ressources alimentaires dans le Sahel central sont semblables à celles des parties occidentales et orientales si l'on se fie à la répartition et à l'abondance des essences d'arbres préférentielles de ces espèces. Le Sahel central semble donc bien être sous-utilisé par les oiseaux migrateurs européens : sa capacité d'accueil n'est pas atteinte. La question de l'existence passée de cette interruption dans la répartition hivernale – le « Trou du Tchad » -, lorsque le nombre d'oiseaux migrateurs était beaucoup plus important, se pose toutefois.

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SUPPLEMENTARY MATERIAL: Gap of Chad in other migrants

Is the Gap of Chad a more widespread phenomenon among migratory birds than revealed by our sub-Saharan surveys? This question might be tackled with the findings from studies which employed geolocators and transmitters to unravel the intricacies of bird migration. The results so far suggest an array of species-specific strategies, ranging from strict site-fidelity (and recurrence in successive years) to itinerancy and every possible variety in between upon reaching the sub-Sahara. Local conditions such as vegetation and climate appear to be the short-term drivers of movement behaviour, these variations being imposed upon the biogeographical legacies from the deep past (Newton 2008). In the Afro-Palearctic migration system, very few tracking studies of passerines were combined with *in situ* research in African wintering quarters, in contrast to the Americas where such studies – including experiments – abound (e.g. Morse 1989, Hagan III & Johnston 1992, Rappole 2022).

Many bird species were found to switch between a succession of two or more wintering sites after having crossed the Sahara, usually in a southward direction and likely triggered by the gradual desiccation of the northern Sahel with a concomitant dwindling of food resources after the last rains have fallen in September:

– European Turtle-doves *Streptopelia turtur* (Eraud *et al.* 2013) remained in the Sahel and were site-faithful in an extremely wet year (2010) but used subsequent wintering sites 150–400 km to the west in a relatively dry year (2009). The birds followed by Schumm *et al.* (2021) used 2 to 4 sites, moving 200–700 km southward and 100–400 to the west or east. One out of four birds remained at a single site for the entire wintering period.

– Montagu's Harriers switched between one and six fixed sites during their stay in the Sahel, undertaking a southward movement in the course of the winter; consecutive sites were on average 229 km (range 10–1434 km) apart (Schlaich *et al.* 2016, Schlaich 2019).

– Sand Martins *Riparia riparia* from eastern Europe spent their full winter period in the surroundings of Lake Chad and the nearby Waza Logone floodplains (Szép *et al.* 2017, Hahn *et al.* 2021).

- Red-rumped Swallows *Cecropis daurica* wintered between 7 and 15°N and used there, probably depending on rainfall, one or more sites (Wong *et al.* 2022).
- Eurasian Reed Warblers from the western flyway remained in western Africa west of 5°W, but birds from the eastern flyway all remained east of 15°E (Adamík *et al.* 2016: see also Procházka *et al.* (2017) for an extensive analysis of the migration of this species).
- Great Reed Warblers *Acrocephalus arundinaceus* (Hedenström *et al.* 1993, Lemke *et al.* 2013) used two consecutive wintering sites south of the Sahara at 235–1352 km from the initial refuelling stopover in West Africa, with a high repeatability in stopover and wintering sites (at least for males; Hasselquist *et al.* 2017).
- European Pied Flycatchers often stayed around six months at the same site, with at most short-distance habitat-related shifts in the second part of their stay (Salewski *et al.* 2002, Ouwehand *et al.* 2015, Ouwehand & Both 2017). A (large?) proportion of the birds spend some weeks in the *Acacia* belt early October in the northern Sahel, 400–500 km north of their wintering quarters (Zwarts *et al.* 2023f).
- Northern Wheatear *Oenanthe oenanthe* in the western Sahel remained near the southern edge of the Sahara until late December, then moved c. 200 km southward (Arlt *et al.* 2015; see also Schmaljohann *et al.* 2012), although the tendency to move southward is almost absent in wet years (Zwarts *et al.* 2023f).
- Tawny Pipits *Anthus campestris* moved c. 400 km SW (five birds; Briedis *et al.* 2016), at least in a relatively dry year and possibly not in wet years (Zwarts *et al.* 2023f).
- Ortolan Buntings *Emberiza hortulana* from NW Europe remained the entire wintering period in West Africa at about 10°W and congeners from Ukraine in Ethiopia occurred at 40°E where the individual birds used different wintering sites, but all sites were situated along the same longitude (Jiguet *et al.* 2019).

Other species spend the northern winter south of the Sahel but use the Sahel zone as temporary staging area. In the course of autumn/winter, they continue their southbound flight to wintering areas in tropical Africa, without diverging to the west or the east:

- European Nightjar *Caprimulgus europaeus* (Evens *et al.* 2017, Norevik *et al.* 2017).
- Great Snipe *Gallinago media* (Lindström *et al.* 2015).
- European Roller *Coracias garrulus* (Emmenegger *et al.* 2014, Rodríguez-Ruiz *et al.* 2014, Finch *et al.* 2015).
- European Bee-eater *Merops apiaster* (Hahn *et al.* 2020).
- Common House Martin *Delichon urbicum* (Szép *et al.* 2017).
- Willow Warbler from Siberia passing through Sudan (Sokolovskis *et al.* 2018).
- Icterine Warbler *Hippolais icterina* (van Noorden *et al.* 2022).
- Thrush Nightingale *Luscinia luscinia* (Stach *et al.* 2012).
- Common Nightingale (Hahn *et al.* 2014).
- Semicollared Flycatcher *Ficedula semitorquata* (Briedis *et al.* 2016).
- Collared Flycatcher *Ficedula albicollis* (Adamík *et al.* 2016).
- Whinchat *Saxicola rubetra* (Blackburn *et al.* 2019).
- Cyprus Wheatear *Oenanthe cypriaca* (Xenophontos *et al.* 2017).

Another strategy is employed by migratory species that, upon reaching sub-Saharan West Africa on a southerly heading during outward migration, make a sharp *Zugknick* (directional shift) before continuing their journey (e.g. Gatter 1987):

- Honey Buzzards *Pernis apivorus* wintering in West Africa cross the Sahara and Sahel from Gibraltar head southwards on a 5°W longitude heading. Birds eventually wintering between 0 and 10°E (Ghana to eastern Nigeria) change to an eastward heading just north of the Gulf of Guinea (Vansteelant *et al.* 2016).
- European Rollers wintering in SW Africa use a stopover site in the eastern Sahel, but Rollers arriving in West Africa use several stopovers to cover the flight of 1500–3000 km to the east before continuing southwards (Emmenegger *et al.* 2014, Catry *et al.* 2014).
- British Common Cuckoos used flyways that resulted in crossings of the Mediterranean and Sahara either via Iberia/West Africa or Italy/central Sahel. The latter birds used prolonged stopovers in the southern Sahel before commencing migration southwards. The birds in West Africa made a directional shift upon reaching the southern Sahel, then flew another 3000 km to the east (Hewson *et al.* 2016). Birds from Sweden followed a similar strategy, but via the eastern Sahel (where prolonged stopovers were recorded) and then made a westward change of direction before their return to the breeding areas (Willemoes *et al.* 2014).
- Pallid Swift *Apus pallidus* from Gibraltar spent two months in the western Sahel (about 17°N) and wintered more than 700 km further south, but those that spent the winter in the Congo Basin had also moved 2500 km eastwards (Finlayson *et al.* 2021).
- Common Swifts *Apus apus* moved eastwards south of the Sahara before they continued their migration to the wintering area in the Congo Basin (Åkesson *et al.* 2012).

Seasonal shifts in habitat choice of birds in the Sahel and the importance of 'refuge trees' for surviving the dry season

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Every year, hundreds of millions of migratory birds cross the Sahara to spend the northern winter in the Sahel. After their arrival in September the region does not receive any rainfall until June while temperatures increase. Birds inhabiting the Sahel have several strategies to cope with this seasonal advent of drought. Most ground-foraging and arboreal migrants actually remain in the desiccating Sahel, although Northern Wheatear *Oenanthe oenanthe* remains in the arid zone only in a wet year, but moves from the arid to the semi-arid zone in a dry year. Some arboreal migrants stay for 1–2 months in the Sahel during the early dry season, but move on to the more humid zone further south for the rest of the northern winter. Common Redstart *Phoenicurus phoenicurus* is the only Sahelian arboreal migrant that moves southward in this period. Counter-intuitively, *Curruca* species move northward after the early dry season to the arid zone where they concentrate in woody plant species whose attractiveness increases later in the dry season. This is either because those plants then gain berries (Toothbrush Tree *Salvadora persica*) or because they develop flowers (six desert species). In the semi-arid zone, tree-dwelling bird species disappear from tree species when these lose their leaves. However, in tree species which do not shed their leaves, bird numbers remain either constant (those using Desert Date *Balanites aegyptiaca*) or increase (those using Winter Thorn *Faidherbia albida*, a tree that foliates during the dry season). On floodplains bird numbers in acacia trees increase during the dry season. As a consequence, birds become concentrated in fewer tree and shrub species during their stay in the Sahel. After wet rainy seasons, trees have more flowers and leaves and shed them later, giving the birds more foraging space. At the end of their stay in Africa after dry rainy seasons, the number of arboreal birds is only half that after wet rainy seasons, suggesting higher mortality in dry years. Clearly, in such years mortality would be even higher without what can be seen as 'refuge trees': the acacias on floodplains, and *Faidherbia* and to a lesser degree *Balanites* in the rest of the Sahel.

Key words: Sahel, migratory birds, tree selection

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In September, when the migratory birds from Europe and Asia arrive in the Sahel, the rainy season is nearly over. The vegetation is still green and the trees are full of leaves, but during the following eight-month long dry period the grass withers and many woody species lose their leaves (Photo 1; Hiernaux *et al.* 1994), and so the prospects for birds would seem bleak (Moreau 1972). His suggestion that living conditions for the migrants progressively deteriorate upon arrival was rectified by Morel (1973), who pointed out that birds might respond to subtle seasonal variations in food availability, for instance by switching between tree species with different flowering regimes. The migratory birds profit from nectar and insects associated with the variety of tree species in the Sahel. Furthermore, as already shown by Ward (1965), foraging conditions for granivorous birds improve only at the onset of the dry season as ripe grass seeds are shed. It is noteworthy then, after these first observations and inferences of half a century ago, that the study of how migratory birds in the Sahel cope with their desiccating winter habitat has shown some progress but many burning questions are still unresolved (Salewski & Jones 2006).

For the birds in the Sahel there are six main sources of food during the long dry season: (1) seeds and (2) insects on the ground, (3) insects, (4) fruit and (5) nectar in woody vegetation, and (6) insects in the air. This aligns with the six main foraging guilds that can be distinguished: granivorous or insectivorous ground-foraging birds, insectivorous, frugivorous or nectarivorous arboreal birds, and aerial insectivorous birds. Each foraging guild requires a different research approach to help understand not only how birds survive the dry season in the Sahel, but also how migrants are able to fatten up sufficiently prior to the return to the breeding grounds.

Many woody plants in the Sahel shed their leaves during the dry season, whilst in some other species the retained leaves wither (Poupon 1979), circumstances likely giving rise to negative effects on food supplies exploited by insectivorous tree-dwelling birds, especially foliage-gleaners (Holmes & Robinson 1981). During and just after the rainy season, insects on leaves of many tree species were up to 25 times more numerous than in the dry season (Morel 1968), except for Winter Thorn *Faidherbia albida* which are leafless in the rainy season (Stoate 1998). Treron (2010), using a mild insecticide, bimonthly collected, identified and counted all insects in three tree species in Namibia. Two of her study species, *Faidherbia albida* and Umbrella Thorn *Acacia tortilis*, are actually the most important trees for migratory birds in the Sahel (Zwarts *et al.* 2023c). In relatively small trees (c. 10 m^2 of canopy surface), she recorded on average 8924 insects per *Faidherbia* and 4555 insects per *A. tortilis*. Insect density was higher during and just after the rainy season and declined during the dry season. Apart from the early studies by Morel (1968) and Stoate (1998), this type of systematic data are still not available for the Sahel, a lament already articulated in 1973 by Elgood *et al.*: "But information on the seasonal abundance of diurnal insects and on their availability to predators in the tropics is almost entirely wanting." On the other hand, much better field data are nowadays available on the phenology of leafing, flowering and fruiting of woody species (Poupon 1979, de Bie *et al.* 1988, Hiernaux *et al.* 1994, Mahamane *et al.* 2007). This information may help us to understand why birds are so selective of, and switch between, woody plants during the course of the season.

The central question in the present study is: do foraging conditions deteriorate after the migratory birds have arrived in the Sahel and, if so, how do the birds adjust to declining food availability? We attempt to answer six specific questions:

(1) Do migratory bird species wintering in the Sahel move to the more humid southern parts to escape the northern drought, and are such moves species-specific?

(2) Is there a seasonal variation in the selection of woody species by tree-dwelling birds and can these switches be explained by tree phenology of the preferred woody species (leaves, flowers, fruit, abundance of insects)?

(3) Does tree preference differ between the European bird species that remain in the Sahel between September and March and the migratory species that migrate through the area in September–October to regions further south?

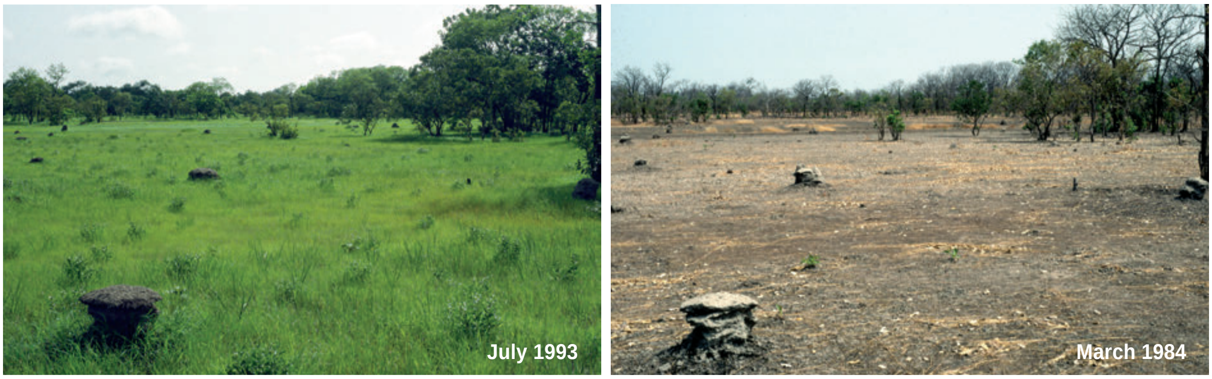


Photo 1. Pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in SE Senegal (13.2°N, 13.1°W; average annual rainfall 890 mm) during the wet and dry season.

(4) Is the seasonal shift in tree choice different for floodplains and drylands?

(5) Is the seasonal shift in tree choice different in dry and wet years?

(6) To what degree do trees which function as a 'refuge' for the birds at the end of the dry season, and especially during dry years, alleviate drought-related mortality?

METHODS

We refer to Zwarts & Bijlsma (2015) for an extensive description of our methods in the field, i.e. counting birds separately per woody plant, and how we measured the canopy surface of woody plants, determined absolute bird density per ha of canopy surface for all woody species, estimated foliage volume for individual trees ('opacity score'), determined food supply of moths in *Faidherbia* trees and registered prey taken by arboreal birds. To describe how the selection of rainfall zone and woody species by birds varies seasonally, we used our counts of birds and woody plants in Africa between 7 and 22°N, as described in Zwarts *et al.* (2023a,b). We used two types of data: systematic random counts in study sites of (mostly) 4.5 ha each and counts of birds in trees in non-random sites. Random counts were used to assess average density per ha, but to calculate average bird density per ha of canopy in different woody species, we used all data available. Field data collected early in the dry season (26 September – 19 November), and not used in the analysis of the dry season distributions (Zwarts *et al.* 2023a,b), were included in the present analysis.

In a strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a wider sense as the transition zone between Sahara in the north and the humid forests in the south. For each study site, we selected per woody species the study sites where they occurred to calculate the average annual rainfall in the distribution area of each tree and shrub species (period 1950–2000, based on Hijmans *et al.* 2005). During our surveys rainfall did not deviate much from the long-term average, except for 2010 (exceptionally high rainfall) and 2014 (relatively dry; see Supplementary Material 4 in Zwarts *et al.* 2023a). In these years, we visited the same sites, or sites nearby, in NW Senegal and SW Mauritania (13.73–16.98°W and 13.65–18.00°N): 114 sites between 21 January and 16 February 2011 and 146 sites between 9 December and 3 March 2015. Rainfall, measured at 7 meteorological stations in North Senegal at 16°N, averaged 601 mm in 2010, i.e. 64% above the long-term average (366 mm/year) and just below the highest annual rainfall ever measured (637 mm in 1933). In contrast, 2014 was dry with 261 mm rain, 29% below the long-term average, but not nearly as dry as the driest year recorded (1982 with 142 mm per year being 61% below the long-term average; Figure 6 in Zwarts *et al.* 2018).

The seasonal variation in bird densities is described for western Senegal where we conducted four series of counts between 26 September and 26 February, mostly in the same sites (26 September – 5 October 2019, 6–17 October 2019, 18 October – 3 November 2015 and between 4 January and 26 February in 2011, 2014 and 2017). The selected area is situated between 13.8 and 16.6°N and west of 15.3°W, with average annual rainfall varying between 229 and 648 mm (see map in Figure 2). We analysed seasonal variation in bird density in seven bird-rich woody species in relation to their phenology (flowers, fruit, foliage). Bird phenology should ideally be studied within the same region, but our limited dataset for September–December requires us to use the entire dataset from various regions despite the longitudinal variation in bird density (Zwarts *et al.* 2023d). We have sufficient data for Egyptian and Umbrella Acacia *Acacia nilotica* and *A. tortilis*, Desert Date *Balanites aegyptiaca* and *Faidherbia albida*, to limit the analyses of seasonal shifts in tree choice to just West Africa (17–0°W). By focussing on West Africa we can circumvent the problems caused by longitudinal variation in bird density (Zwarts *et al.* 2023d). *A. tortilis* (average annual rainfall 328 mm within distribution range) occupies drier habitat than *Balanites* (445 mm), *Faidherbia* (519 mm) and *A. nilotica* (537 mm).

Note that although Subalpine Warbler *Curruca cantillans* has recently been split into three species (Zuccon *et al.* 2020), we here maintained the lumped name for the combination of Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans*.

RESULTS

Seasonal shift in selection of rainfall zone

Of the Palearctic species recorded in the western Sahel, six used the region temporarily whilst heading for wintering sites to the south, mainly during October ('leavers'; Figure 1A). By November the great majority of these transients had left the arid and semi-arid zone. Ten more species started arriving in September, gradually building up in numbers throughout the northern

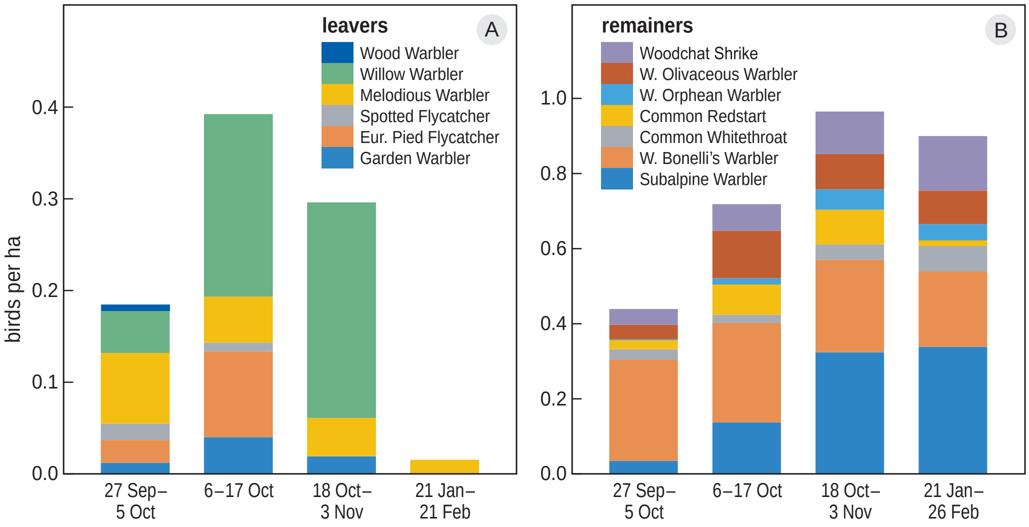


Figure 1. Bird density (*n* per ha) of migratory species in West Senegal between 13.8 and 16.6°N which (A) leave the region in the second half of October or in November to spend the rest of the northern winter further south, and (B) are stationary during their stay in Africa (remainers). Counts grouped in four periods (see text). The average densities are based on counts performed in sites shown on the map in Figure 2.

winter but staying within the same arid and semi-arid region ('remainers'; Figure 1B). The Sahel is their wintering area, where at most small-scale displacements occur during the rest of their stay in Africa.

Of the ten migrants remaining in the Sahel, most showed a (slight) shift towards the south in January/February, as compared to the distribution in the previous three months (Figure 2). The shift was absent for Tawny Pipit *Anthus campestris* and barely noticeable for Woodchat Shrike *Lanius senator* and Western Bonelli's Warbler *Phylloscopus bonelli*. Northern Wheatears *Oenanthe oenanthe* in the Western Sahel ranged between 13 and 18°N (annual rainfall 100–700 mm). Within Senegal, the latitudinal distribution shifted by

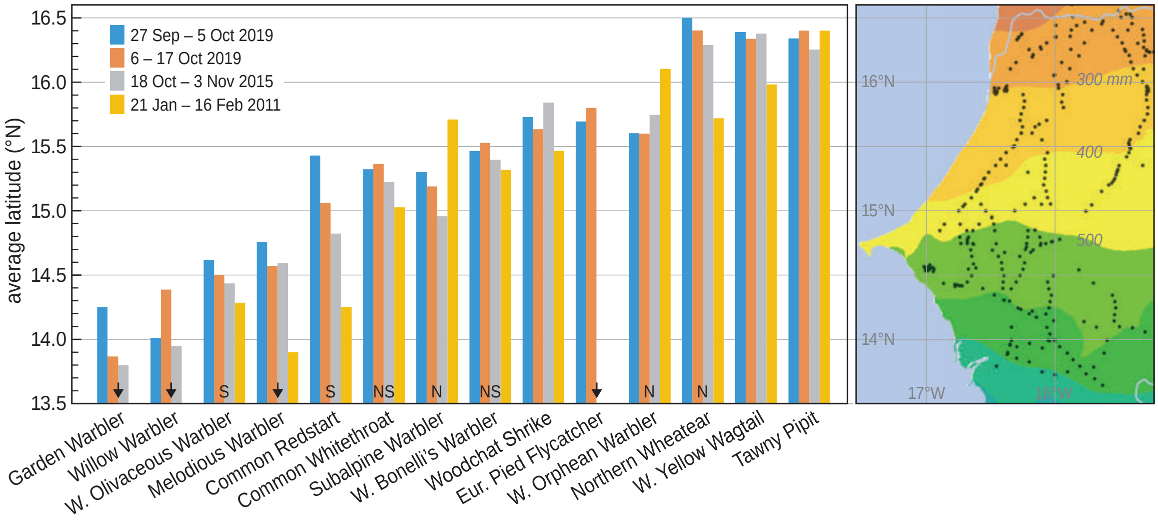


Figure 2. Seasonal shift in the distribution of migrants in West Senegal between 13.8 and 16.6°N. The map shows study sites and average annual rainfall within the 200–700 mm isohyets. Four species leave the area in October or November to more humid wintering areas (↓). Three species (marked N) occur in relatively large numbers in western Africa north of 16.6°, two species (marked S) ditto south of 13.8°N and two species (marked NS) north as well as south of the outlined region; based on Figures S13, S27, S41 and S42 in Zwarts *et al.* (2023a) and on Figures S10, S15, S21, S24, S25 and S28 in Zwarts *et al.* (2023b).

an average of 99 km southwards between October and February (Figure 2). Simultaneously numbers increased from 0.024/ha in October to 0.082/ha in January–February. Melodious Warbler *Hippolais polyglotta* (97 km) also shifted southwards, as expected given its wintering sites to the south of the Sudano-Sahelian vegetation zone. In January/February, Western Orphean Warbler *Curruca hortensis* and Subalpine Warbler were the only species that were, on average, found further to the north than in previous months.

Seasonal shift in tree selection

Willow Warblers *Phylloscopus trochilus* temporarily present in the Sahel in October were abundant in African Birch *Anogeissus leiocarpus*, a common tree in the region but scarcely visited by tree-dwelling birds later on in the dry season when the leaves are shed (Zwarts *et al.* 2023c). However, most common woody species not visited by migratory birds in November–March were also ignored in September–November, among which were very common species like Cashew *Anacardium occidentale* and the shrub *Guiera senegalensis*. Several other woody species preferred in December–March were used much less often in September–November (Figure 3). When a selection was made for bird species remaining in the Sahel, their densities in 28 woody species before and after 20 November were found to be highly correlated ($r = +0.61$, $P < 0.001$). In 19 of the 28 woody species, total bird density per ha of canopy was lower before than after 20 November. Before 20 November transient migrants ('leavers') selected woody species other than those chosen by the 'remainer' migrants. On average, leavers selected woody species that were typical for the region with 500 to 900 mm rain per year, European Pied Flycatcher *Ficedula hypoleuca* and Spotted Flycatcher *Muscicapa striata* being present mainly in *Acacia tortilis* and *A. nilotica* and three warblers (Willow Warbler, Wood Warbler *Phylloscopus sibilatrix* and Melodious Warbler *Hippolais polyglotta*) mainly in *Faidherbia*, Cayor Pear Tree *Cordyla pinnata*, Tamarind *Tamarindus indica* and *Anogeissus leiocarpus*.

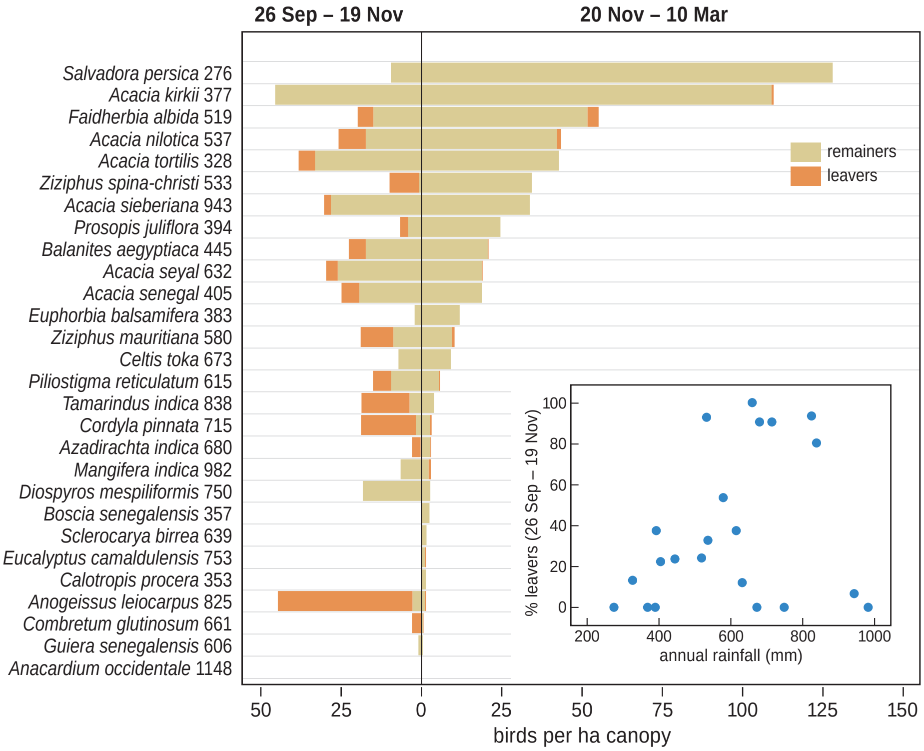


Figure 3. Average density of migratory birds per ha of canopy before and after 20 November in 28 woody species, for birds remaining the full season in the Sahel (remainers, in yellow) and those leaving the region before late November (leavers, in orange). The average densities refer to woody species from western Africa (17–0°W) where bird densities were measured in >1000 m2 of canopy surface. The average annual rainfall per distributional range of woody species is given next to the name. Inset shows the fraction of leavers in 28 woody species as a function of the annual rainfall in the distribution area of the woody species (same data as the bars in main figure).

Woody plants of the arid zone

In this section we analyse for the arid zone whether there is a seasonal shift in how birds use trees and shrubs. In the arid zone (annual rainfall <400 mm), seven of 13 woody species attracted many migrants (>20/ha canopy), three of which attracted up to 75–111 migrants/ha of canopy (Figure 3 in Zwarts *et al.* 2023c). In contrast, three common woody plants from the arid zone were rarely visited by migrants: *Leptadenia pyrotechnica* (2.3 migrants/ha canopy), Sodom Apple *Calotropis procera* (1.0/ha canopy) and *Boscia senegalensis* (2.5/ha canopy).

Toothbrush Tree *Salvadora persica* attracted many birds when ripe berries were available (Figure 4A). It was mostly devoid of birds before November, but from then on, bird density steadily increased to a maximum in March. *Salvadora* has become relatively rare in the Sahel, except in the brackish zone around the Senegal Delta and locally on slightly brackish soils in Chad. In NE Nigeria *Salvadora* formed a dense belt to a height of 4 m on the first dune ridge from the shore of Lake Chad near Malamfatori (Fry *et al.* 1970). Where still present in the arid zone (average annual rainfall 276 mm), *Salvadora* offers birds, especially *Curruca* species, an important food resource in February and March. In the arid zone just south of the Sahara arboreal residents were scarce (see Figure 8 in Zwarts *et al.* 20202b) unless *Salvadora* was present. *Salvadora* shrubs without fruit had, on average, 24 migrants/ha of canopy and 43 residents/ha, while shrubs with fruit held 122 migrants and 148 residents/ha of canopy. The food found in gizzards of 85 Common Whitethroats *Curruca communis* collected in March–April 1967 from the *Salvadora* zone along the western shore of Lake Chad comprised 80% fruits and flowers of *Salvadora*, but also 7800 midgets and other insects (Fry *et al.* 1970). Blue-naped Mousebird *Urocolius macrourus* was the most common resident, irrespective of the presence of berries, and Purple Starling *Lamprotornis purpureus*, Sudan Golden Sparrow *Passer luteus* and Little Weaver *Ploceus luteolus* showed up when ripe berries were available. When in flower, the shrubs were visited by sunbirds. Berries of *Salvadora* ripen asynchronously and were already eaten when partially ripe; competition for berries must be stiff given the continuous and immediate depletion of ripening berries.

A deciduous bushy shrub from the arid zone, Sodad *Capparis decidua*, attracts many migratory birds (Moreau 1972); it occurs where the average annual rainfall is 305 mm (Figure 3 in Zwarts *et al.* 2023c). In the western Sahel it was rather scarce but it was much commoner in Chad and Sudan. In the second part of the dry season Sodad shrubs start to renew their leaves (Nazar *et al.* 2020), at first visible only as minute leaves on young shoots during our surveys in January and February, when respectively 96% and 79% of shrubs showed at least some leaves. The fraction of flowering shrubs remained the same in January and February (48%), i.e. several months after the rainy season. *Capparis* was largely the domain of *Curruca* warblers, with a small scattering of resident species. Bushes with leaves had higher densities than bushes without leaves (Figure 5A) and, especially when flowering, *Capparis* was visited by large numbers of arboreal migrants and residents (Figure 5B).

Salam Tree *Acacia ehrenbergiana* occurred in the arid zone (average rainfall for all trees in our sites was 203 mm) and attracted many birds when in leaf and

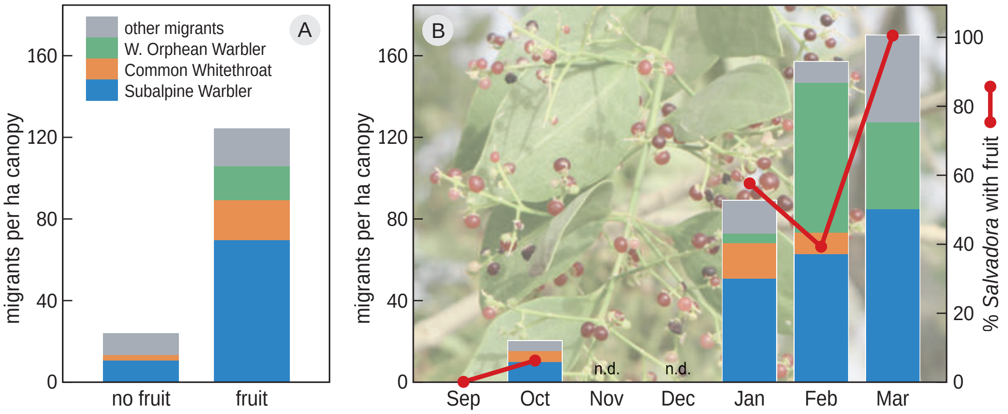


Figure 4. (A) Average bird density of migratory species per ha canopy in *Salvadora persica* with and without berries, based on measurements from late September to mid-March (1585 shrubs with a total canopy surface of 10,338 m^2). (B) Average bird density per ha canopy and the fraction of shrubs bearing fruit per month; n.d. = no data. *Salvadora* are also visited by Afro-tropical birds (see text).

especially when flowering (Figure 6A). Only then do sunbirds favour this tree, but migrants were also much attracted to its flowers (Figure 6B). We found tremendous spatial variation in whether or not trees of this species had leaves or flowers, often within just thousands of square metres: dozens of trees vividly green and full of flowers at one spot stood in stark contrast with nearby groups of living trees that looked dead. In February, twice as many trees were in flower as in January (and even more trees were in leaf). The higher numbers of migrants and sunbirds recorded in *A. ehrenbergiana* in February, though, may be coincidence considering the large spatial, but not necessarily seasonal, variation in tree phenology. Since *A. ehrenbergiana* continues to flower during the dry season and retains much of its leaves throughout winter (Hiernaux *et al.* 1994), it is an attractive tree for birds until at least March (Salewski *et al.* 2006).

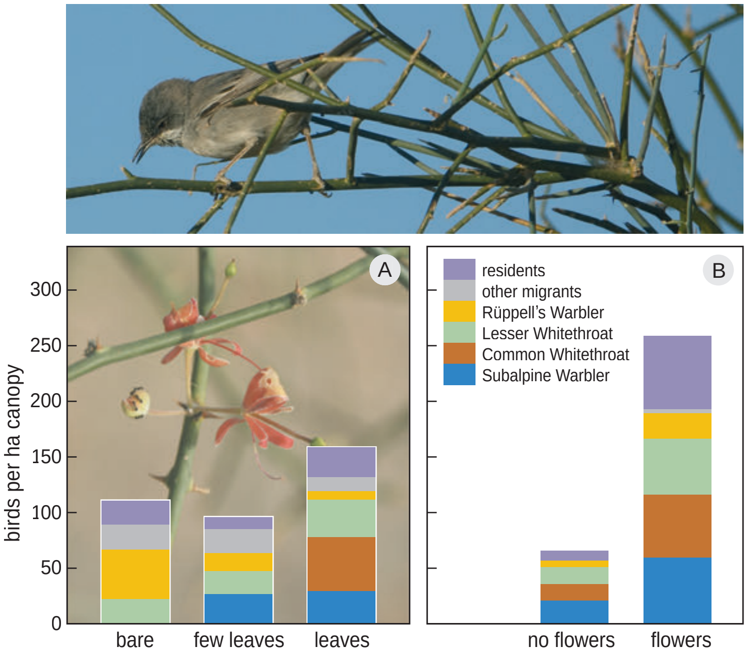


Figure 5. Average bird densities per ha of canopy in *Capparis decidua* (A) with no, few or average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), and (B) with and without flowers (dry season). Average values based on 1454 shrubs with a total canopy surface of 10,232 m^2. Photo shows Rüppell's Warbler *Curruca ruppeli* in a *Capparis* shrub with budding leaves, Sudan, 11 January 2019.

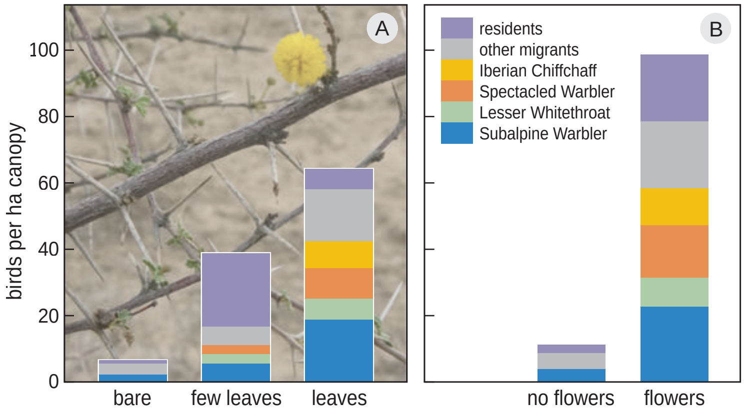


Figure 6. Average bird density per ha canopy in *Acacia ehrenbergiana* (A) with no, few or average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), (B) without and with flowers. Average values based on 3593 woody plants with a total canopy surface of 20,230 m^2.

Balsam Spurge *Euphorbia balsamifera* is often planted in hedgerows around fields (average rainfall for all bushes in our sites was 383 mm). It flowers in the dry season after the leaves are shed (Poupon 1979, Hiernaux *et al.* 1994). In September and October none of the plants was found in flower but in January 29% were flowering. Those shrubs that were still green in September and October contained very few birds, but in December–February we recorded a high density mainly of *Curruca* species (Figure 7), many birds feeding on nectar and on insects that were visiting the flowers.

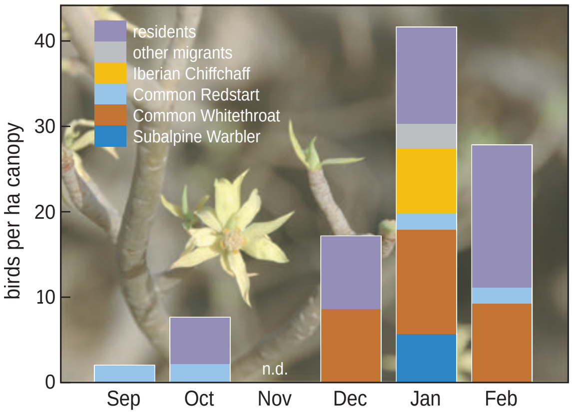


Figure 7. Average bird density per ha canopy in *Euphorbia balsamifera* from September to February; n.d. = no data. Canopy surface measured: 41,541 m^2.

The four woody species mentioned above all attracted increasingly larger numbers of birds in the course of the dry season. Other tree and shrub species from the arid zone that were also highly attractive to birds in the latter part of the dry season included *Maerua crassifolia*, *Acacia etbaica* and *Tamarix senegalensis*. *Maerua crassifolia* is a deciduous evergreen that flowers in both dry and rainy seasons (Arbonnier 2009). In Chad and Sudan, 86% of the trees were in flower in January. Flowering trees had a high bird density of 282/ha of canopy: in Sudan the commonest two bird species were Rüppell's Warbler *Curruca ruppeli* (98/ha of canopy) and Nile Valley Sunbird *Hedydipna metallica* (124/ha of canopy). For all *Maerua* (flowering, non-flowering and unknown), the density was 71 migrants/ha and 41 sunbirds/ha (total measured canopy surface 5609 m^2 of 1657 shrubs).

Acacia etbaica is a small tree species from the hyper-arid eastern Sahel (88 mm rain/year). Most trees still had leaves in January–February. Birds were absent in leafless shrubs, which comprised 18% of the total, compared to 57 migrants/ha of canopy in shrubs with but a few leaves and 156/ha of canopy in shrubs in leaf (503 shrubs; total canopy surface 4062 m^2). All visitors were *Curruca* species, but mainly Rüppell's Warbler and Lesser Whitethroat *Curruca curruca*. Flowering shrubs (26%) were visited by twice as many birds as shrubs without flowers (74%).

Finally, the Tamarisk *Tamarix senegalensis* flowers in the second half of the dry season. The species grows on brackish soils and is common in the Senegal Delta. We measured bird densities in January and in March but made no notes on flowering and presence of leaves (2486 shrubs, 5159 m^2 of canopy). We recorded 35 migrants/ha of canopy in January (17 Subalpine, 9 Common Whitethroat and 9 Iberian Chiffchaff *Phylloscopus ibericus* per ha of canopy) and in March recorded 22 birds/ha of canopy (7 Subalpine Warbler, 4 Common Whitethroat, 7 Iberian Chiffchaff and 4 Yellow-bellied Eremomela *Eremomela icteropygialis* per ha of canopy).

Woody plants of the semi-arid and sub-humid zone

The previous section showed that seven woody species from the arid zone became more attractive to birds in the course of the dry season. A completely different picture emerges from woody plants in the more humid zone, which flower or shed their leaves early in the dry season.

African Birch *Anogeissus leiocarpus* (4788 trees and 224,295 m^2 of canopy) flowers mainly in October–December, when trees start to shed their leaves (Mahamane *et al.* 2007). In October, 72% of the trees were recorded in blossom and all were still fully leafed. In December–March 4% of the trees had leaves, 14% had some leaves and 82% were bare. When in flower, *Anogeissus* attracted many Willow Warblers (36/ha of canopy) and Melodious Warblers (11/ha). In October, *Anogeissus* also attracted European Pied Flycatcher (6/ha) and Western Olivaceous Warbler (10/ha), irrespective of flowering (Figure 8). Birds avoided *Anogeissus* trees in December–March when these lacked flowers and occasionally visited those with some leaves (0.3 migrants/ha of canopy and 3.6 residents/ha); the abundantly available dry fruit was not eaten by birds.

Tamarind usually flowers at the end of the dry season, in April–May (Arbonnier 2019). In our survey, 20% of the trees still had some flowers in September–October but none in November–February. All trees were fully in leaf in September–December. The proportion of bare trees increased from 5% in January to 31% in February. Flowering trees were very attractive (in October 117 birds/ha of canopy, among which Willow and Melodious Warbler were the most common with 27

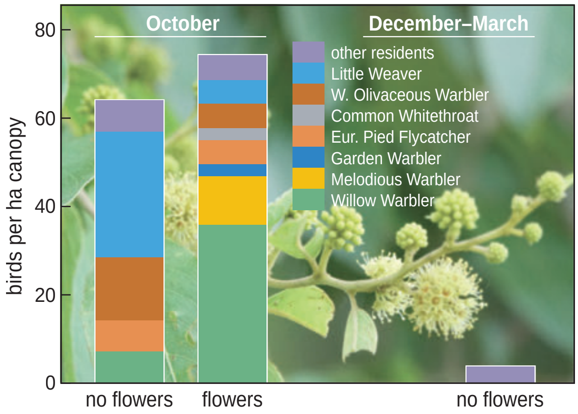


Figure 8. Average bird density per ha of canopy in *Anogeissus leiocarpus* with and without flowers in October and in December–March (always without flowers); 4788 trees measured with a total canopy surface of 224,295 m^2.

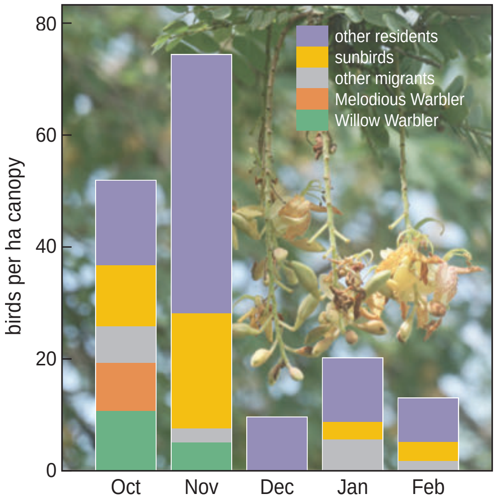


Figure 9. Seasonal variation in average bird density per ha canopy in *Tamarindus indica*; 1181 trees, total canopy surface 76,062 m^2.

and 21 birds/ha respectively). In non-flowering trees, 11 birds/ha, mainly residents, were recorded. Flowering trees were visited by many sunbirds. From December onwards few birds, mainly residents, visited this tree species (Senegal Eremomela *Eremomela pusilla*, Tawny-flanked Prinia *Prinia subflava*; Figure 9).

The Arabic Gum Tree *Acacia senegal* flowers before the first rains and sometimes at the end of the rainy season (Arbonnier 2019), thus in June–October. According to our surveys, 38% were still in flower in October, declining to 15% in January–February. Trees were fully in leaf after the rainy season, with 9% bare trees in October–December and 56% in January–February (see also Hiernaux *et al.* 1994). This tree was attractive to many bird species, among which were relatively many sunbirds and other residents, but only when leafed (Figure 10A). The presence of flowers was by far the most important attractant (Figure 10B). Not many birds remained after Gum Trees had shed their leaves in December (Figure 10C). As in *A. ehrenbergiana*, the spatial variation regarding the occurrence of green and flowering trees was large, but the overall trend was obvious: *A. senegal* attracted many birds in the early dry season after which there was a decline.

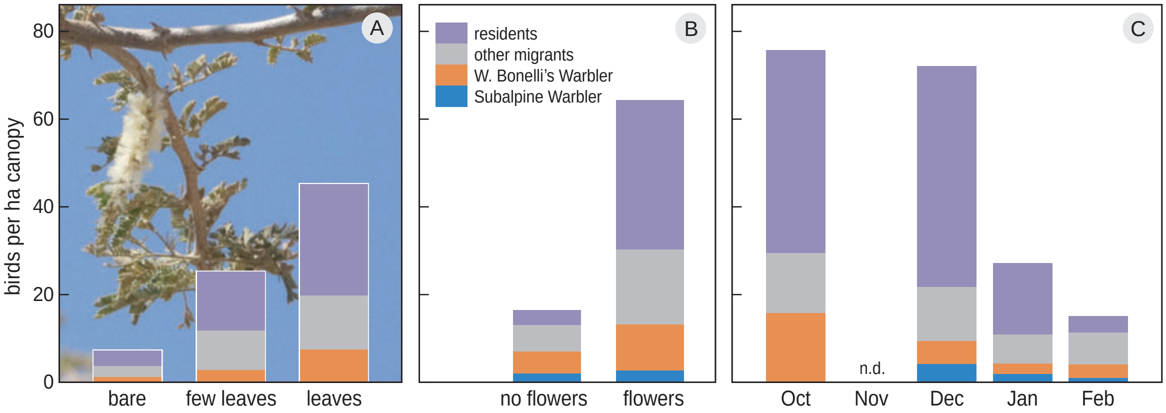


Figure 10. Average bird density of migratory species per ha of canopy in *Acacia senegal* (A) with no, few or an average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), (B) with and without flowers and (C) between October and February. Average values based on 16,350 shrubs and trees with a total canopy surface of 84,176 m^2. n.d. = no data.

Bauhinia rufescens was fully in leaf after the rainy season and gradually lost its foliage during the dry season (in February 29% were bare). It is known to flower all year round, but more trees were in blossom in the early dry season than later in the dry season. The density of migrants (mainly Subalpine Warbler and Common Whitethroat) declined from 40/ha of canopy in December to 13/ha in January and 7/ha in February; for the same three months the density of residents declined from 31 to 20 and 14 birds per ha of canopy (insufficient data from September–November to show bird densities; in total 7304 m^2 of canopy were measured for 1324 woody plants).

African Myrrh *Commiphora africana* is leafless from November onwards (Hiernaux *et al.* 1994). When leafless, *Commiphora* were visited by small numbers of migrants (4.6/ha of canopy; only Subalpine Warbler and Common Whitethroat) and residents such as Cricket Warbler *Spiloptila clamans* (9/ha) and Rufous-tailed Scrub Robin *Cercotrichas galactotes* (3/ha); these averages are based on 4318 m^2 of canopy surface and 1402 shrubs.

Of the tree species specifically mentioned, *Anogeissus* and *Tamarindus* both grow in the sub-humid zone (825 and 838 mm rainfall/year on average, respectively; Figure 3 in Zwarts *et al.* 2023c), south of the zone where most arboreal migrants spend the northern winter (Figure 8 in Zwarts *et al.* 2023b). In October and November, fully leafed and flowering *Anogeissus* and *Tamarindus* attracted transient migrants that are wintering in the south of the Guinean zone (Figure 8 and 9). Similarly, another early flowering species from the same rainfall zone, *Cordyla pinnata* (715 mm rain/year on average) attracted many Willow Warblers (17.1/ha of canopy) and Little Weavers (10.3/ha of canopy) in September–November (266 trees and 5843 m^2). *Acacia senegal*, *Bauhinia rufescens* and *Commiphora africana* are semi-arid species that show declining bird densities during the dry season (average annual rainfall for the sites where the three

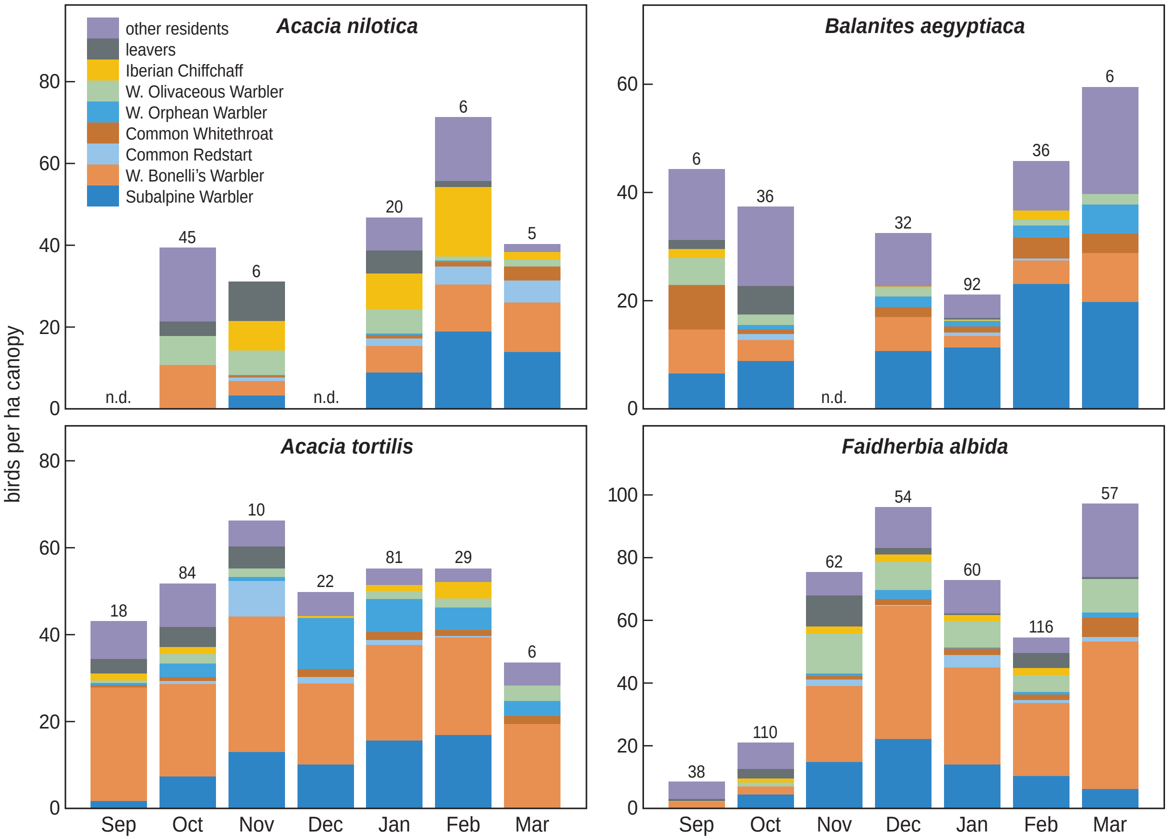


Figure 11. Monthly variation in the average density per ha of canopy in four bird-rich and common woody species. A selection is made for trees from western Africa (17–0°W). Leavers are migrants wintering south of the Sahel but still present in the most southerly trees in the Sahel during the dry season. Numbers above bars indicate total canopy area of surveyed trees (× 1000 m^2); n.d. = no data (i.e. <300 m^2 investigated).

species were found was 405, 503 and 529 mm, respectively). Such declines in bird density are typical of many other woody species, of which most are either scarce or attract so few birds that their impact on the total number of arboreal birds present in the Sahel is negligible.

Photo 2. The coastal rice fields of the Casamance, Senegal, can be thoroughly green in the late wet season, here on 21 September 2007, but *Faidherbia* trees are still bare then and most will not leaf until early November.

Common and bird-rich trees in the semi-arid zone

For the seven most common migrants, densities in four woody species fluctuated in synchrony with tree phenology (Figure 11). *Acacia nilotica* remained in leaf until at least March. The species flowered in the early dry season (97% in flower in October, 76% in November), declining to 40% in January–February. All migrant species foraged in flowering trees in October–November. *A. nilotica* was found mostly in areas that flooded in the rainy season. 49% of the trees were still flooded in October–November, declining to a few percent in March. There were fewer Subalpine Warblers in flooded trees than in unflooded trees in October–November (7.7 and 11.7 birds/ha of canopy, respectively), as was also the case for Western Bonelli's Warbler (3.5 in flooded and 5.0 birds/ha of canopy in unflooded trees). However, Iberian Chiffchaff (11.0 and 4.2 birds/ha) and Willow Warbler (8.6 and 1.7 birds/ha of canopy) were more abundant in *A. nilotica* in areas which remained flooded (average densities are based on 20,996 m^2 of canopy and 1666 trees, all measured in October and November in Senegal or Mali). Iberian Chiffchaffs are typically associated with wetlands and did not disappear from *A. nilotica* till later in the dry season. For all migrants combined, bird density in *A. nilotica* increased in the course of the dry season (Figure 11).

Acacia tortilis flowered in October–December and started to shed its leaves from January onwards (Figure 12). Flowering trees in October–December attracted more migrants and residents than non-flowering trees (36 and 25 migrants and 15 and 11 residents per ha of canopy, respectively; averages based on 89,813 m^2 ha

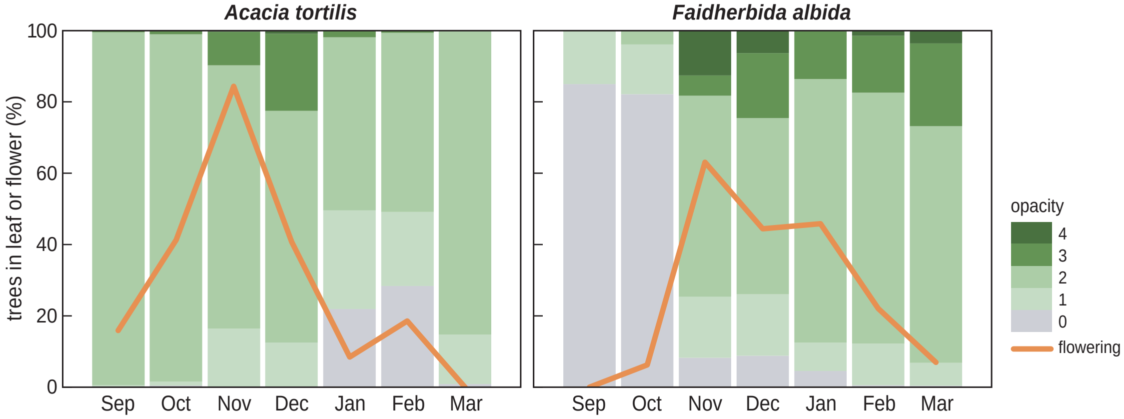


Figure 12. Monthly variation in the opacity score (from 0 = no leaves, 1 = few leaves to 4 = dense foliage) and the percent of flowering trees in *A. tortilis* (*n* = 5241) and *Faidherbia* (*n* = 5855) in the Sahel in Senegal.

of canopy and 2250 trees). After the flowering season, bird density decreased, subsequently remaining stable at a lower density (Figure 11).

Subalpine Warbler was the most common bird species in *Balanites*. Its numbers increased from September through February. Other *Curruca* species were relatively common in February–March. The density of other migrants did not vary seasonally (Figure 11).

Faidherbia is the only woody species in Africa which shows an 'inverse phenology', because it sheds its leaves not in the dry but in the rainy season. Nearly all trees were bare in September and October (Figure 12, Photo 2). The few birds present in *Faidherbia* were (nearly) all concentrated in the few early sprouting trees. The species flowered in November–January. Flowering trees attracted many Subalpine Warblers (20.7/ha of canopy in flowering and 2.4/ha in non-flowering trees), but differences in the use of flowering and non-flowering trees by the other migrants were small (48.7/ha of canopy in flowering and 41.9/ha in non-flowering trees). In contrast, resident species (except sunbirds) were four times less common in flowering trees (4 birds/ha of canopy) than in non-flowering trees (15 birds/ha). From November onwards, the density of birds in *Faidherbia* remained at the same high level, or even increased until March, except for Subalpine Warblers which became scarcer from December onwards.

The food supply in *Faidherbia* probably did not decline during the dry season. Counting the moths coming off disturbed *Faidherbia* trunks, none were recorded in September–October, but numbers increased in later months until at least March (Figure 13). While doing the standard counts, we also recorded the number of birds in *Faidherbia* handling large prey. Of identified prey items, 85% were caterpillars and 7% moths; these proportions did not seem to vary seasonally. Most large prey were recorded taken in November, after which there was a non-significant decline. Compared to other tree species, moth predation by birds foraging in *Faidherbia* remained at a relatively high level throughout the dry season.

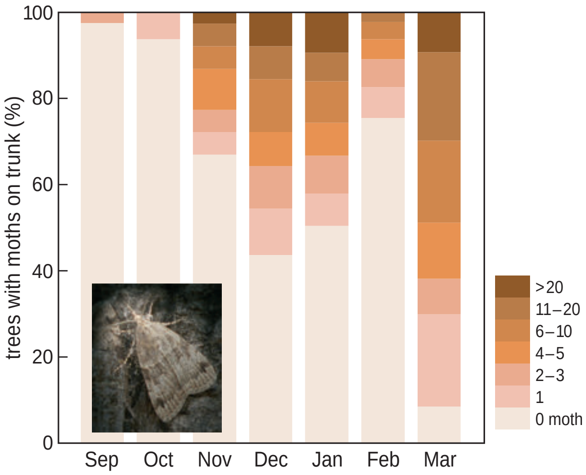


Figure 13. Average number of moths flushed from trunks of *Faidherbia* (>6 m high; $n = 2066$) following three strikes at breast height, shown for seven months. The presence of moths is significantly different between months ($\chi^2_6 = 147, P < 0.001$).

Trees on seasonal floodplains

During the dry season the flood forests in the Sahel are known to attract many arboreal birds, mainly migrants, due to the abundance of insects (Vadifis *et al.* 2014). Western Olivaceous Warblers *Iduna opaca* were common in *Acacia kirkii* in November when the trees were in full bloom and standing in 1–3 m of water. During deflooding, the number of birds increased even further, mainly Iberian Chiffchaff (Figure 14A). Similarly, Red Acacia *Acacia seyal* on floodplains attracted an increasing number of birds later in the season (Figure 14B), reaching densities up to 300–400 birds/ha of canopy when trees were in flower and had a dense canopy (Figure 18 in Zwarts *et al.* 2015). *A. seyal* was also widely distributed further south in the sub-humid zone where the sediment was loamy or clayey. In contrast to the trees on floodplains, *A. seyal* on dry land had already lost their leaves in November– December and were visited by very few birds that mostly appeared in trees in full blossom in February (Figure 14C).

Tree choice in dry and wet years

As shown above, the seasonal variation in tree choice made by arboreal birds depends to a large extent on the phenology of trees, including aspects such as flowering, fruiting, leafing and shedding leaves. Annual variations in the timing of these events depend on rainfall in the preceding wet season. Poor rains result in early desiccation and early shedding of leaves in the dry season, and good rains bring late desiccation and leaf-shedding (Poupon 1979). Tree choice of arboreal birds should therefore differ for dry and wet years. Indeed, compared to the wet year 2010/11, in the dry year 2014/15 *Balanites* had 30% fewer birds (except Orphean Warbler), and *Acacia tortilis* even 51% fewer (except Western Olivaceous Warbler; Figure 15). The difference was also large in *Acacia nilotica* (49% fewer) and very large in *Acacia seyal* (94% fewer). In contrast, in the dry year *Faidherbia* accounted for 30% more birds (except Western Bonelli's and Subalpine Warblers; Figure 15).

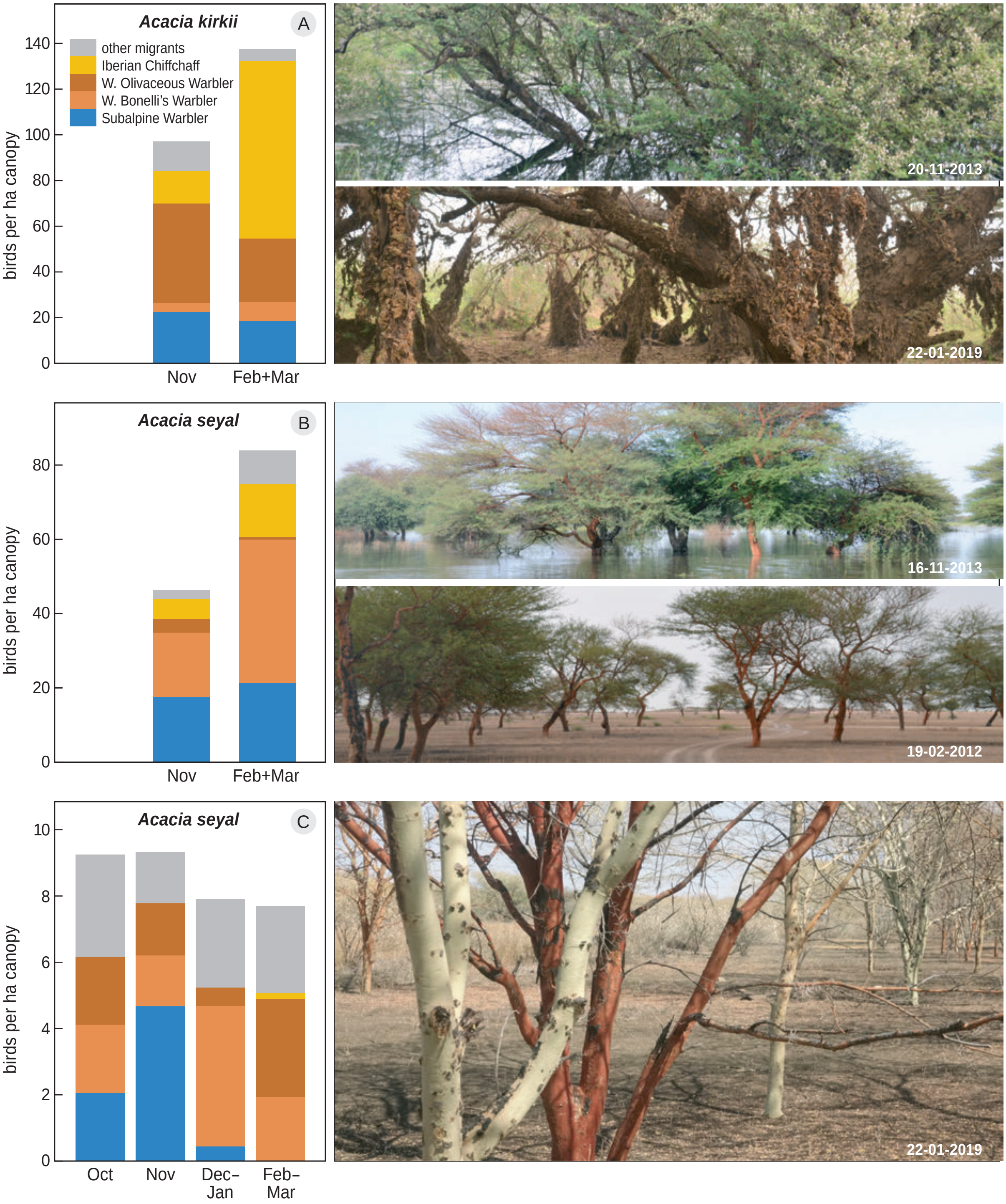


Figure 14. Birds per ha canopy in (A) *Acacia kirkii* forest at Akkagoun, Inner Niger Delta, still flooded in November (top: notice flowers) and when desiccated in February–March (bottom: 10,203 m^2 and 25,629 m^2 surveyed, respectively), (B) scattered *Acacia seyal* near Akka, Inner Niger Delta, still flooded in November (top) and on dried-up ground in February–March (bottom: 24,053 m^2 and 31,523 m^2 surveyed, respectively), (C) leafless *Acacia seyal* on dry ground in West Africa (west of 10°W; 146,180 m^2 surveyed). Note different scales along the vertical axes.

Faidherbia is a particularly attractive tree in dry years, also in a more humid southerly region (Gambia, 13.1–13.2°N, 16.5–16.8°W), where bird density in individually marked *Faidherbia* trees (in total 34,700 m^2 of canopy) was recorded on 3–12 March 2015 (a dry year when we also collected data further north; Figure 15) and again on 23–28 February 2017 when rainfall was very close to the long-term average. Western Bonelli's Warbler reached a density of 51.3 birds/ha of canopy in the dry year against 29.3/ha in the year with an average rainfall (χ^2-test; $P < 0.001$), Western Olivaceous Warblers 12.0 vs. 8.8 birds/ha; (χ^2-test; $P < 0.05$) and other migrants 5.5 vs. 2.0 birds/ha; χ^2-test; $P < 0.001$).

DISCUSSION

Ground-foraging birds

Ground-foraging migratory species were recorded mainly in the arid and semi-arid zone, where movements throughout the dry season – as illustrated by monthly latitudinal averages of occurrence – were either absent or small-scale (Figure 2). Our findings tally with information provided via birds equipped with geolocator or transmitter. Northern Wheatears from Sweden, for example, arrived in the Sahel on 16 October (range 6–26 October for 12 individuals equipped with a geolocator; Arlt *et al.* 2015). These birds first stayed at 16.1 ± 1.2°N (±SE) in October–November, then moved an average of 166 km southwards (range 0–444 km) to spend the rest of their stay

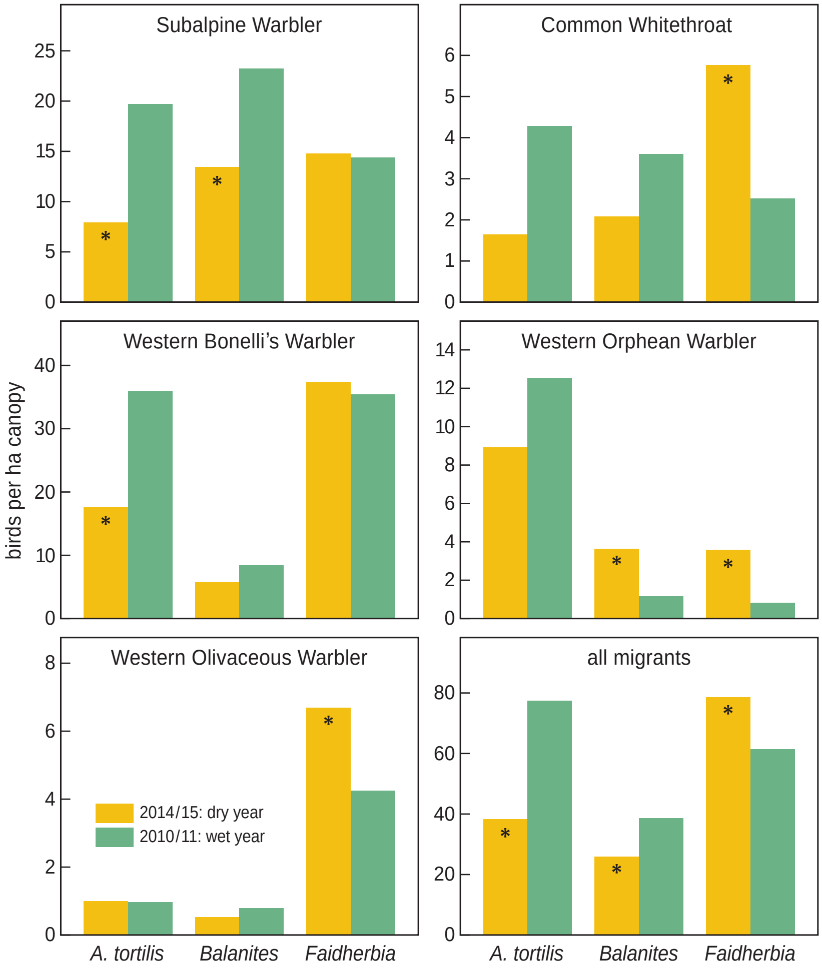


Figure 15. Bird density per ha canopy in three woody species shown for five migratory bird species and all migrants combined in a wet year (2010/11) and a dry year (2014/15). All data are from NW Senegal and SW Mauritania and 20 November – 10 March. Bird density was measured in 60,144, 63,155 and 101,340 m^2 of canopy in *Acacia tortilis*, *Balanites aegyptiaca* and *Faidherbia albida*, respectively. Bird densities that differ highly significantly between a dry and a wet year ($\chi^2_1 > 10.8$, $P < 0.001$) are marked (*).

in Africa at 14.0 ± 1.7°N. This fits well with, and also helps explain, our field data: Northern Wheatears in the Western Sahel ranged between 13 and 18°N (annual rainfall 100–700 mm). Within Senegal, the latitudinal shift southwards in concurrence with an increase in numbers suggests a simultaneous influx of birds from southern Mauritania (16.6–18°N). Such shifts are likely related to rainfall in the previous wet season. Arlt *et al.* (2015) showed the movements of Northern Wheatears in three successive winter periods, the first one preceded by an exceptionally wet season (2010/11; rainfall 64% above long-term average), the other two being relatively dry (11% below average) and wet (+34%). In the extremely wet year, three of four Northern Wheatears stayed the entire northern winter in the north at 16.6°N, the fourth bird moved 200 km southward to a site at 14.1°N. On the other hand, all eight birds left the arid zone in the relatively normal years and moved 230 ± 105 km southward to spend the northern winter at 13.8°N ± 1.2 (distances derived from supplementary data given by Arlt *et al.* 2015).

In contrast to Northern Wheatears, Tawny Pipits remained in the same arid zone between October and February (16.3°N, 230 mm rain/year; Figure 2). Very few birds were recorded north of the southernmost fringe in Mauritania (Figure S42 in Zwarts *et al.* 2023a), reducing the prospect of an influx from the southern Sahara. Our counts suggested that the birds stayed the entire wintering period within the same narrow latitudinal band (Figure 2). The only study of Tawny Pipits equipped with geolocators, however, showed extensive movements (Briedis *et al.* 2016). Six Czech birds arrived in the southern Sahara and northern Sahel on 27 September (range 17 September – 26 October), spent 70 ± 36 days at 17.3°N ± 3.8 and 8.2°W ± 3.4 and moved between mid-November and early January to sites situated at 15.6°N ± 0.9 and 11.0°W ± 4.2. These birds moved on average some 200 km to the south and more than 300 km to the west in the course of the northern winter. These data refer to 2014/15, a dry season preceded by a very poor rainy season (rainfall 29% below long-term average), a condition perhaps instrumental in the relatively large displacements of Czech pipits during their stay in Africa, as just described for Swedish Northern Wheatears during a dry year. This is important as our observations of sedentary Tawny Pipits were based on information from three years with average or abundant rainfall (average annual rainfall 64% above and 2 and 1% below the long-term average in the preceding rainy periods in 2010, 2013 and 2016, respectively).

The most likely explanation of southward shifts within the arid and semi-arid zone during winter is a declining food supply in the footsteps of desiccation and depletion of food resources. However, it should be noted that in September and October, the time that ground-dwelling Palearctic migrants start to arrive in the arid zone, the larger part of the Sahel is still unsuitable for them because of the dense vegetation of knee-high savannah grass (Photo 3A), millet standing at eyelevel (Photo 4A) and the extent of other agricultural crops not yet harvested. Dense vegetation is rare in the hyper-arid zone, but is common in the more humid zones (Figure 1B in Zwarts *et al.* 2023f). After removal of the standing vegetation through grazing, burning and harvesting, in the Sahel usually effected in October–November, these areas become accessible to pipits, larks, wheatears, wagtails and other ground-foraging birds (Photo 3B, 4B). Until then, the presence of Tawny Pipits in NW Senegal is restricted to small patches of bare ground near human settlements where cattle were gathered and grasses removed by grazing, as recorded in October 2015. At that time of year, the surrounding savannah – where we observed Tawny Pipits later during the dry season – was still covered by a dense vegetation of mainly *Cenchrus biflorus*, a grass species known as cram-cram in West Africa (Photo 3A). For the same reason, in the early dry season Northern Wheatears were often seen near villages.

The main food for the bird community in the Sahel comprises grass seeds. Seedeaters are therefore the most numerous guild of birds in the Sahel (Zwarts *et al.* 2023a), mostly comprising of Afro-tropical species and but few Palearctic migrants like the European Turtle Dove *Streptopelia turtur*. Research in northern Senegal shows that after the short rainy season the soil contains, on average, 2000 grass seeds per square metre (Bille 1974) which are mainly eaten by insects and gerbils (Poulet 1974); birds are responsible for 7–10% of the seed consumption (Morel & Morel 1972). The combined predation pressure will have removed 80–90% of the seeds by the end of the dry season. A comparable rate of seed predation was found elsewhere in Senegal where just the birds annually took 6–26% of the available seed (Gillon *et al.* 1983). Seed production varies greatly with annual rainfall (Bille 1974, Grouzis 1992). In dry years many Afro-tropical seed-eaters die, and the survivors often fail to breed (Morel & Morel 1974). Seed production therefore may limit bird populations, especially in dry years (Zwarts *et al.* 2023e). The feeding ecology of European Turtle Dove has been intensively studied in Senegal (Morel 1987, van Tuijl 2018), but to what extent their steep population decline since the 1970s (Woodward *et al.* 2020, Boele *et al.* 2021) may be attributed to a decline of its food supply on the wintering grounds is open to debate (Eraud *et al.* 2009).

For insectivores foraging on the ground or in low vegetation, the food supply also progressively declines during the dry season, as recorded for dry savannah and wetland habitats in northern Senegal (Morel 1968, Gillon & Gillon 1973, Vafadis *et al.* 2014), woody savannah in Ivory Coast (Gillon & Gillon 1974), and various habitats in eastern Africa (Sinclair 1978, Lack 1986a, Owen 1969, Dingle & Khamala 1972). Two studies showed that food intake of birds decreases in the course of the dry season, e.g. for Western Yellow Wagtail *Motacilla flava* (Wood 1979) and for Montagu's Harrier *Circus pygargus* (Schlaich *et al.* 2016, Schlaich 2019). When food supply declines, birds would be expected to leave the affected area and search for alternative locations. Birds in eastern and southern Africa have been shown to use consecutive sites that sometimes are thousands of km apart (Lack 1986b, Pearson & Lack 1992, Herremans 1998, Jones 1999). However, in the western Sahel birds may remain in the transition zone between desert and the forest, moving a few hundred km southwards in the course of their wintering period, as shown by GPS-equipped European Turtle Doves (Lormée *et al.* 2016, Schumm *et al.* 2021), Montagu's Harriers (Schlaich *et al.* 2016, Schlaich 2019; see also Buij & Croes 2014, for supportive evidence from field observations on a raptor guild in Cameroon) and also by geolocator-equipped birds, such as Common Whitethroat (Tapia-Harris *et al.* 2022), Northern Wheatears (Arlt *et al.* 2015), Tawny Pipits (Briedis *et al.* 2016) and European Turtle Doves (Eraud *et al.* 2013). Bird counts in Nigeria in November, repeated in February, revealed that out of nine migratory species, three had moved southwards and two had moved northwards (Cresswell *et al.* 2009).

Arboreal birds: seasonal variation

The majority of the migratory birds wintering in the Sahel arrived in September and left in March–April. Four out of 14 migratory species used the western Sahel only temporarily and left in the second half of October or in November to spend the rest of their stay in Africa further south (Figure 2). In general, bird species staying in the western Sahel throughout the dry season tended to remain in drier rainfall zones in the western Sahel (more northerly, e.g. on average at 15.8°N for Western Orphean Warbler) than species on their way to more southerly wintering areas (e.g. at 13.8°N for Garden Warbler *Sylvia borin*). The only exception to the latter rule was European Pied Flycatcher (Figure 2), presumably coincident with its preference for acacia species in October–November, not unlike the migrants that remain in the acacia belt in the Sahel. In October, and also later in the season, Melodious, Willow and Garden Warblers used other

Photo 3. Most Tawny Pipits in Senegal (16.349°N, 15.528°W) were recorded on pasture land, except when it was still covered with high grass (*Cenchrus biflorus*, picture A: 22 October 2015). The same region had been heavily grazed by cattle by 15 December 2015, as visible from the high density of dung (picture B); pipits and wheatears were now all over the place.

tree species occurring just south of the Sahel, such as *Tamarindus indica*, *Anogeissus leiocarpus* and *Cordyla pinnata* which were rarely visited by other migratory bird species (Figure 3). These tree species were in full blossom in October, and therefore attractive to insectivorous migratory birds (Figure 8, 9). When not in flower during our surveys in November–March, *Tamarindus*, *Anogeissus* and *Cordyla* held few if any insectivorous birds (Figure 3 in Zwarts *et al.* 2023c).

In Senegal, Common Redstarts *Phoenicurus phoenicurus* were less common in January–February than in October (Figure 1). The birds recorded in January were, on average, 129 km farther to the south than in October (Figure 2). This suggests a southward displacement, perhaps even beyond the region surveyed during our study, i.e. to the south of 13.6°N (map in Figure 2). Seven Danish Common Redstarts with geolocators spent the winter in the Western Sahel within the expected distribution area (Figure S28 in Zwarts *et al.* 2023b; Kristensen *et al.* 2015). One of their birds stayed in Senegal but six other redstarts spent the winter inland (mainly in Mali) whilst first making a detour during autum migration via Mauritania and Senegal between late September and mid-October, before turning east/southeast to fly, on average, another 1000 km. These birds passed Mauritania or Senegal probably too quickly (Kristensen *et al.* 2015) to allow us to record seasonal changes in numbers of Common Redstarts in this region.

Most bird species remained in the same rainfall zone during their stay in the western Sahel or shifted only a short distance to the south. Western Orphean Warbler and Subalpine Warbler instead became more common in the arid zone after October (Figure 2). This might be due to an influx of birds from hyper-arid regions north of 16.6°N where small numbers were recorded in winter (Figure S21 and S24 in Zwarts *et al.* 2023b). However, a concomitant increase in numbers in Senegal was not recorded, rather the opposite, a small decline (Figure 1A). Subalpine and Western Orphean Warbler therefore probably moved from the semi-arid to the arid zone (but Cresswell *et al.* 2009 suggested the opposite for Subalpine Warblers in Nigeria). During the dry season, bird numbers in various woody species in the arid zone were found to increase in the wake of fruiting and flowering in the latter part of the dry season (*Salvadora*: Figure 4, *Capparis*: Figure 5A. *Acacia ehrenbergiana*: Figure 6, *Euphorbia*: Figure 7 and four other woody species mentioned in the text).

In the semi-arid zone, most woody species gradually shed their leaves and flowers in the course of the dry season, like *Anogeissus* (Figure 8), *Tamarindus* (Figure 9), *Acacia senegal* (Figure 10) and *A. tortilis* (Figure 12). Insectivorous birds avoided trees without leaves (Figures 5, 6 and 10; see also figures 15 and 18 in Zwarts & Bijlsma 2015). As nearly all woody species lost their leaves later on in the dry season, birds

Photo 4. Northern Wheatears on arable land in W Senegal at 14.464°N and 16.662°W were absent as long as crops were not yet harvested (A: 29 October 2015, ripe millet) or dense grass covered the ground, but as soon as the ground became bare from November onwards ground-foraging birds started to arrive (B: 6 March 2016).

became more selective. Timing and extent of leaf loss varied between species, and tree choice by birds varied accordingly. *A. tortilis* was, in this regard, an anomaly by losing its leaves from January onwards (Figure 12), but without a concomitant decline in density of migrants using this tree (Figure 11). *A. senegal*, on the other hand, was one of the first trees to become bare (Figure 16) and was mostly avoided by birds from December onwards (Figure 10). *Balanites* and *A. nilotica* remained green during the dry season and were visited by an increasing number of migrants between September and March (Figure 11). *Faidherbia*, another anomaly because of their 'inverse' phenology of leafing in the dry season, had a dense canopy in February–March (Figure 12) and shed their leaves only just before the next rainy season (Roupsard *et al.* 1999). When *Faidherbia* was still bare before November, this tree was ignored by migrants, but as soon as budding had started migrants appeared and remained present in high densities (Figure 11). The food supply, using the number of moths as an approximation, increased during the early dry season (Figure 13). This is consistent with the higher density of invertebrates in *Faidherbia* in January than in November in Senegal (Stoate 1998).

Few fruit-bearing woody species in the Sahel are relevant as food plants for birds. Most fruit is inedible

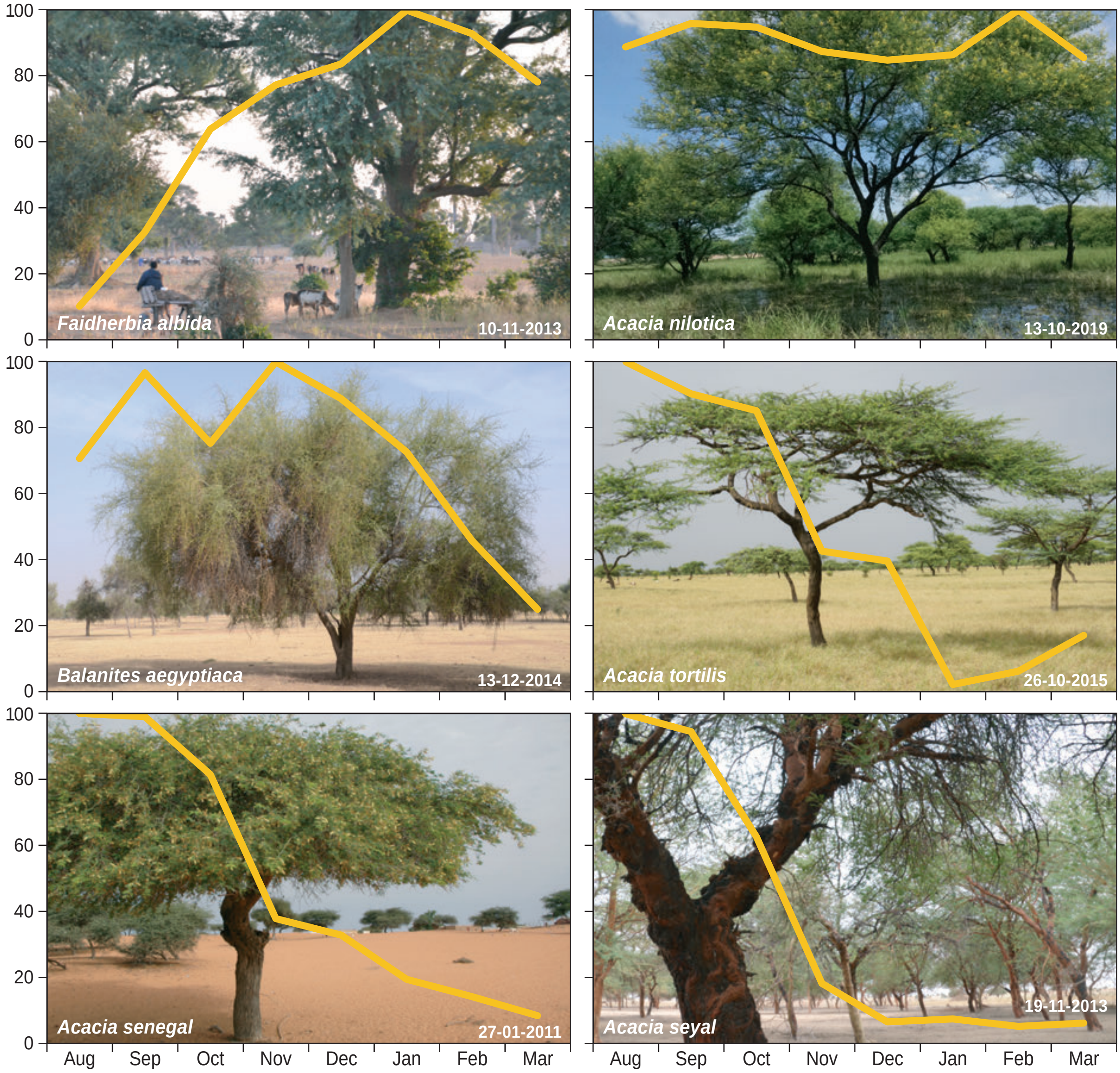


Figure 16. Seasonal variation in leaf biomass in six bird-rich tree species; monthly maximum set at 100 (after Hiernaux *et al.* 1994).

or too large. One of the exceptions is *Salvadora* of which the small berries are eaten by a variety of bird species, among the migrants notably *Curruca* warblers fattening up in February–April (Fry *et al.* 1970, Stoate & Moreby 1995, Wilson & Cresswell 2006). *Salvadora* berries become increasingly available from December onwards (Figure 4). Also *Gymnosporia* (= *Maytenus*) *senegalensis* attracts many birds when fruit is available. *Gymnosporia* is not a common species, despite its wide distribution from Senegal to Ethiopia in the annual rainfall zone of >300 mm. In Gambia, fruit of *Gymnosporia* (diameter 5.5 mm; Schmidt *et al.* 2013) was the main food resource for Blackcap *Sylvia atricapilla* and Common Whitethroat in late March and in April (Hjort *et al.* 1996) and for Garden Warbler and European Pied Flycatcher in Ivory Coast in the same months, at least in 2018 (Comoé NP; Wender Bil & Janne Ouwehand pers. comm.; photo in Oosterveld & Klop 2019: 198). Between November and early February we recorded just a single migrant, a Blackcap, among 963 *Gymnosporia* shrubs with a total woody cover of 2474 m^2, not surprising considering that we noted the first shrubs with fruit only after mid-February (at the end of our observation period).

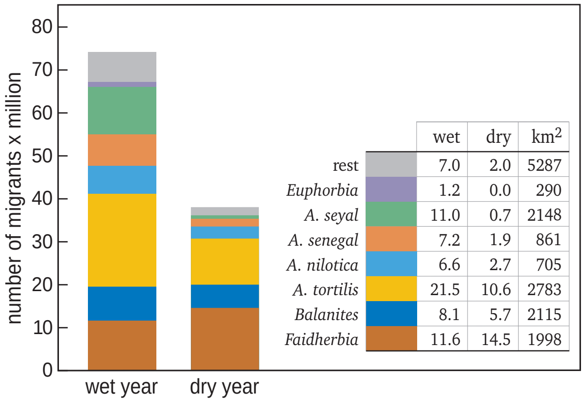
In the course of the dry season bird densities declined in tree species losing leaves and increased in species remaining green (Table 1). Hiernaux *et al.* (1994) measured leaf biomass in 28 woody species of which six feature in Figure 16. The variation in leaf biomass is substantial between individual trees, probably related to the availability of groundwater (Do *et al.* 2005). This also explains why trees may have vivid green leaves in seasonal floodplains that remain inundated well into the dry season, while the same woody species have shed their leaves in nearby dry areas. Such variation is very important for birds. For example, *A. seyal* on the floodplains of the Inner Niger Delta attracted many birds and their numbers increased in the dry season, while *A. seyal* on drylands were visited by few migrants declining in number through the dry season (Figure 14).

Arboreal birds: year to year variation

Seasonal variation in bird density could only be illustrated when combining data from different years (Figure 3–11), masking year-on-year variations in tree phenology, foraging conditions and tree choice of birds. For example, leaf biomass of *A. senegal* in the dry year 1987 (rainfall 24% below long-term average) was a third of that in two years having an average rainfall (1988 and 1989; Hiernaux *et al.* 1994). In the same vein, leaf biomass of *A. seyal* declined to a quarter or a fifth. Poupon & Bille (1974) recorded a large difference in leaf biomass in North Senegal in a dry (1971/1972) and in an extremely dry year (1972/1973), with rainfall 12% and 31% below the long-term average, respectively. Simultaneously, in the extremely dry year, *A. senegal* produced no flowers at all, whereas the flowering period of *Euphorbia balsamifera* was very short. Our data unambiguously show that in a dry year birds disappeared from trees losing leaves and increased in woody species remaining green (Table 1). The increase of migrants in *Faidherbia* in a dry year, not just in the semi-arid zone (Figure 15) but also in the sub-humid zone (Gambia), was probably a consequence of deteriorating foraging conditions in other woody species, on top of being the only tree species in the Sahel leafing in the dry season and with a steadily improving food supply in the course of the dry season (if moth abundance is a reliable indication of food availability; Figure 13). In this respect, *Faidherbia* can be regarded as a refuge tree, which begs the question whether *Faidherbia* is sufficiently abundant and widespread in the Sahel to accommodate birds that have lost foraging habitat in other tree species during dry years. The western Sahel in the rainfall zone of 100–600 mm west of 10°W and covering an area of 0.35 million km^2 holds an estimated 74 million arboreal birds in a wet year, but only 38 million in a dry year (Zwarts *et al.* 2023a: Figure S01 and 2023c: Figures S1–S3). Of all tree species available in this section of the Sahel, *Faidherbia* is the only tree that shows a slight increase in bird density in a dry year (+2.9 million). This constitutes a

Table 1. Leaf biomass in six woody species in February–March relative to the monthly maximum (set to 100%; Hiernaux *et al.* 1994; see Figure 16), ranked from low to high, compared to the seasonal and annual change in numbers of migrants. Season: ratio of bird density in February + March versus October (Figure 10, 11, 14B and 14C). Year: ratio of bird density in December–March in a dry versus and a wet year (Figure 15). [*]Seasonal change in leaf biomass and bird numbers differs substantially for trees on floodplains and drylands, making the comparison less reliable for *A. seyal* and *A. nilotica*.

Species	Leaf biomass (%) Feb–Mar	Ratio bird density	
		Season	Year
A. seyal[*]	5.8	(0.75)	(0.07)
A. senegal	11.6	0.38	0.26
A. tortilis	11.7	1.08	0.49
Balanites	35.8	2.26	0.70
Faidherbia	92.7	6.56	1.75
A. nilotica[*]	92.9	(2.56)	(0.41)



		wet	dry	km^2
rest	⬜	7.0	2.0	5287
Euphorbia	🟪	1.2	0.0	290
A. seyal	🟩	11.0	0.7	2148
A. senegal	🟧	7.2	1.9	861
A. nilotica	🟦	6.6	2.7	705
A. tortilis	🟨	21.5	10.6	2783
Balanites	🟦	8.1	5.7	2115
Faidherbia	🟫	11.6	14.5	1998

Figure 17. Estimated number of arboreal migrants (millions) in 2010/11 (wet year) and 2014/15 (dry year) present in West Africa (10–17°W) between the 100 and 600 mm isohyet (Figure S1 in Zwarts *et al.* 2023a), an area of 0.35 million km^2 with a woody cover of 4.6%; based on the bird density per ha of canopy for both years in all woody species (shown for three woody species in Figure 15) and the woody cover within the region for seven woody species important for birds (last column in inset table).

small compensation for the losses of 11 million arboreal birds in *A. tortilis*, 10 million in *A. seyal* and 18 million in all other woody species. The concentration of migratory birds in fewer trees during a dry year concurred with fewer birds overall. In a dry year, half of the arboreal migrants disappeared from the western Sahel in the zone between 100 and 600 mm (Figure 17). Without the widespread presence of *Faidherbia*, the losses would have been higher.

Possible mechanisms preventing or reducing bird losses during dry years in the Sahel

Several explanations are conceivable for the change in numbers in the Sahel during a dry year.

(1) Birds move to less arid zones during a drought year, as found in the Kalahari (Herremans 2004). It might seem obvious that birds in the Sahel would do the same, except for the fact that the woody vegetation in humid woodland is dominated by non-preferred tree species, many of which shed their leaves during the dry season (Photo 5). Furthermore, drought years in the

Photo 5. This is not a picture of an autumnal forest in the temperate zone, but a forest in the humid zone in West Africa (Burkina Faso; 10.66°N and 4.30°W) during the dry season (28 January 2016). It demonstrates that even in an area with, on average, 1200 mm rain per year, leaves may be desiccated or shed three months after the last rain in October. For arboreal birds, the Sudan vegetation zone is not an attractive alternative to birds for savannah trees in the still drier Sahel, not even in drought years.

Sahel are typically also years with (much) less rain in the humid zone farther south (Nicholson 2005).

(2) In a dry year, birds may move from the western Sahel to the east where their density in the preferred tree species was lower, suggesting undersaturation and hence habitat to expand into (Zwarts *et al.* 2023d). This is possible, but speculative and not likely to occur on a large scale (Zwarts *et al.* 2023d).

(3) Birds may shift to floodplains in the Inner Niger Delta and the lower Senegal Valley (bird numbers in these large wetlands are not included in Figure 17). The relative woody cover of mainly *A. seyal* in the floodplains of the Inner Inner Delta (3.14 million ha) amounted to 1.84% in the 1990s (Zwarts unpubl. data), yielding a total canopy surface of *A. seyal* of some 60,000 ha. These forests harboured 2.7 million migrants in a wet year (46 and 59 migrants per ha canopy in 2009 and 2010, respectively; peak flood level in Akka in both years 497 cm) vs. 5.9 million in a dry year (102 migrants/ha canopy in 2012; peak water level in Akka 404 cm; van der Kamp & Zwarts unpubl. data). These data suggest that at least several millions of migrants may move during a dry year from drylands to wooded floodplains in the Inner Niger Delta and other floodplains.

(4) Mangrove forests remain green during the dry season and attract many migrants. The available data, however, suggest that in drought years West African mangroves harbour fewer migrants than in normal or wet years (Zwarts *et al.* 2014).

(5) The lower numbers in the Sahel in a dry year may result from higher than usual mortality. For a ringed population of British Lesser Whitethroats, only 3% of the adult birds returned after a disastrously dry winter in the eastern Sahel, compared to 10–23% after normal and wet years (Boddy 1994; Figure 256 in Zwarts *et al.* 2009). In British Common Whitethroats, the annual survival rate of adults varied between 11% in 1983 (rainfall in the Sahel 27% below long-term average) and 68% in 1988 (rainfall 1% below average; Boddy 1993). High winter mortality in drought years is clearly a determinant of numbers of birds wintering in the Sahel as suggested by our estimates of bird numbers in wet and dry years (Figure 17). It should be noted that in some years (1972, 1983, 1984 and 1992) rainfall in the Sahel was half that in the dry year 2014. In such years, trees not only lose their leaves but many die (Poupon & Bille 1974, Gonzalez 2001, Tappan *et al.* 2004, Marantz 2009). Among the affected tree species were several that we have identified as a last resort for birds in times of drought, including *Faidherbia*, *Balanites* and *Acacia nilotica* and *A. kirkii* growing on seasonal floodplains, in other words trees that grow, or keep, their leaves during the dry season or are standing in water. These tree species, and notably *Faidherbia*, have higher densities of invertebrates in January than in November (Stoate 1998), particularly of ants, beetles and spiders (and moths, see Figure 13).

Unfortunately, the scarcity of quantitative studies on arthropod densities in savannah trees, and on food availability for insectivorous birds within and between seasons in general, hinders more detailed discussion and analysis (but see e.g. Gillon & Gillon 1973, 1974, Scholtz 1982, Lack 1986a, Stoate & Moreby 1995, Stoate 1997, 1998, Vickery 1999, Dosso *et al.* 2011, Vafidis *et al.* 2014). It seems likely, though, that under drought conditions, food would be in even shorter supply if there were no back-up from trees that could provide food to survive the winter (*Faidherbia*, trees on floodplains). Given the limited extent of southward shifts in European migrant bird distributions in the course of their stay in West Africa, and given that Sudan-Guinean vegetation zones are adversely affected in drought years, when rainfall is poor, high mortality of migrant birds is part of the deal.

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SAMENVATTING

Elk jaar steken honderden miljoenen trekvogels de Sahara over om de noordelijke winter in de Sahel en wijde omgeving door te brengen. De vogels arriveren in de droge tijd, want van september tot juni valt er geen regen in de Sahel. Sterker, na januari lopen de temperaturen op naar boven de 40°C in de schaduw (vanaf maart). Vogels die in de Sahel leven, gebruiken verschillende strategieën om aan deze droogte het hoofd te bieden. Sommige trekvogels die in struiken en bomen foerageren, blijven na aankomst 1 à 2 maanden in de Sahel en vliegen dan nog minstens 500 km naar het zuiden, waar meer regen over een langere periode valt. Ook de Gekraagde Roodstaart *Phoenicurus phoenicurus* schuift iets naar het zuiden op, echter zonder de humide zone te bereiken. De Tapuit *Oenanthe oenanthe* blijft alleen in een nat jaar in de aride zone hangen; in een droog jaar schuift de soort door naar de semi-aride zone. De verschillende grasmussoorten bewegen zich in de loop van het droge seizoen juist noordwaarts, naar de aride gebieden, waar ze zich concentreren in struiken en bomen die later in het droge seizoen aantrekkelijker worden, omdat zij dan bessen hebben gekregen (Tandenborstelboom *Salvadora persica*) of zijn gaan bloeien (zes woestijnsoorten). In de semi-aride zone verliezen de meeste boomsoorten in de loop van de noordelijke winter hun blad, met een navenante leegloop van trekvogels tot gevolg. Bij de weinige boomsoorten die hun bladeren niet verliezen (zoals de Woestijndadel *Balanites aegyptiaca*), blijft het aantal vogels echter constant of neemt het toe (bij de acacia *Faidherbia albida*). Tijdens het droge seizoen neemt het aantal vogels ook toe in acacia's die in vloedvlaktes staan. Als gevolg van dit alles raken vogels tijdens hun verblijf in de Sahel geconcentreerd in steeds minder soorten bomen en struiken. Deze indikking van de verspreiding is des te sterker in jaren met weinig regenval. Omgekeerd, in jaren met veel regen krijgen bomen meer bloemen en bladeren en laten ze die in de droge tijd ook later vallen. Onder natte omstandigheden is er voor de vogels gedurende de droge tijd meer voedsel over een langere tijd beschikbaar, maar in een droog jaar is het voor vogels moeilijker om te overleven. Dat was al bekend op basis van tellingen in het broedgebied (droogte in de Sahel ging gepaard met broedpopulatieafnames). We vonden in de Sahel een rechtstreekse bevestiging van de invloed van droogte op vogelaantallen: het aantal trekvogels was in een droog jaar de helft minder dan het aantal in een nat jaar. De sterfte in de Sahel zou nog veel hoger zijn zonder de acacia's op de vloedvlaktes en de aanwezigheid van *Faidherbia*, en in mindere mate ook *Balanites*, in de rest van de Sahel. Dit handjevol boomsoorten kan met recht worden beschouwd als 'toevluchtsbomen'.

RÉSUMÉ

Chaque année, des centaines de millions d'oiseaux migrateurs traversent le Sahara pour passer l'hiver boréal dans le Sahel et ses environs. Ils y arrivent pendant la saison sèche, qui s'étend de septembre à juin. Au cours de leur séjour, aucune précipitation ne tombe et les températures augmentent graduellement jusqu'à dépasser les 40°C à l'ombre (à partir de mars). Les oiseaux qui vivent dans le Sahel utilisent différentes stratégies pour faire face à cette sécheresse. La plupart des espèces restent au Sahel pendant toute cette période, mais certaines espèces arboricoles ne restent au Sahel que pendant 1 à 2 mois, puis continuent d'au moins 500 km vers le sud, pour rejoindre des zones plus humides. Le Rougequeue à front blanc *Phoenicurus phoenicurus* se déplace également vers le sud, mais sans atteindre la zone humide. Le Traquet motteux *Oenanthe oenanthe* ne reste pour sa part dans la zone aride que lors des années les plus humides. Lors des années sèches, il se déplace vers la zone semi-aride. De façon surprenante, les différentes espèces du genre *Curruca* migrent en début de saison sèche vers les régions arides au Nord, où elles se concentrent dans des essences d'arbustes et d'arbres devenus attractifs, car ils se sont garnis de baies, tel le Siwak *Salvadora persica*, ou ont commencé à fleurir (six essences du désert). Dans la zone semi-aride, la plupart des essences d'arbres perdent leurs feuilles pendant l'hiver boréal, ce qui contraint les migrateurs à se déplacer. Quelques essences ne perdent toutefois pas leurs feuilles et continuent à abriter une quantité d'oiseaux constante (cas du Dattier du désert *Balanites aegyptiaca*) ou en hausse (cas de l'acacia *Faidherbia albida*). Pendant la saison sèche, le nombre d'oiseaux augmente également dans les acacias situés dans les plaines inondables. Les oiseaux se concentrent donc sur une diversité d'essences de plus en plus restreinte pendant leur séjour au Sahel, surtout lors des années sèches. À l'inverse, lors des années humides, les arbres ont plus de fleurs et de feuilles et les conservent plus longtemps : la nourriture disponible et les abris sont plus nombreux. Lors des années sèches, la survie est plus difficile, comme le révèlent les déclins constatés lors des printemps suivants sur les zones de reproduction. Nous avons confirmé par nos inventaires au Sahel l'influence directe de la sécheresse : le nombre d'oiseaux migrateurs restants en fin d'hivernage pendant une année sèche y était inférieur de moitié à celui d'une année humide. La mortalité au Sahel serait encore plus élevée sans la présence d'une poignée d'essences d'arbres jouant le rôle d' « arbres refuges » : le *Faidherbia albida*, les acacias dans les plaines inondables et dans une moindre mesure, le Dattier du désert *Balanites aegyptiaca* dans le reste du Sahel.

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Effects on birds of the conversion of savannah to farmland in the Sahel: habitats are lost, but not everywhere and not for all species

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Many migratory bird species, several of which are in severe decline, and African residents spend the northern winter in the Sahel, by nature a huge savannah, half of which has been converted into farmland. We analyse the impact of such large-scale changes on birds. On average, woody cover is 38% lower on farmland than on savannah. More critically, farmers have drastically changed the vegetation communities of their farmland. In the arid and semi-arid zone, they partly removed bird-rich trees such as Umbrella Thorn *Acacia tortilis* and Desert Date *Balanites aegyptiaca*, yet further south they created a richer bird habitat by replacing the original woody species by Winter Thorn *Faidherbia albida*, a preferred tree species for Afro-Palearctic migrants (but less so for Afro-tropical residents). Still further south, two bird-poor trees, Shea Tree *Vitellaria paradoxa* and African Locust Bean Tree *Parkia biglobosa*, dominate farmland, causing birds, mainly Afro-tropical residents, to lose habitat. As a consequence of farming, arboreal migrants are confronted with habitat degradation in the northern arid zone and in the southern humid zone, but face more favourable wintering conditions in the sub-humid central zone. Ground-foraging birds are more abundant on savannah than on farmland; 24 bird species from this group, including three wheatear species and many residents, are more than twice as abundant on savannah. Conversion of savannah into farmland has mixed outcomes for ground-foraging birds, but were generally negative except for five species (including Western Yellow Wagtail *Motacilla flava*) which were more than twice as abundant on farmland than on savannah. Thus, the conversion of savannah into farmland represents a loss for many but not all bird species.

Key words: Sahel, savannah, farmland, *Faidherbia albida*, *Acacia tortilis*, Shea Tree

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Savannahs, covering about 20% of the land surface worldwide and up to 40% of the African continent (White 1983, Scholes & Walker 1993), are found in the tropics, mainly in two wide bands at about 8°–20°N and 8°–20°S. These bands may be considered as a transition zone between treeless deserts and equatorial rainforest, an ecotone where wood cover gradually increases towards the equatorial region. In Africa, barren desert turns into savannah grassland with shrubs and isolated trees where annual rainfall ranges from 100 to 200 mm. Woody cover increases with increasing rainfall. At 600–700 mm, woody savannah becomes woodland (Sankaran *et al.* 2005). Wooded savannah and humid forests were important habitats for early man, whose imprint on the ecosystem gradually increased through the millennia. The impact of human occupation on savannah ecosystems gained momentum in the 20th century when the huge numbers of wild herbivores roaming the savannah south of the Sahara in the 19th century were eradicated and replaced by several hundred million domestic livestock (Spinage 1968, www.faostat3.fao.org). Despite the vast number of cattle, sheep and goats, the region can still be characterised as an extensive savannah with thorny shrubs and scattered trees. The short rainy season boosts an explosive growth of dense herbaceous vegetation and the subsequent seed production forms the staple food for insects, birds and rodents during the ensuing long dry season (Bille 1974, Morel & Morel 1974, 1978).

The recent ecological changes include the conversion of savannah into cropland, which is usually associated with tree loss and reduced seed production (Photo 1). Farmers growing rice in the floodplains of the Inner Niger Delta (Mali) removed trees on a large scale, as has happened in rice polders in the Senegal Valley, in the agricultural zone of 'Office du Niger' in central Mali and in the vast, fertile plains in southeast Sudan. However, such large-scale tree removal is rather exceptional. In the drylands of the Sahel, farmers grow crops beneath scattered trees. At present, the woody cover on farmland and on savannah is about the same (Brandt *et al.* 2018). The visual impression of farmland in the Sahel, described as agroforestry parkland (Boffa 1999), does not differ much from that of woody savannah. Farmers in the Sahel often use a crop-fallow rotation system to allow soil fertility to recover. Fields are temporarily left uncultivated, and these are covered with a dense vegetation of seed-producing grasses and forbs not unlike savannah vegetation. After the harvest, agricultural land is intensively grazed by livestock during the dry season.

It remains poorly known in which way and to what extent the conversion of savannah into farmland has affected the bird community in the Sahel. Our surveys suggest a negative impact on arboreal and granivorous ground-foraging birds (Zwarts *et al.* 2023d,e), but many variations on this theme are possible. In Burkina Faso, for example, bird density on farmland and savannahs varied with soil type and the duration of farmland left fallow, but the differences were insignificant when savannah and farmland had the same soil type (Söderström *et al.* 2003). However, the effects were large in West Africa for raptors and other large bird species (Thiollay 2006); the encounter rate with larger raptors in agricultural land was 97% lower than in pastoral land and savannahs and 30% lower for smaller raptor species. A similar significant difference was found for raptors and other bird species in Cameroon (Buij *et al.* 2013), Uganda (Bolwig *et al.* 2006, Shaw *et al.* 2019) and South Africa (Malan & Benn 1999). In Zimbabwe, Pringle *et al.* (2019) recorded a decline of larger bird species (>150 g), but an increase of the

Photo 1. Farmland with millet and small *Guiera senegalensis* shrubs bordering savannah with Umbrella Thorn *Acacia tortilis*. Picture taken in Niger (13.983°N, 7.302°E) during the dry season (10 December 2016). Note the bare ground in the millet field and the low, but dense vegetation in the savannah.

smaller ones, after savannah-like, large-scale rangeland was converted into smallholder farmed land. The bird density in the Serengeti savannah (Tanzania) was more than twice as high as in adjacent former savannah converted into agriculture, and the difference was still larger in ground-foraging seedeaters and insectivores (Sinclair *et al.* 2002). In contrast, Whinchats *Saxicola rubetra* in the Central African Republic were exclusively recorded in the sparse agricultural plots amidst vast woody savannahs in December 2017 (own unpubl. data); this species was in Nigeria most common in intensely used farmland (Hulme & Cresswell 2012).

The potential impact of land use changes on birds may be especially large in the Sahel, where 50% of the millions of km^2 of savannah in the 300–1200 mm annual rainfall zone has been converted into farmland. Rainfed farming is not possible in the arid zone. Farmland is therefore scarce (4%) in the 100–200 mm rainfall zone, increasing to 22% at 200–300 mm, 46% at 300–400 mm and 54% at 400–1200 mm rainfall (Figure S46 in Zwarts *et al.* 2023a). The savannah zone is the wintering ground of many millions of Afro-Palearctic migrants and much larger numbers of resident Afro-tropical birds. Among the ground-foraging migrants, three granivorous and ten insectivorous species are almost entirely dependent on this zone (Figure 13A and 14A in Zwarts *et al.* 2023a), as are 13 arboreal migratory species (Figure 5A in Zwarts *et al.* 2023b). The widespread creation of farmland throughout savannahs across the 300–1200 mm annual rainfall zone has drastically changed the wintering habitat of these 26 migratory species, several of which are in steep decline, such as Tawny Pipit *Anthus campestris*, European Turtle Dove *Streptopelia turtur*, Northern Wheatear *Oenanthe oenanthe* and Whinchat (van Turnhout 2005, Eraud *et al.* 2009, Zwarts *et al.* 2009, Vickery *et al.* 2014). These species are known to have faced serious habitat loss and habitat degradation on their breeding grounds (e.g. Brown & Aebischer 2004, Fay *et al.* 2021), but the large-scale changes in land use in their African wintering quarters presents them with double jeopardy, simply because they spend half their lives in the sub-Sahara.

Ideally, in order to address the impact of changing land use in Africa on birds, we should compare bird densities before and after the conversion of savannah vegetation into farmland. Because such data are lacking, we had to adopt the alternative approach of comparing bird densities of Afro-Palearctic migrants and Afro-tropical species between savannah and farmland. This paper focuses on two questions: (1) how many arboreal birds and ground-feeding birds of which species forage on farmland and savannah in the Sahel, and (2) what might have been the impact – in terms of species composition and abundance of birds – of the conversion of savannah into farmland?

METHODS

We refer to Zwarts & Bijlsma (2015) for a description of the methods used to count birds and woody plants and to Zwarts *et al.* (2023a,b,c) for a description of the dataset used in this paper. All 2144 study sites (each usually 4.5 ha) were situated between 7 and 22°N and between 17°W and 42°E. The analysis is based on sites across the entire width of the Sahel, but we excluded Ethiopian sites as being too different from the rest of our study area. In the strictest sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term more loosely as including the full transition zone between Sahara in the north and the humid forests in the south. From the dataset, we selected sites where bird counts had been performed in random plots in the period 20 November – 10 March 2011–2019. Most of these counts were done in January and February two to four months after the crops had been harvested.

The sites were assigned to one of three main habitats: woodland, farmland or savannah. Farmland included fallow land, but savannah encompassed a wider range of habitats including bare desert, rangeland, scrubland and woody savannah. Savannah was heavily grazed by livestock, as was farmland after the harvest, resulting in bare soils after December (Figure 1 in Zwarts *et al.* 2023d). All crops and herbaceous vegetation not yet grazed by November had usually become withered by the time of our surveys. Overall, farmland was often so bare that we sometimes had to search for subtle traces like plough tracks to identify a site as farmland. Since most bird counts used in this paper were from January–February, we sometimes were in doubt whether land was in fallow or had been cultivated some months before, and, if cultivated, what crop the farmers had grown (which shows to what extent farmland is sometimes stripped of leftovers after harvest, both by farmers and by pastoralists passing through with cattle and goats/sheep). The sites not always exclusively consisted of woody vegetation, savannah or farmland. When mixed, the category with the highest coverage was noted. Woodland sites were excluded, as well as stony sites (sandstones, laterite soils, rocks). At first, we only noted Afro-Palearctic birds (from now on called migrants), but in later years also Afro-tropical species (from now on called residents). The number of sites used for the analyses of migrants (675 sites on farmland and 717 sites on savannah) is therefore larger than that for arboreal residents (529 sites on farmland and 633 sites on savannah), and ground-foraging residents (294 sites on farmland and 596 sites on savannah).

The land cover map (Figure 1A) and field data (Figure 1B) agree that half of the surface area in the 300–1000 mm rainfall zone is farmland, but the regional differences that we found are large. A comparison between our 2144 ground-truthing study plots and the land cover classification identified from remote sensing data shows that the satellite-based map slightly overestimated the coverage of farmland, mainly in the zones where the rainfall is less than 500 mm/year. Three older land use maps underestimated the extent of farmland and were less accurate (Table 1 in Zwarts *et al.* 2023a).

Between 13 and 16°N, nearly 100% of the area in W Senegal (13–17°W), N Nigeria, S Niger (4–11°E) and SE Sudan (30–36°E) comprises farmland, but much less so in E Senegal, W Mali (8–14°W) and in Chad (15–25°E). This variation is largely explained by soil characteristics, which are excellent for agriculture in W Senegal (fine sand) but poor in E Senegal and W Mali (laterite soils; Figure 1C). In less populous Chad, however, large parts of the zones that receive between 300 and 1200 mm of rainfall and are suitable for cultivation remain free of farming. To compare the average density of arboreal birds between farmland and savannah, we selected all sites where the annual rainfall was >300 mm, representing an area where half of the savannah had been modified into farmland.

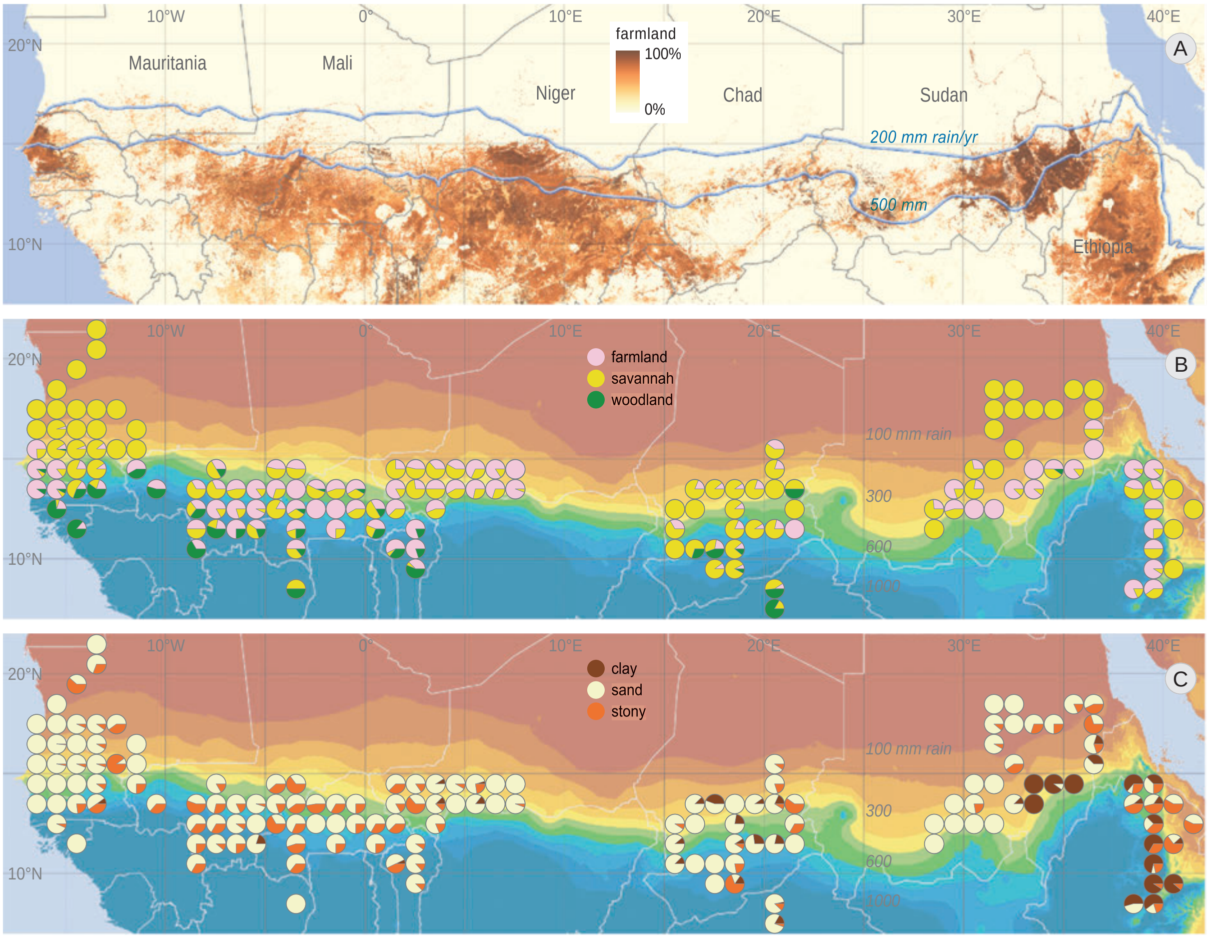

Figure 1. (A) Percent farmland in 2015 expressed per 100×100 m based on remote sensing data (source: Buchhorn *et al.* 2020), (B) percentage of study sites (n = 2144) categorised as farmland, savannah or woodland, averaged for 150 1° latitude × 1° longitude grid cells with annual rainfall as background (source: Hijmans *et al.* 2005), (C) percentage of the study sites in 150 grid cells classified as having a clayish, sandy or rocky soil.

RESULTS

Woody vegetation

Woody cover on farmland and savannah increased significantly with rainfall (Figure 2A) but, on average, woody cover on farmland was significantly lower (38%) than on savannah. Fewer woody species were expected on farmland due to selective felling, but this effect was recorded only in the humid zone (>800 mm rain; Figure 2B). In drier habitats the number of woody species on farmland was similar to that on savannah (Figure 2B).

The reduced woody vegetation on farmland might imply habitat loss for arboreal bird species, but actually does so only when tree loss occurred in bird-preferred woody species. Four tree species stand out because they attract many birds and are also common (Zwarts *et al.* 2023c). The most important woody species for birds was Umbrella Thorn *Acacia tortilis*, common and widespread in the savannah in the 100–500 mm/year rainfall zone, but far less so on farmland (Figure 3A). Desert Date *Balanites aegyptiaca* also attracted many birds, occurring across the wider rainfall range of 100–600 mm and in Chad even including the subhumid rainfall zone of 600–900 mm. Overall, *Balanites* was less common on farmland than on savannah (Figure 3B). Red Acacia *Acacia seyal* was typically confined to floodplains and clayish soils (Figure 3C). Winter Thorn *Faidherbia* (=*Acacia*) *albida* was found almost exclusively on farmland in the 300–700 mm rainfall zone (Figure 3D).

Of the widespread tree species usually avoided by arboreal birds (Zwarts *et al.* 2023c), *Guiera senegalensis* was a very common shrub in the 400–700 mm rainfall zones (Figure 4A). Farmers frequently removed *Guiera* shrubs, and the remaining shrubs were mostly 1 m high, their woody cover on farmland being half that for savannah (Figure 4A). *Combretum glutinosum* can become a large tree on the savannah in the 500–1000 mm rainfall zone, but on farmland most were removed, any remaining trees being small (Figure 4B). As an economically important tree, Shea Tree *Vitellaria paradoxa* (Figure 4C) was treated with care by farmers and was often the dominant tree species on farmland in southern Mali and Burkina Faso (annual rainfall >700 mm). This tree species was rarely found in woodland or savannah. African Locust Bean Tree *Parkia biglobosa* was characteristic of farmland in the humid zone, but almost completely absent on savannah except where annual rainfall exceeded 1000 mm (Figure 4D).

Very few woody species were common on both farmland and savannah. Most were either common on savannah and rare on farmland or vice versa (Figure 5A). *Faidherbia albida* and several fruit-bearing trees, such as Mango *Mangifera indica*, were not found beyond farmland. Common savannah species such as camel's foot *Piliostigma* spp., *Combretum* spp. and tallow tree *Detarium* spp. were common on farmland, but rarely as large trees because of frequent cutting; total woody cover therefore remained low.

Arboreal birds

Shea Tree *Vitellaria paradoxa* was poor in birds (Figure 5B), and would have held even fewer birds were it not for the large-scale presence of the parasite *Tapinanthus* spp. which attracted birds taking their berries and,

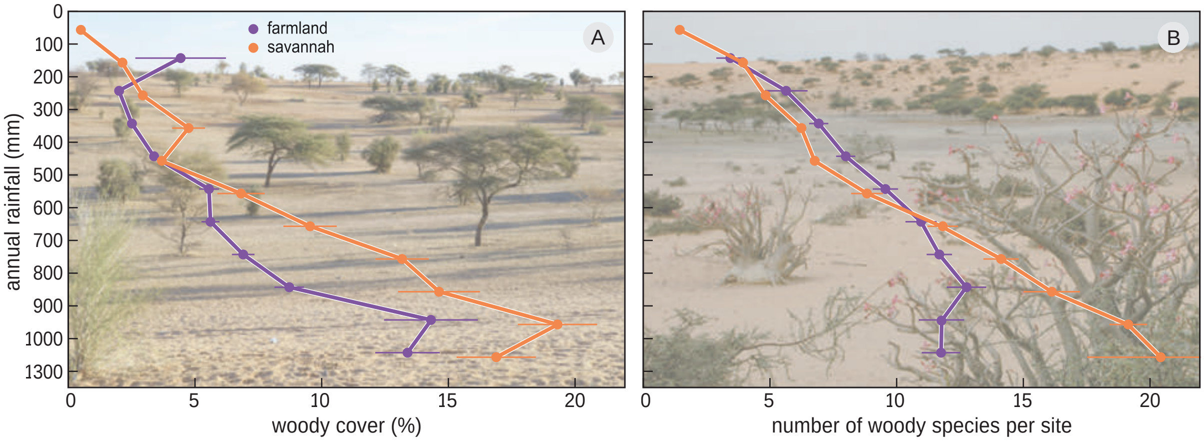

Figure 2. (A) Average woody cover (%) ± SE and (B) number of woody species ± SE on farmland and savannah in 11 annual rainfall zones. Woody cover and number of woody species differ significantly for land use (2 classes), rainfall (11 classes) and the interaction term (two-way ANOVA for A: $r^2 = 0.39$, $n = 1392$, $P < 0.001$ and for B: $r^2 = 0.44$, $n = 1392$, $P < 0.001$). Photos show dunes and valleys in southern Mauritania, with (A) mainly Umbrella Thorn *Acacia tortilis* and (B) Desert Rose *Adenium obosum*.

when flowering, sunbirds (73% of *Vitellaria* in Chad were infested with this parasite, in Burkina Faso up to 95% (Lamien *et al.* 2006, Kanika *et al.* 2020). The expansion of *Vitellaria* parkland must have inevitably had a negative impact on arboreal birds in the humid zone where this woody species is widespread. On the other hand, farmers in the sub-humid zone have created a bird-rich agroforestry parkland dominated by *Faidherbia*. The conversion of savannah into farmland again has had a negative impact yet farther north in the semi-arid zone where bird-rich tree species such as *A. tortilis* and *Balanites* were partly removed from farmland.

The species composition of the woody vegetation on farmland differed substantially from that on savannah (Figure 5), with far-reaching consequences for birds. Because farmers removed bird-rich trees in the semi-arid zone (especially *A. tortilis* & *Balanites*), fewer arboreal migrants were found on farmland than on savannah in the 100–400 mm rainfall zone (Figure 6A). In contrast, farmland in the 400–700 mm rainfall zone, where bird-rich *Faidherbia* (Figure 5B) was most abundant (Figure 3D), was highly attractive to arboreal migrants. The more humid zone held few migrants (Figure 6A) on farmland or savannah, but insectivorous residents were more abundant, albeit at much lower densities on farmland than on savannah (Figure 6B), as was also the case for nectarivorous residents (Figure 6C) and frugivorous residents (Figure 6D).

Ground-foraging birds

Insectivorous ground-foraging migrants were most abundant in the drier zones. In the zone with 100–300 mm rainfall/year, their density was on farmland twice as high as on savannah. On the contrary, there were fewer birds on farmland than on savannah in the more humid zones (Figure 7A). For ground-foraging residents taking insects (Figure 7B) or seeds (Figure 7C), bird densities increased with rainfall in both farmland

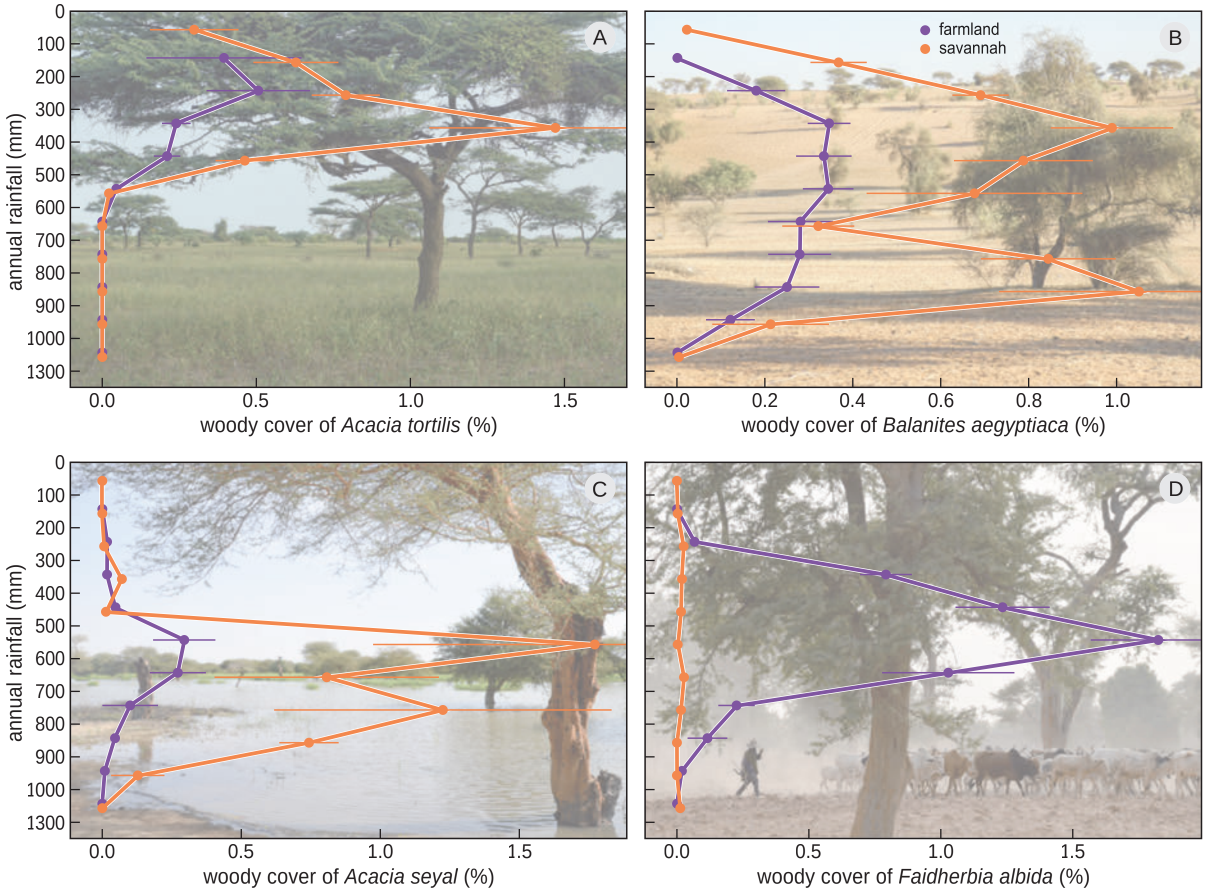

Figure 3. Average woody cover (%) ± SE of four bird-rich woody species on farmland and savannah in 11 annual rainfall zones. Woody cover in the four tree species differs significantly for land use, rainfall and the interaction term ($P < 0.001$), but $P < 0.01$ for the interaction term in *A. tortilis* and *Balanites* and not significant for land use in *A. tortilis* (two-way ANOVA; n =1392 in the four tree species; A: $r^2 = 0.05$, B: $r^2 = 0.09$, C: $r^2 = 0.05$, D: $r^2 = 0.18$).

and savannah but there were no perceivable differences in bird density between these two land uses.

The overall densities of ground-foraging birds were quite similar when comparing farmland and savannah (Figure 7). However, at the species level distinct variations were evident (Table 2). Bird densities for eight migratory species were higher on savannah (significant for the three wheatear species), while in two other migratory species densities were higher (non-significant) on farmland, namely Woodchat Shrike *Lanius senator* and Western Yellow Wagtail *Motacilla flava*, the latter associating with farmland near wetlands. Residents were also found in higher densities on savannah (36 species, 9 significant) than on farmland (10 species, 1 significant). The fraction of granivorous species occurring in higher densities on savannah (76%, 25 out of 33 species) was similar to the fraction of insectivorous species (79%, 19 out of 24 species). Bird densities on farmland and savannah differed significantly in 14 of the 57 ground-foraging species, of which only one species, Laughing Dove *Spilopelia senegalensis*, reached a higher density on farmland; in 13 other species densities were higher on savannah.

DISCUSSION

Most bird species (63%, 57 of 90) were recorded in a higher density on savannah than on farmland (Table 1 and 2). The densities of arboreal birds differed significantly between savannah and farmland in 36% of the bird species overall, ranging from 42% of insectivorous ground-feeding birds to 12% of the granivorous bird species (Table 1). This does not necessarily mean that conversion into farmland had a smaller impact on granivores. Granivorous birds often feed in flocks and recorded densities were therefore more variable (Figure 12 in Zwarts *et al.* 2023a). An extreme example is the

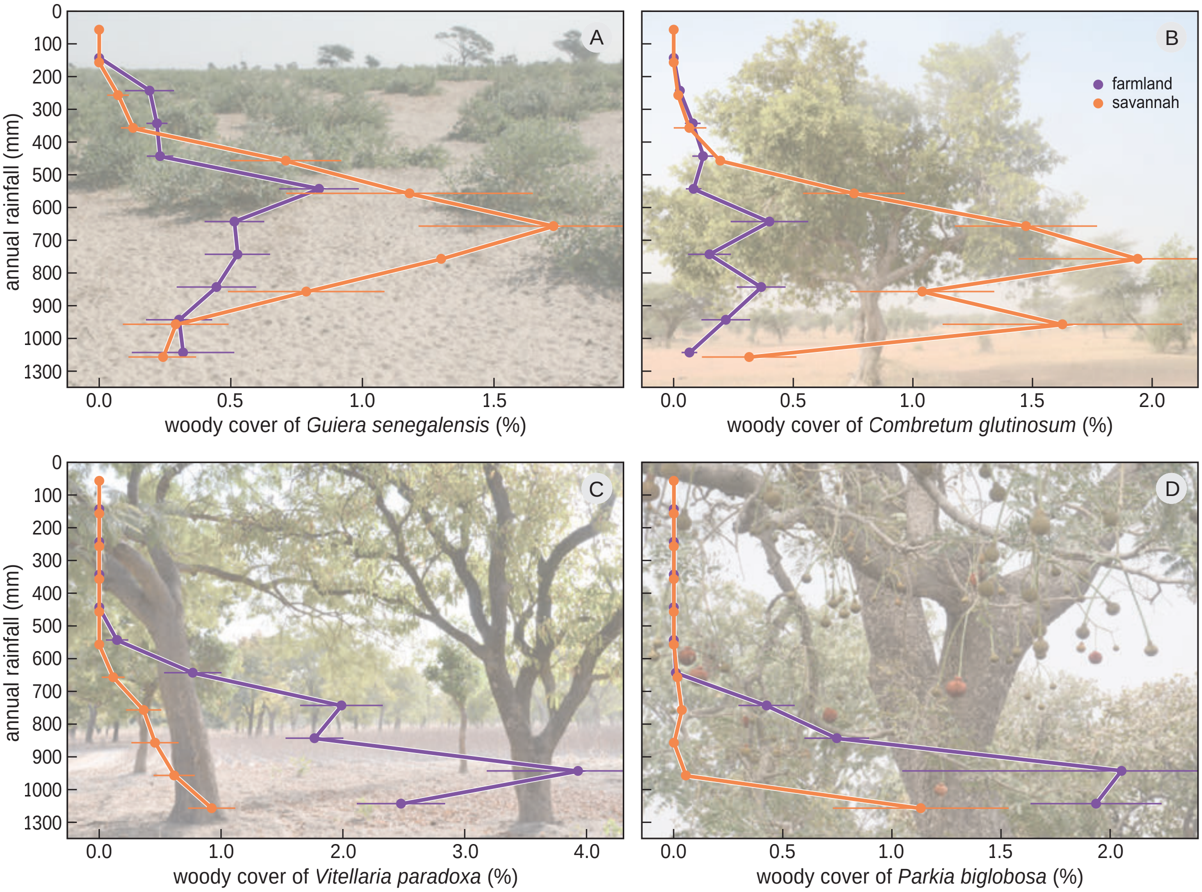

Figure 4. Average woody cover (%) ± SE of four most common woody species on farmland and savannah in 11 annual rainfall zones. Woody cover in the four woody species differs significantly for land use, rainfall and the interaction term ($P < 0.001$), but $P < 0.01$ for land use and interaction term in *Guiera* (two-way ANOVA; $n = 1392$ in the four tree species; A: $r^2 = 0.06$, B: $r^2 = 0.12$, C: $r^2 = 0.28$, D: $r^2 = 0.15$).

European Turtle Dove observed in only four savannah sites (0.6%), once in a flock of 28 birds. We saw none on our farmland sites, nor in the agricultural west of Senegal where van Tuijl (2018) found a large concentration of European Turtle Doves. To obtain reliable data for flock-feeding granivorous bird species more or larger counting sites are necessary.

Even when excluding Ethiopia, as we did in the face of its divergent habitats, regional and local variations in bird densities remained large (Zwarts *et al.* 2023a,b). Furthermore, we inevitably enlarged the variation by lumping all farmland habitats into a single category. Bird densities not only differ between fallow and recently cultivated land (Söderström *et al.* 2003) but also between the various crops (e.g. millet, sorghum, fonio, peanuts, bissap and cotton). The highest densities were recorded in well-tended and watered vegetable gardens. Even though we excluded sites with stony soil, sites categorised as savannah also consisted of a wide range of different sub-habitats, such as bare sandflats, grassland, scrubland and areas with few or many trees. Seasonal variation was to some extent reduced by selecting bird counts performed between 20 November and 10 March, corresponding with the middle of the dry season. Bird counts were always performed after harvest, the latter usually in September and October.

Savannah and farmland may sometimes look the same in the dry season, but the difference is substantial when it comes to the presence and identity of woody species, especially concerning trees either highly or rarely preferred by birds. On average, arboreal migrants on the savannah reached peak densities between the 100-mm and 400-mm rainfall zones. The conversion of savannah into farmland in this rainfall zone reduced the woody cover of bird-rich trees such as *A. tortilis* and *Balanites* (Figures 3A and 3B), leading to a reduction of bird densities on farmland by 34% compared to the original savannah (Figure 6A). However, further south, in the 400–600 mm rainfall zone *Faidherbia* was retained and protected by farmers (Figure 3D); the density of arboreal birds in this zone was 71% higher than on savannah (Figure 6A). To quantify the overall gain for arboreal migrants in the *Faidherbia* agroforestry zone and the losses following removal of preferred trees in the *Acacia* belt in the north, we calculated total bird numbers per rainfall zone and habitat. Bird densities on savannah and farmland (Figures 6 and 7) were multiplied by their respective total surface areas within the region covered (Figure 8A; see also Supplementary Material 1 in Zwarts *et al.* 2023a), while accounting for the percentage coverage of farmland and savannah (Figure S46 in Zwarts *et al.* 2023a;

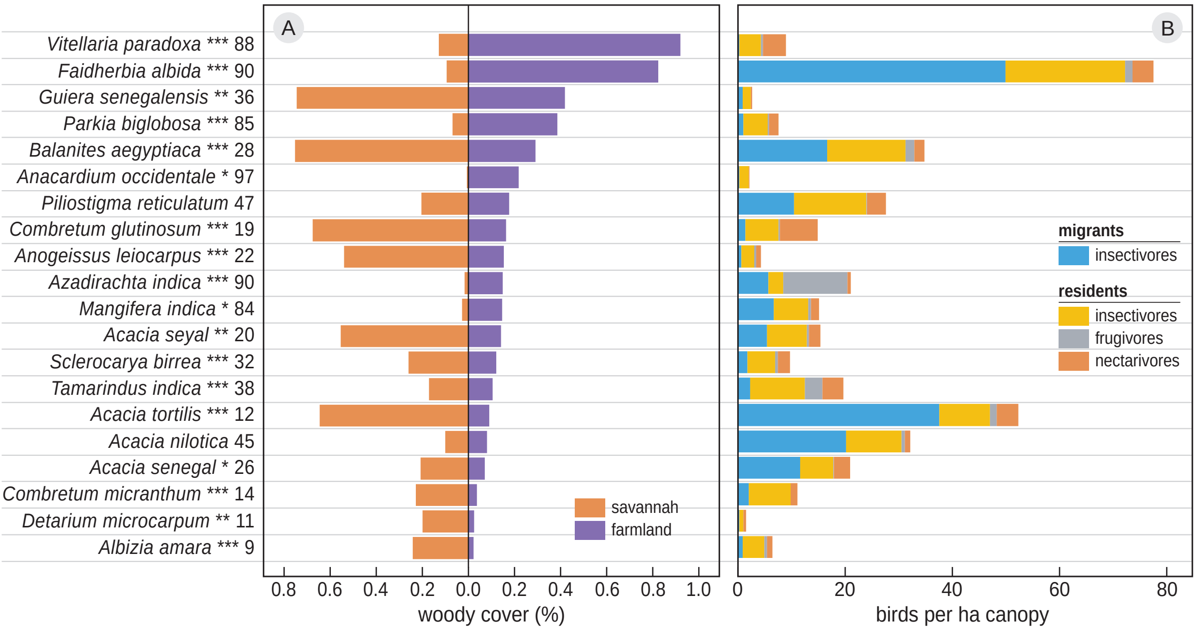

Figure 5. (A) Woody cover (%) of twenty common woody species on farmland and savannah. A selection is made for sites in the rainfall zones of >300 mm/year (n = 406 for savannah and n = 681 for farmland). Seventeen of the 20 woody species occurred significantly more often on either savannah or farmland (one-way ANOVA; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$). Occurrence on farmland (relative to occurrence on farmland + savannah), varying between 2 and 98% of the total woody cover, is shown along the vertical axis next to the tree name. (B) Average bird density per ha of canopy (data from Figure 3 in Zwarts *et al.* 2023c).

Figure 8B). We omitted the farmlands and savannahs of Ethiopia. The estimate arrived at a total of 145 million arboreal migrants using farmland and savannah between Senegal and Sudan as a wintering site in the 2010s: of that total 72 million arboreal migrants used farmland and 73 million savannah (Figure 8C).

The historical numbers of arboreal birds per rainfall zone could be derived on the assumptions that all existing farmlands in the zone under study had originally been savannah and that it had held the same bird densities per rainfall zone as calculated for the 2010s (Figure 8C). In the absence of farmland in the continuous savannah vegetation of the past, we back-calculated that the region must have harboured an estimated 141 million arboreal migrants, some 4 million fewer than in the present situation. This suggests that arboreal migrants have not suffered from the conversion of savannah to farmland. However, the extent to which numbers were gained or lost are species-specific. Bird species abundant in *Faidherbia*, such as Western Olivaceous Warbler *Iduna pallida* (up by 53% in the current situation compared to the theoretical situation without farmland), Western Bonelli's Warbler (+33%) and Rüppell's Warbler *Curruca ruppeli* (+23%) profited from the conversion of savannah into farmland (because of the increase of *Faidherbia*), but Western Orphean Warbler *Curruca hortensis*, which concentrates in the northern Sahel and is largely dependent on *Acacia tortilis* (a typical savannah tree), would be down by 39%. For several other Palearctic passerines, occurring in a wide range of rainfall zones, changes in fortunes as a result of the conversion were probably minor, such as for Subalpine Warbler *Curruca iberiae* + *C. subalpina* + *C. cantillans* –5%, Lesser Whitethroat *Curruca curruca* +2% and Common Redstart *Phoenicurus phoenicurus* +6%.

Because arboreal migrants are less common in the more humid zones within the studied region, the

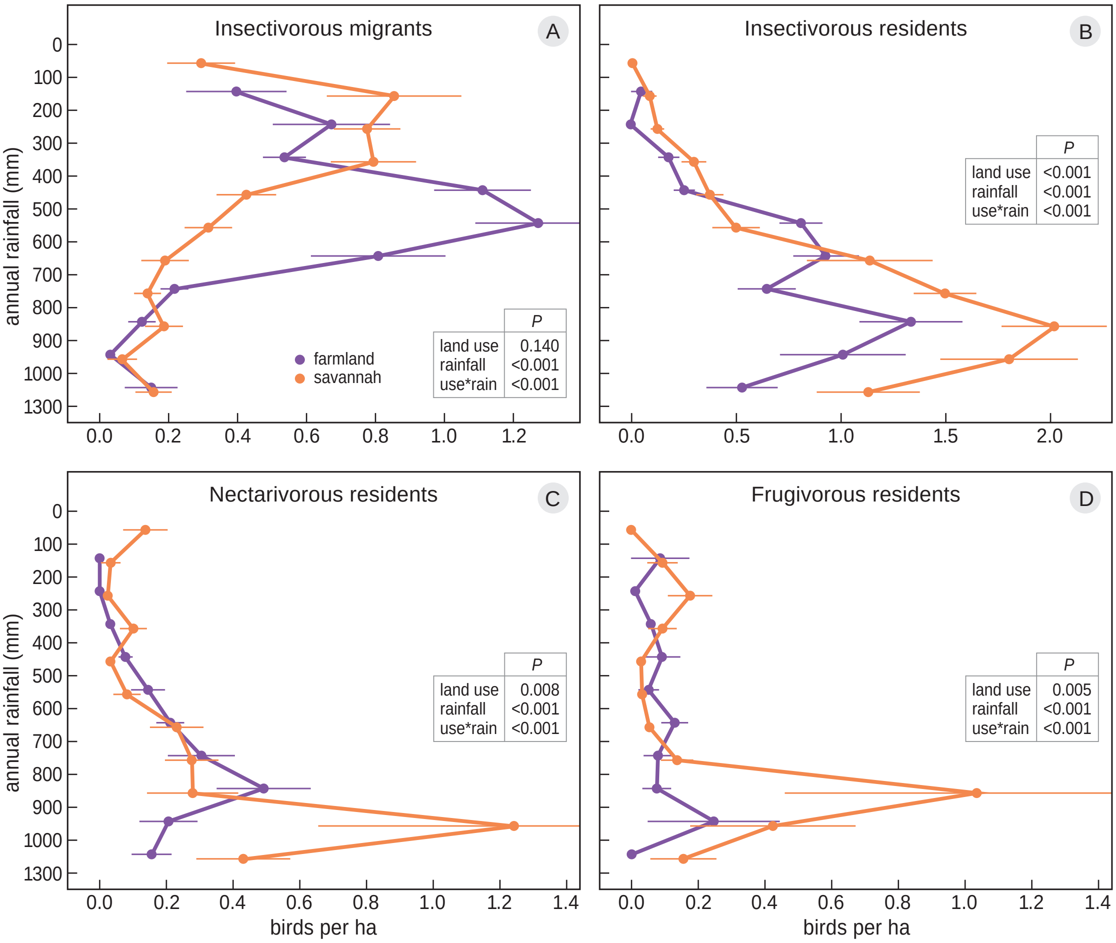

Figure 6. Bird densities per ha ± SE of four categories of arboreal birds on farmland and savannah, in 11 rainfall zones. The significance of the statistics comparing between land uses, rainfall values and their interaction term are given (two-way ANOVA).

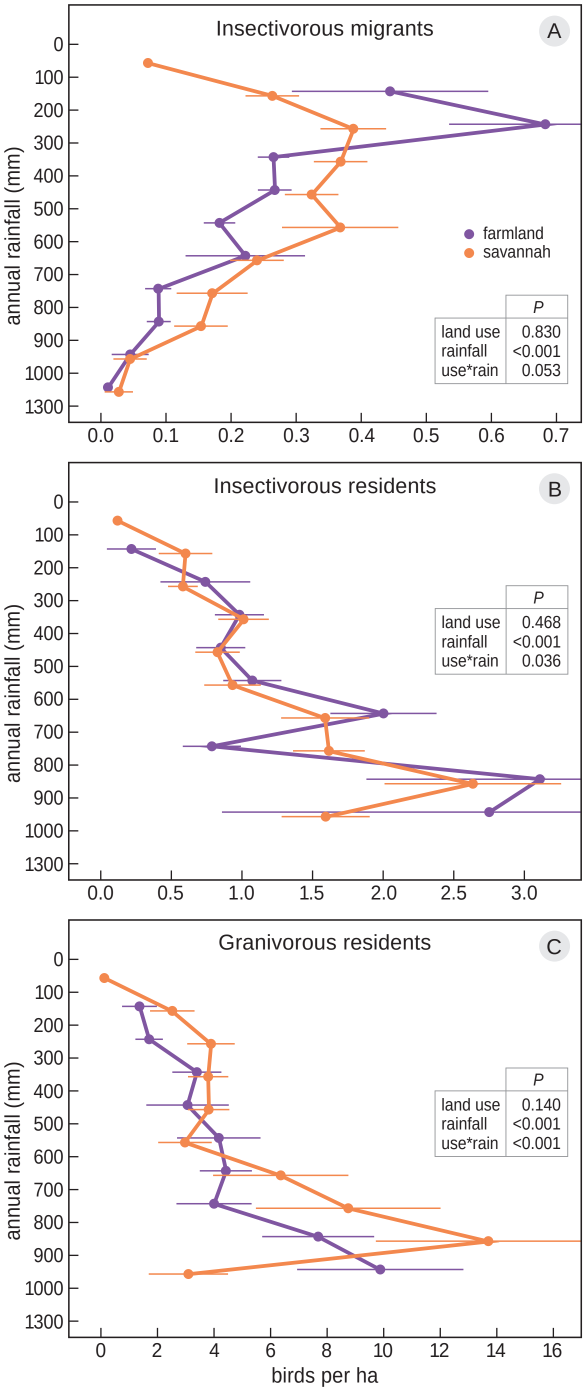

Figure 7. Densities of three categories of ground-foraging birds per ha ± SE on farmland and savannah in 11 annual rainfall zones. The statistical significance of the differences in bird densities between land uses, rainfall values and their interaction term are given (two-way ANOVA).

conversion of woodland savannah into *Vitellaria* parkland (which is almost completely devoid of arboreal migrants) is not likely to have had a significant impact on their total population (Figure 8C). However, in that part of the humid zone which mainly lies south of our study area's southern limit (7°N), species like Willow Warbler *Phylloscopus trochilus*, Wood Warbler *Phylloscopus sibilatrix*, Melodious Warbler *Hippolais polyglotta* and European Pied Flycatcher *Ficedula hypoleuca* might have suffered from the conversion of woody savannah into parkland dominated by *Vitellaria* and *Parkia*. The post-conversion losses must have been especially large for the many arboreal residents that are common in this rainfall zone (Figure 6).

During the dry season, the ground of farmland and savannah is typically largely bare in the northern Sahel region, but food supply for ground-foraging birds at this time of year potentially differs between the two habitats. In the rainy season savannah is covered by a dense vegetation of annual grasses in the arid part of the Sahel and by perennial grasses in the humid zone, which to a lesser degree also may be covered by forbs. Seed production, except in drought years, was in pre-conversion times sufficiently high to constitute a reliable food resource for the many ground-foraging granivorous birds during the long dry season (Zwarts *et al.* 2023e). On farmland, however, weeds are actively removed by farmers, as are crops during harvest. Consequently, food supply for ground-foraging birds has become much more reduced on farmland than on savannah, as evident from the higher numbers of granivores (+36%) and insectivores (+33%) on savannah during the dry season (Table 2). The difference is even larger for seven dove species (but not for Laughing Dove) and for three wheatear species.

We were unable to determine bird densities separately for cropped and fallow fields. Both field types were therefore merged into a single 'farmland' class. In the long run, fallow land will turn again into savannah and may until that time be considered as an intermediate stage between farmland and savannah. Farmers keep their land under fallow for an average of 4 to 6 years, and as a result 63% of the farmland in the Sahel is under fallow (Tong *et al.* 2020). In the dry season, the soil of farmland in China was found to contain between 90% (Hu *et al.* 2015) and 71% (Li *et al.* 2017) fewer seeds than on savannah; intermediate values applied for mixed land use. The same goes for insects. Kaiser *et al.* (2015), for example, found more ants (an important prey for birds, especially in arid regions (Dean & Milton 2018), more in fallow fields than on farmland. Hence, we suspect that a negative impact of

Table 1. Average density (*n*/ha) on farmland and on savannah of 33 arboreal bird species, excluding Ethiopia, stony sites, and sites where the average rainfall was less than 300 mm/year. **Food**: ins = insect, nec = nectar; **r-m**: r = residents, m = migrants; **rain** : average annual rainfall (mm) in the distribution area of the bird species, marked light blue <500 mm and dark blue >800 mm. **Farmland** is marked light green when density on farmland was higher than on savannah and dark green when it was twice as high; **savannah** is marked light yellow when density on savannah was higher than on farmland and dark yellow when it was twice as high. $n = 1392$ (migrants) or 1162 (residents); *P*: statistical significance of the difference between farmland and savannah: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one-way ANOVA).

					Farmland		Savannah		
Bird species		**Food**	**r-m**	**Rain**	Mean	SE	Mean	SE	***P***
Blue-naped Mousebird	*Urocolius macrourus*	fruit	r	519	0.027	0.011	0.086	0.011	
Green Woodhoopoe	*Phoeniculus purpureus*	ins	r	589	0.024	0.010	0.007	0.010	
African Grey Hornbill	*Lophoceros nasutus*	ins	r	673	0.014	0.004	0.018	0.004	
Vieillot's Barbet	*Lybius vieilloti*	fruit	r	658	0.014	0.004	0.016	0.004	
African Grey Woodpecker	*Dendropicos goertae*	ins	r	562	0.009	0.003	0.009	0.003	
Rose-ringed Parakeet	*Psittacula krameri*	fruit	r	710	0.014	0.006	0.015	0.006	
Senegal Batis	*Batis senegalensis*	ins	r	668	0.000	0.000	0.017	0.000	*
Yellow-crowned Gonolek	*Laniarius barbarus*	ins	r	706	0.009	0.004	0.015	0.004	
Black-headed Gonolek	*Laniarius erythrogaster*	ins	r	888	0.004	0.001	0.015	0.001	*
Brubru	*Nilaus afer*	ins	r	718	0.005	0.002	0.014	0.002	
Sennar Penduline Tit	*Anthoscopus punctifrons*	ins	r	517	0.002	0.001	0.018	0.003	***
Common Bulbul	*Pycnonotus barbatus*	fruit	r	885	0.018	0.003	0.020	0.003	
Northern Crombec	*Sylvietta brachyura*	ins	r	643	0.020	0.005	0.050	0.005	**
Western Bonelli's Warbler	*Phylloscopus bonelli*	ins	m	450	0.237	0.025	0.054	0.025	***
Common Chiffchaff	*Phylloscopus collybita*	ins	m	586	0.008	0.005	0.019	0.005	
Eastern Olivaceous Warbler	*Iduna pallida*	ins	m	468	0.017	0.003	0.011	0.003	*
Western Olivaceous Warbler	*Iduna opaca*	ins	m	534	0.057	0.004	0.008	0.003	***
Tawny-flanked Prinia	*Prinia subflava*	ins	r	727	0.148	0.013	0.237	0.013	**
Green-backed Camaroptera	*Camaroptera brachyura*	ins	r	752	0.090	0.011	0.172	0.011	***
Yellow-bellied Eremomela	*Eremomela icteropygialis*	ins	r	493	0.004	0.002	0.016	0.002	*
Senegal Eremomela	*Eremomela pusilla*	ins	r	775	0.058	0.011	0.066	0.011	
Lesser Whitethroat	*Curruca curruca*	ins	m	433	0.018	0.006	0.037	0.006	*
Western Orphean Warbler	*Curruca hortensis*	ins	m	287	0.012	0.003	0.021	0.003	
Subalpine Warbler	*Curruca cantillans*	ins	m	368	0.166	0.016	0.120	0.015	
Common Whitethroat	*Curruca communis*	ins	m	471	0.076	0.007	0.090	0.007	
Northern Yellow White-eye	*Zosterops senegalensis*	ins	r	1017	0.012	0.005	0.003	0.003	
European Pied Flycatcher	*Ficedula hypoleuca*	ins	m	1128	0.006	0.002	0.007	0.002	
Common Redstart	*Phoenicurus phoenicurus*	ins	m	616	0.035	0.006	0.037	0.006	
Pygmy Sunbird	*Hedydipna platura*	nect	r	699	0.092	0.013	0.127	0.013	
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	nect	r	913	0.032	0.011	0.022	0.011	
Beautiful Sunbird	*Cinnyris pulchellus*	nect	r	838	0.028	0.005	0.028	0.005	
Variable Sunbird	*Cinnyris venustus*	nect	r	773	0.007	0.003	0.012	0.003	
Little Weaver	*Ploceus luteolus*	ins	r	591	0.154	0.018	0.076	0.018	**
TOTAL					1.421		1.467		

Table 2. Average density (n/ha) of 57 ground-foraging bird species on farmland and on savannah, excluding Ethiopia, stony sites and sites where average rainfall was less than 300 mm/year. **Food**: gran (incl. g+i, g+i+f) = granivores, ins (incl. i+f) = insectivores (g = grain, i = insect, f = fruit):, r-m: r = resident, m = migrant, rm = both; **rain**: average annual rainfall (mm) in the distribution area of the bird species, marked light blue <500 mm and dark blue >800 mm. **Farmland** is marked light green when density on farmland was higher than on savannah and dark green when it was twice as high; **savannah** is marked light yellow when density on savannah was higher than on farmland and dark yellow when it was twice as high. $n = 1392$ (migrants) or 890 (residents); P = statistical significance of the difference between farmland and savannah: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$ (one-way ANOVA).

					Farmland		Savannah		
Bird species		**Food**	**r-m**	**Rain**	Mean	SE	Mean	SE	***P***
Double-spurred Spurfowl	*Pternistis bicalcaratus*	gran	r	570	0.001	0.001	0.017	0.004	*
Speckled Pigeon	*Columba guinea*	gran	r	708	0.003	0.001	0.012	0.001	
European Turtle Dove	*Streptopelia turtur*	gran	m	407	0.000	0.000	0.016	0.000	
African Collared Dove	*Streptopelia roseogrisea*	gran	r	507	0.022	0.009	0.065	0.009	**
Mourning Collared Dove	*Streptopelia decipiens*	gran	r	770	0.019	0.003	0.031	0.003	
Vinaceous Dove	*Streptopelia vinacea*	gran	r	754	0.128	0.018	0.159	0.018	
Laughing Dove	*Spilopelia senegalensis*	gran	r	537	0.252	0.046	0.107	0.046	**
Black-billed Wood Dove	*Turtur abyssinicus*	gran	r	825	0.030	0.003	0.048	0.003	
Namaqua Dove	*Oena capensis*	gran	r	432	0.082	0.013	0.245	0.013	**
Black-headed Lapwing	*Vanellus tectus*	ins	r	494	0.017	0.006	0.050	0.006	*
Eurasian Hoopoe	*Upupa epops*	ins	rm	484	0.011	0.002	0.017	0.003	
Northern Red-billed Hornbill	*Tockus erythrorhynchus*	ins	r	663	0.080	0.015	0.130	0.012	
Abyssinian Roller	*Coracias abyssinicus*	ins	r	647	0.025	0.003	0.022	0.003	
Black-crowned Tchagra	*Tchagra senegalus*	ins	r	622	0.011	0.004	0.028	0.004	*
Yellow-billed Shrike	*Corvinella corvina*	ins	r	820	0.020	0.009	0.028	0.009	
Great Grey Shrike	*Lanius excubitor*	car	r	308	0.013	0.003	0.025	0.003	**
Woodchat Shrike	*Lanius senator*	ins	m	426	0.043	0.004	0.033	0.004	
Piapiac	*Ptilostomus afer*	g+i+f	r	635	0.021	0.013	0.001	0.013	
Black-crowned Sparrow-Lark	*Eremopterix nigriceps*	gran	r	297	0.067	0.029	0.149	0.029	
Chestnut-backed Sparrow-Lark	*Eremopterix leucotis*	gran	r	502	0.138	0.026	0.139	0.026	
Singing Bush Lark	*Mirafra cantillans*	ins	r	438	0.022	0.005	0.032	0.007	
Greater Short-toed Lark	*Calandrella brachydactyla*	ins	m	180	0.002	0.052	0.019	0.052	
Red-pate Cisticola	*Cisticola ruficeps*	ins	r	664	0.024	0.004	0.059	0.004	**
Cricket Warbler	*Spiloptila clamans*	ins	r	323	0.044	0.008	0.057	0.008	
Brown Babbler	*Turdoides plebejus*	ins	r	835	0.013	0.007	0.050	0.007	*
Greater Blue-eared Starling	*Lamprotornis chalybaeus*	i+f	r	866	0.054	0.004	0.070	0.004	
Purple Starling	*Lamprotornis purpureus*	i+f	r	811	0.090	0.019	0.046	0.019	
Long-tailed Glossy Starling	*Lamprotornis caudatus*	i+f	r	743	0.044	0.014	0.049	0.014	
Chestnut-bellied Starling	*Lamprotornis pulcher*	ins	r	382	0.235	0.037	0.181	0.037	
Black Scrub Robin	*Cercotrichas podobe*	ins	r	429	0.019	0.004	0.067	0.004	***
Rufous-tailed Scrub Robin	*Cercotrichas galactotes*	ins	rm	557	0.019	0.003	0.049	0.004	***
Northern Wheatear	*Oenanthe oenanthe*	ins	m	450	0.041	0.004	0.071	0.004	***
Isabelline Wheatear	*Oenanthe isabellina*	ins	m	463	0.017	0.004	0.041	0.004	*
Black-eared Wheatear	*Oenanthe hispanica*	ins	m	335	0.003	0.001	0.012	0.001	***
Sahel Bush Sparrow	*Gymnoris dentata*	g+i	r	869	0.017	0.006	0.035	0.005	
North. Grey-headed Sparrow	*Passer griseus*	gran	r	555	0.395	0.094	0.313	0.034	
House Sparrow	*Passer domesticus*	gran	r	322	0.025	0.009	0.010	0.009	
Sudan Golden Sparrow	*Passer luteus*	gran	r	369	1.243	0.201	1.414	0.201	
White-billed Buffalo Weaver	*Dinemellia dinemelli*	g+i	r	442	0.170	0.048	0.097	0.023	
Chestnut-cr. Sparrow-Weaver	*Plocepasser superciliosus*	gran	r	815	0.002	0.001	0.012	0.002	
Speckle-fronted Weaver	*Sporopipes frontalis*	gran	r	530	0.248	0.029	0.277	0.029	
Vitelline Masked Weaver	*Ploceus vitellinus*	g+i	r	623	0.106	0.030	0.113	0.030	

Table 2. Continued.

					Farmland		Savannah		
Bird species		**Food**	**r-m**	**Rain**	Mean	SE	Mean	SE	***P***
Village Weaver	*Ploceus cucullatus*	gran	r	841	0.002	0.000	0.009	0.000	
Red-billed Quelea	*Red-billed Quelea*	gran	r	696	0.151	0.413	1.009	0.413	
Northern Red Bishop	*Euplectes franciscanus*	gran	r	908	0.040	0.001	0.130	0.063	
African Silverbill	*Euodice cantans*	gran	r	364	0.174	0.044	0.088	0.044	
Black-rumped Waxbill	*Estrilda troglodytes*	gran	r	682	0.090	0.022	0.102	0.022	
Cut-throat Finch	*Amadina fasciata*	gran	r	600	0.019	0.005	0.087	0.005	
Red-cheeked Cordon-bleu	*Uraeginthus bengalus*	gran	r	717	0.454	0.063	0.688	0.059	
Green-winged Pytilia	*Pytilia melba*	gran	r	615	0.017	0.005	0.032	0.005	
Red-billed Firefinch	*Lagonosticta senegala*	gran	r	669	0.066	0.019	0.047	0.019	
Sahel Paradise Whydah	*Vidua orientalis*	gran	r	668	0.002	0.001	0.011	0.001	
Western Yellow Wagtail	*Motacilla flava*	ins	m	593	0.024	0.014	0.011	0.014	
Tawny Pipit	*Anthus campestris*	ins	m	362	0.008	0.003	0.015	0.003	
White-rumped Seedeater	*Crithagra leucopygia*	gran	r	669	0.050	0.009	0.022	0.009	
Gosling's Bunting	*Emberiza goslingi*	gran	r	742	0.002	0.001	0.009	0.002	
Golden-breasted Bunting	*Emberiza flaviventris*	gran	r	675	0.008	0.002	0.013	0.002	
TOTAL					4.924		6.667		

Photo 2. Two pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in central Senegal, south of Kaffrine, during the dry season in November 1994 (still savannah, shortly after a grass fire) and March 2010 (farmland with millet and peanut, after harvest).

Photo 3. When the landscape in the Sahel has some relief, farming is usually restricted to the valleys (here Sourou Valley in E. Mali in the early dry season; photo by Richard Julia), where the sediment is slightly more clayey and more resistant to water runoff than on sandy hill slopes with shallow soils or rocky outcrops (in the background).

farming on granivorous and insectivorous birds was not evident in our data because so much farmland was under fallow.

There are two reasons to assume that the actual impact of the conversion of natural savannah to farmland is larger than our bird counts indicate. First, Pringle *et al.* (2019) in Zimbabwe found an increase in small (<150 g) bird species, but a decline in larger bird species after savannah was turned into farmland (see also Thiollay 2006). Our data seem at variance, but it should be noted that all bird species listed in Table 1 and 2 are small because large bird species either had already disappeared or had become very rare by the time we started our fieldwork. Second, we compared

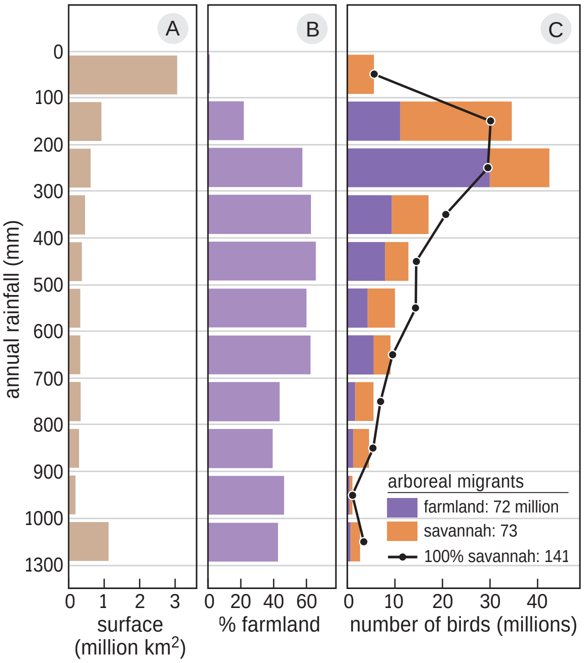

Figure 8. (A) Surface (million km^2) of farmland + savannah in 11 rainfall zones between 7 and 22°N (excluding Ethiopia). (B) Percent farmland relative to farmland + savannah (excluding woodland and Ethiopia). (C) Estimated number of insectivorous arboreal migrants feeding in woody vegetation. The black line gives the predicted numbers if the original savannah had not been partly converted to farmland.

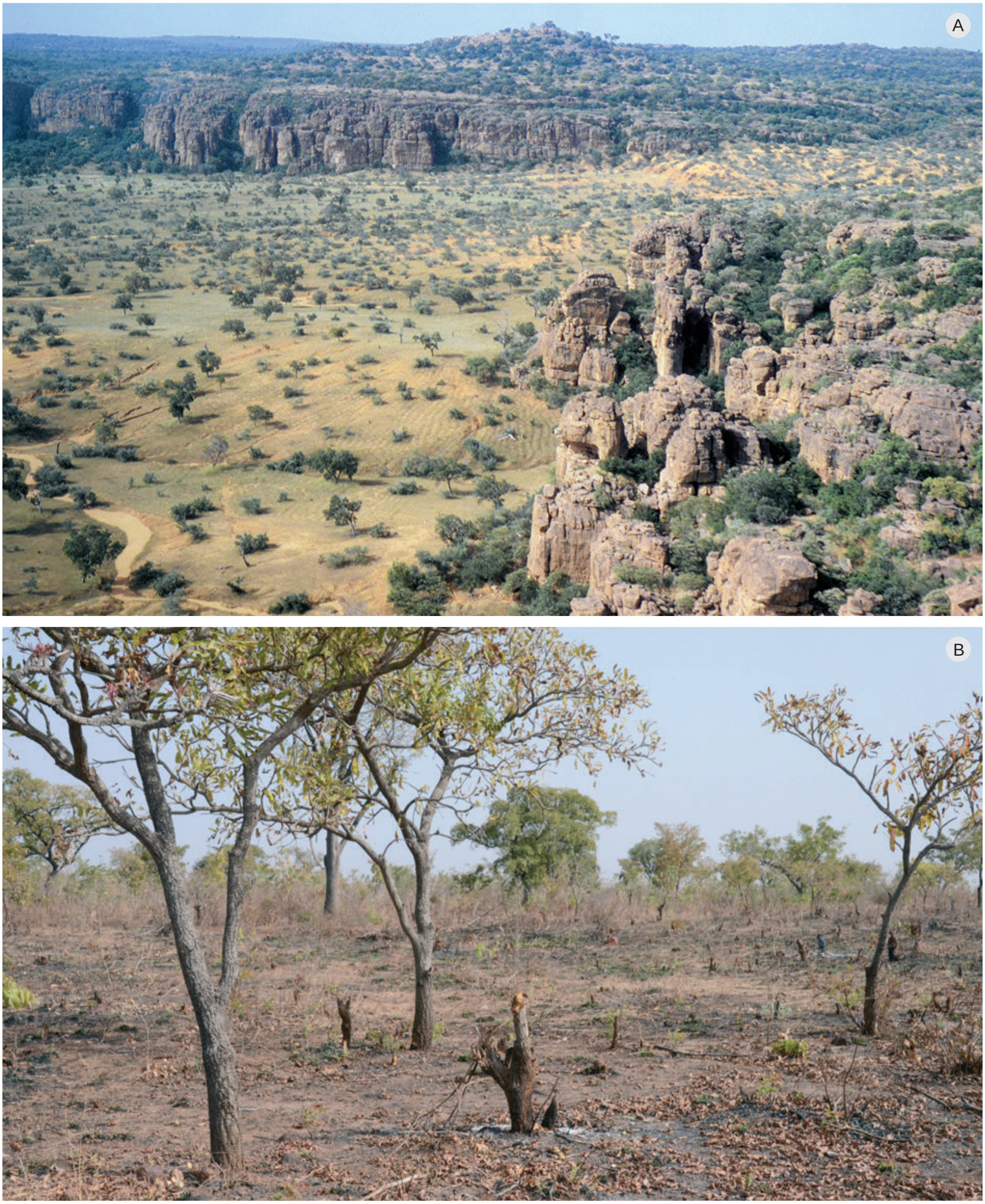

Photo 4. (A) Semi-arid savannah in eastern Mali near the Bandiagara escarpment has been mainly converted into agricultural land (see plow tracks), but tree density is about the same as on the remaining savannah (photo G. Gray Tappan, U.S. Geological Survey, EROS Center, USA) (B) To facilitate agriculture in the woody humid zone, farmers cut down and burn the woody vegetation to create a more open landscape (S. Mali; 11.42°N, 6.73°W). Note that the few remaining woody plants are Shea trees *Vittelaria paradoxa*. In the humid zone the conversion of savannah into agro-forestry parkland has a larger negative impact on arboreal birds than in the arid zone (Figure 6).

bird densities between existing savannah and farmland and not densities before and after conversion of the land; the latter comparison might have yielded bigger losses. To make a fair comparison between farmland and savannah, we excluded stony sites (5.0% and 21.2% of the sites with farmland and savannah, respectively), but other differences in soil composition between farmland and savannah remained, particularly for sandy/clayey soils. For example, conversion of savannah into farmland is often deployed in topographic depressions where the soil is relatively fine-grained, rather than on hillsides which comprise coarse, sandy soil (Photo 3). Also, farmland established in seasonal floodplains or near water courses always attracts many birds. The savannah nearby will most likely have poor soils less conducive to farming (e.g. Hiernaux *et al.* 2009). This difference in productivity is further exacerbated by enriching arable land with manure collected from nearby savannah used as rangeland.

The shift in food supply following the conversion of savannah into farmland has a bearing on the respective bird communities (though needs better quantification where food resources are considered), but it is probably not the sole explanation. Many more changes have taken place in the wake of increasingly intensive human exploitation: more people, houses, tracks, dogs, chickens and other livestock can be found on farmland than on savannah. This may have had an additional effect on birds (Pringle *et al.* 2019). Our savannah sites were indeed more remote than our farmland sites. The average distance to the nearest house was 1273 ± 1523 m (±SD, n = 846) for savannah sites and 697 ± 1069 m (n = 879) for farmland sites, excluding the sites in the <200 m rainfall zone (using the data from Figure S47 in Zwarts *et al.* 2023a).

The rate at which farmland in the Sahel and neighbouring vegetation zones has expanded since the 1960s varied locally between 0.7% per year in Senegal (Tappan *et al.* 2004), 2% in SW Niger (Hiernaux *et al.* 2009) and 3.9% in SW Burkina Faso (Augusseau *et al.* 2006). For West Africa overall it is estimated at 2% (CILSS 2016). Agricultural expansion has levelled off in areas where nearly all suitable land is under cultivation, but is unabated in 'empty' quarters, for example in Senegal in the most northern semi-arid regions and in the humid southern parts of the country (Tappan *et al.* 2004, CILSS 2016). Expansion of farmland in the semi-arid zone signifies loss of wintering habitat for arboreal Palearctic birds like Western Orphean Warblers, and similarly in the south for residents and for such migrants as Willow Warblers.

Half of the arboreal migrants (Figure 8C) and 37% of the ground-foraging migrants spend the northern winter in the Sahel on farmland. The future of more than twenty Eurasian species depends on how farmers in the Sahel continue to manage their agricultural parkland. The expansion of farmland has not yet been accompanied with serious intensification of agricultural practices. However, the increasing shortage of suitable arable land has resulted in shorter fallow cycles in the crop-fallow rotation system (e.g. Augusseau *et al.* 2006, Hiernaux *et al.* 2009), with possible negative impacts on birds. In Europe, it was not the expansion of agricultural land as such that caused substantial declines in birds, but rather the large-scale changes of agricultural practices in the second half of the 20th century (Newton 2017). This may yet happen in Africa.

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SAMENVATTING

Tientallen trekvogelsoorten, waarvan er vele sterk zijn afgenomen, overwinteren in de Sahel, van nature een uitgestrekte savanne die inmiddels voor de helft is omgevormd tot landbouwgrond. Welk effect heeft deze grootschalige verandering in landgebruik gehad op de vogels voor wie het gebied tijdelijk of permanent het leefgebied is? Zou de achteruitgang misschien deels kunnen worden verklaard door die conversie, gezien ook de afhankelijkheid van bomen als bron van voedsel voor de meeste trekvogels? Op boerenland staan namelijk minder bomen dan op de savanne, gemiddeld zelfs 38% minder. Nog belangrijker dan een afname van bomen sec bij de omzetting van savanne in akkerland is het feit dat de boeren bepaalde boomsoorten systematisch hebben weggehaald en andere hebben laten staan of hebben aangeplant. In de aride en semiaride zone hebben zij voor vogels aantrekkelijke bomen als *Acacia tortilis* en Woestijndadel *Balanites aegyptiaca* gedeeltelijk verwijderd. Meer naar het zuiden hebben de boeren echter een rijk vogelhabitat gecreëerd door de oorspronkelijke bomen te vervangen door *Faidherbia albida*, een acaciasoort die favoriet is bij trekvogels (en in mindere mate ook bij lokale vogels). Nog verder naar het zuiden, in de meer humide zone, is vooral de Karitéboom *Vitellaria paradoxa* in het boerenland gaan overheersen, een bij uitstek voor vogels onaantrekkelijke boomsoort; deze omslag heeft veel leefgebied, hoofdzakelijk van lokale vogelsoorten, verloren doen gaan. Al deze veranderingen hebben ertoe geleid dat boom- en struikbewonende vogelsoorten in de noordelijke aride zone en in de zuidelijke humide zone aanzienlijk terrein hebben verloren, maar in de tussenliggende sub-humide zone vooralsnog hebben geprofiteerd van de omzetting. Voor de vogels die op de grond foerageren, liggen de zaken anders. Die zijn talrijker op de savanne dan op landbouwgrond: 24 vogelsoorten (waaronder drie tapuitensoorten) waren meer dan tweemaal zo talrijk op de savanne als op landbouwgrond. Vijf soorten echter (waaronder de Gele Kwikstaart *Motacilla flava*) waren meer dan tweemaal zo talrijk op landbouwgrond als op de savanne (met de kanttekening: mits in de buurt van water). Per saldo kan de omzetting van savanne in landbouwgrond als habitatverlies voor vogels worden aangemerkt, maar dat geldt dus niet voor alle soorten. Bedenk daarbij dat de landbouw in Afrika nog betrekkelijk extensief is; intensivering onder invloed van stijgende bevolking kan de zaken op den duur drastisch negatiever laten uitpakken.

RÉSUMÉ

Des dizaines d'espèces d'oiseaux migrateurs, dont beaucoup ont fortement décliné, hivernent au Sahel. Cette vaste zone était originellement une savane, mais la moitié a déjà été convertie en terres agricoles. Quel effet ce changement à grande échelle de l'utilisation des terres a-t-il eu sur les oiseaux qui l'habitent en permanence ou temporairement ? Leur déclin pourrait-il s'expliquer en partie par cette conversion, compte tenu de la dépendance de la plupart de ces espèces à des habitats arborés ou arbustifs ? En moyenne, les terres agricoles accueillent en effet 38% d'arbres en moins que la savane et, plus préjudiciable encore, les agriculteurs ont systématiquement éliminé certaines essences et les ont remplacées par d'autres. Dans la zone semiaride, notamment, ce sont des arbres très attractifs pour les oiseaux comme l'Acacia faux-gommier *Acacia tortilis* et le Dattier du désert *Balanites aegyptiaca* qui en ont fait les frais. A l'opposé, plus au Sud, les agriculteurs ont créé un habitat favorable en remplaçant les essences indigènes par *Faidherbia albida*, une espèce d'acacia appréciée des oiseaux migrateurs et dans une moindre mesure des oiseaux locaux. Plus au Sud encore, dans la zone plus humide, le Karité *Vitellaria paradoxa*, peu attractif pour les oiseaux, est devenu dominant dans les zones cultivées. Ce changement a entraîné d'importantes pertes d'habitats, principalement pour les espèces locales. En raison de ces changements, les espèces arboricoles ont perdu de grandes surfaces d'habitat au Sahel dans la zone septentrionale aride et dans la zone méridionale humide. Au contraire, dans la zone intermédiaire subhumide, elles en ont pour le moment bénéficié. La situation est différente pour les espèces qui se nourrissent au sol : vingt-quatre des espèces étudiées, dont trois de traquets, étaient plus de deux fois plus abondantes sur les savanes que sur les terres agricoles, alors que seulement cinq espèces (dont la Bergeronnette printanière *Motacilla flava*) étaient plus de deux fois plus abondantes sur les terres agricoles que sur les savanes. Dans l'ensemble, la conversion de la savane en terres agricoles entraîne donc une perte d'habitat pour les oiseaux, mais pas pour toutes les espèces.

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Downstream ecological consequences of livestock grazing in the Sahel: a space-for-time analysis of the relations between livestock and birds

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Bird counts in the Ferlo, NW Senegal had shown that the density of ground-foraging birds was much lower in grazed than in ungrazed savannah: 84% fewer granivorous birds and 64% fewer insectivorous birds. Between 1960 and 2010, in three areas within the same region, granivores declined by 39–97% and insectivores by 61–91%, losses attributable to the steadily increasing livestock grazing pressure. If these trends hold for all Sahelian rangelands, the extrapolation at the time indicated that 1.5 billion birds would have been lost in just half a century. The aim of this space-for-time substitution study was to investigate whether that extrapolation can be substantiated with data from the eastern Sahel. To permit analysis of the spatial and seasonal variation in grazing pressure and its impact on ground-foraging granivorous and insectivorous birds, we counted birds in 1901 sites across the entire region (Mauritania to Ethiopia) and took landscape photos of these sites to evaluate livestock presence. We also estimated livestock density from our counts of cowpats and of droppings of sheep and goats, and the cover of the soil vegetation. Within the same rainfall zone (200–400 mm/year), the grazing pressure was higher in the Ferlo than elsewhere in the Sahel. Grazing pressure declined in the Ferlo in the course of the dry season, indicating that cattle food supply became depleted. No such seasonal decline was recorded elsewhere in the Sahel. The same pattern was found for ground-foraging birds: a decline during the dry season in the Ferlo, but nowhere else in the same Sahel rainfall zone. Indeed, in the 1960s and 1970s, when the grazing pressure was much lower than today, there were no records of a seasonal decline of ground-foraging birds in the Ferlo. The much lower densities of seed-eating birds in the Ferlo were not exhibited elsewhere in the Sahel, which is consistent with the phenomenon of local overgrazing. The previous extrapolated loss of 1.5 billion birds is therefore too high, because conditions in the Ferlo were found to differ from those experienced elsewhere in Sahel's arid zone. The actual overall loss cannot be specified due to lack of bird counts from the past in the eastern Sahel. The comparison of grazing pressure and bird densities across all rainfall zones of the western and eastern Sahel shows that increasing livestock densities negatively impact bird numbers. Livestock grazing pressure in the west was higher than in the east and most ground-foraging bird species were less common in the west than in the east. Furthermore, the majority of ground-foraging species in West Sahelian savannahs were exclusively confined to the arid and semi-arid zone, but in the east, these species were more widely distributed and also occupied the more humid zone to the south.

Key words: Sahel, livestock, ground-foraging birds

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With a land surface of 30 million km^2, Africa is a large continent that is home to millions of long-distance migratory birds from Europe and Asia in winter (Moreau 1972). The question to what extent the decline of many European breeding populations of migratory birds is due to changes in their African wintering grounds has proven difficult to answer (Salewski & Jones 2006, Sanderson 2006, Zwarts *et al.* 2009, Morrison *et al.* 2013, Adams *et al.* 2014, Atkinson *et al.* 2014). Deforestation, conversion of savannah into cropland, and short- and long-term changes in annual rainfall act on vast geographic scales and are no doubt major factors in the fortunes of long-distance migrants. This paper investigates another factor that might have a large negative impact on migratory bird numbers: the overall increase of livestock. In particular, the region between 7 and 22°N, an area of 10 million km^2, has experienced significant increases in the numbers of grazing herds of cows, goats and sheep since at least 1960. For instance, FAO data (www.fao.org/faostat/en/#data/TP) showed that cattle numbers in 21 countries, fully or partly situated between these latitudes, on average have increased exponentially by 2.30% per year, from a total of 60 million in 1961 to 231 million in 2019. Sheep increased by 2.78% per year from 50 million in 1961 to 256 million to 2019, goats by 3.45% per year from 45 to 311 million. The accuracy of the FAO data is uncertain, but there can be no doubt that grazing pressure is mounting, driven by the 2.61% annual increase of the human population in the same 21 countries, from 106 million in 1950 to 607 million in 2020 (https://esa.un.org/unpd/wpp). In fact, Bonnet-Dupeyron's (1945) estimate for the same region (excluding Sudan and Ethiopia) in the early 1940s amounted to only 7 million cattle, an indication that cattle numbers have been increasing for a long time indeed.

Grazing alters the age structure and density of the vegetation and the species composition of the plant community (Chapin *et al.* 2002). Such changes have substantial impact on breeding and foraging birds in multiple ways (e.g. Barzan *et al.* 2021). The impact of grazing is evident in semi-arid and humid tropical areas where in the absence of livestock, savannah turns into acacia woodland within a brief period of time (Photo 1D). In contrast, when arid areas lack domestic grazing, a savannah landscape with scattered trees will hardly change (Photo 1B). This does not imply, however, that grazing on savannahs in the arid zone does not affect foraging birds. In the Sahel, as in other drylands, grasses and forbs grow during the short rainy season after which they die back; during this stage seeds ripen and are shed. For example, in Argentinian drylands, seed density on the ground during the dry season was 74% lower in grazed sites than in ungrazed, and the density of seed-eating finches was 48% lower (Gonnet 2001). In heavily grazed sites, seed density was reduced by 95% and bird density by 70%. The finches preferred grass seeds, taking 52–92% of the annual production during the dry season (Pol *et al.* 2014). When the density of preferred seeds became too low, some birds switched to other food resources, but most dispersed to other places (Marone *et al.* 2017). In Britain, nine ground-foraging bird species in winter foraged in lower densities when seed density had become depressed, sites being abandoned when seed density dropped too low (Stephens *et al.* 2003).

During the long dry season (October–June), the seeds produced by annual grasses and forbs in the Sahelian savannah are the only food resource for many ground-foraging bird species (Keith *et al.* 1992, Fry & Keith 2004). In Fété Olé, a site in the arid north of Senegal, on average, 80 grasses and forbs per m^2 produce 50,000 seeds at the end of the rainy season. Nine months later at the start of the next rainy season, 500 seeds per m^2 remain to germinate. Only 80 seeds/m^2 survive to begin the next annual cycle (Bille 1992). Rodent predation is a prime cause of the 90% decline of seeds during the dry season (Poulet 1974), followed by birds (Morel & Morel 1970, 1972a) and insects (Gillon & Gillon 1974; Gillon *et al.* 1983). The annual variation in seed predation is large and is dependent mostly on the variation of annual rainfall (Bille 1974). In dry years with low seed production, many seed-eating birds die, and the survivors are in poor condition and often unable to breed (Morel & Morel 1974). When grazing pressure structurally reduces seed availability, bird populations of granivorous birds will decline (Zwarts *et al.* 2023c).

Previous research had shown that in the Ferlo granivorous birds had declined by 39–97% and insectivorous birds by 61–91% over the last 20–50 years (Zwarts *et al.* 2018). Bird counts from 20–50 years ago, such as performed in the Ferlo (Supplementary Material), have not been carried out elsewhere in the Sahel, at least to our knowledge. We therefore do not know whether birds in the Sahel have declined as much as in the Ferlo, but if they have done so, the implications would be large, given the size of the Sahel, which extends by 6000 km from the Atlantic Ocean to the Red Sea. If the birds in the Sahel have declined as much as in the western Ferlo, an extrapolated 1.5–2 billion birds, among which 300–400 million Afro-Palearctic migrants, would have been lost in just half a century (Zwarts *et al.* 2018).

However, the Ferlo may not be representative of the arid Sahelian savannah at large. First, the western Sahel is more densely populated than the eastern Sahel (see Figure 8 in Zwarts *et al.* 2023a). Second, the grazing pressure in NW Senegal may be especially high because of the proximity of the Senegal River and seasonal waterbodies (see Photo 1 in Zwarts *et al.* 2023c). Third, the density of large, mechanised boreholes in the western Ferlo is unprecedented, facilitating the conversion of remote drylands into grazing grounds (Photo 2).

In this paper we use a space-for-time approach (i.e. analysing spatially separated sites where environmental gradients serve as proxies to understand temporal processes) to re-examine the hypothesis that livestock grazing reduces ground-foraging bird populations in the Sahel. We compare recent bird densities and grazing pressure of the Ferlo with those elsewhere in the Sahel, and also of the western and eastern Sahel, under the assumption that grazing is the main cause of declines of ground-foraging birds.

Photo 1. Grazed and ungrazed savannah during the dry season; average annual rainfall (based on Hijmans *et al.* 2005) is given on each image. (A) The history of this Mauritanian exclosure is unknown. (B) In the NW Senegal site, livestock had been excluded from the fenced area since 1992 (Miehe 2007), 22 years before the picture was taken. The density of seed-eating birds in the exclosure was six times higher than in the grazed area beyond the fence. (C) When the picture was taken, this exclosure in Mali was less than two years old (visible on Google Earth on 10 January 2008, but not on 15 April 2007). Note the high density of cowpats on the bare ground in the grazed areas of A, B and C. (D) A fence with a track on both sides separates open savannah (with tall baobabs) grazed daily by livestock from a nearby village (left of the fence) and woody savannah (with low Red Acacia *Acacia seyal*) in the West Senegal Bandia Reserve (right of the fence), subject to low grazing pressure of wild herbivores. Satellite photos from 1968 and high-resolution satellite images available since 2003 show that a densely wooded savannah in 1968 has turned into an almost bare savannah in 2003, but since the construction of the fence in 2004, the Bandia Reserve transformed back into a densely wooded savannah within a few years (Hejcmanová *et al.* 2009, Zwarts *et al.* 2015).

METHODS

For a Sahel-wide comparison of grazing and bird numbers we have data at our disposal that were collected in 2144 study sites between 7 and 22°N and between 17°W and 42°E between 2011 and 2019 (Zwarts *et al.* 2023a). At each site, we counted birds and trees in triangular transects with three legs of 300 by 50 m each (Figure 2 in Zwarts *et al.* 2023a); methods are described in detail by Zwarts & Bijlsma (2015). All sites were categorised as woodland, farmland (including fallow) or savannah (including desert, scrubland and woody savannah). This study is based on a selection of savannah sites, excluding those few sites that comprised rocky or stony soil. For the description of the average bird density per rainfall zone and/or longitudinal band, we used only random sites. Unless stated otherwise, we selected data collected in the dry season (20 November – 10 March; most data collection occured in January and early February, but we excluded data from Ethiopia. In the strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a much wider sense as covering the full transition zone between Sahara in the north and the humid forests in the south.

We visited the western Ferlo more frequently than the rest of the Sahel (January and December 2014, February–March and October 2015 and October 2019), not least to compare the recent situation with the one described in great detail for the 1960s, 1970s and 1990s (Figure 1, Supplementary material; see also Zwarts *et al.* 2018). The average annual rainfall in this region varies between 200 mm in the north (16.5°N) and 400 mm in the south (15°N). The data collected in the western Ferlo are compared to other study sites in sandy savannahs of the 200 to 400 mm rainfall zone between Senegal and Sudan. The average annual rainfall (calculated over the period 1950–2000) per site was taken from Hijmans *et al.* (2005) and does not deviate, on average, from the rainfall during our period of observation (2011–2019). Rainfall (in mm) preceding our visits in the Ferlo and in the dry zone of the rest of the Sahel varied little over the years of our study, except in 2010 (much rain) and 2013 (little rain). The annual rainfall during the four years when we visited the Ferlo did not differ, on average, from the seven years when we did fieldwork in the same rainfall zone elsewhere in the Sahel.

We used various methods to quantify the presence of livestock, the grazing pressure, and its impact on the ground vegetation:

Photo 2. In the past, large parts of the Sahelian savannah were left ungrazed by livestock in the dry season due to lack of water. Grazing was limited to river valleys and emerging floodplains and their surroundings, up to a walking distance of 5–10 km from watering points. After the construction of mechanised boreholes (watering points), much larger areas could be grazed in the dry season. This further increased in the 1980s when people started to use donkey carts to transport water to the animals. The photo, taken in the western Ferlo on 30 October 2015, shows that the ground vegetation has already completely disappeared early in the dry season. 1000-litre containers are better for transporting water than using large inner tubes, the method prevalent when donkey carts had become the popular method of water transportation.

(1) To quantify the presence of livestock, we used landscape photos we had taken of the study sites. Regarding the presence of livestock, we consider these images to be unbiased, because our primary purpose was to document per site the landscape and its constituent trees, the latter to validate our field measurements of tree dimensions. For each study site, we noted the presence or absence of livestock (cattle, goats, sheep or dromedaries), enumerating the images in each category; when more than one photo was taken of the same scene, we selected the first one.

(2) To quantify the grazing pressure within the study sites, at each 100 m of transect, we counted the number of small droppings of goats and sheep and cowpats per 4 m^2.

(3) To quantify the vegetation cover in the study sites, we estimated the percentage of the soil surface covered by vegetation within a square of 2 × 2 m, irrespective of greenness (including dried vegetation and leftovers from harvest), standing or lying, and crops or natural vegetation. Two by two meter plots were chosen at intervals of c. 100 m, on average 9.7 squares per site.

RESULTS

Grazing, vegetation and birds in the Ferlo compared to the rest of the Sahel

GRAZING AND VEGETATION

The photos from our study sites revealed that cattle density in the western Ferlo, averaged for the entire dry season, was quite similar to that elsewhere in the Sahel in the same rainfall zone (200–400 mm/year; 5.1 vs. 4.8% of the pictures; one-way ANOVA: $P > 0.05$, $n = 1754$). However, seasonal differences in the Ferlo were large. In the western Ferlo cattle density was high in the early dry season (livestock visible on 7.4% of the pictures in October–December), declining to 0.8% in February–March ($\chi^2_1 = 4.1$; $P = 0.01$). Elsewhere within the same rainfall zone, the number of cattle visible on the photos remained constant during the dry season. Goats and sheep were more common in the Ferlo than elsewhere (14.8 vs. 9.5%; $\chi^2_1 = 15.4$; $P < 0.001$), with a weak increase between October and March ($P < 0.001$) in the Ferlo ($\chi^2_2 = 15.4$) and elsewhere ($\chi^2_1 = 14.7$).

Counts of cowpats showed that the grazing pressure in the Ferlo, averaged for October–March, was somewhat higher than elsewhere in the rainfall zone of 200–400 mm (2.95 vs. 2.76/4 m^2; one-way ANOVA: $P = 0.01$), and significantly different between months (2-way ANOVA: $n = 3036$, $P = 0.006$). Beyond the western Ferlo, the density of cowpats linearly increased from 0.23 in October to 4.43/4 m^2 in March. Cowpat density in the Ferlo only increased between October and December; after December, the density of cowpats remained stable. For goats and sheep, the density of their droppings increased non-significantly during the dry season and was higher in the Ferlo than elsewhere (9.83 vs. 8.16/m^2; 2-way ANOVA: $n = 1750$, $P = 0.001$).

The vegetation cover declined over the dry season and was overall sparser in the western Ferlo (8.4 vs. 16.2%; Figure 1; see also Photo 1B). The three data sets (pictures, cowpats, vegetation) show the western Ferlo to be more intensively grazed than the rest of our arid study zone. In the western Ferlo, grazing pressure was particularly high in the first months of the dry season (October–December), resulting in a complete loss of ground vegetation. In this area, most herders and their cattle had left by January.

BIRDS

The density of granivorous birds in the western Ferlo was much lower than elsewhere in the arid zone (Table 1). The difference was most striking for Sudan Golden Sparrow *Passer luteus* (0.37/ha in the Ferlo vs. 2.70/ha elsewhere; one-way ANOVA: $n = 255$, $P = 0.02$) and African Silverbill *Euodice cantans* (0.01 vs. 0.20; $P = 0.03$). For several dove species the differences were small (e.g. Namaqua Dove *Oena capensis*: 0.32 vs. 0.40, Laughing Dove *Spilopelia senegalensis*: 0.11 vs. 0.17). The density of insectivorous birds in the Ferlo did not differ from elsewhere in the arid zone. In the Ferlo, bird densities declined during the dry season (Table 1), but no such trend was found elsewhere in the arid zone (based on bird densities averaged for five months between September and March).

Grazing, vegetation and birds across the Sahel

GRAZING AND VEGETATION

The presence and composition of livestock differed per rainfall zone and longitudinally (Figure 2). In the western Sahel, dromedaries were restricted mostly to the arid zone (<200 mm rainfall/year) while cattle, goats and sheep were more common in the zone with 200–600 mm rainfall/year. In the eastern Sahel, all livestock species roamed extensively across the 200 to 1100 mm rainfall/year zones, but at a lower density. In the western Sahel, cattle and goats+sheep were twice as common as in the eastern Sahel.

The density of cowpats showed a similar trend to livestock presence across the Sahel. In the western

Sahel, cowpat density was three times higher than in the eastern Sahel (Figure 3). The density of droppings of goats and sheep increased from 1.73/4 m^2 at <100 mm rainfall/year to 20.5/4 m^2 at 200–300 mm, and linearly declined in the more humid zones to 3.5/4 m^2 at 900–1000 mm. Rainfall was strongly correlated ($P < 0.001$) to density of droppings; land use, longitude and their interaction terms were not significant (3-way ANOVA: $r^2 = 0.109$; $n = 495$ sites).

BIRDS

The density of ground-foraging birds increased with the rainfall gradient but in the western Sahel lower densities were recorded in the humid zone than in the eastern Sahel (Figure 4). The single exception, recorded in a single grid cell in the western 1000–1100 mm rainfall zone (Figure 4A), refers to high numbers of seedeaters in the Comoé National Park (Côte d'Ivoire) in December, which are unlikely to be representative of the humid zone in West Africa in general. Within the arid zone, bird densities did not differ much between the eastern and western halves of the Sahel (Figure 4). Differences are more pronounced when a comparison is made at species level (Table 2). The Red-billed Quelea *Quelea quelea*, for example, was rare in the Sahel when annual rainfall was less than 500 mm, and also rare in

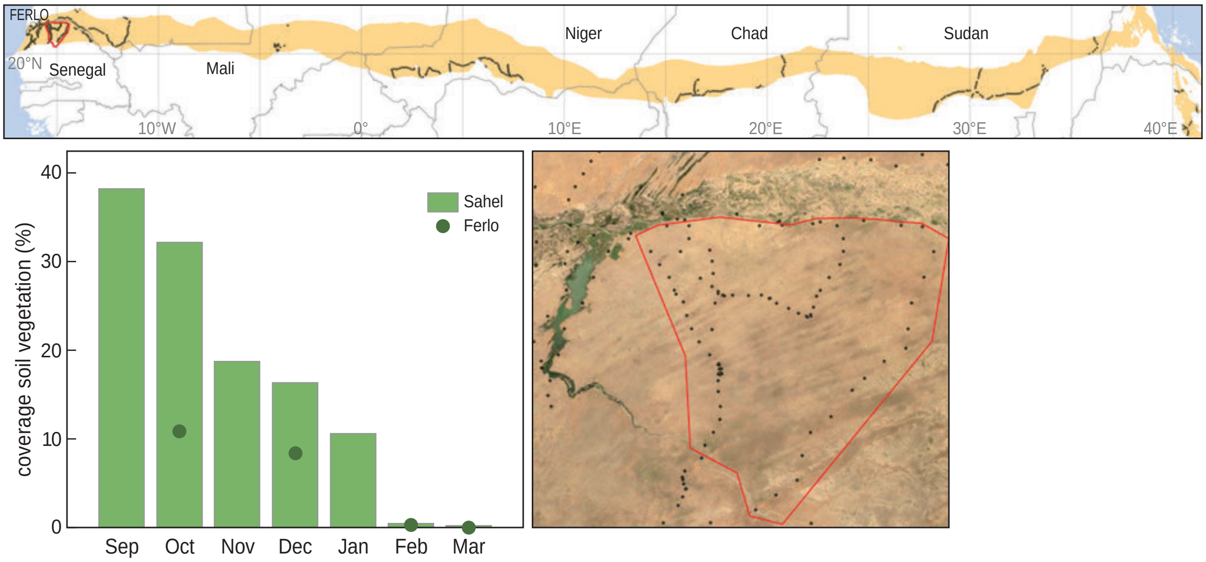
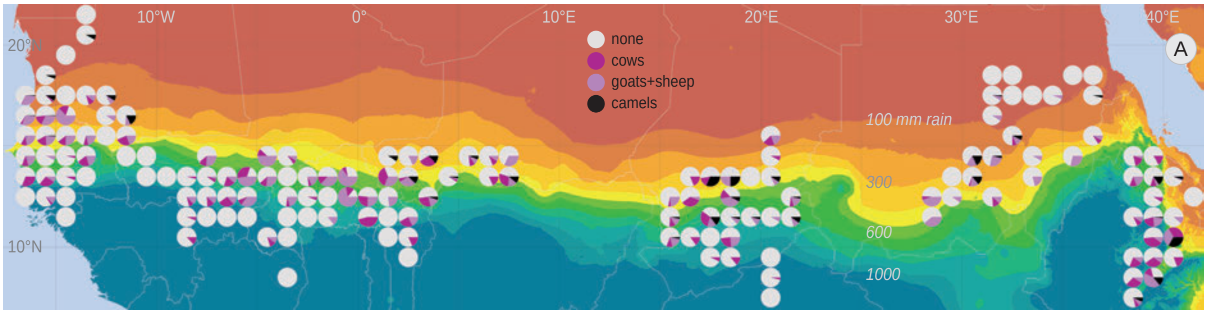


Figure 1. Seasonal decline of the vegetation cover (%) of sandy savannah during the dry season, separately for the western Ferlo and all other sites across the Sahel with an average annual rainfall of 200–400 mm/year (2-way ANOVA: season: $P < 0.001$, Ferlo: $P = 0.002$; season×Ferlo: $n = 2183$, $r^2 = 0.103$, $P < 0.001$). The map shows the study sites (•) within the 200–400 rainfall zone (yellow band). The western Ferlo is enclosed by a red line (inset).

Table 1. (Left) Average bird density per ha during the dry season (October–March) in the Ferlo and elsewhere in the Sahel on sandy savannah within the 200–400 mm rainfall zones (Figure 1), being significantly different for granivores but not for insectivores (one-way ANOVA; *P* value given in table). (Right) Bird densities of granivores and insectivores significantly declined during the dry season in the Ferlo (one-way ANOVA; *P* value given in table). In the three bird groups, there was no seasonal decline between October and March elsewhere in the arid zone (one-way ANOVA's; results not given). There were no granivorous migrants in the Ferlo and 0.064/ha elsewhere in the arid zone ($P = 0.238$).

	Sahel	**Ferlo**	***P***	**Ferlo**			***P***
	Oct–Mar	Oct–Mar		Sep–Oct	Dec	Feb–Mar	
granivorous residents	4.75	1.95	0.005	3.15	2.50	1.03	0.011
insectivorous residents	0.72	0.80	N.S.	1.34	1.06	0.38	0.003
insectivorous migrants	0.40	0.46	N.S.	0.79	0.51	0.29	0.014
Number of sites	**176**	**79**		**21**	**19**	**39**	



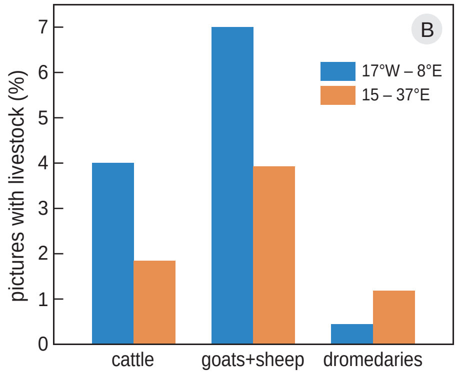


Figure 2. (A) The presence of livestock (%) across the Sahel between 20 November and 10 March, scored on 11,883 landscape photos taken in 150 grid cells (excluding woodland sites). Livestock was present on 7% of the photos, on average, and varied for the grid cells between 0 and 33%. To improve the clarity of the pie charts, the maximum percentage of livestock in the grid cells (33.3%) was set at 100%. (B) The presence of livestock on photos (%) in the western and eastern Sahel (annual rainfall <1300 mm, based on 7616 and 2446 photos, respectively. The differences are highly significant (cattle: $\chi^2_1 = 20.8$, goats+sheep: $\chi^2_1 = 22.3$, dromedaries: $\chi^2_1 = 15.59$; $P < 0.0001$).

the more humid zone in the western Sahel. In the eastern Sahel, however, Queleas reached densities of 5.4–6.2 birds/ha in the 700–900 mm rainfall zone. A similar pattern was found for the Red-cheeked Cordon-bleu *Uraeginthus bengalus*, which was uncommon in the western Sahel (<0.8/ha in the 400–800 mm rainfall zone), but common in the eastern Sahel (1.6–2.7/ha in the 500–1000 mm rainfall zone). Very few species showed a reverse pattern of lower densities in the eastern Sahel, notably Cut-throat Finch *Amadina fasciata* (Table 2). The humid zone in the eastern Sahel held many more birds than the same zone in the western Sahel (see last two columns in Table 2). This difference is not just evident for resident bird species, but also for two Wheatear species that reached their highest densities in the west in the zones between 100 and 400 mm of rainfall, and in the east between the 300- and 900-mm-rainfall zones (Figure 5). Woodchat Shrike *Lanius senator* has a more southerly distribution in the east, but the difference with the western Sahel is small. No difference was found in Tawny Pipit *Anthus campestris* (Figure 5).

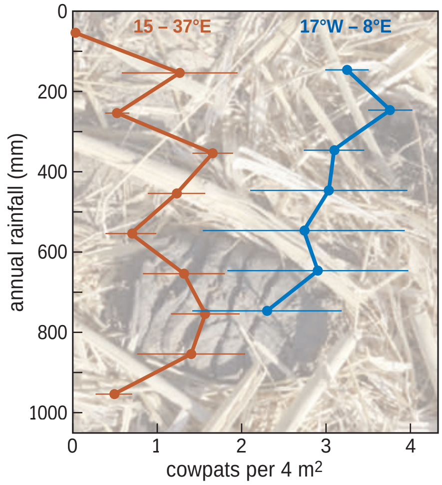


Figure 3. The average density of cowpats per 4 m^2 (±SE) on sandy savannah in the dry season, given for ten rainfall zones in the western (17°W–8°E) and eastern Sahel (15–37°E). Rainfall, longitude and their interaction term were all significant ($P < 0.001$, 2-way ANOVA: $r^2 = 0.207$, 495 sites). The graph did not change when 269 farmland sites were included; land use was non-significant ($P = 0.157$) in a 3-way ANOVA.

DISCUSSION

Decline of ground-foraging birds in the Sahel

Ground-feeding birds showed a large decline in the Ferlo since at least the 1960s, following increased grazing pressure and droughts (Zwarts *et al.* 2018). Two landscape pictures taken at the same site in 1994 and 2011 illustrate how much the savannah in NW Senegal has changed under heavy grazing in a period of just 17 years (Photo 3). Did similar changes occur in Sahelian regions further east, with similar consequences for ground-foraging birds? If so, the overall decline of ground-feeding birds must have been massive. However, the number of livestock (Figure 2) and density of cowpats (Figure 3) showed that the grazing pressure in the western Ferlo in the 2010s was higher than in the corresponding rainfall zone elsewhere in the Sahel. The exceptionally high grazing pressure explains why the ground vegetation in the western Ferlo in October had completely disappeared by December (Figure 1). No such depletion of grassy vegetation was recorded in the eastern Sahel, where

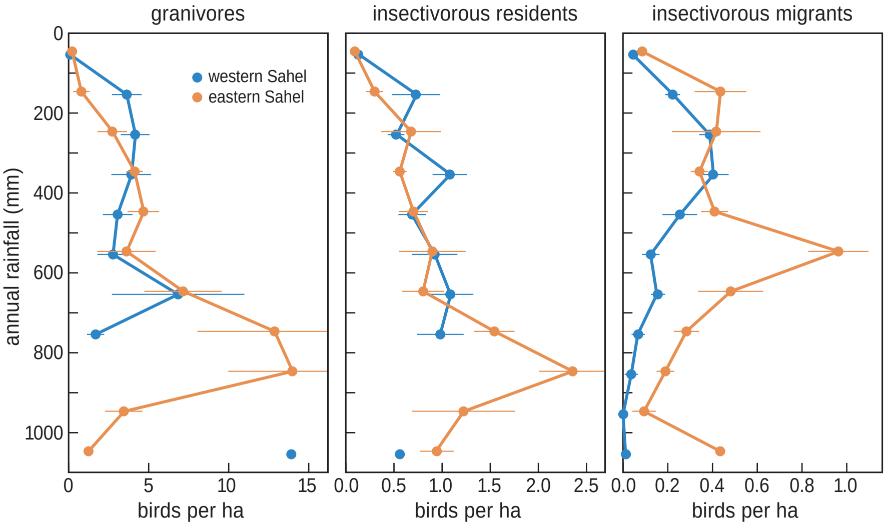
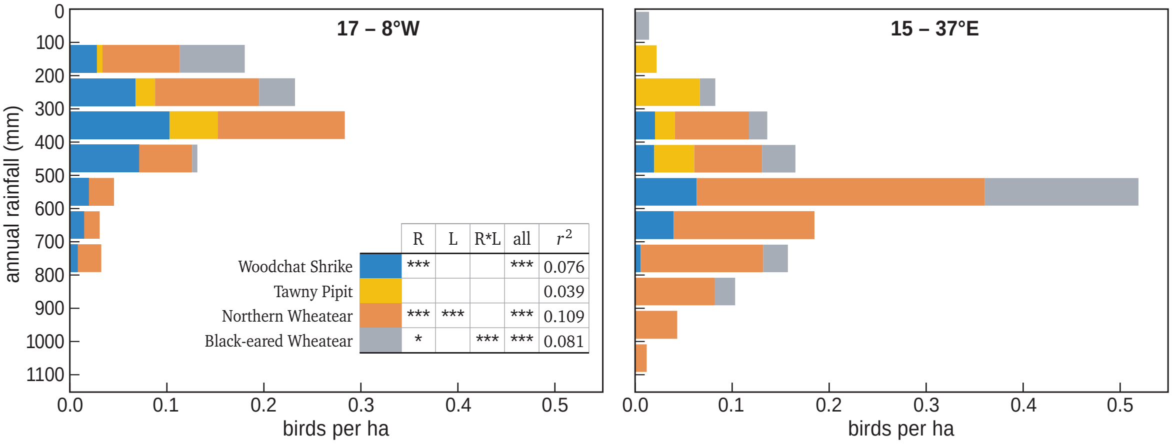


Figure 4. Density of three groups of ground-foraging birds per rainfall zone on sandy savannah in the western (17°W–8°E) and eastern Sahel (15–37°E) during winter. The effect of rainfall is significant for all three groups ($P < 0.001$), longitude only in migrants ($P < 0.001$) and the interaction term in granivores ($P = 0.042$) and migrants ($P = 0.003$); r^2 is 0.119 in granivores, 0.155 in insectivorous residents and 0.131 in insectivorous migrants (2-way ANOVA; $n = 578$ sites); note that the scales of the horizontal axes vary.



	R	L	R*L	all	r^2
Woodchat Shrike	***			***	0.076
Tawny Pipit					0.039
Northern Wheatear	***	***		***	0.109
Black-eared Wheatear	*		***	***	0.081

Figure 5. Density of four ground-foraging insectivorous migrants on sandy savannah in 11 rainfall zones, given separately for the western (left) and eastern Sahel (right). The density differed significantly per rainfall zone (R; except for Tawny Pipit), non-significantly for longitude (L; except for Northern Wheatear) and for the interaction term (R×L; except for Black-eared Wheatear *Oenanthe melanoleuca*; 2-way ANOVA; $n = 716$ sites; $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$).

the grazing pressure was much lower than in the western Ferlo.

The 70% lower density of seed-eating birds in the western Sahel compared to the rest of the arid Sahel can be explained by differences in grazing pressure and therefore by vegetation cover (Table 1). Granivorous birds and ground-foraging insectivorous birds largely left the Ferlo during the dry season (Table 1), unlike elsewhere in the same rainfall zone and in the Ferlo in the 1970s, except in an extremely dry year (Morel & Morel 1974, 1978). As the rainfall during our study period in the Ferlo did not deviate from average (Zwarts *et al.* 2015), the current situation of rapid depletion of the limited food supply will force ground-foraging birds to leave the Ferlo during the dry season, and/or cause high mortality. Our tentative conclusion is that ground-foraging birds in the Ferlo have been more negatively affected by increased grazing pressure than elsewhere in the northern Sahel. It is unlikely that bird numbers in the Sahel in general have declined quite as much as in the Ferlo, at least so far.

Table 2. The maximum average density (*n*/ha) per rainfall zone on sandy savannah in the western (W) and eastern (E) Sahel (W = 431 sites; 17°W–8°E and E = 285 sites; 15–37°E). The rainfall zones where the birds reached their maximum densities are shown in the last two columns (0 = rainfall zone 0–100 mm/year, 1 = 100–200 mm, etc.). Granivores are printed in bold. Selection is made of 34 common bird species which occur in both the eastern and western parts of the Sahel.

Bird species	**birds/ha**		**rain**	
	W	E	W	E
African Collared Dove	0.120	0.207	7	6
Vinaceous Dove	0.089	0.550	5	7
Laughing Dove	0.231	0.186	2	7
Black-billed Wood Dove	0.017	0.166	7	7
Namaqua Dove	0.463	0.264	3	7
Black-headed Lapwing	0.209	0.222	6	5
Eurasian Hoopoe	0.023	0.060	1	7
Northern Red-billed Hornbill	0.260	0.241	6	5
Abyssinian Roller	0.067	0.058	7	8
Great Grey Shrike	0.069	0.065	1	3
Woodchat Shrike	0.103	0.063	3	5
Black-crowned Sparrow-Lark	0.439	0.424	1	3
Chestnut-backed Sparrow-Lark	0.118	0.394	6	5
Greater Short-toed Lark	0.021	2.584	0	1
Cricket Warbler	0.144	0.172	1	2
Purple Starling	0.031	0.317	3	7
Long-tailed Glossy Starling	0.137	0.267	7	7
Chestnut-bellied Starling	0.468	0.286	3	4
Black Scrub Robin	0.115	0.184	3	2
Rufous-tailed Scrub Robin	0.103	0.218	6	6
Northern Wheatear	0.131	0.297	3	5
Black-eared Wheatear	0.067	0.159	1	5
Sahel Bush Sparrow	0.205	0.089	7	6
Northern Grey-headed Sparrow	0.332	0.433	3	6
Sudan Golden Sparrow	2.212	2.578	2	4
White-billed Buffalo-Weaver	0.124	0.290	3	3
Speckle-fronted Weaver	0.308	0.928	3	6
Vitelline Masked Weaver	0.621	0.415	6	6
Red-billed Quelea	1.869	6.172	6	7
African Silverbill	0.341	0.173	1	3
Black-rumped Waxbill	0.185	0.741	5	6
Cut-throat Finch	0.993	0.057	6	5
Red-cheeked Cordon-bleu	0.431	2.702	5	8
Red-billed Firefinch	0.256	0.133	7	6

Seed-eating birds and their food supply

There are several bird species in the Sahel which cling to grass stems to harvest attached seeds, such as Yellow-fronted Canary *Crithagra mozambica*, Bronze Mannikin *Spermestes cucullata* and various waxbill *Estrilda* species and seedeater *Crithagra* species (Fry & Keith 2004). Other seed-eating bird species may incidentally feed in grass tufts or pull them down to take seeds off the panicle, but most would wait until the plants shed their seeds. From then on, all granivorous birds, including the aforementioned species, forage exclusively on the ground. At first, many seeds are not yet accessible to ground-feeding birds due to the dense vegetation; the tall grasses form a blanket covering the fallen seeds (Ward 1965). By removing the standing grasses and forbs during the early dry season, grazing livestock facilitate seed-eating birds without substantially reducing the total food supply because the seeds have already been shed at the end of the wet season (Hiernaux *et al.* 2009). Timing of grazing has thus far-reaching consequences for the seed supply. Grazing during the wet season reduces seed formation and potential soil seed stocks (Sternberg *et al.* 2003), and consequently the food supply for granivorous birds. In contrast, dry-season grazing by cattle, sheep and goats does not deplete the remaining seed supply.

Our estimates of grazing pressure (counts of cowpats and droppings, presence of livestock on photos) refer to dry-season grazing and seem – in the light of the above – less relevant to ascertain the local impact of grazing on ground-foraging birds. However, overall cattle density in the western Sahel is much higher than in the eastern part, both during the wet and the dry season. For this reason, we would expect that ground-foraging birds must have declined more severely in the

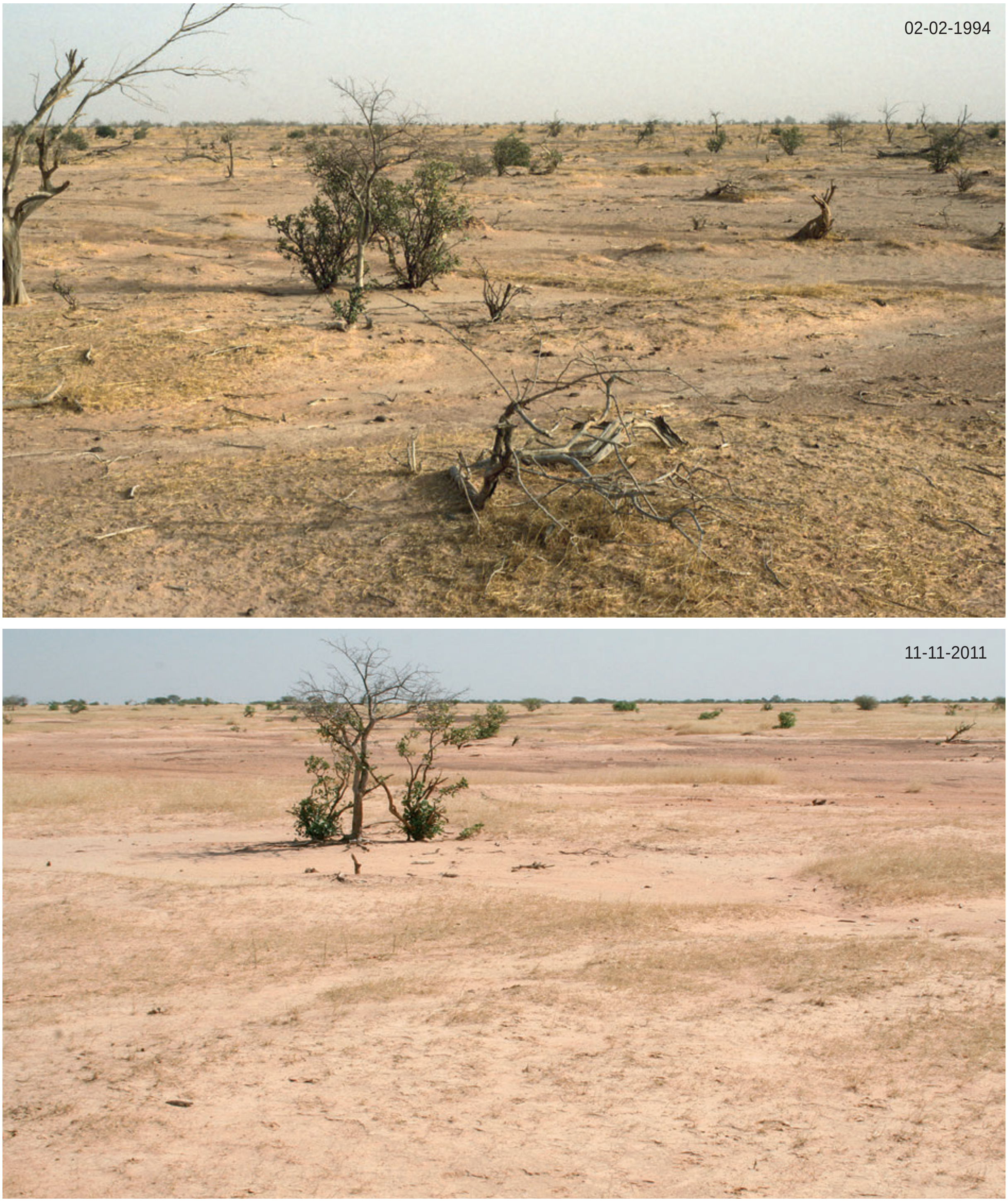


Photo 3. Two pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in the Ferlo near Révane (15.6°W, 14.4°N; average annual rainfall 390 mm) during the dry season in 1994 and 2011. The savannah with scattered trees (mainly *Acacia tortilis* and *A. senegal*) had already been transformed into an almost treeless landscape (mainly *Boscia senegalensis* bushes) before 1994 but had become even more desolate 17 years later. The extent of grassy vegetation die-back during the dry season (Figure 1), a process markedly prevalent in February 1994, is much more evident in November 2011; the difference cannot be explained by variation in annual rainfall (the same for both years; Figure 6 in Zwarts *et al.* 2018). See also www.usgs.gov/media/before-after/expansion-degraded-land-ferlo-region-senegal/.

western than in the eastern Sahel. The lack of systematic bird counts from the eastern Sahel in the past prevents any quantified statement to this effect. In the current situation (2010s), insectivorous migrants were 2–8 times more common in most rainfall zones in the eastern than in the western Sahel (Figure 5C). In contrast, insectivorous and granivorous residents were equally common in the (semi) arid zone of the western and eastern Sahel, but in the humid zone reached higher densities in the east than in the west (Figure 5A and 5B).

The 500-mm isohyet in Chad lies some 280 km further south than in Senegal (15°N and 17–18°N, respectively) and the 1000-mm isohyet even further at 780 km (17°N and 9°N, respectively; Figure 4 in Zwarts *et al.* 2023a). Assuming that the distribution of birds is governed by annual rainfall (Figure 13 and 14 in Zwarts *et al.* 2023a), we expected an equally large shift to the south in the distribution of ground-foraging birds in Chad compared to Senegal. The actual shift is larger, in fact, since most of the bird species reach their maximum densities in the eastern Sahel in more humid rainfall zones than the same species in the western Sahel (Table 2, Figure 5 and 6). It is of interest to note that the same applies for the Desert Date *Balanites aegyptiaca* and other characteristic savannah tree species, found in Senegal mostly at 15–17°N (c. 300 mm rain/year) but in Chad at 10–14°N (600–700 mm/year; Figure S3 in Zwarts *et al.* 2023b). The same southward extended distribution was recorded for dromedaries, cattle and sheep and goats (Figure 2).

In sparsely populated Chad and Sudan, the vegetation typical of the savannah zone with an annual rainfall of 500–1000 mm still exists more or less intact, a stark contrast to the densely populated western Sahel (Figure 8 in Zwarts *et al.* 2023a) where the composition of the plant community has changed radically under the influence of mounting grazing pressure. The outlier in West Africa is the high density of many seed-eating birds recorded at >1000 mm rainfall/year (Figure 5), deduced from data collected within the Comoé National Park (11,500 km^2). It is unlikely that Comoé NP is representative of the remaining sandy savannah at >1000 mm rainfall in present-day West Africa, given the lack of protection beyond the NP borders. Comoé NP probably is representative of the humid savannahs once typical of West Africa (and still partly found in E Sahel), a glimpse of the past, when huge flocks of seedeaters roamed the savannahs and floodplains to the horror of local farmers (Bruggers & Elliott 1989).

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SAMENVATTING

Vogeltellingen in de Ferlo, in het noordwesten van Senegal, hadden laten zien dat de dichtheid van vogels die op de grond foerageren, geringer was in begraasde dan in onbegraasde savannes. Het verschil was enorm: 84% minder zaadeters en 64% minder insecteneters. In drie telgebieden in de Ferlo waren zaadeters tussen 1960 en 2010 met 39–97% afgenomen, insecteneters met 61–91%. Deze verliezen werden toegeschreven aan de toegenomen begrazingsdruk van vee. Dat fenomeen beperkt zich niet tot de Ferlo. Overal in de Sahel is de graasdruk toegenomen. Als de bevinding in Senegal algemene geldigheid zou hebben, moeten we voor de afgelopen halve eeuw rekening houden met een verlies van 1,5 miljard vogels in alleen al het aride deel van de Sahel. Helaas is deze rekensom niet te verifiëren, omdat vogeltellingen van een halve eeuw geleden, zoals die er wel zijn voor de Ferlo, ontbreken voor de rest van de Sahel. De verificatie is daarom toegespitst op het recente heden: zijn vogeldichtheid en begrazingsdruk in de Ferlo maatgevend voor de rest van de Sahel? Om die vraag te beantwoorden zijn tussen 2011 en 2019 in 1901 random gekozen vakjes van 4,5 ha, verspreid over de hele regio (van Mauritanië tot Ethiopië), systematisch vogels geteld en is de begrazingsdruk geschat door de dichtheid te meten van koeienvlaaien en schapen- en geitenkeutels. Duizenden landschapsfoto's, genomen tijdens het veldwerk in de onderzochte plotjes, zijn bekeken op de aanwezigheid van vee. Bovendien is in alle vakjes de bedekking van de bodemvegetatie geschat. De begrazingsdruk was in de Ferlo aan het begin van de droge tijd (oktober–november) groter dan elders in de Sahel binnen dezelfde neerslagzone (200–400 mm regen per jaar). Ook de bodemvegetatie was er eerder verdwenen dan elders. In de Ferlo vonden we veel minder zaadeters dan elders. De vogels die er wel waren, verdwenen grotendeels in de loop van het droge seizoen uit het gebied. Elders in de Sahel was de graasdruk minder en bleven de vogels gedurende oktober–maart in dezelfde aantallen aanwezig. In de jaren zestig en zeventig, toen de begrazingsdruk veel kleiner was dan nu, was er in de Ferlo evenmin een afname van de vogels in de loop van het droge seizoen, behalve in extreem droge jaren wanneer veel vogels doodgingen door gebrek aan voedsel. De conclusie moet dan ook zijn dat de graasdruk van vee in de Ferlo veel groter is dan elders in dezelfde regenvalzone. Het is daarom onwaarschijnlijk dat de vogels in de rest van de Sahel even hard zouden zijn afgenomen als in Noord-Senegal. Niettemin blijkt uit een vergelijking van de begrazingsdruk en de vogeldichtheid in alle neerslagzones van de westelijke en oostelijke Sahel dat een toename van de veedichtheid een negatief effect heeft op vogels. De begrazingsdruk van het vee was in het westen groter dan in het oosten en de meeste vogelsoorten die op de grond foerageren, kwamen in het westen minder algemeen voor dan in het oosten. Bovendien foerageerden de meeste van deze vogelsoorten in het westen van de Sahel in de aride en semi-aride savannes, maar hadden zij een veel bredere verspreiding in het oosten, waar ze ook in groten getale aanwezig waren in savannes binnen de humide zone.

RÉSUMÉ

Des comptages d'oiseaux réalisés dans le Ferlo, au nord-ouest du Sénégal, ont montré que la densité d'oiseaux se nourrissant au sol est plus faible dans les savanes pâturées que dans les savanes non pâturées. La différence est énorme : 84 % de granivores et 64 % d'insectivores en moins. Dans trois secteurs du Ferlo, les populations de granivores ont diminué de 39 à 97 % entre 1960 et 2010, et celles d'insectivores de 61 à 91 %. Ces pertes ont été attribuées à l'intensification de la pression de pâturage due à une augmentation du nombre de têtes de bétail, phénomène qui n'est pas limité au Ferlo, mais généralisé dans tout le Sahel. Si le constat fait au Sénégal se vérifiait partout, alors les populations d'oiseaux dans la seule partie aride du Sahel pourraient avoir diminué d'1,5 milliard d'oiseaux au cours du dernier demi-siècle. Malheureusement, ce calcul n'est pas vérifiable, faute d'anciennes données disponibles. Afin de vérifier si le Ferlo est un cas particulier ou pas, nous avons cherché à vérifier si la densité d'oiseaux et la pression de pâturage dans cette région sont comparables à celles du reste du Sahel. Pour répondre à cette question, nous avons inventorié, entre 2011 et 2019, les oiseaux présents et la couverture végétale dans 1901 parcelles de 4,5 ha sélectionnées aléatoirement dans tout le Sahel, de la Mauritanie à l'Ethiopie. Nous y avons également estimé la pression de pâturage en analysant la présence de bétail sur des milliers de photographies de paysages et en relevant la densité de déjections de vaches, moutons et chèvres. Nos résultats montrent que la pression de pâturage est plus élevée dans le Ferlo au début de la saison sèche (octobre–novembre) que dans les zones de précipitations équivalentes ailleurs au Sahel (200–400 mm de pluie par an) et que la végétation au sol y disparaît plus tôt. La densité d'oiseaux granivores est bien plus faible dans le Ferlo qu'ailleurs, et une bonne partie de ceux qui y sont en disparaissent pendant la saison sèche. Ailleurs dans le Sahel, la pression du pâturage est moindre et la densité d'oiseaux reste stable de septembre à mars. Dans les années 1960 et 1970, lorsque la quantité de bétail était beaucoup plus faible qu'aujourd'hui, la population d'oiseaux ne diminuait pas pendant la saison sèche, sauf lors des années extrêmement sèches où de nombreux oiseaux mourraient par manque de nourriture. La pression de pâturage du bétail dans le Ferlo est donc beaucoup plus importante qu'ailleurs dans la même zone pluviométrique : il est par conséquent peu probable que les oiseaux du reste du Sahel aient décliné autant que ceux du Nord du Sénégal. Néanmoins, la comparaison de la pression de pâturage et de la densité d'oiseaux réalisée pour l'ensemble du Sahel, toutes zones pluviométriques confondues, montre que l'augmentation de la densité du bétail a un effet négatif sur les populations d'oiseaux. La pression de pâturage est plus importante à l'Ouest qu'à l'Est, alors que la densité des espèces d'oiseaux qui se nourrissent au sol est plus faible à l'Ouest qu'à l'Est. De plus, la répartition de la plupart des espèces concernées est restreinte aux savanes (semi-)arides dans le Sahel occidental, alors qu'elle est beaucoup plus large à l'Est, où ces espèces fréquentent également en grand nombre les savanes de la zone humide.

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SUPPLEMENTARY MATERIAL: Bird counts in the Ferlo, NW Senegal, between 1960 and 2015

The bird counts in Fété Olé and two other sites in the 1960s–1990s were repeated in 2014–2015 in order to investigate the impact of mounting grazing pressure on bird populations (Zwarts *et al.* 2018). At another site, bird density was compared in grazed and ungrazed savannah. All four sites are situated in NW Senegal, a region known as the western or sandy Ferlo (Tappan *et al.* 2004), at about 16.2°N and 15.4°W:

(1) The Fété Olé study area was not grazed by livestock when Morel & Morel (1974, 1992) carried out their bird counts between 1969 and 1976. During the 1970s, bird density during the dry season had peaked at 8.2 birds/ha in a wet year (311 mm/year), declining linearly to 1.9 birds/ha in a very dry year (33 mm/year; Figure 13 in Zwarts *et al.* 2018). The region had been heavily grazed in the months preceding our visit in February 2015. Given the local rainfall of 161 mm/year in 2014/15, 3.52 birds/ha were expected, but only 1.16 birds/ha were present (–67%). Most of the birds counted by Morel & Morel were seedeaters (although no precise data on species were given), which suggests that granivorous birds must have been affected most, given their density of only 0.16/ha in 2015.

(2) When Tréca *et al.* (1996) performed systematic monthly bird counts in 1993/94, livestock were excluded from their study site, but in 2014/15 their site was being grazed. Granivorous ground-feeding birds had declined from 20.89 birds/ha in 1993/94 to only 0.64 in 2014/15 (–97%) and insectivorous ground-feeding birds from 3.69 birds/ha to 1.46 (– 61%; Figure 11 in Zwarts *et al.* 2018).

(3) Livestock were not excluded from the study site of Morel (1968) when he counted birds in 1960–1962, nor during our repeat survey in 2014/15. Granivorous ground-feeding birds had declined from 1.45 birds/ha in 1960–62 to 0.88 in 2014/15 (–39%), and insectivorous ground-feeding birds from 0.91 to 0.06 (–93%; Figure 12 in Zwarts *et al.* 2018).

(4) In the fenced experimental site of Widou Thiengoly (Miehe *et al.* 2010), we counted birds in 2014/15 not only in exclosures that were still intact but also in the adjoining areas that had been heavily grazed (Photo 1B). Granivorous ground-foraging birds were much more common in the ungrazed than in the grazed savannah (18.29 birds/ha vs. 2.92; –84%). That difference was also substantial for insectivorous ground-feeding birds (4.08 birds/ha vs. 1.48; –64%; Figure 14 in Zwarts *et al.* 2018).

The data sets 1–3 show that in the Ferlo granivorous birds declined by 39–97% and insectivorous birds by 61–91% over the last 20–50 years. In data set 4 (Widou Thiengoly) a similarly large difference in bird density was found between ungrazed and grazed habitat. The losses due to grazing are particularly telling because grazed and ungrazed areas were surveyed simultaneously within the same region. In study sites (1) and (2) that were being grazed but had lacked grazing in the past, it is difficult to assign the large loss of birds to grazing, to overall habitat deterioration independent of grazing, or to both. In study site (3), grazed currently and in the past (though probably by fewer livestock), bird loss was also considerable.

Photo 4. The Ferlo in the dry season during a sand storm (26 February 2015, 16.264°N, 15.313°W).

Granivorous birds in the Sahel: is seed supply limiting bird numbers?

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During the dry season four billion African and European granivorous birds in the Sahel consume, by grand average, 15 g seeds/ha/day, equivalent to an average annual consumption of 4.5 kg/ha. This represents only 4–15% of the estimated average total soil seed bank of some 30–100 kg/ha in the early dry season. Despite this apparent abundance of food, there are many reasons to presume that the number of seed-eating birds is limited by their food supply. First, the birds have to share the seed supply with rodents and insects that eat more seeds than all the birds combined. Second, granivorous birds are constrained by foraging time available to them. They avoid foraging during the midday heat and feeding time is mostly restricted to the early morning and late afternoon, totalling about 4 h per day. This forces them to achieve high intake rates and thus to select feeding sites where the available seeds can be handled quickly and/or are so abundant that the encounter rate is high. Third, only a proportion of the seeds lies on the surface where they are easy to find. Most grass seeds are tiny and even small birds need to eat thousands per day. Because they have so little time to look for food, they cannot afford to search for seeds hidden in the sand. Doves rapidly swallow seeds whole, but all smaller seedeaters have to separate the husk from the seed, a process that takes time too. Fourth, seed-eating birds in the Sahel discriminate between seeds. They ignore 'empty seeds' (husks) and also avoid feeding on common graminoids whose seeds have long awns (*Aristida*) or spines (*Cenchrus*) and which are time-consuming to process. Occasionally, granivorous birds may select seeds from forbs, but these, being low in digestibility, are not the preferred choice. Granivorous birds prefer the seeds of *Panicum* grass and other grass species with highly soluble carbohydrate fractions. Birds switch to marginal seed types at the end of the dry season, when the seed bank of the preferred species is depleted. Fifth, soil seed bank of preferred grass species is much reduced in dry years. *Panicum* and other preferred annual grasses are found mostly on riverine floodplains and in depressions that are prone to ephemeral flooding during the rainy season. Such sites attract many seed-eating birds, but the total surface area of floodplains is relatively small compared to the extensive drylands, on top of being very much smaller in dry years, circumstances that account for high mortality among seed-eating birds in drought years. The final argument for food-limitation is that the mounting grazing pressure of livestock over the last decades has severely reduced the annual soil seed bank and changed the plant community (preferred grass species replaced by non-preferred grasses and forbs). The combination of these factors caused a very large decline of seed-eating bird populations in the Sahel between the 1970s and 2010, including a handful of Eurasian species. The Sahel is still home to some four billion granivorous birds during the dry season, but just half a century ago the numbers must have been much higher.

Key words: granivorous birds, prey depletion, Sahel

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Eurasian bird species spending the northern winter in Africa leave their breeding grounds in August–September and do not usually return until April–May. Most insectivorous birds have no choice but to leave the temperate zone in late summer when their arthropod food supply dwindles. In contrast, seed-eating birds have the option not to migrate because seed stocks remain available throughout winter, albeit in decreasing amounts. This inference is generally valid. Very few granivorous species from the temperate zone cross the Sahara to winter in the tropics (Alerstam 1990: 192–193). Apart from omnivorous waterbirds that also take seeds (i.e. ducks and waders), five Eurasian granivorous bird species winter south of the Sahara: Common Quail *Coturnix coturnix*, European Turtle Dove *Streptopelia turtur*, Greater Short-toed Lark *Calandrella brachydactyla*, Ortolan Bunting *Emberiza hortulana* and Cretzschmar's Bunting *Emberiza caesia* (Moreau 1972). Breeding populations of each of these species are declining (BirdLife International 2021). The Pan-European decline of European Turtle Dove (–84%) and Ortolan (–69%) in 1980–2009 is larger than in any insectivorous migrant species (Vickery *et al.* 2014).

In less than half a century, European Turtle Dove, once a common bird in Europe, has become rare, experiencing a >90% decline at the northwestern fringe of the breeding range between the 1970s and 2010 in Great-Britain (Browne & Aebischer 2004, Woodward *et al.* 2020) and in The Netherlands (de Vries *et al.* 2022). The species is also declining in the core breeding range (e.g. –37% between 1996 and 2018 in Spain; Moreno-Zarate *et al.* 2019). The population crash is associated with habitat loss and declining food supplies on the breeding grounds (Browne & Aebischer 2003, Moreno-Zarate *et al.* 2019, Dunn 2021) and to intense hunting during migration (Hirschfeld *et al.* 2019, Lormée *et al.* 2020). Changes in seed availability and hunting are probably important players also in their African wintering areas (Eraud *et al.* 2009, Zwarts *et al.* 2009).

Ortolan Buntings have declined by 88% in Europe between 1980 and 2015 (Jiguet *et al.* 2016) due to habitat changes on the breeding grounds (Vepsäläinen *et al.* 2005, Berg 2008), exacerbated by hunting during migration (Jiguet *et al.* 2019). The overall decline is larger, as the sparse data from older sources show that the species was already in decline in the 1950s (Stolt 1993). Whether the long-term decline involves changes in the African wintering grounds, as suggested by Stolt (1993), is still in question. Cretzschmar's Bunting has declined in SE Europe and probably also in Turkey where most breed (Keller *et al.* 2020).

Recent bird counts in the Sahel suggest crashing wintering populations of the Greater Short-toed Lark and Common Quail between about 1980 and 2020 (Zwarts *et al.* 2023a,c). Greater Short-toed Larks have declined in Europe, including a contraction of the breeding range. Most birds breed in Spain, where there was a decline of perhaps >30% between 1990 and 2000 (de Juana *et al.* 2020). Fluctuations in numbers of Common Quail on the breeding grounds have been linked to variations in rainfall and to farming practices, but numbers appeared to be rather stable at the turn of the century (Puigcerver *et al.* 2012). Declines of the Common Quail have been attributed to increased hunting pressure during migration (Zuckerbrod *et al.* 1980, Caruana-Galizia & Fenech 2016, Eason *et al.* 2016), but a negative impact of reduced food supply in the Sahel is also implicated, as suggested for European Turtle Dove (Eraud *et al.* 2009).

These five Afro-Palearctic seedeaters together amount to a few hundred million birds that overwinter in a wide band between the Sahara and tropical woodland in the northern half of Africa (estimates based on BirdLife International 2021). This number pales into insignificance compared to the four billion granivorous Afro-tropical birds in the same region (Zwarts *et al.* 2023a). Is the long-term decline of seed-eating migrants an indication of deteriorating conditions in the Sahel and if so, is it a corollary of a massive undocumented decline in Afro-tropical seedeaters? Bird counts in NW Senegal in the 2010s suggest that African granivorous passerines were much less common than in the 1970s and 1980s, a decline attributed to the mounting grazing pressure from livestock (Zwarts *et al.* 2018). Livestock has increased in all Sahelian countries, and seedeaters therefore face grazing-related problems across the entire Sahel (Zwarts *et al.* 2023c). This paper reviews the available literature to determine whether seed-eating birds in the Sahel suffer from a decline in their food supply. We focus our analysis on four topics, embedded in our own data from bird counts in random sites in tropical northern Africa between 7 and 22°N (see Zwarts *et al.* 2023a):

(1) What is known about the food supply of seed-eating birds in the Sahel?

(2) Which seeds are selected (and ignored), and why?

(3) Has the increase in livestock numbers resulted in a decline of the food supply for seed-eating birds?

(4) Is the population size of seed-eating birds limited by the annual seed production of preferred plant species?

METHODS

In the strictest sense, the Sahel is the climate zone where annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a wider sense as the transition zone between the Sahara in the north and the humid forests in the south. This region covers several vegetation and climate zones.

We derived the average seed predation by seed-eaters in the Sahel from the average bird density of granivorous bird species (Zwarts *et al.* 2023a,b,c) and the estimated daily consumption per species. To estimate seed consumption, we took body mass values of seed-eating birds given by Urban *et al.* (1986), Keith *et al.* (1992) and Fry & Keith (2004) and derived the daily food consumption from the relationship between daily seed consumption (DSC, g dry weight) and body mass (BM, g; Figure 1):

$$\mathrm{DSC} = 0.473\mathrm{BM}^{0.657} \qquad (1)$$

Using equation (1), the daily seed consumption would vary between 1.9 g/day for the smallest seedeater in the Sahel, Common Waxbill *Estrilda astrild* (8 g), to 25.6 g/day for the largest, Double-spurred Spurfowl *Pternistis bicalcaratus* (440 g). From these data, and using the bird density counts from Zwarts *et al.* (2023a), we calculated for each 4.5-ha study site and for each granivorous bird species the daily seed consumption per ha.

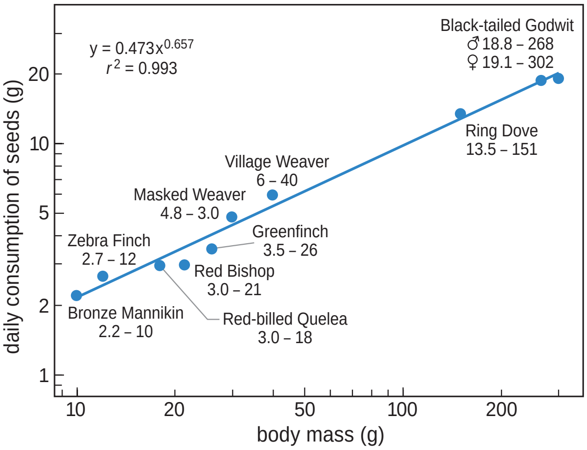


Figure 1. Daily food consumption (g unhusked seed) of nine bird species (captive birds in thermo-neutral conditions) as a function of body mass (g); *y*- and *x*-values given below the bird names. Sources: Woodall (1975), Gillespie (1982), Da Camara-Smeets & Manikowski (1981), Brisbin (1969), Meijer *et al.* (1996), Whittington-Jones 2001 and Santiago-Quesada *et al.* (2009).

In our study sites, we measured on 1226 occasions the soil temperature at the surface between November and March (accuracy 0.1°C, not calibrated), during every hour of the daylight period, always in the full sun, and simultaneously on 682 of these occasions the soil temperature in a shady spot in the immediate surroundings. The average rainfall data (determined over the period 1950–2000) were taken from Hijmans *et al.* (2005).

RESULTS

Food supply and seed selection by granivorous birds in the Sahel

FOOD SUPPLY

The vegetation in Africa in the dry belt of the northern tropics reflects the transition from the bare Sahara to savannah grasslands. When less than 100 mm rain/year, herbaceous vegetation is absent. The annual above-ground primary production (dry biomass) of herbaceous vegetation in the 100–200 mm rainfall zone of 0.4 ton/ha increases to 2–3 ton/ha in the 200–400 mm rainfall zone (Le Houérou 1980). Breman & de Wit (1983) provided somewhat higher average annual values: 1 ton/ha at 200 mm of rainfall, increasing linearly to 4 ton/ha at 1000 mm rainfall. Grouzis (1988) measured lower average annual values: 0.2–0.3 ton/ha at 100 mm of rainfall linearly increasing to 1.2–1.8 ton/ha at 600 mm of rainfall. Adding spatial and temporal variation, estimates differ substantially per region and between years depending on annual rainfall. For example, the primary production of the herbaceous layer in Fété-Olé (Senegal, see Figure 2A; 289 mm rainfall/year on average) was measured between 1969 and 1975. The annual rainfall varied between 33 mm (1972) and 450 mm (1969) and the respective annual biomass production between 0 and 1.0 ton/ha on sandy dunes and between 0.02 and 4.1 tons/ha in the valleys (Bille 1977). An equally large variation was measured around Lake Oursi (Burkina Faso, see Figure 2A; 374 mm rainfall/year), with 0.3 tons on sandy dunes and 3.5 tons in low-lying areas with loamy soil (Grouzis 1988). In four African floodplains (Inner Niger Delta, Logone, Kafue and Sudd), the above-ground biomass increased with maximum flood depth (Scholte 2007). The semi-aquatic perennial grasses *Echinochloa stagnina* and *Vossia cuspidata* reached biomass values of 30 to 80 dry tons per ha when the maximum flood depth was 4–8 m (Leauthaud *et al.* 2019). Floodplains are very productive when compared to Sahelian drylands.

Some 1500 plant species occur in the Sahel, but only 15–30 species (often fewer than 5) usually occur within a randomly chosen homogenous site of some hundreds of m^2 (Hiernaux & Le Houérou 2006). Within the Sahel, the vegetation is dominated by annual grasses, except on the floodplains where perennial grasses are more common. The total annual seed production ranges from 6 to 30% of the annual above-ground primary biomass production (Grouzis 1988). Seedfall occurs at the end of the rainy season (September). Seed densities can be high. For example, near Kaédi (Mauritania, see Figure 2) 176,000 seeds per m^2 were recorded, mainly *Panicum laetum* (Carrière 1989). With such a density, and with *Panicum* seeds measuring 1 × 2 mm, more than one third of the surface would have been covered by seeds, though a proportion of the seeds lies buried in the soil. Even so, at this site seeds represented a very large, potential food supply of 167 g/m^2 for granivores.

The variation in seed production on the Sahelian savannah is considerable (Table 1). Exceptionally high seed biomass values (1457–2238 kg/ha) were recorded in years with above-average rainfall in temporarily flooded areas covered mainly by *Panicum*. In Maltam, along the Chari River (Chad, see Figure 2A), seed production varied from 2236 kg/ha in a wet year to 206 kg/ha in a dry year (Gaston 1976); the latter value is higher than seed production during wet years in drylands. In contrast, very low seed biomass was found on sandy dunes covered by vegetation of *Aristida* species (awngrass) and Sandbur *Cenchrus biflorus* (known in West Africa as cram-cram), especially in dry years. In the drought year of 1972, sandy dunes in Fété-Olé were devoid of herbaceous vegetation and the few seeds present were leftovers from the previous year (Bille 1977).

We do not know whether the cited studies distinguished between viable ('full') and non-viable ('empty') seeds and, if not, to what extent the seed density may have been overestimated by including empty seeds without nutritional values for birds. On the other hand, by counting 'fallen seed on the ground', total seed production is underestimated, because birds also take seeds from the panicles (Price & Joyner 1997, Fry & Keith 2004) and livestock consume grass including seeds. Seed density on the soil declines gradually during the dry season due to consumption by birds, rodents and insects. For instance, from the 20,000 (in 1973) or 120,000 (in 1975) seeds/m^2 present in the study area of Gaston (1976) during the early dry season, less than 2000 were left 10 months later in April and May, presumably mainly due to heavy predation by Red-billed Quelea *Quelea quelea*.

The large variation in seed production (Table 1) may relate to how seed density was measured (e.g. depth of top layer of the soil being sampled, varying

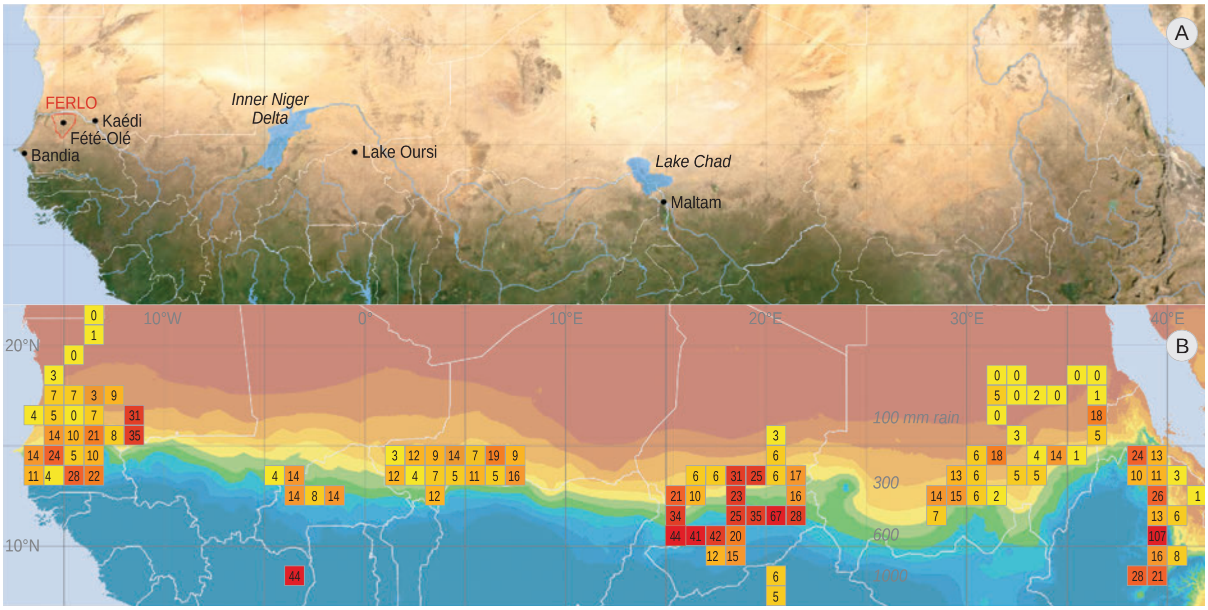


Figure 2. (A) Study areas and large wetlands mentioned in the text. (B) Estimated daily seed consumption (g/ha) by granivorous bird species during the dry season (20 November – 10 March) on savannah or farmland, averaged for 111 grid cells of 1° latitude × 1° longitude.

between 0.5 cm (Bille 1977) to 8 cm (Carrière 1989) and whether 'empty' seeds were included or not. We assume that methodological variations were small compared to the large differences found in seed production between areas and between years. Within the Fété-Olé site, seed production in the valleys was 184 kg/ha, 5.3 times higher than on the surrounding drylands (34 kg/ha). The five study sites of Grouzis (1988) around Lake Oursi had highest seed biomass (1457 kg/ha) on the floodplain and the lowest (77 kg/ha) on the extensive drylands surrounding the lake. From this we tentatively conclude that the initial biomass of the soil seed bank in the early dry season amounted to, on average, 30 to 100 kg/ha on drylands, but much less in a dry year. These values are equal to seed resource levels in North American drylands (Pulliam & Dunning 1987, Desmond *et al.* 2008). However, the seed production can reach 1000–2000 kg/ha after floodplains and valleys become inundated in the rainy season, but such highly productive areas comprise but a small part of the Sahel.

SEED CONSUMPTION

Gaston (1976) suggested that seed density in his Chad study site declined by 100,000 seeds/m^2 within several months due to heavy predation by Red-billed Queleas. This figure seems realistic given the feeding ecology of Red-billed Queleas. Red-billed Queleas weigh 18 g and their daily consumption of unhusked seeds is estimated at 3.0 g (Figure 1), or 32,000 seeds of 0.95 mg, per individual. To achieve Gaston's claimed consumption rate (100,000 seeds/m^2, each seed weighing just 0.95 mg), requires 3.1 queleas foraging on a square metre each day the species was present. Extrapolating this to a 1.0-ha site, requires 31,000 Queleas, or 3100 Queleas feeding for 10 days on a single ha. Queleas are known to occur locally in the millions (Crook & Ward 1968) and have evolved efficient foraging techniques in large groups, including a 'roller feeding' strategy for dense flocks of hundreds or thousands of Queleas sweeping across the plains (Ward 1965). Birds in front of the group take so many seeds that fewer remain for the birds at the back. Once the seeds available to the rear rank become too sparse, the rear rank leapfrogs forwards to form a new front rank, a fluid and regular process. Ward (1965) did not quantify seed depletion, but suggests that dense flocks can reduce local seed density very quickly.

Bird density counts in our study sites (Zwarts *et al.* 2023a) and estimated daily consumption per bird species derived from their body weight (Figure 1) were used to calculate the average seed consumption per grid cell of 1° latitude × 1° longitude (Figure 2B). Seed consumption was very low in the desert and increased with rainfall, reaching higher levels in Chad than in West Africa.

On our study sites, but excluding desert (rainfall < 100 mm/year) and woodland sites, the average daily consumption of all seed-eating birds was estimated at 15 g/ha/day. The variation, however, was large, as no granivores were recorded in 22.5% of the sites. For other sites daily seed consumption levels of over 100 g/ha were calculated (Figure 3). The maximum estimated daily seed consumption (1197 g/ha) was not calculated for a typical Sahel site, but referred to one at the edge of the Danakil Desert (eastern Ethiopia), an area where larger seed-eating bird species were still common (sandgrouse and francolins, nowadays rare

Table 1. Seed (kg/ha) present in the soil during the early dry season in five study areas, with 1–5 vegetation types in a single year (but over five years in Oursi in Burkina Faso). Annual rainfall (mm/year) calculated for the 1950–2000 period (data from the nearest meteorological stations or from Hijmans *et al.* 2005); rainfall during year(s) of observation is given as percent deviation from this 50–year average.

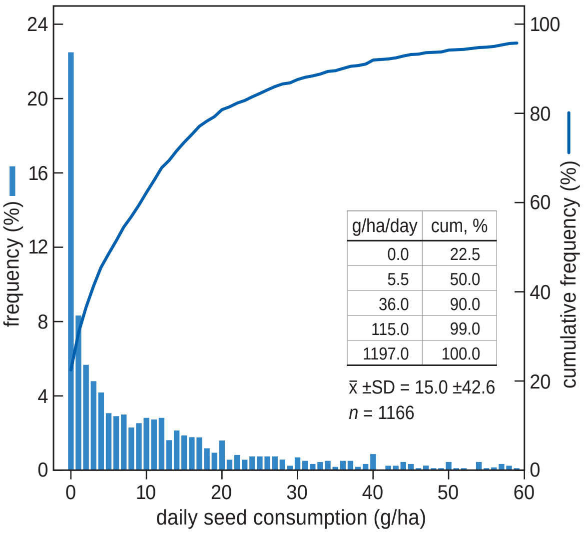
Site	Coordinates	Rainfall/year		Year	Vegetation types	kg/ha	Source
		avg.	dev.%				
Fété-Olé, Senegal	15.01°W, 16.10°N	289	–30	1971	3	34–184	Bille 1977
Fété-Olé, Senegal	15.01°W, 16.10°N	289	–89	1972	3	24–171	Bille 1977
Kaédi, Mauritania	13.43°W, 16.19°N	298	–3	1986	7	268–2170	Carrière 1989
Oursi, Burkina Faso	0.50°W, 14.58°N	374	–10	'77–'81	5	77–1475	Grouzis 1988
Maltam, Chad	14.88°E, 12.15°N	466	–32	1973	1	206	Gaston 1976
Maltam, Chad	14.88°E, 12.15°N	466	62	1975	1	2238	Gaston 1976
Bandia, Senegal	16.97°W, 14.57°N	540	14	1978	1	1061	Gillon *et al.* 1983
Bandia, Senegal	16.97°W, 14.57°N	540	10	1979	1	286	Gillon *et al.* 1983
Bandia, Senegal	16.97°W, 15.57°N	540	–35	1980	1	803	Gillon *et al.* 1983

elsewhere in the Sahel). The large variation in seed consumption hinges on several factors, including the large variation in seed density (Table 1), the avoidance by seedeaters of sites lacking seeds and the tendency of granivorous birds to congregate in feeding flocks. Flocking birds cause sampling problems (Figure 12 in Zwarts *et al.* 2023a), and particularly so when sites are visited only once (as in our survey).

The estimated daily seed consumption is based on bird counts during the first half of the dry season. To estimate the total annual seed consumption, we assumed that the birds remained strictly granivorous during 300 days of the year (switching to insect food during the July–September rainy season; Ward 1965, Da Camara-Smeets & Manikowski 1981, Adegoke 1983). An average daily consumption of 15 g/ha/day equates to an annual consumption of 4.5 kg/ha/year, which represents only 4–15% of the estimated total seed supply present on the soil in the early dry season (30–100 kg/ha). Does this mean that food is always plentiful for Sahel's granivores? And are all seeds equally attractive to all seedeaters?

DIET

'The Birds of Africa' (Urban *et al.* 1986, Keith *et al.* 1992, Fry & Keith 2004) and additional sources (Table 2) provided a baseline for seeds taken by African bird species. A comparison with the original papers (e.g. Morel & Morel 1972, Morel 1987) showed that the information in 'The Birds of Africa' concerned a selection of the most commonly eaten seeds. A seed species omitted from Table 2 does therefore not necessarily equate with absence of that seed in a species' diet. The body masses of the 34 bird species in Table 2 vary between 8 and 440 g, but most are in the 10–20 g range. Seed-eating bird species in Africa showed a preference for a limited number of grass genera. *Panicum* grasses were a main food item for 27 of the 34 bird species: *P. turgidum* in the arid zone (Black-crowned Sparrow-Lark *Eremopterix nigriceps*), *P. laetum* mainly in the Sahel and *P. maximum* also elsewhere in Africa. Seeds of other millet genera were taken relatively often (lines marked blue in Table 2). Some genera of very common grasses were hardly ever mentioned as being part of avian diets. For example, *Aristida* spp. (awngrass) belong to the most common grass species in the arid and semi-arid zone (Rattray 1968, Le Houérou 1980, Breman & de Wit 1983, Hiernaux *et al.* 2009a), but were taken only by the Desert Sparrow *Passer simplex*. Another very common grass species from the arid and semi-arid region, *Schoenefeldia gracilis*, is mentioned only as food for Red-billed Quelea (Ward 1965), and the even more common and widespread *Cenchrus biflorus* is absent from the literature on avian diets (with one exception; see below).



g/ha/day	cum, %
0.0	22.5
5.5	50.0
36.0	90.0
115.0	99.0
1197.0	100.0

x̄ ±SD = 15.0 ±42.6
n = 1166

Figure 3. Frequency (%, left) and cumulative frequency distribution (%, right) of the calculated daily seed consumption (g/ha), derived from bird counts in 1166 sites during the dry season in the grid cells shown in Figure 2. Selection made of random sites with an annual rainfall >100 mm not covered by woodland.

Seeds of African grasses mostly weigh about 1 mg, varying between 0.07 mg (*Sporobolus*) and 14 mg (Wild Rice *Oryza barthii*). The seeds of cultivars are heavier: rice 17.5 mg, *Sorghum* 19.5 mg, *Pennisetum* (millet) 25 mg and still higher in two species rarely found in the arid and semi-arid zone: *Hordeum* (barley) 35 mg and *Zea* (maize) 262 mg. Two crops in the Sahel have minute seeds: Fonio *Digitaria exilis* (0.5 mg) and Tef *Eragrostis tef* (0.3 mg; Table 2). The selection of seeds according to mass differs for large and small seedeaters, but the overlap is considerable (Table 2). Large seeds, such as those of cultivated rice (17.5 mg), are selected as often by small as by large bird species. Even a bird like the Bronze Mannikin *Spermestes cucullata* (10 g) feeds on rice grains. Very small grass seeds (≤ 0.1 mg), e.g. *Sporobolus* and *Cymbopogon*, are not mentioned in diets of bird species with body masses of >64 g, but seeds that are only slightly less small (≥0.25 mg) are important for larger bird species as well.

Seeds may be 'empty', consisting of a hull only, but it is unknown whether they were included in published density counts of seeds present on the surface and in the soil. Seedeaters are known to reject empty seeds. A Common Woodpigeon *Columba palumbus* stomach

Table 2. Thirty grass genera and six forb genera recorded in the diets of 34 seed-eating bird species occurring in the Sahel and elsewhere in Africa. Diet data extracted from 'The Birds of Africa' (Urban *et al.* 1986, Keith *et al.* 1992, Fry & Keith 2004), with supplementary data from Da Camera-Smeets & Manikowski (1981), Adegoke (1983), Badenhorst & Kerley (1996) and https://birdsoftheworld.org/bow/home. Body mass of bird species (g; after English names, top of the table) are from 'The Birds of Africa' and Tieleman *et al.* (2003) for Dunn's Lark. Mass of grass seeds (mg; after scientific names of genera on left of the table) are taken mainly from Bille (1977), but also from Ward (1965), Grouzis (1988), Gallinato *et al.* (1999), Peco *et al.* (2013), Török *et al.* (2013), Jedmoski *et al.* (2015), Titulaer *et al.* (2018) and Musso *et al.* (2019). Grasses with awned seeds are marked grey when all, or at least most, species within the genus have awns (Clayton *et al.* 2021). For instance, within *Oryza* (rice) the wild species *O. barthii* has awns but not the cultivated *O. sativa* and *O. glaberrima*. Birds predate 11 millet genera (all awnless, marked blue) three times more often on average than other grasses.

Genus seed mg	Common Quail 110	Double-spurred Spurfowl 440	Speckled Pigeon 300	European Turtle Dove 172	African Collared Dove 126	Mourning Collared Dove 149	Vinaceous Dove 110	Laughing Dove 91	Black-billed Wood Dove 66	Namaqua Dove 36	Black-crowned Sparrow-Lark 14	Greater Short-toed Lark 20	Dunn's Lark 20	Desert Sparrow 19	Sudan Golden Sparrow 13	Village Weaver 40	Red-headed Quelea 19	Red-billed Quelea 20	yellow-crowned Bishop 15	Black-winged Bishop 23	Northern Red Bishop 17	Fan-tailed Widowbird 28	Pin-tailed Whydah 16	Red-collared Widowbird 23	Bronze Mannikin 10	Common Waxbill 8	Cut-throat Finch 20	Green-winged Pytilia 15	Red-billed Firefinch 9	Village Indigobird 12	Cameroon Indigobird 12	White-rumped Seedeater 11	Yellow-fronted Canary 13	Golden-breasted Bunting 19
Grass genera																																		
Andropogon 3.6																●									●									
Aristida 0.64														●																				
Brachiaria 1.2							●		●							●			●						●									
Chloris 0.37–0.51																										●	●		●					●
Cymbopogon 0.1																			●															
Cynodon 0.26																										●				●				
Dactyloctenium 0.25		●				●			●	●								●	●										●	●				
Digitaria 0.3																●		●	●			●	●		●	●			●	●	●		●	
Echinochloa 1.94		●															●	●	●			●	●		●	●			●	●				
Eleusine 0.3								●		●		●											●		●				●	●				
Eragrostis 0.33			●							●		●				●		●							●	●								●
Hordeum 35	●	●																																
Hyparrhenia 0.77																				●			●		●	●	●							
Hyperthelia ?																			●							●								
Ischaemum 0.7																		●																
Melinis 0.65																										●		●						
Oryza 14–17.5									●	●						●	●	●		●	●	●			●									
Panicum 0.95	●	●		●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●			●	●	●	●	●	●	●				●	●
Paspalum 1.08																		●				●			●	●								
Pennisetum 2.3–25			●					●	●	●				●	●	●	●	●			●				●				●			●		
Phalaris 0.6																										●								●
Poa 0.15								●																									●	
Rottboellia 10.6																●	●			●														
Schoenefeldia 0.11																		●																
Setaria 0.75				●								●						●	●			●	●		●	●	●	●	●	●				
Sorghum 19.5	●		●		●			●	●	●					●	●		●			●			●	●								●	
Sporobolus 0.07																			●						●	●		●	●					
Tricholaena ?																										●								
Urochloa 1.3																		●					●		●	●		●	●					
Zea 262			●					●								●	●			●		●												
Forb genera																																		
Arachis 500					●	●	●	●																										
Alysicarpus 3.6							●			●																								
Citrullus 55					●	●	●	●																										
Gisekia 0.26					●	●	●	●		●																								
Tribulus 6.4			●	●	●	●		●																										
Zornia 1.9							●	●								●																		

contained full beechnuts only (average weight 0.17 g, compared to 0.08 g for a random sample), whereas 11% of the nuts available on its foraging patch had been empty (Bijlsma 1995). Another study, on Black-tailed Godwits *Limosa limosa* feeding on rice grains in Portuguese farmland (Blomert & Zwarts unpubl. data), found that available rice grains varied in weight between 2 and 27 mg. The godwits ignored all grains <8 mg, took some of 9–11 mg, but preferred to take the larger grains of which 80% of the mass was digestible (against <20% for all grains <8 mg). The fraction of empty rice grains in the field was high (34%), probably not much different from that in Sahelian grass and forb species (Hérault & Hiernaux 2004).

Most granivorous birds in the Sahel predominantly feed on seeds of annual grasses, but they also take the seeds of some forbs, from the very small (*Mollugo* and *Cleone*; 0.1 mg) to the very large (*Citrullus colocynthis*; 55 mg and *Arachis*; 500 mg). The latter two are taken by Speckled Pigeon *Columba guinea* and by four of the larger dove species (91–300 g body mass) but not by Namaqua Dove *Oena capensis* (36 g) which preferred the small *Mollugo* and *Cleone* seeds that were ignored by the larger doves (Morel & Morel 1972b).

We combined the data summarised in Table 2 to test whether the selection of seed by mass differs for small and large birds. Although the smallest seeds are not taken by the largest birds, the overlap in seed size between small and large granivorous species is nearly complete because the smaller bird species also take the larger seeds ($\chi^2_{24} = 14.7$, $P = 0.93$; bird species in weight classes of 7–10, 11–15, 16–20, 35–91 and 110–440 g, and seeds in weight classes of 0.07–0.1, 0.11–0.37, 0.64–1.4, 1.94–5 and 14–500 mg). A similar large overlap in seed size was found for seed-eating bird species of the Monte Desert, Argentina (Cueto *et al.* 2006, Marone *et al.* 2008, Camín *et al.* 2015, Marone *et al.* 2022).

The grass species often mentioned in diets of granivorous bird species have awnless seeds, whereas grass species infrequently reported as food have awns (Table 2). Some very common grass species with awned (*Diheteropogon, Loudetia*) or spiny seeds (*Cenchrus*) are not mentioned at all as bird food. The exception is queleas feeding their young with *Cenchrus* seeds in September (Morel *et al.* 1957), when the seeds are still soft. Once these seeds have hardened, the spines can even injure livestock and humans. Another very common food resource, the awned seed of *Aristida*, is ignored as food by birds in Africa and N America (Pulliam & Brand 1975, Titulaer *et al.* 2017, Desmond *et al.* 2008) and ignored by small, but not by large seed-eating birds in S America (Marone *et al.* 2008, 2017). Granivorous bird species are able to husk most seeds (Kear 1962, Newton 1967, Pulliam 1985), even some that are large or hardy (van der Meij & Bout 2004, 2007). They are also able to separate awns (up to 7 cm long) from seeds, but some awned seeds are more difficult to handle than others (Pulliam & Brand 1975, Titulaer *et al.* 2018). Overall, birds prefer seeds that are easier to handle, to make their foraging strategy as profitable as possible (Hrabar & Perrin 2002, Soobramoney & Perrin 2007, Marone *et al.* 2022).

Seed masses as cited in Table 2 refer to total dry mass including hull and awns, the standard way of expressing seed mass in studies of birds' seed selection. These values are a far cry from the mass and energy content of the digestible fraction of the seed when the indigestible husks, awns and hairs are excluded. The seed hull consists of crude fibre and is indigestible by birds. The indigestible fraction can be as high as 50–70% in seeds with a heavy hull and/or with large awns or many hairs, but in grasses mostly comprises 20–30% and in grass seeds lacking hairs or awns even less (Kear 1962, Hespenheide 1966, Pulliam 1985, Hrabar & Perrin 2002). Most grass seeds are easy to handle by birds due to their soft and thin hull, in contrast to the seeds of forbs that are often equipped with a sturdy seed coat. Puncture Vine *Tribulus terrestris*, for instance, has nutlets (37 mg) containing 3 seeds (6.4 mg, only partly digestible due to its thick hull; Bille 1977, Grouzis 1988, Morel 1987), so more than half of the nutlet is indigestible. Most granivorous bird species in the Sahel are unable to crack the nutlet, but five larger pigeon and dove species swallow the nutlets whole (Morel & Morel 1972b), much to the surprise of Morel (1987) that these birds were able to process nutlets with such hard spines. In the light of these findings it is not surprising that savannah birds take grass seeds relatively more often than forb seeds (Cueto *et al.* 2006, Marone *et al.* 2008, Díos *et al.* 2012a, Camín *et al.* 2015, Marone *et al.* 2017, 2022), in addition to the fact that some forb seeds are (slightly) toxic (Díos *et al.* 2012a,b), such as *Senna tora* which contains phytohaemagglutinins (Gillon *et al.* 1983). *Senna tora* is locally a very common forb in West Africa which produces a lot of large seeds (19 mg) that are eaten by insects but refused by birds.

Apart from mass, the energy content of seed kernels also varies greatly, i.e. between 17 and 30 kJ/g. Energy content is higher in fat seeds (e.g. sunflower, rape) but only 17–19 kJ in most grass seeds (Willson 1971, Willson & Harmeson 1973, Hrabar & Perrin 2002, Soobramoney & Perrin 2006). Birds, rodents and insects prefer highly nutritional seeds with a high soluble carbohydrate fraction that are easy to digest (Kelrick *et al.* 1986). The carbohydrate fraction is particularly high in *Panicum* and other millet species' seeds (*Echinochloa*, *Eleusine*, *Paspalum*; Kelrick *et al.* 1986, Gupta *et al.* 2014), which may encourage their selection by seed-eating birds (Ríos *et al.* 2012a), also in Africa (Table 2).

Heat stress at midday

Seed-eating birds in the Sahel roost communally at night (e.g. Ward 1985) and forage only during daylight hours (12 h a day available). However, the middle of the day is usually too hot to exploit for foraging. Even in a desert-dwelling species, such as Dune Lark *Calendulauda erythrochlamys*, heat stress manifested itself in a change of behaviour (searching for shade or remaining immobile) when sand temperatures exceeded some 35°C (Wolf *et al.* 1996, Cox 1983, Williams 2001). Soil temperature in our study sites in the Sahel increased from an average of 15°C in the early morning to a maximum of 46.5°C between 11:30 and 13:30, after which it cooled down to 27°C at sunset (Figure 4). These are average values, with daily maxima sometimes exceeding 50°C or even 60°C on clear sunny days. On dusty days when the sun was scarcely visible, maximum temperatures may not rise above 30°C, however. Temperatures varied in the course of the dry season from late November to early March, with surface temperatures around midday (11:30–13:30) increasing from an average of 44.8°C ± 0.8 (±SE) in December ($n = 37$), to 45.6°C ± 0.5 in January ($n = 68$), 46.9°C ± 1.2 in February ($n = 42$) and 50.8°C ± 1.3 in early March ($n = 17$; sunny days only). The threshold of a maximum temperature of 35°C at ground level for seedeaters would limit the foraging windows to 3 h in the morning and 1.5 h in the late afternoon. We lack quantitative data to confirm this threshold for ground-foraging birds, but it fits the observation of Ward (1965) that Red-billed Queleas feed 2–3 h in the early morning and about 2 h in the late afternoon, later revised to two hours in each period (Ward 1978).

Non-feeding birds were often seen resting in the shadow, where it was always cooler even when still on the ground. The soil temperature in the shadow was, on average, 4.7°C lower than in the sun, but the difference increased at high temperatures, to 6.2°C when soil temperature in the sun exceeded 35°C, with a linear relationship between soil temperature in the shadow and in the sun:

$$T_{shadow}\ (°C) = 2.82 + 0.79T_{sun} \qquad (2)$$

based on 682 simultaneous measurements of soil temperature in the sun and a shady spot in the immediate surrounding; $r^2 = 0.88$; range 8.8–56.8°C (T_{sun}) and 7.9–50.2°C (T_{shadow}).

In arid and semi-arid savannahs, the presence of solitary trees and pockets of trees may extend the duration of foraging bouts for ground-foraging birds at high temperatures, but we lack empirical data on this subject. Trees can also act as 'thermal refugia' in a heat-stressed environment, as suggested for arboreal and, especially, ground-foraging birds (in the Kalahari; Martin *et al.* 2015).

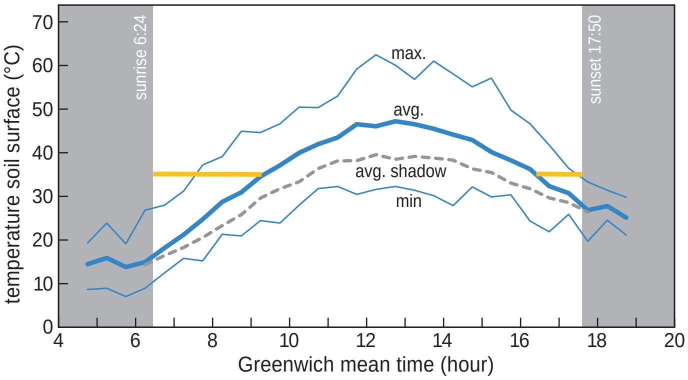


Figure 4. Diurnal variation in the average, maximum and minimum temperature of the exposed soil surface, and the average temperature of soil surface in the shadow, between 20 November and 10 March. Based on 1226 measurements in the region shown in Figure 2 (but excluding Ethiopia) from three time zones converted to Greenwich mean time. The horizontal yellow lines indicate the feeding periods of seedeaters during daylight, assuming birds avoid foraging when average soil temperature is >35°C, yellow time slots cover 6:24–9:20 h and 16:20–17:50 h.

Intermezzo: Foraging theory applied to Sahelian granivores

A reduction of foraging time has consequences for the intake rate needed to meet the daily energy requirements. The daily food consumption is determined by five variables: energy content of the prey (E), handling time per prey (H), searching time per prey (S), number of prey and total daily foraging time, where E/H is the profitability (intake rate during handling the prey) and E/(H+S) the intake rate during feeding.

Intake rate

When the available foraging time is restricted, birds need to raise their intake rate to meet the required daily food consumption. Assuming seed-eating birds in the Sahel have to meet their energy demand during a foraging period of 4 h per day (avoiding heat stress), instead of the full daylight period of 12 h (Figure 4), their intake rate must be three times higher. The required intake rate during feeding can be derived from the daily consumption as determined by body mass (Figure 1; Eq. 1), assuming they forage nonstop in the time (4 h) available:

$$\text{intake rate} = 0.0328\text{bm}^{0.657}, \qquad (3)$$

where intake rate = mg dry mass/s feeding and bm = body mass of the bird (g).

Handling time

Seeds may be ignored when they take too much handling time and intake rate during prey handling becomes lower than the intake rate during feeding. Most seed-eating birds husk the seeds to get rid of indigestible material, but doves and waders swallow seeds whole. Swallowing a seed whole takes 0.3–1.2 s, depending on size and dimensions of the seed relative to the gape width of the bird (Pulliam 1985, Hrabar & Perrin 2002, Zwarts & Wanink 1993, Marone *et al.* 2022). To crack and husk seeds takes additional time. Husking canary grass *Phalaria* seeds (7 mg) and hemp *Cannabis* seeds (18.5 mg) amounts to 2–4 seconds of handling time in birds with a body mass of >25 g but varies in smaller birds between 3 and 16 s (van der Meij & Bout 2004, 2006). We found 13 studies where seed mass (for 38 species) and seed handling time by birds (in 48 species) were given in detail (full list of handling times given in Supplementary Material). The handling time varies per bird species, depending on bill size, bill shape, biting force, seed handling method (with or without husking) and seed species (e.g. size, shape, hardness of the husk, presence of awns or stiff spines). An analysis of the pooled data showed that handling time depends mainly on seed mass, and to a lesser degree on body mass of the bird and width and depth of its bill. It also makes a difference whether or not husk and kernel are separated. For seeds swallowed whole, the expected decrease of handling time with body size and increase with seed mass is small and far from significant. In contrast, the relationship is highly significant for husked seeds. Handling time is a function of seed mass, body mass, bill width and bill depth with all (log-transformed) variables being highly significant ($r^2 = 0.74$, $n = 151$; multiple regression analysis). However, heavier bird species have a sturdier bill ($r = +0.66$ for bill depth vs. body mass and $r = +0.50$ for bill width vs. body mass) which complicates the interpretation of handling time. Bill dimensions are known for only a few Sahelian seed-eating birds. Therefore, we disregard bill dimensions in the equation for handling time:

$$\text{ht} = \exp(1.188 \pm 0.419 + 0.609 \pm 0.038 \times \ln(\text{sm}) - 0.211 \pm 0.139 \times \ln(\text{bm})), \qquad (4)$$

where ht = handling time (s), sm = seed mass (mg ± SE; $P < 0.001$), bm = body mass of bird species (g ± SE; $P = 0.131$), $r^2 = 0.59$, $n = 192$; raw data in Supplementary Material.

Search time

Equation 3 gives the required intake rate of birds assuming they forage 4 h a day and equation 4 gives the handling time of birds feeding on seeds varying in

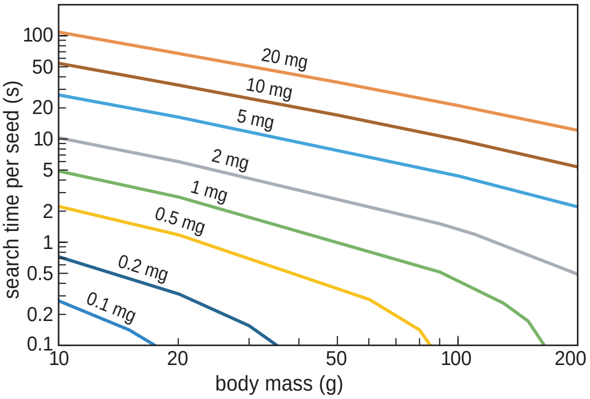


Figure 5. The search time needed per seed, varying in mass between 0.1 and 20 mg, as a function of the body mass of bird species feeding on those seeds. The prediction is based on the assumption that birds have to meet their daily food demand (Figure 1) in 4 h (Figure 4) and intake rate and handling times of seeds are according to equation 3 and 4, respectively.

mass. To estimate the search time per seed as a function of seed mass and body mass of the bird species we subtracted estimated handling time from the total time needed to find and handle a seed (Equation 3). The estimation of search time (Figure 5) was based on the assumption that the birds foraged continuously during the available daily foraging time of 4 h. In practice, foraging times will be shorter as birds have to spend time searching for rich feeding sites, meanwhile dealing with disturbances, experiencing interactions with other birds and resorting to comfort behaviour. According to Figure 5, seeds of 0.1 mg, and even of 0.2 mg, would be worthwhile to take by only the smallest bird species. This prediction refers to birds that husk the seeds. Doves swallowing seeds whole have shorter handling times, allowing them the valuable option of feeding also on small seeds that are unprofitable for husking seedeaters.

PROFITABILITY

A bird as small as a Bronze Mannikin (10 g) has to take 2.15 g seeds per day (Figure 1) and therefore needs to find 154 rice grains (14 mg each). Given an available foraging period of 4 h (Figure 4), mannikins have to find one rice grain per 94 s. The much larger Double-spurred Spurfowl (440 g) needs to take a rice grain every 7.6 s which seems feasible at high seed density. But if the same species had to feed on seeds of 1 mg, it would have to take a seed every 0.5 s which would only be possible at a very high encounter rate. Most seed-eating birds in the Sahel weigh 10–20 g. For a 4-hour feeding time, the bird's search time per seed would vary between 0.2 s for a seed of 0.1 mg taken by a bird of 20 g to 4.6 s for a bird of 10 g feeding on seeds of 1 mg (Figure 5). Obviously, seed-eating birds in (hot) Sahelian drylands feeding on small seeds cannot spend a long time searching for each and every seed and therefore must be dependent on sites where seeds are abundant. The available studies clearly show the impact of seed density on birds' intake rates and feeding density (Green 1978, Bock & Bock 1999, Whittingham & Markland 2001, Moorcroft *et al.* 2002, Stephens *et al.* 2003, Tsurim *et al.* 2007). The intake rate increases with seed density but levels off when the density is high enough to reduce search time effectively to zero: the maximal intake rate is determined by the profitability, i.e. the intake rate while handling the prey. When the birds face reduced foraging times, they must increase their intake rate by selecting profitable prey and sites where seed density is high (Figure 6A). However, when they are forced to feed on unprofitable prey, their foraging time may be too short even when the seed density is very high (Figure 6B).

DISCUSSION

Searching for visible seeds

Seed-eating birds in the Sahel, being time-constrained in their search for small grass seeds (Figure 5), also have the problem that not all seeds are accessible at the surface and, when accessible, are not always visible. 30

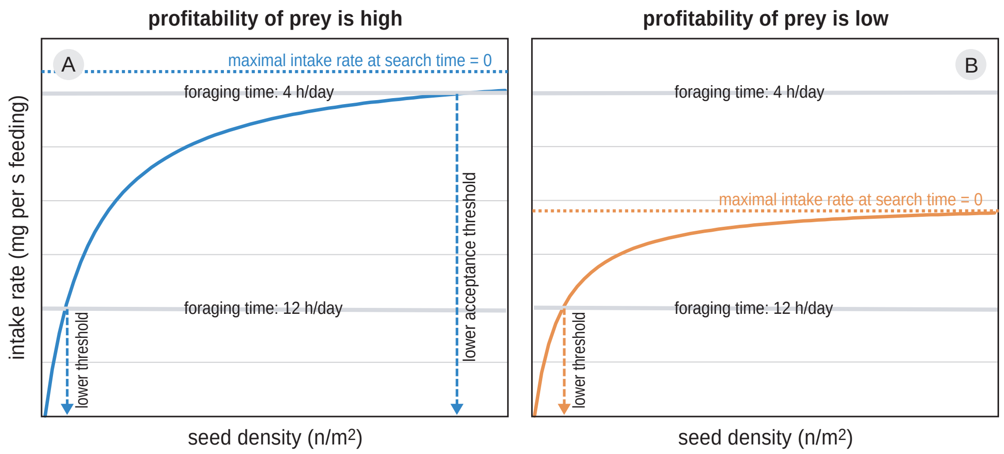


Figure 6. Functional response, the expected relationship between intake rate and seed density when the prey has (A) a high or (B) a low profitability. The dashed lines show the threshold values below which the seed density becomes too low to achieve the intake rate required to survive at a daily foraging time of 4 or 12 h/day. In a restricted foraging time period, birds need a higher intake rate and so will select sites where the search time per seed is less. In this example, birds foraging on seeds with a low profitability cannot meet their energy requirement when the feeding time is only 4 hours a day, even if seeds are so abundant that the search time is 0 (dotted line).

to 40% of the seeds of savannah grasses are buried more than 1 cm below the surface, but as the dry season progresses this proportion increased to about 50% (Carrière 1989). This increase may be a consequence of selective predation of shallow seeds, but if so, larger declines would be expected for grass species that are eaten more often. This difference was not evident from the data in Carrière (1989), but nevertheless such depletions of shallow seeds may well occur, given that experiments with captive birds showed that birds focused on visible seeds. Three finch species and a sparrow species had to search for seeds both on the surface and buried at different depths. When there were no visible seeds, the birds opted for the shallowest seeds (Cueto *et al.* 2013). Some bird species such as indigobirds and whydahs may scratch the soil in search of more deeply buried seeds (Fry & Keith 2004, Whalen & Watts 2010), but most seed-eating birds do not, likely because it would be too time-consuming. When the ground is covered by a blanket of (dead) vegetation, any seeds present on the soil surface are more difficult to detect. Indeed, the intake rate of seed-eating canaries in captivity was 36% higher on bare ground than on grass-covered ground (Whittingham & Markland 2002). Most of the soil in the Sahel is bare in the dry season, but in the humid zone a large part of the ground is covered by (dead) vegetation, unless it has been burned (Zwarts *et al.* 2023d).

Is heat stress at midday a constraint for ground-foraging birds?

Morel *et al.* (1957), Morel (1968) and Morel & Morel (1978a) noted that the length of the midday roosting period was reduced at lower temperatures, but extended when food was abundantly available (e.g. after rice had been harvested). However, bird species apparently differ in their susceptibility to heat stress; larger species tolerate higher air temperatures (Whitfield *et al.* 2015). Drinking regularly is also important (e.g. Morel 1975). Curry (1974) noted that European Turtle Doves, in contrast to African dove species, continued to feed throughout the day on the floodplains of the Inner Niger Delta, probably because water was always nearby, and also because moist areas on floodplains were not as hot as the surrounding drylands; Nobel & Geller (1987) showed that on dry and wet desert soils daily peak temperatures reached 56 and 28°C, respectively.

If birds are forced to forsake foraging during the hottest parts of days, several predictions can be made. First, due to the daily variation in midday temperatures, the reduced food consumption rate of ground-foraging birds in effect makes that resource less predictable. Birds may adopt the compensatory behaviour of enhancing their consumption during cooler days, so that their fat deposits tide them over the hot spells (e.g. Bednekoff & Krebs 1995). Second, the length of the overall daily feeding period will fluctuate more during the hot season (March–May) than during the cooler season (December–January), particularly apparent in the (hot) arid zone rather than in the (less hot) humid zone. Body mass should show a corresponding day-to day-variation. The fat content of Red-billed Weavers amounted to 5–6% relative to their total body mass during the dry season (Ward 1965), but whether the 'lean-season fat' varies in relation to temperature remained unexamined. If the temperatures in the Sahel keep rising, having already increased in April–May by an average of 1.8°C between 1950 and 2010 (Barbier *et al.* 2018), more research is surely warranted on whether midday temperatures are an increasing constraint for ground-foraging birds.

Significance of temporary wetlands in the dry Sahel

The Fété-Olé site in NW Senegal consists of low sandy dunes where small valleys are temporarily inundated during the wet season (Photo 1). Seed biomass was 2.32 g/m^2 on the dunes, but in depressions was five times higher: 11.97 g/m^2 (Bille & Poupon 1974). However, when the seeds not taken by birds are excluded (*Aristida*, *Cenchrus*, *Diheteropogon* and *Schoenefeldia*), seed biomass on the dunes was 74% lower at 0.61 g/m^2, but in depressions only 4% lower, at 11.46 g/m^2. As a result, density of preferred seeds in depressions was 19 times greater than on dry land. Floodplains and depressions (often with a clayish soil) accordingly attract seedeaters because (1) they are much more productive and (2) awnless grass species typical of seasonal ephemeral wetlands are preferred by all seedeaters, *Panicum* being first choice, followed by *Echinochloa*. The opposite applies to the arid savannah's commonest grass species (such as *Aristida* and *Cenchrus*), which are ignored.

The third reason why temporary wetlands are attractive to seedeaters is the lower soil temperatures in wet terrain, enabling European Turtle Dove to continue feeding during the middle of the day (Curry 1974). The total daily seed consumption of the European Turtle Dove (body mass: 156 g) may be estimated at 13.1 g (Figure 1). When the doves feed on *Panicum* seeds (0.95 mg), they need 12,400 seeds/day. Before their departure in April, they increase their body mass up to >190 g (Morel 1986); to attain this mass, an increase of the daily consumption is required. Indeed, Morel

(1987) found in March up to 15,000 *Panicum* seeds (14 g) in the gullet and gizzard (an underestimate of total daily intake, since seeds eaten hours before had already been digested). Handling a seed of the size of a *Panicum* would take a Turtle Dove 0.5–1.0 s (Anne-Marie Blomert pers. comm.), and so just to handle 15,000 seeds would take 125–250 minutes. Data are lacking on encounter rates of seeds by doves in the Sahel, but assuming that birds need at least 1 s to find a *Panicum* seed, they have to forage at least 6.2 to 8.3 h to consume 15,000 *Panicum* seeds. It would be much more difficult for European Turtle Doves to fuel up in drylands where soil temperature in March is still higher than in the preceding months (Figure 4).

Red-billed Queleas in NE Nigeria were concentrated in the inundation zone around Lake Chad, where they fed on a large variety of seeds from cereals (rice, sorghum) and wild grasses (especially *Echinochloa* and *Panicum*; Ward 1975, Conert 1987). On the low-lying areas of fertile alluvial soil of the dry zone, they fed on their preferred *Panicum* seed (Ward 1975). In North Senegal the queleas concentrated on floodplains along the Senegal River, where they took the same grass species as their congeners in NE Nigeria, *Echinochloa*, *Panicum* and Wild Rice, and later on in the dry season also *Chloris* and *Dactyloctenium* (Morel & Morel 1978a, 1980, 1992). This supports Ward's conclusion that food supply in drylands is insufficient to feed the many millions of queleas, hence the large gatherings of queleas in floodplains along the Rivers Senegal, Niger, Chari and Logone, and in comparable areas elsewhere in Africa. However, in dry years, seed-rich floodplains are not as extensive as in wet years (Zwarts *et al.* 2009) and far fewer ephemeral lakes can be found in the drylands. Consequently, grass species restricted to these habitats, such as *Panicum* and *Echinochloa*, will be thin on the ground, forcing seed-eating birds to switch to seeds of other graminoids or to disperse to other feeding areas.

Impact of grazing

Wet-season grazing has a large negative impact on seed-dependent birds during the dry season (Pol *et al.* 2014). Soil seed banks are reduced if livestock graze the swards before seed has fallen on the ground (Sternberg *et al.* 2003). The impact of grazing becomes

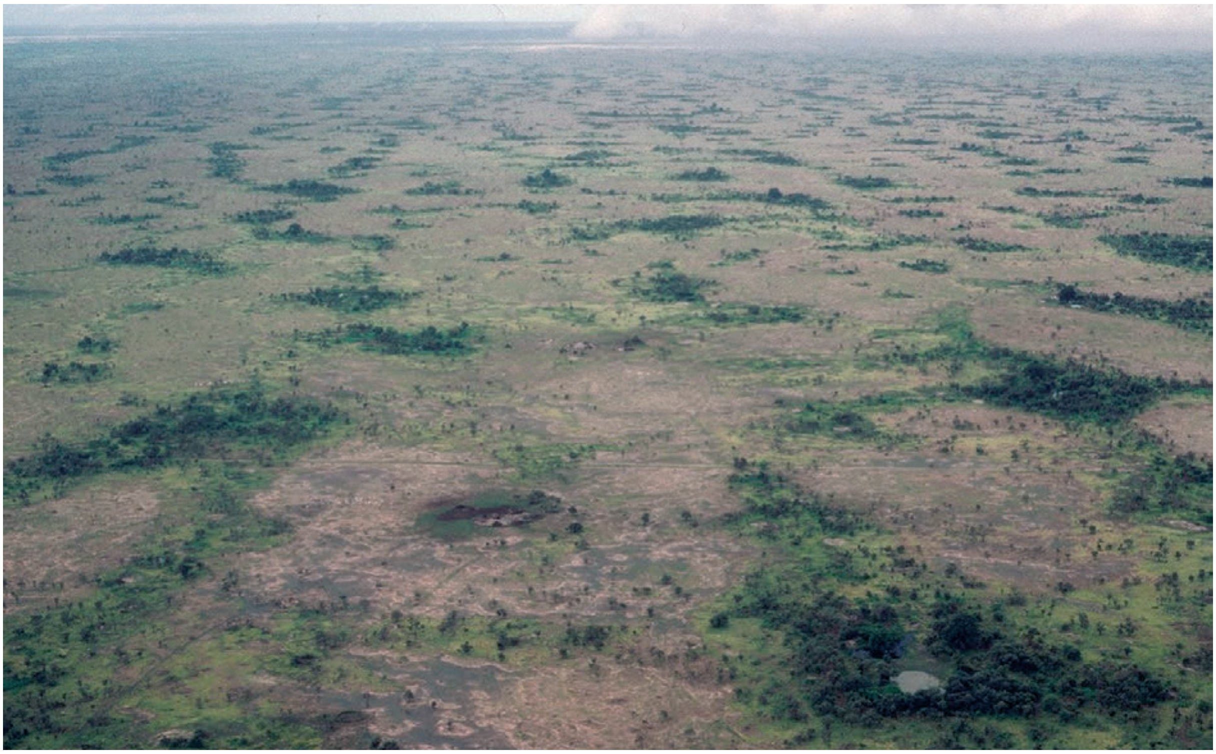


Photo 1. The landscape of the Ferlo, N Senegal, is flat, but subtle differences in elevation produce a mosaic of vegetations. The lower areas retain water for some time after the short rainy season and are covered by a dense mat of annual grasses, mainly *Panicum* and *Echinochloa*, preferred by seed-eating birds. Other grass species (e.g. *Aristida* and *Cenchrus*), ignored by birds, dominate the surrounding low dunes. The photo, taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) in the early dry season, shows these low depressions as green spots, often speckled with trees and shrubs, among light brown drylands.

greater still if heavy grazing leads to a change in the herbaceous community and birds' preferred seed plants are reduced or eliminated, leading to the predominance of grasses whose seeds are mostly ignored by birds. This vegetational shift is not unexpected because the softer seeds preferred by birds do not survive digestion by livestock, whereas the seeds ignored by birds, do (Gardener *et al.* 1993). Long-term studies in the Sahel are in agreement of changes in plant communities in the wake of increased grazing pressure. At a site in Niger (annual rainfall 575 mm) most plant species that benefited from grazing (*Aristida*, *Cenchrus*, *Schoenefeldia*) are not taken by birds, or may be taken as a last resort (*Zornia glochidiata*; 1.92 mg) when other seeds are no longer present (Hiernaux 1998). At elevated grazing pressure near Niono, Mali (570 mm rain/year) *Andropogon gayanus* was replaced by the annual herb *Zornia glochidiata* (Breman & Cissé 1977). A long history of heavy grazing and trampling at Gourma, Mali (200–500 mm rain/year) promoted an increase of the perennial *Tribulus* and the short-cycle annual *Zornia* (Hiernaux *et al.* 2009a). Heavy grazing impinges on the composition of the vegetation (Hiernaux *et al.* 2016), which in the long run will create plant communities consisting of grasses and forbs that birds dislike or avoid. The result equates a year-round qualitative and quantitative degradation of the food supply for granivorous birds (but not necessarily for livestock). In the Sahel, this scenario is based on sparse evidence as far as birds are concerned, but it corresponds with the results from detailed research in the Monte Desert of Argentina (Pol *et al.* 2014, Marone *et al.* 2017, Marone & Pol 2021, Sagario *et al.* 2020).

The impact of pastoralism on the savannah ecosystem is particularly evident in the vicinity of natural and man-made watering points. Within the heavily grazed first km from the watering points in NW Senegal, the soil vegetation was dominated by species with non-preferred seeds: *Dactylotenium* (a grass with minute seeds) and *Zornia* (Poissenet *et al.* 1992). At 1–2.5 km from the watering points the situation was much the same, the vegetation being dominated by *Zornia* and two grasses whose seeds are not taken by birds (*Aristida* and *Cenchrus*). At a distance of more than 4 km grass diversity became greater, with four species taken by birds (*Chloris*, *Digitaris*, *Eragrostis*, *Panicum*) and one species less favoured (*Schoenefeldia*). The density of seed-eating birds increased with distance from watering points in NW Senegal, but trends were not significant (Zwarts *et al.* 2018). These counts, however, referred to all birds present in the study sites, partly feeding on the ground but mostly roosting in trees, including those near watering points. Seed-eating birds are known to drink regularly (Morel 1975) and watering points are therefore magnets for seed-eating birds, obscuring any trend of expected increase of density of seed-eating birds with increasing distances from the watering points.

The heavy grazing pressure of livestock on Sahelian drylands makes floodplains and depressions even more important as refuges for seed-eating birds. It is therefore of relevance to establish the impact of grazing livestock on the herbaceous vegetation in temporary wetlands. In the absence of grazing in the low-lying parts around Lake Oursi, *Panicum* was replaced by *Aeschynomene indica* (Grouzis 1988), a tall legume with toxic seeds (7.5 mg) and probably not taken by seed-eating birds. Grazing on low-lying wet soils in this particular region helped to create and maintain an abundant food resource for seed-eating birds (but probably with negatively effects on birds like Sedge Warbler *Acrocephalus schoenobaenus*, which reaches high densities in dense vegetation of *Aeschynomene*; own unpubl. data). And exclusion of cattle from the floodplains of the Somone River in the Bandia reserve (W Senegal) resulted within a few years in the colonization of grasslands by Red Acacia *Acacia seyal* (Hejcmanová *et al.* 2009; Photo 1D in Zwarts *et al.* 2023c). Similarly, exclosures in the Inner Niger Delta (Mali) led to the establishment of flooded forests of *Acacia kirkii* (Beintema *et al.* 2007). Hence, and contrasting with drylands, seed-eating birds lose foraging habitat in Sahelian floodplains and depressions when grazing is completely absent. It is evident that seed-eating birds on the savannahs and floodplains profit from light or moderate grazing regimes, but not from the heavy grazing which is becoming the standard across the Sahel and which reduces the soil seed bank of selected plant species.

Does the available food supply limit the number of seed-eating birds?

Savannahs, at first sight perhaps perceived as simple ecosystems, are in reality complex webs with many actors on various trophic levels. This complexity is stressed again and again by plant ecologists with a long history of research in Sahelian ecosystems (e.g. Hiernaux *et al.* 2016). In the words of Peter Ward (1965) "Only those who have never seen tropical grasslands or savannah in the dry-season could suppose that there were no seasonal variations in food supply. Certainly, queleas experience a time of severe shortage of food at the onset of the rains and evidence has been given that considerable mortality occurs at this time.

Allee & Schmidt (1951) stated that in the African grassland "With the first rains, the vicissitudes of the dry season are over...", but as far as Quelea is concerned, nothing could be further from the truth." In fact, 'Quelea' in this quotation can be substituted for any seed-eating bird species.

During the early dry season, Red-billed Quelea in NE Nigeria took mainly small seeds (*Panicum*, *Echinochloa*), but later in the season they switched to minute (*Digitaria*, *Dactyloctenium*) and large seeds (sorghum, wild rice), presumably because the small seeds were depleted (Ward 1965). Morel & Morel (1978a) agreed that queleas in the late dry season in NW Senegal began to take minute seeds (*Chloris* and *Dactyloctenium*; <0.5 mg). Variation in dietary choices is typical in seasonal habitats, as evident in European Turtle Doves in N Senegal, which fed mainly on *Panicum* in August–November, on wild and cultivated rice in December–February and on the forb *Tribulus* in March–July (Morel & Morel 1979). Six Afro-tropical dove species studied by Morel & Morel (1972b) also took *Panicum* in the early dry season but forb seeds such as *Tribulus*, *Gisekia pharnaceoides* (0.26 mg) and *Zornia* in the late dry season.

The seed supply varies from year to year but is always lower in dry years (Table 1). Ward (1965) concluded that for queleas the food shortage at the end of the dry season was larger in a dry than in a wet year. In NW Senegal, seven dove species mainly fed on *Panicum* in a wet year but switched to forb seeds (*Gisekia*, *Tribulus* and *Zornia*) and small grass seeds (*Dactyloctenium*) which were normally taken only at the end of the dry season when their preferred seeds had been depleted (Morel & Morel 1972b, Urban *et al.* 1986). In the Fété-Olé study site, the density of ground-foraging birds remained stable at about 7 birds/ha between July and February in a year with a normal rainfall, but in a dry year, the numbers declined to 2–3 birds/ha in November–February (Morel & Morel 1974). The larger decline in the dry year may be due to birds leaving the area, but also to high mortality. The birds that survived the dry season were in such a poor condition that they refrained from breeding (Morel & Morel 1978b, 1992). Seed supply declines during the dry season, and much more so in years with little rain. Seeds of *Tribulus* and *Zornia*, taken during periods of food shortage, are inadequate replacements of preferred seeds, possibly due to their low digestible fraction.

Morel & Morel (1972a) estimated that in the Fété-Olé study site seed-eating birds took 2.6 g/ha in a dry year and 4.3 g/ha in a wet year, which equates to 7% of the total annual seed production (40–60 g/ha; Bille *et al.* 1972). Seed-eating birds ignored the seeds of *Aristida*, *Cenchrus*, *Diheteropogon* and *Schoenefeldia* (Morel & Morel 1972b), representing a staggering 64% of the total seed biomass (Bille & Poupon 1974). Predation pressure on the seeds of the remaining species is estimated at 20%. It must have been much higher in *Panicum* (1.8 g/ha), considering that the total annual seed consumption by birds amounted to 2.6–4.3 g/ha and *Panicum* being the main prey for seed-eating bird species. Other studies indeed found that seed-eating animals depleted the food supply during the dry season (or during winter in the temperate zone) by 50–90% and for this reason populations of seed-eating birds are often considered as limited by food (Noy-Meir 1979, Dunning & Brown 1982, Pulliam 1985, Robinson & Sutherland 1999, Gonnet 2001, Robinson *et al.* 2004, Desmond *et al.* 2008, Siriwardena *et al.* 2008, Pol *et al.* 2014, Marone *et al.* 2017). This is no different in the Sahelian savannahs.

Which leads to the conclusion, following the initial questions asked, that (1) food supply of seedeaters in the Sahel is declining, (2) seedeaters in the Sahel are highly selective in their seed choice, (3) heavy grazing has in general a negative impact on the food resources in the Sahel, and (4) present overall conditions in the Sahel are indeed limiting numbers of granivorous birds to the extent of causing steep declines in populations of most species involved, including the few species breeding in Eurasia.

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SAMENVATTING

Zaadetende vogels eten in de Sahel dagelijks met zijn alle gemiddeld ongeveer 15 gram zaad per ha. Dat is berekend aan de hand van systematische tellingen van vogels in vakjes van 4,5 ha en een geschatte dagelijkse voedselconsumptie afgeleid van hun lichaamsgewicht. Gedurende de korte regentijd stappen veel zaadeters over op ander voedsel. Als we daarmee rekening houden, zouden zaadetende vogels jaarlijks gemiddeld 4,5 kg zaad per ha consumeren. Het gaat daarbij om zaden van kruiden en grassen, vooral eenjarige soorten die aan het eind van de regentijd afsterven. Hoeveel zaad er dan op de grond ligt, verschilt naar locatie. Voor de gehele Sahel zal de gemiddelde zaadproductie tussen 30 en 100 kg per ha liggen. Als deze schattingen juist zijn, zouden zaadetende vogels niet meer dan 4 tot 15% van de jaarlijkse zaadvoorraad opeten, ogenschijnlijk geen aanwijzing voor voedselschaarste. Toch zijn er diverse redenen om aan te nemen dat het aantal zaadetende vogels wordt beperkt door hun voedselaanbod. Ten eerste moeten de vogels de zaadvoorraad delen met knaagdieren en insecten die bij elkaar meer zaden eten dan alle vogels samen. Ten tweede hebben de vogels per dag niet veel tijd om te foerageren, omdat ze ermee stoppen als de bodemtemperatuur

boven 35°C stijgt. Midden op de dag kan de bodemtemperatuur, zonder schaduw, oplopen tot 50°C of hoger. Dat is de belangrijkste reden dat grondfoeragerende vogels grosso modo vooral in de vroege ochtend en de late middag naar voedsel zoeken, in totaal ongeveer 4 uur per dag. Dit beperkte tijdvak zou in de toekomst nog verder kunnen worden ingeperkt; tussen 1950 en 2010 zijn de temperaturen in de Sahel in de heetste maanden april en mei al met 1,8° C gestegen. Hittestress dwingt vogels ertoe om in weinig tijd veel te eten. Ze zijn daardoor afhankelijk van plekken waar de beschikbare zaden zo talrijk zijn dat ze gemakkelijk kunnen worden gevonden (korte zoektijd). Maar de zaden moeten ook heel snel kunnen worden verwerkt (korte hannestijd). Duiven slikken de zaden in één keer in en dat gaat heel snel. Maar alle kleinere zaadeters scheiden eerst het kaf van het zaadje en dat kost meer tijd. Een derde reden om te denken dat het voedselaanbod beperkt is, heeft te maken met het feit dat slechts een deel van de zaden aan het oppervlak ligt en daardoor gemakkelijk te vinden is. De meeste graszaden liggen verborgen in het zand en zijn ook nog eens heel klein. Zo klein dat zelfs vogels van minder dan 10 gram er duizenden per dag moeten eten om rond te komen. Maar omdat ze zo weinig tijd hebben om voedsel te zoeken, kunnen ze het zich niet permitteren om te zoeken naar zaden die onder het zand verborgen liggen. Zelfs in overvloed kan voedsel toch onbereikbaar zijn. Ten vierde laten vogels in de Sahel veel zaad links liggen. Ze weigeren 'lege zaden' (zaden bestaande uit alleen het onverteerbaar kafje, dus zonder inhoud). Ook de zaden van juist de meest voorkomende grassoorten worden vermeden, zoals van *Aristida* waar aan de zaden lange naalden zitten of van *Cenchrus*, een soort kleefkruid met keiharde stekels. Deze zaden worden waarschijnlijk niet gegeten omdat het te veel hannestijd zou kosten om ze naar binnen te kunnen werken. Sommige zaden van kruidachtigen worden wel gegeten, maar genieten niet de voorkeur, waarschijnlijk vanwege hun geringe verteerbaarheid. Zaadetende vogels eten het liefst de zaden van het gras *Panicum* en andere wilde gierstsoorten die geen naalden of stekels hebben en gemakkelijk verteerbaar zijn. Vogels schakelen pas over op marginale zaadsoorten wanneer, aan het einde van de droge tijd, de zaadvoorraad van de voorkeurssoorten is uitgeput. Ten vijfde worden *Panicum* en andere preferente eenjarige grassen meestal aangetroffen op vloedvlakten en lage plekken die tijdens het regenseizoen tijdelijk onder water komen te staan. Deze gebieden trekken veel zaadetende vogels aan, maar de totale oppervlakte van vochtige foerageergebieden is relatief klein vergeleken met de uitgestrekte droge gebieden. En nog veel kleiner in droge jaren, waaraan geen gebrek was in de afgelopen ruim halve eeuw. In dergelijke jaren is de sterfte onder zaadetende vogels enorm. Het zesde en laatste argument voor beperkt voedselaanbod is dat de hoeveelheid zaad op de bodem is geslonken door de gestegen begrazingsdruk van vee die met het gras ook de zaden opeten. De hogere graasdruk heeft er tevens voor gezorgd dat de voor zaadetende vogels favoriete grassoorten zijn vervangen door niet-preferente grassen en kruiden die beter bestand zijn tegen graasdruk of daar zelfs van profiteren. Al deze factoren tezamen hebben bijgedragen aan de fenomenale achteruitgang van zaadetende vogels in de Sahel tussen 1970 en 2010. Het zijn er nu nog vier miljard, maar een halve eeuw geleden moeten dat er miljarden meer zijn geweest. Ook het handjevol Euraziatische zaadeters dat in de Sahel overwintert kan daarover meespreken.

RÉSUMÉ

Les oiseaux granivores du Sahel mangent en moyenne environ 15 grammes de graines par hectare. Ce chiffre a été calculé à partir de comptages systématiques des oiseaux dans des parcelles de 4,5 ha et d'une estimation de la consommation alimentaire quotidienne dérivée de leur poids corporel. Pendant la courte saison des pluies, de nombreux oiseaux granivores se tournent vers d'autres aliments. Compte tenu de ce facteur, les oiseaux granivores consommeraient en moyenne 4,5 kg de graines par ha et par an. Il s'agit de graines d'herbes et de graminées, en particulier d'espèces annuelles qui meurent à la fin de la saison des pluies. La quantité de semences laissée sur le sol varie alors d'un endroit à l'autre. Pour l'ensemble du Sahel, la production moyenne de semences se situera entre 30 et 100 kg par ha. Si correcte, les oiseaux granivores ne mangeraient pas plus de 4 à 15% de l'approvisionnement annuel en graines. Cependant, il y a plusieurs raisons de supposer que le nombre d'oiseaux granivores est limité par leur nourriture. (1) Les oiseaux doivent partager l'approvisionnement en graines avec les rongeurs et les insectes qui, ensemble, mangent plus de graines que tous les oiseaux réunis. (2) Les oiseaux n'ont pas beaucoup de temps par jour pour fourrager car ils s'arrêtent lorsque la température du sol dépasse 35°C. Au milieu de la journée, sans ombre, la température du sol peut atteindre 50 ou 60°C. C'est la principale raison pour laquelle les oiseaux butinant au sol ne s'alimentent qu' en début de matinée et en fin d'après-midi, pour un total d'environ 4 heures par jour. Le stress thermique oblige les oiseaux à manger beaucoup en peu de temps. Ils dépendent donc des endroits où les graines disponibles sont si abondantes qu'elles peuvent être trouvées facilement (temps de recherche court). Mais il faut aussi que les graines soient traitées très rapidement (temps d'accrochage court). Les pigeons avalent les graines d'un seul coup et très rapidement. Mais tous les petits mangeurs de graines séparent d'abord l'enveloppe de la graine et cela prend plus de temps. (3) Seules certaines des graines sont à la surface et donc faciles à trouver. La plupart des graines d'herbe, très petites, sont cachées dans le sable. Si petites que même les oiseaux pesant moins de 10 grammes doivent en manger des milliers par jour pour joindre les deux bouts. Mais comme ils ont si peu de temps pour se nourrir, ils ne peuvent pas se permettre de chercher des graines cachées sous le sable. Même en abondance, la nourriture peut encore être inaccessible. (4) Les oiseaux du Sahel ignorent de nombreuses graines. Ils refusent les "graines vides" (graines constituées uniquement de l'enveloppe indigeste, donc sans contenu). Ils évitent également les graines des espèces de graminées les plus courantes, telles que l'*Aristide*, dont les graines sont munies de longues aiguilles, ou le *Cenchrus*, un type de gaillet gratteron aux épines très dures. Ces graines ne sont probablement pas consommées car il faudrait une trop grande envie pour les ingérer. Certaines graines d'herbacées sont consommées, mais ne sont pas préférées, probablement en raison de leur faible digestibilité. Les oiseaux granivores préfèrent les graines de l'herbe *Panicum* et d'autres espèces de millet sauvage qui n'ont pas d'aiguilles ou d'épines et sont faciles à digérer. Les oiseaux ne passent à des espèces marginales que lorsque, à la fin de la saison sèche, les réserves de graines de l'espèce préférée sont épuisées. (5) Le *Panicum* et d'autres herbes annuelles préférées se trouvent généralement dans les plaines inondables. Ces zones attirent de nombreux oiseaux granivores, mais la superficie totale de ces zones est relativement faible par rapport aux vastes zones sèches. Et encore moins pendant les années sèches, qui n'ont pas manqué au cours du dernier demi-siècle. Ces années-là, la mortalité des oiseaux granivores est énorme. (6) La quantité de graines sur le sol a diminué en raison de la pression accrue du bétail, qui mange les graines en même temps que l'herbe. La pression de pâturage plus élevée a également entraîné le remplacement des espèces de graminées favorisées par les oiseaux granivores par des graminées et des herbes non préférées qui sont plus résistantes à la pression de pâturage, voire qui en bénéficient. Tous ces facteurs ont contribué au déclin phénoménal des oiseaux granivores du Sahel entre 1970 et 2010. Aujourd'hui, ils sont encore quatre milliards, mais il y a un demi-siècle, ils devaient être beaucoup plus nombreux.

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SUPPLEMENTARY MATERIAL: Handling time in seed-eating birds

Table S1. The handling time in seconds (ht), defined as the time needed to husk and ingest a seed, for 48 seed-eating bird species with body masses (bm) varying between 9.6 and 70 g, and for 38 seed species varying between 0.1 and 146 mg. A selection is made for seeds that are husked (thus excluding seeds swallowed whole, as typical of doves and waterbirds). The 197 handling times and seed weights are taken from 13 sources (#): (1) Carrillo *et al.* 2007, (2) Goldstein & Baker 1984, (3) Hespenheide 1966, (4) Hrabar & Perrin 2002, (5) Kear 1962, (6) Marone *et al.* 2022, (7) Pulliam 1985, (8) Soobramoney & Perrin 2007, (9) Titulaer 2018, (10) van der Meij & Bout 2004, (11) van der Meij & Bout 2006, (12) Willson 1971 and (13) Willson & Harmeson 1973.

Bird species	**bm**	**Seed species**	**seed** (mg)	**ht**	**#**
Fischer's Lovebird	46.6	*Echinochloa frumentacea*	3.5	6.0	4
Fischer's Lovebird	46.6	*Panicum maximum*	5.6	6.6	4
Fischer's Lovebird	46.6	*Phalaris canariensis*	7.0	5.3	4
Fischer's Lovebird	46.6	*Setaria italica*	5.4	7.1	4
Cape Sparrow	24.6	*Echinochloa frumentacea*	3.3	2.2	8
Cape Sparrow	24.6	*Guizotia abyssinica*	2.9	7.1	8
Cape Sparrow	24.6	*Panicum maximum*	3.6	3.1	8
Cape Sparrow	24.6	*Phalaris canariensis*	7.0	2.7	8
Cape Sparrow	24.6	*Setaria italica*	5.1	2.9	8
Cape Sparrow	24.6	*Sorghum bicolor*	20.8	22.3	8
Thick-billed Weaver	43.9	*Echinochloa frumentacea*	3.3	5.9	8
Thick-billed Weaver	43.9	*Guizotia abyssinica*	2.9	8.3	8
Thick-billed Weaver	43.9	*Panicum maximum*	3.6	6.4	8
Thick-billed Weaver	43.9	*Phalaris canariensis*	7.0	4.7	8
Thick-billed Weaver	43.9	*Setaria italica*	5.1	7.3	8
Thick-billed Weaver	43.9	*Sorghum bicolor*	20.8	16.5	8
Black-winged Red Bishop	22.0	*Cannabis sativa*	18.5	5.5	10
Southern Red Bishop	21.1	*Echinochloa frumentacea*	3.3	3.2	8
Southern Red Bishop	21.1	*Guizotia abyssinica*	2.9	6.4	8
Southern Red Bishop	21.1	*Panicum maximum*	3.6	2.7	8
Southern Red Bishop	21.1	*Phalaris canariensis*	7.0	3.5	8
Southern Red Bishop	21.1	*Setaria italica*	5.1	4.1	8
Southern Red Bishop	21.1	*Sorghum bicolor*	20.8	24.5	8
Sunda Zebra Finch	22.7	*Phalaris canariensis*	7.0	16.0	11
Bronze Mannikin	9.6	*Echinochloa frumentacea*	3.3	5.0	8
Bronze Mannikin	9.6	*Guizotia abyssinica*	2.9	5.8	8
Bronze Mannikin	9.6	*Panicum maximum*	3.6	1.6	8
Bronze Mannikin	9.6	*Phalaris canariensis*	7.0	8.9	8
Bronze Mannikin	9.6	*Setaria italica*	5.1	6.4	8
Bronze Mannikin	9.6	*Sorghum bicolor*	20.8	32.2	8
Magpie Mannikin	16.2	*Phalaris canariensis*	7.0	7.9	11
Java Sparrow	30.4	*Cannabis sativa*	18.5	4.1	10
Java Sparrow	26.9	*Echinochloa frumentacea*	3.5	2.3	4
Java Sparrow	26.9	*Panicum maximum*	5.6	2.7	4
Java Sparrow	26.9	*Phalaris canariensis*	7.0	2.6	4
Java Sparrow	30.4	*Phalaris canariensis*	7.0	2.6	11
Java Sparrow	26.9	*Setaria italica*	5.4	3.1	4
Scaly-breasted Munia	12.4	*Phalaris canariensis*	7.0	11.6	11
White-rumped Munia	13.6	*Echinochloa frumentacea*	3.3	3.7	8
White-rumped Munia	13.6	*Guizotia abyssinica*	2.9	4.5	8
White-rumped Munia	13.6	*Panicum maximum*	3.6	2.3	8
White-rumped Munia	13.6	*Phalaris canariensis*	7.0	6.7	8
White-rumped Munia	13.6	*Setaria italica*	5.1	5.9	8
White-rumped Munia	13.6	*Sorghum bicolor*	20.8	29.7	8
Gouldian Finch	15.2	*Phalaris canariensis*	7.0	12.5	11
Blue-faced Parrotfinch	13.1	*Phalaris canariensis*	7.0	7.8	11
Cut-throat Finch	18.5	*Phalaris canariensis*	7.0	5.4	11
Common Chaffinch	22.0	*Brassica napus*	5.3	2.4	5
Common Chaffinch	22.0	*Cannabis sativa*	25.0	5.0	5
Common Chaffinch	22.0	*Helianthus annuus*	143.0	41.0	5
Common Chaffinch	22.0	*Linum usitatissimum*	7.8	6.5	5
Common Chaffinch	22.0	*Phalaris canariensis*	11.0	2.8	5
Common Chaffinch	22.0	*Setaria italica*	4.9	3.2	5
Collared Grosbeak	70.0	*Phalaris canariensis*	7.0	2.4	11
Evening Grosbeak	55.0	*Cannabis sativa*	25.0	2.3	5
Evening Grosbeak	55.0	*Helianthus annuus*	143.0	4.3	5
Hawfinch	21.8	*Cannabis sativa*	25.0	3.1	5
Hawfinch	21.8	*Helianthus annuus*	143.0	4.3	5
Hawfinch	21.8	*Linum usitatissimum*	7.8	5.6	5
Hawfinch	21.8	*Phalaris canariensis*	11.0	2.8	5
Chinese Grosbeak	52.0	*Phalaris canariensis*	7.0	2.1	11
Eurasian Bullfinch	20.9	*Phalaris canariensis*	7.0	4.9	11
Trumpeter Finch	19.2	*Avena sativa*	16.0	11.9	1
Trumpeter Finch	19.2	*Brassica napus*	4.0	2.3	1
Trumpeter Finch	19.2	*Linum usitatissimum*	4.8	4.3	1
Trumpeter Finch	19.2	*Phalaris canariensis*	6.5	2.8	1
Trumpeter Finch	19.2	*Setaria italica*	6.7	6.3	1
Common Rosefinch	21.6	*Phalaris canariensis*	7.0	3.4	11
European Greenfinch	25.1	*Cannabis sativa*	25.0	2.8	5
European Greenfinch	28.3	*Cannabis sativa*	18.5	2.2	10
European Greenfinch	25.1	*Helianthus annuus*	143.0	5.9	5
European Greenfinch	25.1	*Linum usitatissimum*	7.8	4.8	5
European Greenfinch	25.1	*Phalaris canariensis*	11.0	2.8	5
European Greenfinch	28.3	*Phalaris canariensis*	7.0	2.6	11
Grey-capped Greenfinch	20.0	*Phalaris canariensis*	7.0	2.9	11
Desert Finch	22.5	*Phalaris canariensis*	7.0	4.0	11

Table S1. Continued.

Bird species	**bm**	**Seed species**	**seed** (mg)	**ht**	**#**
Yellow-fronted Canary	12.0	*Cannabis sativa*	18.5	12.6	10
Yellow-fronted Canary	12.0	*Phalaris canariensis*	7.0	12.6	11
Common Redpoll	12.6	*Phalaris canariensis*	7.0	9.8	11
Red Crossbill	44.0	*Phalaris canariensis*	7.0	3.7	11
Atlantic Canary	24.9	*Brassica napus*	5.3	2.3	5
Atlantic Canary	24.9	*Cannabis sativa*	25.0	4.6	5
Atlantic Canary	24.9	*Linum usitatissimum*	7.8	8.3	5
Atlantic Canary	24.9	*Phalaris canariensis*	11.0	3.3	5
Atlantic Canary	24.9	*Setaria italica*	4.9	3.3	5
Eurasian Siskin	13.0	*Phalaris canariensis*	7.0	9.2	11
Yellowhammer	25.0	*Cannabis sativa*	18.5	4.8	10
Grasshopper Sparrow	16.6	*Bouteloua aristidoides*	0.3	0.4	9
Grasshopper Sparrow	16.6	*Bouteloua curtipendula*	2.4	0.4	9
Grasshopper Sparrow	16.6	*Cenchrus ciliaris*	2.9	0.9	9
Grasshopper Sparrow	16.6	*Disakisperma dubium*	0.6	0.7	9
Grasshopper Sparrow	16.6	*Eragrostis lehmanniana*	0.1	0.5	9
Grasshopper Sparrow	16.6	*Melinis repens*	0.7	0.3	9
Chipping Sparrow	12.6	*Aristida divaricata*	1.0	3.2	7
Chipping Sparrow	12.6	*Aristida hamulosa*	0.8	2.8	7
Chipping Sparrow	12.6	*Aristida ternipes*	1.0	4.4	7
Chipping Sparrow	12.6	*Bidens leptocephala*	1.2	6.3	7
Chipping Sparrow	12.6	*Bouteloua aristidoides*	0.8	1.3	7
Chipping Sparrow	12.6	*Bouteloua curtipendula*	0.8	1.4	7
Chipping Sparrow	12.6	*Bouteloua hirsuta*	0.7	1.5	7
Chipping Sparrow	12.6	*Digitaria californica*	0.6	2.3	7
Chipping Sparrow	12.6	*Disakisperma dubium*	0.7	1.2	7
Chipping Sparrow	12.6	*Eragrostis lehmanniana*	0.1	0.6	7
Chipping Sparrow	12.6	*Glinus oppositifolius*	0.1	0.1	7
Chipping Sparrow	12.6	*Hexasepalum teres*	4.1	5.9	7
Chipping Sparrow	12.6	*Hopia obtusum*	1.8	4.5	7
Chipping Sparrow	12.6	*Lycurus phleioides*	0.2	0.9	7
Chipping Sparrow	12.6	*Portulaca oleracea*	0.1	0.9	7
Chipping Sparrow	12.6	*Portulaca oleracea*	0.2	0.6	7
Chipping Sparrow	12.6	*Schkuhria pinnata*	3.1	4.7	7
Chipping Sparrow	12.6	*Sida abutilifolia*	1.6	5.5	7
Field Sparrow	13.1	*Setaria italica*	3.4	3.2	12
Red Fox Sparrow	31.0	*Cannabis sativa*	16.8	8.1	12
Red Fox Sparrow	31.0	*Guizotia abyssinica*	2.9	2.0	12
Red Fox Sparrow	31.0	*Linum usitatissimum*	5.5	6.2	12
Red Fox Sparrow	31.0	*Phalaris canariensis*	6.5	2.8	12
Red Fox Sparrow	31.0	*Setaria italica*	3.4	4.0	12
American Tree Sparrow	17.8	*Cannabis sativa*	16.8	19.0	12
American Tree Sparrow	17.8	*Guizotia abyssinica*	2.9	4.6	12
American Tree Sparrow	17.8	*Phalaris canariensis*	6.5	4.4	12
American Tree Sparrow	17.8	*Setaria italica*	3.4	1.6	12
Dark-eyed Junco	19.8	*Aristida hamulosa*	0.8	2.5	7
Dark-eyed Junco	21.0	*Cannabis sativa*	16.8	30.3	12
Dark-eyed Junco	19.8	*Digitaria californica*	0.6	1.3	7
Dark-eyed Junco	19.8	*Disakisperma dubium*	0.7	1.0	7
Dark-eyed Junco	19.8	*Eriochloa acuminata*		4.1	7
Dark-eyed Junco	19.8	*Guizotia abyssinica*	3.1	4.9	2
Dark-eyed Junco	21.0	*Guizotia abyssinica*	2.9	3.4	12
Dark-eyed Junco	21.1	*Helianthus annuus*	86.0	228.0	3
Dark-eyed Junco	21.1	*Helianthus annuus*	93.0	166.0	3
Dark-eyed Junco	21.0	*Linum usitatissimum*	5.5	7.8	12
Dark-eyed Junco	19.8	*Lycurus phleioides*	0.2	0.7	7
Dark-eyed Junco	19.8	*Phalaris canariensis*	7.0	5.9	2
Dark-eyed Junco	21.0	*Phalaris canariensis*	6.5	5.3	12
Dark-eyed Junco	21.0	*Setaria italica*	3.4	3.9	12
Rufous-collared Sparrow	19.2	*Digitaria californica*	1.52	0.4	6
Rufous-collared Sparrow	19.2	*Parthenium hysterophus*	1.85	0.4	6
Rufous-collared Sparrow	19.2	*Pappophorum* spp.	1.45	0.7	6
Rufous-collared Sparrow	19.2	*Setaria leucopila*	2.05	0.8	6
White-crowned Sparrow	27.0	*Aristida divaricata*	1.0	1.4	7
White-crowned Sparrow	27.0	*Aristida hamulosa*	0.8	2.2	7
White-crowned Sparrow	27.0	*Aristida ternipes*	1.0	2.0	7
White-crowned Sparrow	27.0	*Bouteloua aristidoides*	0.8	1.0	7
White-crowned Sparrow	27.0	*Bouteloua hirsuta*	0.7	1.1	7
White-crowned Sparrow	23.2	*Helianthus annuus*	86.0	72.0	3
White-crowned Sparrow	27.0	*Lycurus phleioides*	0.2	0.8	7
White-throated Sparrow	23.2	*Avena sativa*	29.6	13.2	12
White-throated Sparrow	23.2	*Cannabis sativa*	16.8	13.9	12
White-throated Sparrow	23.2	*Guizotia abyssinica*	2.9	4.8	12
White-throated Sparrow	23.2	*Helianthus annuus*	93.0	103.0	3
White-throated Sparrow	23.2	*Helianthus annuus*	122.0	121.0	3
White-throated Sparrow	23.2	*Helianthus annuus*	146.0	158.0	3
White-throated Sparrow	23.2	*Phalaris canariensis*	6.5	3.3	12
White-throated Sparrow	23.2	*Setaria italica*	3.4	4.9	12
Baird’s Sparrow	17.5	*Bouteloua aristidoides*	0.3	0.5	9
Baird’s Sparrow	17.5	*Bouteloua curtipendula*	2.4	0.8	9
Baird’s Sparrow	17.5	*Cenchrus ciliaris*	2.9	0.8	9
Baird’s Sparrow	17.5	*Disakisperma dubium*	0.6	0.6	9
Baird’s Sparrow	17.5	*Eragrostis lehmanniana*	0.1	0.5	9
Baird’s Sparrow	17.5	*Melinis repens*	0.7	0.3	9
Savannah sparrow	16.5	*Bouteloua aristidoides*	0.3	0.7	9
Savannah sparrow	16.5	*Bouteloua curtipendula*	2.4	1.1	9
Savannah sparrow	16.5	*Disakisperma dubium*	0.6	0.7	9
Savannah sparrow	16.5	*Melinis repens*	0.7	0.3	9
Song Sparrow	25.0	*Amaranthus retroflexus*	0.3	2.2	13
Song Sparrow	25.0	*Cannabis sativa*	16.8	12.8	12
Song Sparrow	25.0	*Cannabis sativa*	7.0	11.4	13
Song Sparrow	25.0	*Guizotia abyssinica*	2.9	4.5	12
Song Sparrow	25.0	*Persicaria bungeana*	4.8	10.1	13
Song Sparrow	25.0	*Phalaris canariensis*	6.5	3.5	12
Song Sparrow	25.0	*Setaria faberi*	1.2	2.0	13
Song Sparrow	25.0	*Setaria italica*	3.4	2.9	12
Swamp Sparrow	16.0	*Guizotia abyssinica*	2.9	3.1	12
Swamp Sparrow	16.0	*Phalaris canariensis*	6.5	3.5	12
Swamp Sparrow	16.0	*Setaria italica*	3.4	2.8	12
Northern Cardinal	44.0	*Ambrosia trifida*	35.7	80.7	13
Northern Cardinal	44.0	*Ambrosia trifida*	35.7	43.6	13
Northern Cardinal	44.0	*Avena sativa*	29.6	28.9	12
Northern Cardinal	44.0	*Cannabis sativa*	16.8	13.5	12
Northern Cardinal	44.0	*Cannabis sativa*	7.0	5.5	13
Northern Cardinal	44.0	*Guizotia abyssinica*	2.9	2.7	12
Northern Cardinal	44.0	*Helianthus annuus*	120.0	36.8	12
Northern Cardinal	44.0	*Persicaria bungeana*	4.8	11.7	13
Northern Cardinal	44.0	*Phalaris canariensis*	6.5	4.3	12
Northern Cardinal	44.0	*Setaria faberi*	1.2	3.0	13
Northern Cardinal	44.0	*Setaria italica*	3.4	5.4	12
Many-colored Chaco Finch	22.4	*Digitaria californica*	1.32	0.4	6
Many-colored Chaco Finch	22.4	*Parthenium hysterophus*	2.28	0.4	6
Many-colored Chaco Finch	22.4	*Pappophorum* spp.	1.59	0.7	6
Many-colored Chaco Finch	22.4	*Setaria leucopila*	2.13	0.8	6
Cinnamon Warbling Finch	12.7	*Digitaria californica*	1.33	0.4	6
Cinnamon Warbling Finch	12.7	*Parthenium hysterophus*	1.89	0.4	6
Cinnamon Warbling Finch	12.7	*Pappophorum* spp.	1.7	0.7	6
Cinnamon Warbling Finch	19.2	*Setaria leucopila*	3.09	0.8	6
Diuca Finch	25.0	*Digitaria californica*	1.72	0.4	6
Diuca Finch	25.0	*Parthenium hysterophus*	1.63	0.4	6
Diuca Finch	25.0	*Pappophorum* spp.	3.86	0.7	6
Diuca Finch	25.0	*Setaria leucopila*	1.04	0.8	6

Birds and bush fires in African savannahs

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Bush fires are widespread in African savannahs. Their impact on birds varies. Many insectivores temporarily profit from the insects escaping fire and smoke, whereas the burnt-through grass and herb layer facilitates feeding for some ground-foraging bird species. Nevertheless, bush fires have a direct, negative impact on many other ground-foraging birds. The average density of seed-eating birds in humid, African savannahs (annual rainfall >800 mm) was 15.9 birds/ha in unburned savannahs, compared to 3.3 birds/ ha (–72%) in recently burned areas. No such difference was found for insectivorous bird species. Eleven of the 13 common ground-foraging migratory bird species were not affected by bush fires in Africa because they spend the northern winter in the arid and semi-arid zone, beyond the main bush-fire zone. In the long run, savannah-inhabitant birds profit from bush fires, simply because fires prevent open landscape from becoming overgrown with trees. However, the short-term implications of bush fires might be severe for seed-eating birds that rely on humid savannah, because of the more than 3 million km^2 in Africa burned annually, most comprises humid savannah.

Key words: bush fire, granivorous birds, insectivorous birds, savannah, Sahel

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Bush fires play a key role in determining the structure, functioning and dynamics of savannahs (Scholes & Archer 1977, Saab & Powell 2005, Hegazy & Lovett-Doust 2016). This has been the case in fire-prone regions from long before humans began to dominate the Earth (Pausas *et al.* 2009). At present, most bush fires – at least in the Sahel – are established by local people. Fires are ignited for a wide range of purposes, such as for land clearance or regeneration of plant food and for controlled burning in order to reduce the potential fuel load that would feed larger fires. Each year, Earth's surface experiences fires over an area totalling 4.9 million km^2, 70% of which comprises sub-Saharan Africa (Rano *et al.* 2021). Every year, 11% of African savannahs and other fire-prone landscapes is burnt. In climate zones with >800 mm rainfall per annum, bush fires are the instruments that create and maintain open savannah and prevent the landscape from being dominated by trees.

Bush fires promptly attract a variety of avian predators of various plumage to feast upon the small mammals, reptiles and large insects (especially orthopterans) escaping from the flames and smoke, finding them easy prey. Egrets, herons, storks, kites, buzzards, hawks, falcons, pratincoles, terns, nightjars, kingfishers, bee-eaters, rollers, hornbills, swallows, fiscals, drongos, crows and starlings have long been known to congregate at bush fires in Africa and elsewhere (Büttikofer 1890, Thiollay 1971, Barnard 1987, Dean 1987, Schulz 1998, Bouwman & Hoffman 2007, Krook *et al.* 2007, Hovick *et al.* 2017). Even small fires are quickly detected and exploited. When food is hard to detect in the tall grasses of the humid savannahs (early dry season) or when food supplies are dwindling (later on in the dry season), bush fires not only expose large insects and vertebrates to ground-foraging birds, but also expose smaller insects to aerial insectivores (Thiollay 1971). We observed a typical example on 11 January 2017, when a recently ignited bush fire in Senegal (14.022°N, 15.151°W) attracted at least 110 Abyssinian Rollers *Coracias abyssinicus*. The Rollers began to arrive from all directions as soon as smoke columns emerged from the fire scene. In West Africa, Abyssinian Rollers are territorial and widely spaced. Prior to the fire, we had recorded their territorial density in the immediate surroundings of the bush fire as 0.099/ha (25 counting sites, in a total area of 111 ha). Given this density, the bush fire may have attracted every individual within a radius of 1.94 km. Some 15 minutes after the fire had begun to attract birds, only an occasional straggler still headed towards the fire scene, but many Rollers had already made the return trip to their territories. We were unable to assess whether the returning birds had reached their digestive bottleneck (Karasov & McWilliams 2005), or whether the temporary food bounty had become depleted.

The after-effects of bush fires are manifold. Much of the ground vegetation is scorched and bare soil is covered by sooty debris (Photo 1). However, the intensity of a fire may vary greatly across its footprint. A fire sometimes bypasses patches of vegetation or travels so fast that part of the food supply of birds (seeds, insects) remains unaffected. Furthermore, many grasses have seeds with awns that facilitate their burial in the ground (Peart 1984). Seeds of *Hyparrhenia* grasses with long awns were found at a greater depth than those with shorter awns, enhancing their survival during intense bush fires (Garnier & Dajoz 2001). Seeds without awns can also end up below the surface, the smooth elliptical seeds of *Panicum* grass descending even to greater depths than awned seeds of *Aristida* (Carrière 1989). More than half of the grass seeds were found at >1 cm below the surface.

In this paper, we address three questions: (1) Which parts of the northern sub-Saharan Africa are most prone to bush fires and which bird species occur in this fire zone, (2) What are the densities of ground-foraging birds in burned areas compared to unburned areas in the same zone, and (3) Is the response of insectivorous birds – in terms of densities in burned and unburned sites – similar to that of granivorous birds?

RESULTS

Extent and timing of grass fires

The fraction of burned sites in the savannah decreased with decreasing rainfall (Figure 1A), and fires were completely absent in sub-Saharan zones with an average annual rainfall of 500 mm or less. A similar trend was recorded for sites categorised as farmland or woodland, albeit at a lower level. The lack of bush fires in the arid zone equated with a lack of flammable vegetation, i.e. a vegetation cover in the dry season of less than 15% at annual rainfall < 600 mm (Figure 1B). The cover of the herbaceous layer increased up to 80% when rainfall exceeded 600 mm per annum, and on average was twice as low in burned sites than in unburned.

Our field data suggest that a large part of the savannah in the humid zone was burned (Figure 1A). Some sites were visited in December, but most were visited in January and February; the final burned area on these sites during the dry season must therefore have been larger than we measured, given the ongoing process of setting fire to savannah.

Remote sensing data confirm that a large part of the savannah is burned annually. The total surface of the

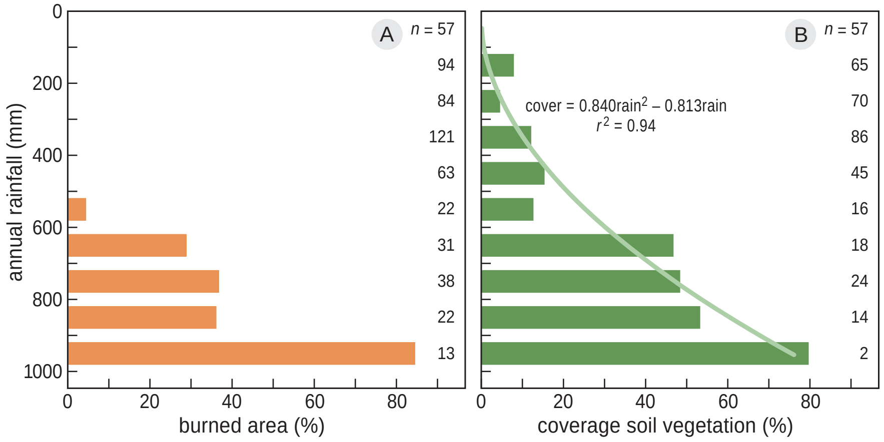
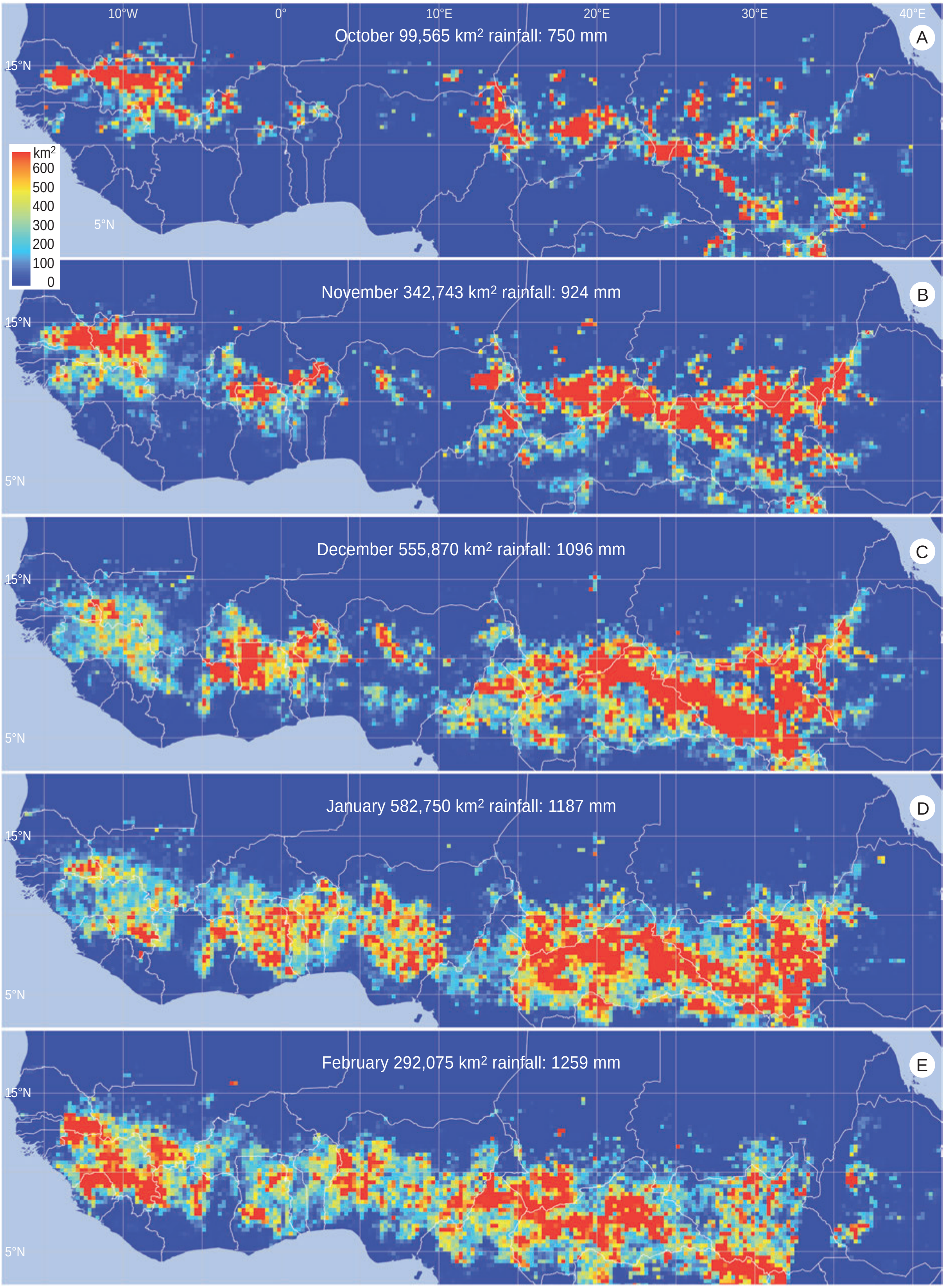


Figure 1. (A) Percentage of burned sites in savannah in the dry season (20 November – 10 March) between 7 and 22°N as a function of average annual rainfall. (B) Coverage of the herbaceous layer (%) on unburned savannah in January or February as a function of average annual rainfall. For location of the sites, see Zwarts *et al.* (2023a); not included are sites from Ethiopia, sites with a stony soil or sites classified as farmland or woodland. Number of sites (*n*) per rainfall zone is shown.

Photo 1. Grass fires in savannahs in the humid zone, (A and B) still burning or (C) shortly after the fire. The grass vegetation in the semi-arid (400–600 mm rain/year) and semi-humid zone (600–800 mm rain/year) is too sparse to fuel extensive grass fires, in contrast to the humid zone where tall grasses dominate. People establish fires mostly at the beginning of the dry season when the grass vegetation is not yet fully withered, to prevent fires from running rampant. Consequently, the grass vegetation is often only partially burned (photo C).


10°W
0°
10°E
20°E
30°E
40°E
15°N
5°N
km^2
600
500
400
300
200
100
0
October 99,565 km^2 rainfall: 750 mm
A
November 342,743 km^2 rainfall: 924 mm
B
December 555,870 km^2 rainfall: 1096 mm
C
January 582,750 km^2 rainfall: 1187 mm
D
February 292,075 km^2 rainfall: 1259 mm
E

burned area within the region shown increased from 0.10 million km^2 in November to 0.58 million km^2 in January and then declined to 0.08 million km^2 in April (Figure 2). The sum of the monthly total burned area (2.13 million km^2) overestimates the total surface of the burned area because some sites will have been classified as burned in more than one month. Using the maximum area burned per month per grid cell during seven months would give a total burned area of 1.03 million km^2 for the entire region. This is an underestimate, because within grid cells the areas burned during the different months in the dry season will not always overlap.

The fire zone shows a seasonal shift southward (Figure 2). Most bush fires in October and November were recorded in the rainfall zone of 600–800 mm (5 and 13% of total surface, respectively), in the 700–1200 mm rainfall zone in December (13–16%) and in the 1000–1300 mm rainfall zone in January (15–17%). With a further increase of the annual rainfall and a larger part of the area covered by humid forests, the surface of burned areas declined (Figure 3).

In the semi-humid and humid zone (600–1200 mm) with a high coverage of farmland, such as in West Senegal, Nigeria and Ethiopia, far fewer bush fires were recorded than in the same zone with less farmland in Chad, Central African Republic and South Sudan (Figure 2H). On average, in grid cells without farmland, 46–61% of the area was burned, compared to just 7–9% in grid cells with >40% farmland (Figure 4).

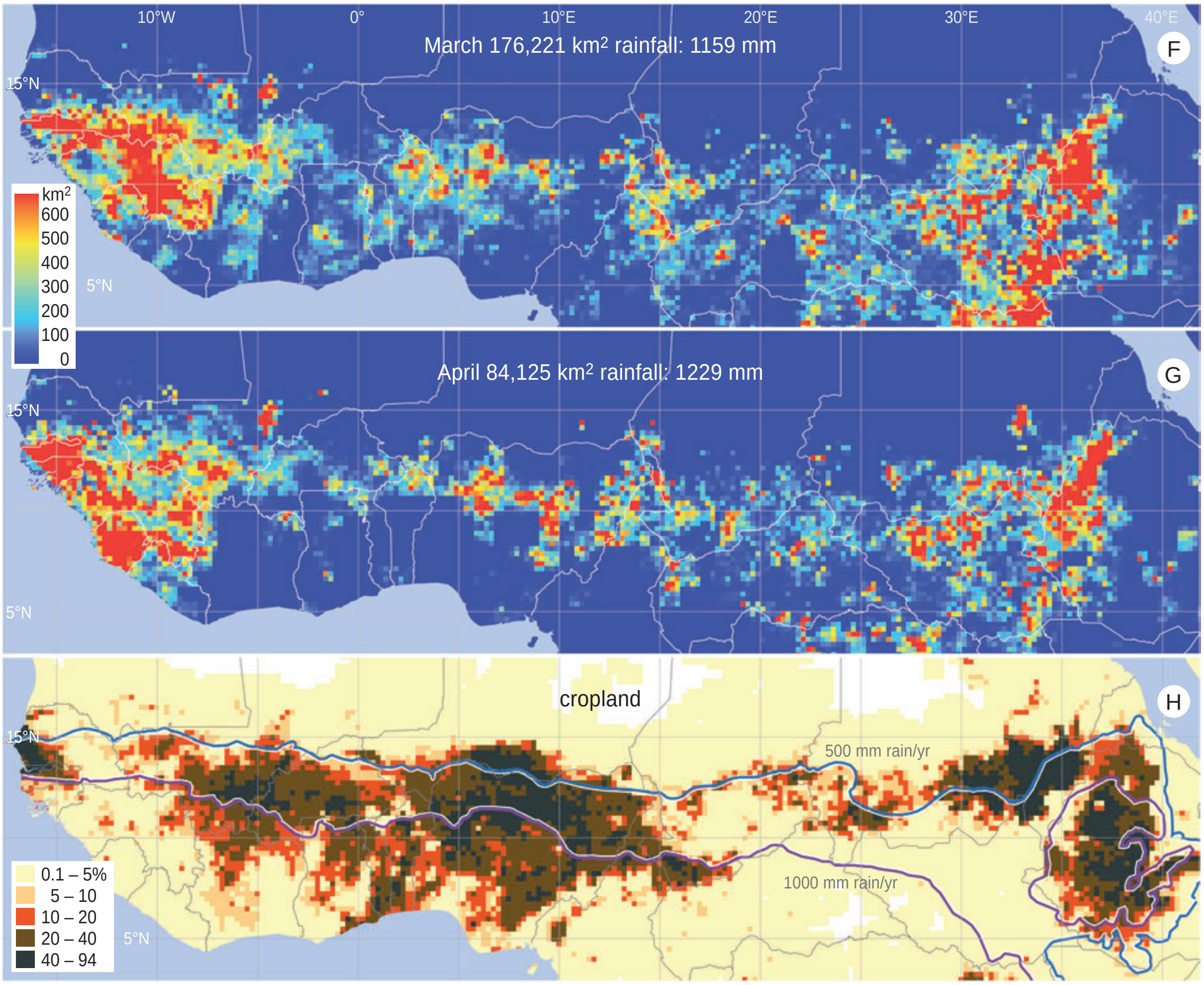


Figure 2. (A–G) Burned area (km^2) in ¼-degree grid cells between 3 and 20°N in six months in 2016 (Chuvieco *et al.* 2019). In red grid cells, at least half of the area is burned. Note that the surface area of grid cells varies per latitude and declines from 766 km^2 at 3°N to 711 km^2 at 20°N. Total burned area and average annual rainfall in the burned area were calculated for the region shown on the maps (source: Hijmans *et al.* 2005). (H) % cropland (source: Buchhorn *et al.* 2020) with 500- and 1000-mm isohyets.

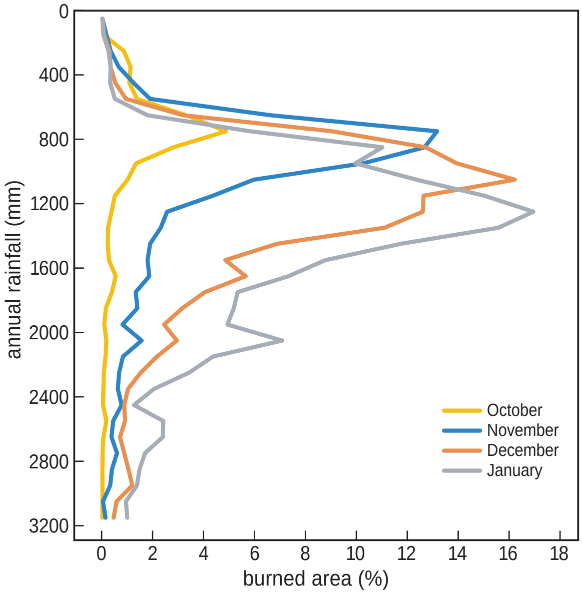


Figure 3. Area indicated as burned (%) during each of the first four months of the dry season in 2016 as a function of average annual rainfall; same data as Figures 2A–D. Source of data: Chuvieco *et al.* (2019).

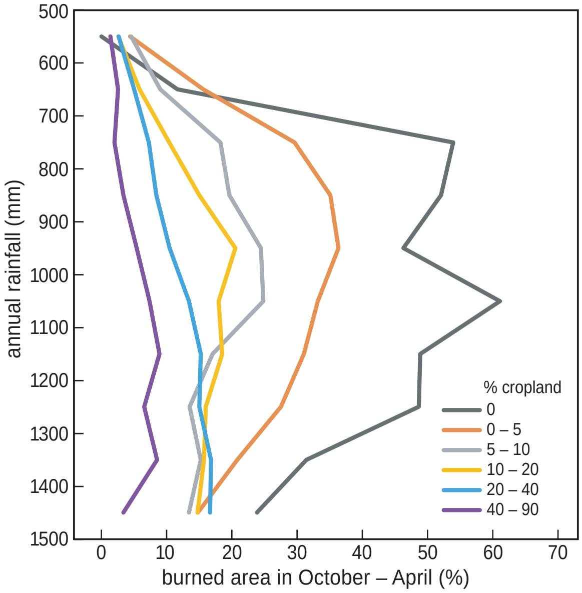


Figure 4. Area burned (%) in October–April in ten rainfall zones between 500 and 1500 mm/year (same data as Figure 2), given separately for ¼-degree grid cells where the coverage of cropland varied between 0% and 40–90% (data from Figure 2H; for each grid cell the maximum burned area between October and April was used to calculate the average burned area per rainfall zone. Source of data: Chuvieco *et al.* (2019) for burned area and Buchhorn *et al.* (2020) for cropland.

Densities of ground-foraging birds in relation to burns

The average density (±SE) of ground-foraging granivores amounted to 15.9 ± 4.2 birds/ha in 18 unburned sites and 3.3 ± 0.8 birds/ha in 20 burned sites (Figure 5A). The overall density of Afro-tropical ground-foraging insectivores was much lower and differed only marginally between unburned (2.0 ± 0.5 birds/ha) and burned sites (1.4 ± 0.4 birds/ha). The difference was significant for granivores (ANOVA: r^2 = 0.21, n = 38, P = 0.004), but not for insectivores (ANOVA: r^2 = 0.02, n = 38, P = 0.398).

To assess the robustness of our results, we repeated the analysis for a smaller data set, excluding the only site from Ivory Coast, and for a larger data set by including the sites in Chad in a wider range of rainfall zones (62 sites with >700 mm rainfall, or 78 sites with >600 mm). The outcome was the same: significantly lower densities of seedeaters in burned areas, but no difference in densities of insectivores. The results were also unaffected when adding vegetation cover as a (non-significant) covariate.

Ground-foraging migrants were present in low densities in humid savannahs, but were significantly more common in unburned (0.25 ± 0.5 birds/ha) than in burned areas (0.07 ± 0.03 birds/ha, ANOVA: P = 0.008). Northern Wheatears *Oenanthe oenanthe* were

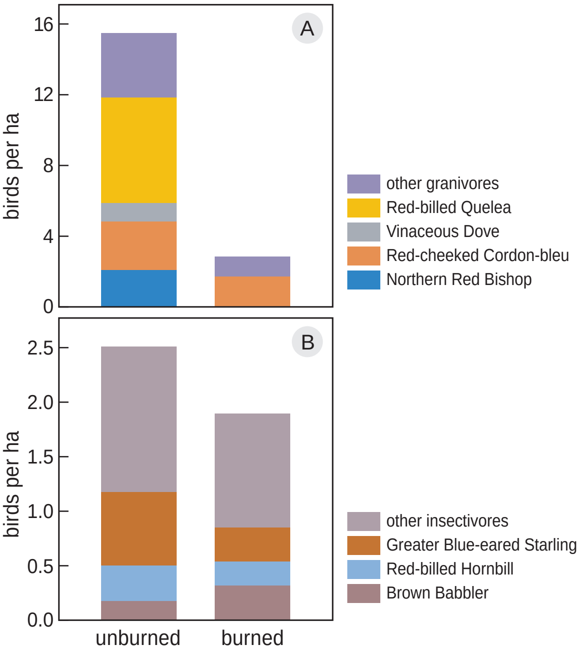


Figure 5. (A) Number of Afro-tropical ground-foraging birds per ha on recently burned (n = 20) or unburned (n = 18) savannah sites where annual rainfall was >800 mm, separately for (A) granivores and (B) insectivores.

Photo 2. Unburned savannah during the dry season in the semi-humid zone. (A) The vegetation consists mainly of annual grasses 10–40 cm high in the semi-humid zone. (B and C) In the humid zone, the savannah is mainly covered by tall perennial grasses such as *Andropogon* spp. and *Hyparrhenia* spp. of 60–120 cm height. Most grasses and herbs have already disappeared just after the rainy season in the arid and semi-humid zone due to heavy grazing of cattle, goats and sheep. The grazing pressure in the humid zone typically is lower, but is sufficiently high to create open spaces locally by grazing and trampling (Photo B).

rarely seen in burned areas, Western Yellow Wagtails *Motacilla flava* not at all. Tree Pipit *Anthus trivialis* and Whinchat *Saxicola rubetra* reached low densities in both burned and unburned sites. The low density of migrants in humid savannahs prevents any firm statement as to avoidance of burned areas or not.

DISCUSSION

Because many seeds on the surface are destroyed, grass fires are considered to have a negative impact on seed-eating birds, at least in the short term (Esque *et al.* 2010). In the longer term, undamaged seeds may become accessible after the fire-assisted removal of the vegetation, but this does not compensate for the initial losses. Furthermore, the seed bank will not be replenished until the next rainy season. Nevertheless, in the longer run, savannah-inhabiting birds will profit from bush fires, simply because fires prevent the open landscape from becoming overgrown with trees (Van Auken 2000, Staver *et al.* 2011, Smit & Prins 2015, Devine *et al.* 2017), facilitating feeding for ground-foraging granivorous birds. This is particularly evident in the more humid landscapes (>800 mm rainfall per annum) of sub-Saharan Africa, which experience lower grazing pressure than drier areas. In the semi-arid zone where fires are scarce anyway, the fortunes of eleven common ground-foraging migrants were unaffected by fires (compare Figure 3 in this paper with Figure 13A and 14A in Zwarts *et al.* 2023a). In the humid savannahs, the impact of grass fires on insectivorous ground-foraging birds is smaller than in the semi-humid savannahs for Afro-tropical species (Figure 5) and for two migrants, Tree Pipit and Whinchat. Essentially the same results were found in Kruger National Park (South Africa), where fire had a negative impact on the density of seed-eating birds and on birds that prefer cover of vegetation, but not on other bird species (Mills 2004). In Australia, the impact of fire was also found to be detrimental to most bird species, especially when the fires occurred in the late dry season (Woinarski & Recher 1997, Reside *et al.* 2012).

With a growing human population, a concomitant increase in frequency of bush fires would be expected. Surprisingly then, in northern sub-Saharan Africa the trend was downwards, at least between 1981 and 2018 (Otón *et al.* 2021). The decline in the frequency of fires occurred against a varied context:

(1) Due to the increase in livestock and higher grazing pressure, less grass is left in the dry season, and therefore less fuel is available for bush fires (Archibald & Hempson 2016). Bush fires were, for instance, common in northern Senegal in the 1960s (visible on CORONA satellite photos), the 1970s (Morel & Morel 1978) and the 1980s (Le Houérou 1989), but in the same region we did not record any bush fires between 2011 and 2019. Since the 1960s, grazing pressure has increased to such an extent that grass is now completely removed by livestock early in the dry season (Zwarts *et al.* 2018, 2023b).

(2) At the same time, farmers converted savannah (fire-prone) into cropland (with much less fire; Wei *et al.* 2020).

(3) Rainfall in northern sub-Saharan Africa has (partly) recovered after the extremely dry period of 1969–1992. As long as the savannah vegetation remains wet, bush fires may be inhibited (Zubkova *et al.* 2019), although the opposite has been suggested for semi-arid savannahs where the fuel load of dead grass is higher in wet years (Le Houérou 1989, Smit & Prins 2015).

(4) Millions of ha of woody savanna and agroforestry parkland has been converted into cashew plantations in West Africa since 1980, resulting in a decline of bush fires because plantation owners protect the fire-sensitive cashew trees (Temudo & Abrantes 2014).

(5) Due to the increase of the human population and expansion of farmland and cashew plantations, at the expense of savannah, fires are probably smaller than in the past and consequently increasingly remain undetected by satellites using a sensor with coarse resolution (Rano *et al.* 2021).

Our study shows that the density of seed-eating birds in unburned savannah was 3.6 times higher than on recently burned savannah (Figure 5). This suggests a large impact of bush fires on the fortunes of an estimated four thousand million seedeaters between 7° and 22°N (Table 2 in Zwarts *et al.* 2023a). Our survey, however, has some caveats. First, the much lower densities in burned areas may be a methodological artefact if densities of birds had been higher in the sampled unburned sites compared with densities at the burned sites before the fires. We sought to mitigate this confounding factor by selecting counts from the same period (late February) and within a single region (36 of 38 sites in southern Chad). Thus, we selected sites where rainfall and woody cover in burned and unburned sites were similar, on average. Second, we do not know to what degree differences in the density of birds on burned and unburned sites was due to birds having moved from burned to unburned areas. The burned sites in southern Chad in February 2018 were largely situated around 18 and 19°E longitude in an area of at least 150 × 350 km. This region had been almost completely burned, not just savannah but also farmland and woodland. When burned areas are this extensive, movements to unburned sites must have involved long flights. Third, in Chad, ground-foraging birds reached higher densities on humid savannahs than in West Africa (Figure 4 in Zwarts *et al.* 2023b), complicating estimates of how many birds are affected within the more than 1 million km^2 that is annually burned in Africa between 3 and 20°N (Figure 2). Clearly, here is scope for systematic fieldwork in fixed study plots before and after bushfire, as has been done in South Africa (Mills 2004, Krook *et al.* 2007, Bouwman & Hoffman 2007).

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SAMENVATTING

Natuurbranden zijn wijdverbreid in Afrikaanse savannes, vooral in regenrijke gebieden waar de bodem na de regentijd bedekt is met een dichte vegetatie van hoge grassen. Wanneer aan het begin van de droge tijd het verdorde savannegras massaal in brand wordt gestoken, heeft dat zowel positieve als negatieve effecten op de vogels. Veel insecteneters profiteren tijdelijk van de insecten die ontsnappen aan vuur en rook. Ook vogels die op de grond foerageren, hebben profijt van branden. Normaliter mijden zij savannes vanwege de hoge en dichte grasvegetatie. Een brand zorgt dan voor een toegankelijke, zij het zwartgeblakerde, vlakte. Savannebranden hebben echter ook een negatief effect doordat een deel van het potentiële vogelvoedsel (zaden, insecten) verbrandt. De gemiddelde dichtheid van zaadetende vogels in vochtige, Afrikaanse savannes (jaarlijkse regenval >800 mm) was tijdens het droge seizoen 15,9 vogels/ha in niet-verbrande savannes, vergeleken met 3,3 vogels/ha (–72%) in recent verbrande savannes. Een dergelijk verschil werd niet gevonden bij insectenetende vogelsoorten die op de grond foerageren. Boompieper *Anthus trivialis* en Paapje *Saxicola rubetra* overwinteren in Afrika in de natte savannegebieden en hebben daarom veelvuldig te maken met savannebranden. Elf andere soorten trekvogels, alle op de grond foeragerend, werden echter niet getroffen door savannebranden in Afrika, omdat ze de noordelijke winter doorbrengen in droge gebieden en daardoor buiten de belangrijkste brandzone blijven. Op de lange termijn is het waarschijnlijk dat savannevogels profiteren van bosbranden, simpelweg omdat branden voorkomen dat open landschap overgroeid raakt met bomen. Maar op de korte termijn is het effect negatief. Jaarlijks wordt in Afrika meer dan 3 miljoen km^2 savanne in brand gestoken. Door de schaal waarop het gebeurt, heeft het branden grote gevolgen voor zaadetende vogels van vochtige savannes.

RÉSUMÉ

Les feux de brousse sont très répandus dans les savanes africaines, en particulier dans les zones les plus humides où le sol est envahi par une végétation dense de hautes herbes après la saison des pluies. Les incendies qui surviennent en début de saison sèche ont des effets variés sur les oiseaux. De nombreux insectivores profitent de la manne temporaire des insectes qui fuient le feu et la fumée, tandis que certaines espèces granivores qui se nourrissent au sol profitent de la disparition de la végétation herbacée dense et haute qu'ils évitent habituellement pour accéder à de nouvelles ressources alimentaires. Cependant, ces feux ont également un impact négatif direct, car ils détruisent une partie de la nourriture disponible (graines, insectes). Ainsi, la densité moyenne d'oiseaux granivores dans les savanes africaines humides (précipitations annuelles >800 mm) pendant la saison sèche est de 15,9 oiseaux/ha dans les savanes non brûlées, contre 3,3 oiseaux/ha (–72 %) dans les savanes récemment brûlées. Cette diminution d'abondance ne se retrouve pas chez les espèces insectivores se nourrissant au sol parmi lesquelles, sur les 13 espèces migratrices étudiées, seuls le Pipit des arbres *Anthus trivialis* et le Tarier des prés *Saxicola rubetra* qui hivernent dans les zones de savane humide subissent les effets néfastes des feux de brousse. Les 11 autres espèces passent l'hiver septentrional dans des zones sèches et restent donc en dehors de la principale zone d'incendies. À long terme, les oiseaux de la savane bénéficient vraisemblablement des feux de brousse qui empêchent la fermeture des habitats. Mais à court terme, les espèces qui dépendent des graines de graminées des savanes humides pourraient être sévèrement touchées : la majeure partie des plus de 3 millions de km^2 de savane brûlés chaque année en Afrique concernent ces habitats.

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Shrub-dwelling birds in the Sahel forage less often on the ground in grazed areas

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Shrub-dwelling birds may resort to ground-foraging in the Sahel when opportunities are favourable. Several arboreal and semi-arboreal passerines, both African and European, were frequently recorded foraging on the ground, but not in heavily grazed areas. Grazed, dry savannah probably has fewer insects on the ground, which is often devoid of vegetation in the dry season. Shrub-dwelling birds foraged more frequently on the ground in the eastern Sahel, where grazing pressure is lower. In the Sahel grazing pressure increased fourfold since the 1960s, presumably reducing opportunities for arboreal bird species to facultatively forage on the ground. Due to increased grazing pressure, Common Whitethroats *Curruca communis* and other shrub-dwelling passerines may have lost a specific niche within their foraging habitat. This has compounded the greater losses associated with declines of woody vegetation during the drought years since the late 1960s.

Key words: shrub-dwelling birds, Sahel, grazing pressure

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Numbers of cattle, sheep and goats in Africa grazing in the dry belt of the northern tropics have quadrupled between the 1960s and the 2010s (www.fao.org/faostat/en/#data/TP). At first glance, the impact of grazing on the vegetation might seem small. After all, each rainy season, whether of short or long duration, transforms a desert-like landscape into a green plain with lush vegetation of mainly annual grasses grazed by livestock, the standard feature of the Sahelian savannah. However, a closer look reveals that the mounting grazing pressure has negatively impacted a multitude of bird species that inhabit this region during the dry season. This is particularly evident in granivorous birds, for which grass seeds are a staple food, but insects and rodents are equally affected. The soil seed bank is a key factor in the entire savannah ecosystem, across several trophic levels (Le Houérou 1989). Take, for example, raptors and owls, which suffer from the after-effects of drought, namely that rodent numbers plummet due to the paucity of grass seeds in a parched landscape (Morel & Morel 1978). Seed production in the herbaceous layer is extremely variable, depending on vegetation type, soil type, annual rainfall and grazing pressure of livestock (e.g. Bille 1977, Grouzis 1988, Le Houérou 1989, Sternberg *et al.* 2003). The huge decline in seed-eating birds, as ascertained for NW Senegal between the 1970s and the 2010s, is the inevitable outcome of these processes, heavy grazing being the most consistent driver (Zwarts *et al.* 2018, 2022c).

Arboreal birds feeding on insects, fruit and nectar in tree canopies are, by the very nature of their foraging niche, exempt from the negative impact of declining seed stock and ground-dwelling insects. However, they are not exempt from the negative impact of grazing per se. Although most arboreal bird species strictly forage in tree canopies, several species will leave the trees and shrubs to additionally forage for insects on the ground beneath. We expected adverse effects of grazing on insect abundance on the ground, resulting in fewer opportunities for arboreal bird species to forage on the ground, especially in heavily grazed areas. Additionally, we expected a seasonal decline in the frequency of ground-foraging among arboreal birds due to the gradual removal of ground vegetation by grazing livestock over the course of the dry season (Figure 1 in Zwarts *et al.* 2022b).

METHODS

The basic methods used to record birds are described in Zwarts & Bijlsma (2015). Upon detection, all birds were assigned to either tree/shrub or ground/herbaceous layer. The categories do not necessarily equate to foraging habitats. Some species, such as European Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*, may search for insects in the lower canopy, performing sallies from a branch to capture flying prey or to pounce on ground-dwelling insects. These sit-and-wait predators are excluded from the present analysis. Cricket Warblers *Spiloptila clamans*, mainly foraging in *Leptadenia pyrotechnica*, a desert shrub which was often <1 m high, were also excluded because of inconclusive foraging niches (ground or low vegetation).

For five relevant bird species and one species-pair, sufficient data were collected to test our expectations, i.e. three common Afro-tropical species (Tawny-Flanked Prinia *Prinia subflava*, Black Scrub Robin *Cercotrichas podobe*, Green-backed Camaroptera *Camaroptera brachyura*), one Afro-Palearctic species (Rufous-tailed Scrub Robin *Cercotrichas galactotes*) and three Palearctic migrants (Common Whitethroat *Curruca communis* and the species-pair Iberian Chiffchaff *Phylloscopus ibericus*/Common Chiffchaff *P. collybita*). Among the Palearctic migrants, Common Whitethroat is the only arboreal species in the Sahelian drylands that routinely forages in low woody vegetation and sometimes on the ground (Cramp 1992), just as it does during the breeding season in Europe (Mason 1976, Halupka *et al.* 2002). Iberian Chiffchaffs were recorded in West Africa, all North of 13°N and West of 4°W, partly overlapping with Common Chiffchaff (all North of 10°N and West of 2°W), but these species were sometimes not specifically identified and therefore lumped under 'Chiffchaff'. As in the breeding area, Chiffchaffs in Africa are supposed to be essentially woodland birds (Cramp 1992), but in West Africa we recorded most Chiffchaffs in flooded forests or near water, sometimes even foraging on floating vegetation. Incidentally, all Chiffchaffs recorded in Ethiopia were Common Chiffchaff.

The data set used in this paper is described in Zwarts *et al.* (2022a). To investigate the impact of grazing on birds, we also specifically targeted three areas in western Senegal where domestic livestock had been excluded:

Widou Thiengoly exclosure, total surface 23.6 ha, where grazing was excluded for 33 years (Miehe *et al.* 2010); situated at 15.94°N and 15.29°W; average annual rainfall 338 mm; visited in January and December 2014 (see Photo 1B in Zwarts *et al.* 2022b; Figure 4 in Zwarts *et al.* 2018); rainfall data, averaged over the period 1969–1990, are taken from Hijmans *et al.* (2005).

Guembeul Natural Reserve (720 ha), a lagoon surrounded by drylands with a dense woody vegetation of mainly *Acacia tortilis* and locally *Prosopis juliflora* and *Salvadora persica* (https://rsis.ramsar.org/ris/338). Grazing pressure is extremely low with no livestock and

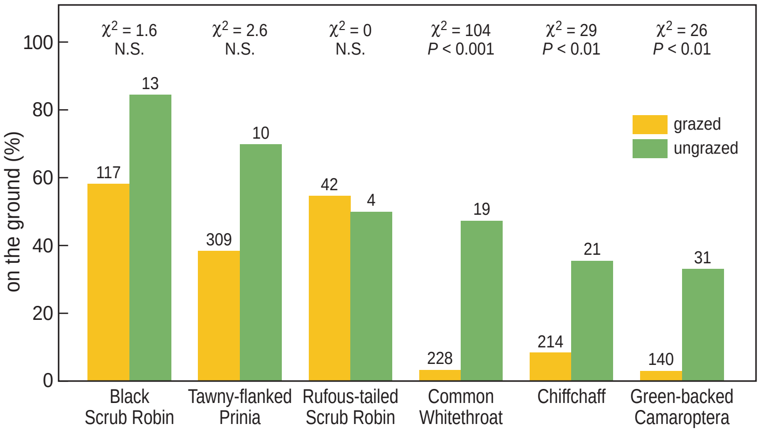

Figure 1. Percentage of shrub-dwelling birds foraging on the ground in Senegal in three areas where livestock were excluded ('ungrazed') and elsewhere in West Africa ('grazed'; 17–9°W). Number of birds observed is shown at the top of the bars. The results of six χ^2-tests ($df = 1$) are given above the bars.

only few Scimitar Oryx *Oryx dammah* and Dama Gazelles *Gazella dama*. The area is situated at 15.92°N and 16.46°W; average annual rainfall 302 mm; visited in January 2014.

Bandia Wildlife Reserve (3400 ha) comprises a fenced area with reintroduced populations of Warthog *Phacochoerus africanus*, Buffalo *Syncerus caffer*, Roan Antelope *Hippotragus equinus*, Giraffe *Giraffa camelopardalis*, etc. (Vincke *et al.* 2005, Hejcmanová *et al.* 2010). Within the reserve, the grazing pressure is low, contrasting strongly with that of livestock in the area outside the fence. The reserve was established in 1986 and expanded in 1998, 2004 and 2007. It gradually turned from open heavily grazed savannah into woody savanna comparable to the savanna existing in 1968 (Zwarts *et al.* 2015b); situated at 14.54°N and 16.98°W; average annual rainfall 542 mm; visited in November 2013 and 2015 and January 2014 (see Photo 1D in Zwarts *et al.* 2022b).

The two ungrazed sites in the arid zone of northern Senegal (Widou Thiengoly and Guembeul) had a low vegetation of grasses and forbs during the dry season in contrast to the grazed surroundings where the ground was completely bare at the time of our visits. This contrast was less pronounced in Bandia. In all sites the remaining above-ground vegetation was completely withered during our visits in November–February.

To test longitudinal variation in the fraction of birds foraging on the ground, all data were split in six bands covering the entire width of the Sahel (limits at 9°W, 0°, 10°E, 25°E, 34°E and 42°E (see map in Figure 2).

RESULTS

In the Widou Thiengoly exclosure, all three Common Whitethroats present foraged on the ground, as did 6 out of 16 birds in the two other areas without grazing. In grazed areas in West Africa (west of 9°W) only 3.5% (8 out of 228 birds) of Common Whitethroats were recorded as foraging on the ground. A similar difference, albeit less pronounced, was found for Chiffchaff, Green-backed Camaroptera and (statistically not significant) Tawny-flanked Prinia and Black Scrub-Robin. In contrast, half of the very few Rufous-tailed Scrub Robins in ungrazed sites were recorded on the ground, very similar to those in grazed areas (Figure 1).

If grazing has a negative impact on ground-foraging of shrub-dwelling passerines, we would expect a lower incidence of ground-foraging in the western Sahel than in the eastern Sahel due to substantial differences in grazing pressure (Figure 2 and 3 in Zwarts *et al.* 2022b). Excluding the birds from non-grazing exclosures in the westernmost section of the Sahel, all investigated shrub-dwelling species, except Common Whitethroat, showed the expected trend (Figure 2). Birds foraged less frequently on the ground in the three western longitudinal zones than in the three eastern zones.

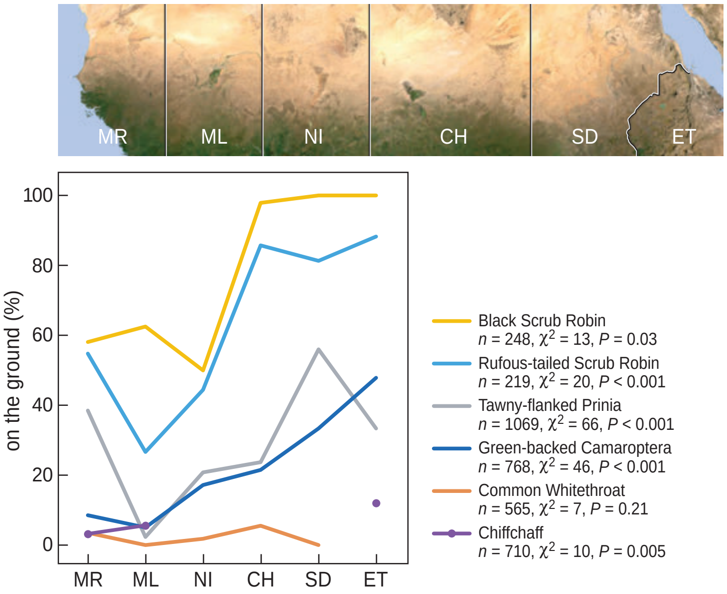

Figure 2. Percent of six tree-dwelling bird species foraging on the ground in six longitudinal bands between 7 and 22°N. The results of the six χ^2-tests (df = 5) are given. Satellite image: Earthstar Geographics.

Using the same data set as in Figure 2, we calculated the seasonal variation in ground-foraging across September through March. The expected decline in the average percent of ground-foraging in grazed plots was found only for Tawny-flanked Prinia ($P < 0.001$; linear regression declining from 44% in September to 0% in March), but not in the other five species.

DISCUSSION

The impact of grazing on the frequency of ground-foraging was, as expected, high for essentially arboreal species that normally forage low in trees and in shrubs with the occasional foray into herbs and on the ground below woody vegetation (Figure 1). For these species, like Chiffchaff, Common Whitethroat and Green-backed Camaroptera, grazing *de facto* reduced the foraging repertoire to near-exclusive foraging in woody vegetation. A large difference was also found in species for which ground-foraging is essentially the main strategy of obtaining food, as in the scrub robins (Figure 1 and 2). The Tawny-flanked Prinia (for which we had insufficient data for the ungrazed sites; Figure 1) is a shrub-dwelling species that also forages on the ground. Detailed observations by McLean (2017) showed that even when on the ground food items were taken from the vegetation. Ground vegetation in the Sahel vanishes during the dry season soon after the last rain in October (Figure 1 in Zwarts *et al.* 2022b), which may explain why the fraction of ground-foraging Tawny-flanked Prinias declined from 44% in October to 0% in March. No such seasonal decline was obvious in the other five species, probably because these species are not bound to vegetation when they forage on the ground and search for insects on bare patches where they probe the soil, hop among leaf litter, peer under dead leaves, peck among stones and make sallies to catch insects from plants or from the air.

In Europe, many species largely or partly depend on insect food or seed gathered from the ground. For example, when captive Common Redstart were offered the choice to either forage on bare ground with few insects or in dense vegetation with many insects, they selected bare ground, probably because the few prey on bare ground are easier to detect than insect prey in dense vegetation (Martinez *et al.* 2010). This probably also applies to other sit-and-wait predators as Woodchat Shrike *Lanius senator* and Great Grey Shrike *Lanius excubitor* which need a good view from a perch. Other ground-foraging long-distance migrants, like Eurasian Hoopoe *Upupa epops*, Eurasian Wryneck *Jynx torquilla*, European Turtle Dove *Streptopelia turtur* and Ortolan Bunting *Emberiza hortulana*, prefer as foraging habitat a mixture of bare and sparsely vegetated ground. Their decline in Europe is associated with the loss of half-open habitats. The former mosaic of varied ground vegetation has transformed into a dense and more homogeneous, herbaceous layer where their main food (e.g. seeds, ants and their pupae) is more difficult to access (Schaub *et al.* 2010, Menz & Arlettaz 2011, Weisshaupt *et al.* 2011, Dunn 2021). During the dry season in Africa, ground-foraging birds in savannahs face the very opposite, though equally negative in its outcome: due to mounting grazing pressure, the Sahel has become more barren. Ungrazed areas with some vegetation remaining are getting scarcer. In the western Sahel, exclosures were eye-catching pinpricks amidst savannah resembling a desert (Figure 4 in Zwarts *et al.* 2018; Photos 1 and 3 in Zwarts *et al.* 2022b). Foraging conditions for ground-foraging arboreal birds deteriorate when the herbaceous layer has been removed by heavy grazing. Several studies found a decline of insects at high grazing pressure and loss of herbaceous layer (e.g. Seymour & Dean 1999, DeBano 2006, Moran 2014, Kaiser *et al.* 2015, Zhu *et al.* 2015, Ma *et al.* 2017). Intensively grazed land is littered with cowpats and droppings of goats and sheep, but our observations showed that dung when dehydrated did not attract insects in noteworthy numbers (R.G. Bijlsma unpubl. data).

Our preliminary conclusion is that due to increased grazing pressure, Common Whitethroats and other shrub-dwelling passerines have lost part of their foraging habitat, especially in the western Sahel where the grazing pressure is higher. This loss compounds greater losses associated with declines in woody vegetation during the drought years since the late 1960s (Gonzalez 2001, Zwarts *et al.* 2018), probably more so for Common Whitethroat, Chiffchaff and possibly Common Redstart (given their frequent forays to the ground), than for strictly arboreal migrants, such as Western Bonelli's Warbler *Phylloscopus bonelli*.

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SAMENVATTING

De meeste vogels die in bomen foerageren, komen zelden aan de grond. Dat ligt anders voor soorten die zich veel in struiken ophouden en geregeld een uitstapje naar de grond maken om een insect op te pikken. In de Sahel is dat niet anders. Hier zijn het vooral Grasmussen *Curruca communis*, Tjiftjaffen *Phylloscopus collybita* en Iberische Tjiftjaffen *P. ibericus* die tijdens het droge seizoen onder struiken op de grond naar insecten zoeken. Hetzelfde gedrag zien we bij Afrikaanse struikbewoners als Roestflankprinia *Prinia subflava* en Mekkercamaroptera *Camaroptera brachyura*. De Sahel wordt intensief begraasd door runderen, schapen en geiten, vooral in het westelijke deel. Er zijn maar heel weinig gebieden waar vee wordt buitengesloten. Juist in die exclosures vonden we opvallend vaak dat de genoemde soorten op de grond foerageerden. In begraasde gebieden kwam dat veel minder voor. Dat begrazing van bodemvegetatie door vee een grote rol speelt bij wel of niet op de grond foerageren, bleek bij een vergelijking van de mate van grondfoerageren door struikbewoners in de westelijke en oostelijke Sahel. In de westelijke Sahel (intensief begraasd) werden voornoemde soorten minder vaak foeragerend aan de grond gezien dan in de oostelijke Sahel (minder intensief begraasd). De vermoedelijke verklaring is dat begrazing de bodemvegetatie elimineert, en daarmee het leefgebied voor insecten. Voor vogels die zowel in bomen en struiken als op de grond foerageren is het dan niet langer de moeite waard om in intensief begraasde gebieden op de grond naar insecten te zoeken. De graasdruk is in de Sahel verviervoudigd tussen 1960 en 2010. We weten niet of de struikvogels vroeger vaker op de grond foerageerden dan nu, maar dat ligt wel voor de hand. Voor bijna alle Europese vogelsoorten die in de Sahel overwinteren, zijn de omstandigheden in de afgelopen ruime halve eeuw verslechterd. We vermoeden dat in het bijzonder de Grasmus in de Sahel meer terrein heeft verloren (bomen, struiken én bodemvegetatie) dan andere trekvogels die uitsluitend in boomkronen foerageren.

RÉSUMÉ

La plupart des oiseaux qui se nourrissent dans les arbres descendent rarement au sol. A l’inverse, les espèces qui fréquentent préférentiellement les arbustes s’y posent régulièrement pour y capturer des insectes. Au Sahel, ce sont principalement la Fauvette grisette *Curruca communis*, le Pouillot véloce *Phylloscopus collybita* et le Pouillot ibérique *P. ibericus* qui cherchent des insectes au sol sous les buissons pendant la saison sèche. Le même comportement peut être observé chez les passereaux sédentaires de la brousse africaine comme la Prinia modeste *Prinia subflava* et le Camaroptère à tête grise *Camaroptera brachyura*. Le Sahel est intensivement pâturé par des bovins, des ovins et des caprins, surtout dans sa partie occidentale, et rares sont les zones dont le bétail est exclu. C’est précisément dans celles-ci que nous avons rencontré les espèces susmentionnées à une fréquence remarquablement élevée, alors que nous les avons trouvées moins fréquemment dans les zones pâturées. La comparaison des fréquences d’alimentation au sol entre l’Ouest (intensivement pâturé) et l’Est du Sahel (moins intensivement pâturé) révèle le rôle majeur du pâturage dans le comportement alimentaire des espèces des milieux arbustifs. Ces espèces sont moins fréquemment observées au sol dans le Sahel occidental, probablement car le pâturage élimine la végétation au sol, donc l’habitat des insectes. La pression de pâturage au Sahel a quadruplé entre 1960 et 2010 et a donc vraisemblablement fortement réduit les opportunités alimentaires au sol pour les insectivores des arbustes. Pour la quasi-totalité des espèces d’oiseaux européens hivernant au Sahel, les conditions se sont détériorées au cours du demi-siècle dernier. Nous soupçonnons que la Fauvette grisette, en particulier, a souffert d’une perte d’habitat plus importante que les espèces migratrices qui se nourrissent exclusivement dans le houppier des arbres.

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On the wintering ecology of Montagu's Harriers in West Africa: itinerancy in relation to varying annual environmental conditions

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Palearctic migrants wintering in Africa commonly use several sites throughout the winter, a strategy known as 'itinerancy'. In this way, migrants track spatio-temporal variation in resources. Despite the importance of this strategy for migratory landbirds, we still lack detailed understanding of how variation in environmental conditions affects site use and the timing of movements between sites. We tracked 125 adult Montagu's Harriers *Circus pygargus* from Western European breeding populations between 2005 and 2018 using satellite transmitters and GPS trackers. In total, data on 129 complete wintering seasons were obtained, including 33 individuals that were followed in two or more winters. Montagu's Harriers were itinerant, using on average 3.3 wintering sites, to which they showed high site fidelity between years. The first sites harriers used after arriving in their wintering range were situated in the northern Sahel and were dominated by natural and sparse vegetation. Subsequent sites, situated further south in the Sahel, were mainly dominated by agricultural and natural habitats. Sites used by harriers had higher habitat diversity compared to random sites. Home range size and activity (time flying per day, daily distance) peaked at the last sites harriers used (i.e. the site from which they commenced spring migration). For individuals tracked in multiple seasons, we showed that home range size did not depend on vegetation greenness. However, the birds covered longer daily distances at the same site in drier years compared to greener (wetter) years. Importantly, the timing of the movements between wintering sites was affected by local environmental conditions, with individuals staying for shorter durations and departing earlier from first sites in drier years and arriving earlier at last sites in greener years. We conclude that within the context of a strategy of itinerancy, Montagu's Harriers are faithful to the sites they use between years (spatial component), but flexible in the timing of use of these sites (temporal component), which they adjust to annual variation in environmental conditions.

Key words: winter ecology, site fidelity, Sahel, NDVI, long-distance migrants, *Circus pygargus*

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Most long-distance migrants spend more than half of their annual cycle outside their breeding areas (Newton 2008). In recent years, migration patterns of many species have been mapped thanks to advances in tracking technologies (Bridge *et al.* 2011, López-López 2016). Although we consequently have a much better idea about where birds spend the winter, this does not mean that we have achieved a better understanding of their ecology and how they are impacted by (varying) environmental conditions during winter. This is a serious omission, since many long-distance migrants are in decline (Sanderson *et al.* 2006, Vickery *et al.* 2014), and these declines have been associated with changes in environmental conditions (e.g. variation in rainfall; Baillie & Peach 1992, Szép 1995, Zwarts *et al.* 2009), including human-induced changes in land use (e.g. overuse of natural habitats; Zwarts *et al.* 2015).

Palearctic migrants wintering in Africa commonly use several sites throughout the winter, a strategy known as 'itinerancy' by Moreau (1972). The alternative strategy of residency is notably rare, especially among terrestrial species (landbirds), where species that appear resident (e.g. Pied Flycatcher *Ficedula hypoleuca*) might still perform small-scale seasonal movements within their winter home ranges (Salewski *et al.* 2002, Bil *et al.* 2023). The strategy of itinerancy is believed to be a way to track spatiotemporal variation in resources throughout the winter (Moreau 1972, Thorup *et al.* 2017). This does not mean that the birds are continuously on the move. Instead they use multiple distinct non-breeding residency sites (hereafter wintering sites). Intra-tropical movements between wintering sites can occur at relatively small scales of some hundred kilometres, as for example found in the Turtle Dove *Streptopelia turtur* moving between the Sahel and the Sudanian savannah (Eraud *et al.* 2013). But more commonly, these movements occur over thousands of kilometres, such as in the Red-backed Shrike *Lanius collurio* which moves from the Sahel to the Kalahari south of the equator (Tøttrup *et al.* 2012).

Although it is well-established that a strategy of itinerancy allows migrants to profit from ephemeral resources, we still lack a more detailed understanding of how individual wintering sites are used within and between years and the factors steering the timing of movements between sites. This was also acknowledged by Moreau who posed the question "The great problem is to know the extent to which an individual's movements in Africa, before settling into identically the same wintering site each year, are replicated during the lifetime of the migrant." (Moreau 1972, page 266). One possible way to answer this question is by tracking individual migrants in multiple winters.

The subject of this study is the Montagu's Harrier *Circus pygargus*, a long-distance migratory raptor (Ferguson-Lees & Christie 2001). European breeding birds winter in the western part of the Sahel (Limiñana *et al.* 2012c, Trierweiler *et al.* 2014), a relatively narrow zone with open savannah vegetation sandwiched between the Sahara in the north and wooded savannah in the south (Moreau 1972, Zwarts *et al.* 2009). On the basis of satellite tracking telemetry Trierweiler *et al.* (2013) described the strategy of itinerancy adopted by Montagu's Harriers, in which individuals use on average four distinct sites during the winter. Montagu's Harriers arrive in the Sahel at the end of the wet season, and wintering conditions progressively get drier during their stay (Schlaich *et al.* 2016). By moving between different sites during the winter, harriers track a shifting 'green belt' of vegetation (Normalized Difference Vegetation Index: NDVI) indicative of higher grasshopper abundance, their main prey in Africa (Mullié 2009, Mullié & Guèye 2010, Trierweiler *et al.* 2013). Only at their final wintering site, often located in the southern Sahel just at the southern edge of open savannah vegetation, do they face deteriorating environmental conditions. Harriers respond to declining grasshopper numbers at their last wintering sites by increasing their daily foraging time (Schlaich *et al.* 2016).

Since Trierweiler *et al.* (2013), we accumulated additional tracking data. Moreover, since 2009 we have also been tracking Montagu's Harriers with more accurate GPS trackers (Bouten *et al.* 2013). This allows for detailed analyses of site use, including many individual harriers that were tracked in several consecutive years. Specifically, with this dataset we are able to analyse within-individual differences in timing and site use between years in order to answer Moreau's longstanding question of how variation in environmental conditions affects site use and the timing of movements between sites.

METHODS

Overview

Since this study comprises several analyses, we provide here a short overview of the following sections. First, the two datasets we used, satellite-tracking data and GPS-tracking data, are described. This is followed by a description of site use, including the number of sites used, distance and direction between sites, arrival and departure date, and duration of stay. The following definition of site categories is used throughout the paper: first site, i.e. wintering site used after arrival from autumn migration, last site, i.e. wintering site used before departure on spring migration, and intermediate site, i.e. all wintering sites used in-between, which could be more than one depending on how many sites an individual used. The next section describes the habitat composition at wintering sites and how this compares to random sites regarding habitat categories, habitat diversity and vegetation greenness. This is followed by a section on home range size and activity measures where daily home range size, daily time flying and daily distance covered are compared between site categories and total home range size is related to environmental variables (habitat and vegetation greenness). The next section describes site fidelity using a subset of birds that were tracked in at least three winters. In the last section, we investigated, for sites used in several years, the relation between site use (number of sites used, home range size, time spent flying and mean daily distance) to environmental conditions (vegetation greenness). Furthermore, within-individual differences in the timing of movements between sites in different years were analysed in relation to vegetation greenness.

All data selection procedures and analyses were performed in R v. 3.5.1 (R Core Team 2018). The specific R-packages and R-functions used are stated in the respective sections below.

Satellite-tracking data

We tracked 60 adult Montagu's Harriers (24 males and 36 females) using solar-powered satellite transmitters (PTT-100 series, Microwave Telemetry Inc., Columbia, MD, USA) between 2005 and 2018. Birds were captured in breeding areas in Germany (*n* = 15), The Netherlands (*n* = 13), the United Kingdom (*n* = 12), Belarus (*n* = 8), Denmark (*n* = 8) and Poland (*n* = 4). Of those, 49 individuals (23 males and 26 females) produced tracks including wintering movements. Due to birds being tracked in consecutive years, we recorded a total of 99 wintering tracks (year × individual combinations). After removal of incomplete tracks (start or end missing, gaps), the final satellite-tracking dataset comprised of 78 tracks of 38 individuals (16 males and 22 females; Table S1).

Satellite-transmitters were programmed either to a longer duty cycle of 10:48 h on:off (9.5-g and part of the 12-g tags) or a shorter duty cycle of 6:16 h on:off (12-g tags only) to recharge their batteries. Data were received via the ARGOS system (CLS, Toulouse, France). Raw data were filtered using R-function 'sdafilter' from package 'argosfilter' v. 0.63 (Freitas 2012). This function filters location data obtained from Argos, using the Freitas *et al.* (2008) algorithm. Filtered data were checked visually and remaining outliers were removed by hand.

GPS-tracking data

We tracked 65 adult Montagu's Harriers (45 males and 20 females) using UvA-BiTS GPS trackers (Bouten *et al.* 2013; www.uva-bits.nl) between 2009 and 2018. Birds were captured in breeding areas in The Netherlands (*n* = 39), France (*n* = 12) and Denmark (*n* = 9), plus five at a wintering site in the area of Khelcom near the village of Diabel, Senegal. Of those, 39 individuals (28 males and 11 females) returned to the study areas and tracks including wintering movements could be downloaded via the local UvA-BiTS antenna system. A Danish male that over-summered in Africa (Sørensen *et al.* 2017) was removed from the dataset. Due to birds being tracked in consecutive years, we recorded a total of 63 wintering tracks (year × individual combinations). After removal of incomplete tracks (start or end missing, gaps), the final GPS-tracking dataset comprised of 51 tracks of 34 individuals (24 males and 10 females; Table S1).

GPS trackers were programmed to collect GPS positions at an interval of 5 min (*n* = 15 tracks), 10 min (10), 15 min (20) or 30 min (6) during the day and at maximum once per hour during the night. Intervals differed because memory storage increased with newer trackers. Positions with instantaneous speeds or trajectory speeds higher than 25 m/s were removed from the dataset. In addition, data were visually checked for outliers.

General description of the strategy of itinerancy

Each point, in the satellite-tracking data, or each day, for GPS-tracking data, was annotated as 'wintering site' (clustered movements within a site south of the Sahara), 'trip' (explorative movement outside a wintering site that could last one or several days but returned to the same site) or 'movement between sites' (movement between consecutive wintering sites). For examples see Figure S1. A stay at a wintering site was defined as lasting at least three days. Within a site, several night roosts could be used, but distances between consecutive roosts at a site were generally small (Figure S1D and E). Consecutive wintering sites were defined as being at least 10 km apart with no overlapping tracks (see Figure S1B). These annotations were done manually, since automated annotation using a threshold of distance between consecutive roosts did not define all wintering sites correctly. This was due to birds with large home ranges occasionally having inter-roost distances of more than 10 km. A geographical wintering site could be revisited during the same winter. For each site, we calculated a centroid using mean latitude and longitude of all positions at this site. Sites were grouped into the categories first, intermediate and last (definition see above). In case only a single site was used, this was classified as last site.

Distance between consecutive sites was calculated using the R-function 'distMeeus', which calculates the shortest distance between two points on an ellipsoid, from the package 'geosphere' v. 1.5-7 (Hijmans 2017). To test whether the distance of movements between sites changed over time (e.g. shorter distances between consecutive sites earlier in the winter) we used Linear Mixed-Effects Models (LMM) with 'track' as random effect by means of R-function 'lme' from package 'nlme' v. 3.1-137 (Pinheiro *et al.* 2018).

Direction between sites was calculated using the R-function 'bearing', which calculates the initial bearing between two positions following the shortest path on an ellipsoid, from the package 'geosphere'. Change of direction of movements between sites during the course of the winter was modelled using LMM with 'track' as random effect. The difference in direction of movements between sites during the first and second half of the winter (before and after 15 December) was compared using a Pearson's Chi-squared test.

Arrival date at and departure date from the wintering grounds were defined as the first and last day at a stationary wintering site, as derived from the annotated dataset. Differences in mean arrival and departure date between the sexes were investigated using LMM with 'track' as random effect.

The length of stay at a site was the number of days spent at that site during a visit. The difference in length of stay at last sites compared to preceding sites was investigated using LMM with 'track' as random effect and the R-function 'testInteractions', which calculates and tests contrasts for factor interactions, from package 'phia' v. 0.2-1 (De Rosario-Martinez 2015).

Habitat composition at wintering sites and site selection

We used the GlobCover 2009 V2.3 land use map (ESA GlobCover 2009 Project: http://due.esrin.esa.int/page_globcover.php) with a 300-m resolution to investigate habitat composition at Montagu's Harriers' wintering sites. The whole wintering zone of our tracked birds was defined as the 100% MCP (maximum convex polygon) around all wintering sites ($n = 449$, except for one site that was beyond the natural wintering range at the southern coast of Ghana; Figure S2). Sixteen of the 23 GlobCover land use categories occurred in the MCP (Figure S3, Table S2), with only seven categories covering more than 5% of the surface area. Habitat types ranged from bare and sparsely vegetated to grassland and shrubland savannahs and mosaic or agriculture dominated habitats. These subsequent habitat types were spatially correlated and approximately form a gradient from north to south with increasing vegetation cover and agricultural productivity. Habitat types may overlap except when at either end of the gradient (e.g. 'bare' and 'crops' seldom occur at the same site; Figure S4). The habitat composition at Montagu's Harriers' wintering sites was determined by extracting habitat information from all GlobCover map cells within a radius of 3.53 km around a site's centroid. Each such circle consisted of about 430 pixels of 300 × 300 m (c. 39 km^2) which is similar to the average wintering home range size (median: 35 km^2, 193 sites; see Results). To illustrate variation in habitat composition across sites, we gave each habitat type a value (from 1 for sparsely vegetated habitats up to 13 for agricultural habitats; see Table S2) and subsequently calculated a habitat score for each site which is the average habitat value weighted by the habitats' surface areas. To determine which habitat types were dominant at each site, we combined similar categories into three main habitat groups: agricultural, natural and bare (see Table S2). Colours in graphs match these main groups: blues for bare and sparsely vegetated zones, greens for natural habitat types and reddish colours for agricultural habitats. A site was considered being dominated by one of these groups if the sum of all habitat types in one of the groups covered more than 50% of the surface area. If none of them did, the site was categorised into a fourth group called 'other'. Frequencies were compared using Pearson's Chi-squared tests.

The selection of wintering sites within the whole wintering zone (MCP) was analysed by compositional analysis (Aebischer *et al.* 1993) with the R-function 'compana' from package 'adehabitatHS' (Calenge 2006). This analysis was conducted for all wintering sites together and for the three subsets of sites (first, intermediate, last) separately. The habitat composition at harrier sites was compared to the habitat composition at random sites. For this, 4500 (ten times the number of harrier wintering sites) random points were created within the maximum and minimum latitude and longitude of harrier sites using R-function 'runifpoint' from package 'spatstat' v. 1.56-0 (Baddeley *et al.* 2015). As for the harrier wintering sites, habitat information from all GlobCover map cells within a radius of 3.53 km around each random point was extracted. Subsets of random sites were created for all, first, intermediate and last sites based on their respective MCPs (MCP-all see red polygon Figure S2, MCP-first, MCP-intermediate and MCP-last see Figure 4A). Sample sizes for random sites were 3295 for all, 1585 for first, 2408 for intermediate and 2490 for last sites. The average habitat composition at the random sites was compared to the habitat composition at sites used by harriers. Habitat categories that occurred less than 1% were excluded (nine habitat categories remained in the compositional analyses).

To investigate habitat diversity we compared Shannon's diversity indexes calculated using R-function 'diversity' from package 'vegan' v. 2.5-2 (Oksanen *et al.* 2018). Habitat diversity was compared between random sites and those used by the harriers. Frequency distributions of indexes were compared using *t*-tests.

In addition to habitat types, we used vegetation greenness at wintering and random sites as another environmental variable. It has been shown previously that vegetation greenness can be used as proxy for food availability (grasshoppers being the main prey in the winter diet of Montagu's Harriers (Szép & Møller 2005, Trierweiler & Koks 2009, Trierweiler *et al.* 2013, Schlaich *et al.* 2016). Therefore, we used NASA's MODerate resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) remotely sensed data (product MOD13Q1: data provided every 16 days at 250-m spatial resolution) downloaded from The Land Processes Distributed Active Archive Center (LP DAAC; https://lpdaac.usgs.gov) using R-package 'MODISTools' (Tuck *et al.* 2014). Around each harrier wintering site centroid, 25 × 25 = 625 pixels of 250 × 250 m (c. 39 km^2, which is similar to the average wintering home range size (median = 35 km^2, n = 193 sites; see Results)) were downloaded for the winters 2006/2007 till 2017/2018. The average of the 625 pixels was calculated for each 16-day period after removal of fill values (–3000) and then multiplied by the scaling factor of 0.0001 to get NDVI values between –0.2 and 1 (Zhu *et al.* 2013). The same was done for 750 of the random points within the MCP-all. Of those, 346 lay within MCP-first, 550 within MCP-int and 567 within MCP-last. To compare vegetation greenness between harrier sites and random sites, we used the closest NDVI values to three dates: the peak of harrier presence at first, intermediate and last sites (derived from Figure 1B). These were NDVI measures on 30 September, 1 November and 6 March, respectively (in the leap years 2008, 2012 and 2016 these dates were 29 September, 31 October and 5 March, respectively). We selected the values on those dates of all 12 winters for harrier sites (5400 NDVI measures, first: 1500, intermediate: 2352, last: 1548) as well as random sites (n = 17,556, first: 4152, intermediate: 6600, last: 6804) and compared the frequency distributions using *t*-tests. To determine how dry or wet a year was in general, we calculated a 'yearNDVI' value for each year. This was done by using the mean NDVI values of the three dates for the 750 random points and calculating a median NDVI over these 750 values per year.

Home range size and activity measures

For this part, we only used data of the GPS-tracked Montagu's Harriers since these were more precise and denser (on average 92 positions per day for GPS-tracks compared to on average four positions per day for satellite tracks). Days with fewer than 75% of expected positions (<108 for 5-min, <54 for 10-min, <36 for 15-min, <27 for 20-min and <18 for 30-min interval tracks) were removed from this dataset. Two tracks had too many days with insufficient data and were removed, thus 49 tracks remained. For this analysis, days of movements between sites and trip days were excluded.

Daily home ranges were calculated as 90% kernel density estimation using R-function 'rhrKDE' from package 'rhr' v. 1.2.909 (Signer & Balkenhol 2015) with bandwidth parameter h determined by reference bandwidth estimation using R-function 'rhrHref'. Surface area of daily home ranges was retrieved using R-function 'rhrArea'. For the calculation of daily activity measures, only positions during daylight were used (daylight defined as being between nautical dawn and nautical dusk). Time spent flying and distance covered were calculated for each day. We determined for each GPS-position if the bird was sitting or flying using instantaneous speed and a threshold of 1.2 m/s (local minimum of a two-peaked frequency distribution of instantaneous speeds). The percentage of positions in flight was corrected by day length to determine the number of hours spent flying per day. Cumulative daily distance was calculated as the sum of distances between positions during a day. Temporal patterns in daily home range size, hours flying per day, and daily distance were analysed using LMM with 'site category' as fixed effect and 'year' as well as 'site ID' nested in 'individual' as random effects by means of R-function 'lmer' from package 'lme4' v. 1.1-17 (Bates *et al.* 2015) in combination with package 'lmerTest' v. 3.0-1 (Kuznetsova *et al.* 2017) and R-function 'testInteractions'.

We calculated the total size of wintering site home ranges (using all positions at a wintering site) using the Biased Random Bridge Movement Model (BRBMM; Benhamou 2011) which is a movement-based kernel density estimation to estimate the Utilization Distribution (UD) of an animal with serial autocorrelation of the relocations using R-function 'BRB' from package 'adehabitatHR' v. 0.4.15 (Calenge 2006). Tmax was set to 15 times the GPS-interval since home range size became stable from this value onwards for the different intervals (data not shown). We used the surface area of the 90% contour of the UD retrieved using R-function 'getverticeshr' from package 'adehabitatHR' to determine total home range size. Differences in total home range size between first, intermediate and last sites were analysed using LMM with 'site category' as fixed effect and 'year' as well as 'site ID' nested in 'individual' and 'number of days' as random effects and R-function 'testInteractions'. Spatial patterns in total home range size were modelled using a Linear Model (LM) with 'latitude' and 'longitude' as fixed effects. The effect of environmental variables on total home range size was investigated using LMM with 'NDVI' or 'habitat score' as fixed effects as well as 'site ID' nested in 'individual' as random effects. If total home range size differed between dry and wet years, it was also analysed using LMM with 'yearNDVI' as a fixed effect as well as 'site ID' nested in 'individual' as random effects.

Site fidelity

The dataset of repeated tracks comprised of 33 individuals of which 19 were tracked in two years, six in three years, six in four years and two in five years. In total, these birds used 164 different wintering sites. Each geographical site was given a 'site ID' and classified into one of the three site categories (first/intermediate/last). A site classified as 'first' in any one year was classified as such in all years. Similarly, a site classified as 'last' was classified as such in all years. In two cases, a site was used as first site in one and as last site in a second year and these two sites were classified as 'last'. Sites that were only used as intermediate sites but never as first or last, were called 'intermediate'.

Overall site fidelity was calculated as the percentage of sites reused by an individual between two years. For this, we took the sites visited by an individual in year 1 and counted how many of those it reused in year 2. If all sites were used in both years, the individual showed 100% site-faithfulness. If for example only one out of two of the sites were re-visited in year 2, it showed 50% site-faithfulness, irrespective of new sites used in year 2. We did several two-year comparisons for birds with more than two years of tracking, i.e. we compared year 1 to year 2, year 2 to year 3, and so on.

To investigate in more detail how often a site was reused in relation to site category and duration of stay, we created a new dataset using only birds that were tracked in at least three years ($n = 14$). In case a bird was tracked in more than three years, we used its first three years for this analysis. With this balanced dataset we could determine if a site was used in all three years or only in one or two of the three years ('reuse category' 1, 2 or 3). Differences in duration of stay between sites were tested for using a Linear Model with 'reuse category' and 'site category' as fixed effects.

Within-individual differences in relation to environmental conditions

The variation within an individual between years and between individuals was investigated for several variables using within-subject centring in mixed models as described in Van de Pol & Wright (2009). This procedure allows to separate within-individual effects from between-individual effects by using the relative values (observation(ind,year) – mean observation (ind)) as well as the individual's mean as predictor variables in a mixed model with individual as random effect. For example, to explain the number of sites that an individual used in a winter in response to the environment 'yearNDVI', the model looked like this:

> lme(number of sites ~ relative 'yearNDVI' + mean individual 'yearNDVI', random =~1|individual)

We used this procedure to investigate within- and between-individual effects of local NDVI on several response variables. For this, we used all sites that were at least used twice ($n = 71$) and calculated a mean NDVI value for the period that the bird had stayed at this site. These NDVI values thus are the mean of a different number of NDVI measurements (one every 16 days) depending on duration of stay. If no NDVI measurement lay exactly within the period that the bird used the site (short visit), we used the first NDVI measurement after the bird had left. For each site, a mean NDVI value was calculated over the years the site had been used, as well as the relative NDVI (difference of the NDVI at the site in that year minus the mean site NDVI).

Home range size and activity measures for GPS-tracked birds were available at 24 sites of 10 individuals used in two ($n = 16$), three (4) or four (4) years. Using one of the following response variables: site home range size, mean hours flying per day, mean daily distance, we investigated within- and between-individual effects by including 'relative NDVI' and 'mean-site NDVI' as fixed effects and 'siteID' nested in 'individual' as random effect.

Timing of movements between sites was investigated for all birds, irrespective of tracking method. Within-individual differences in timing of movement between sites in relation to NDVI were tested in the same way. We used the departure date from first sites as well as the duration of stay at first sites (subset of 20 sites from 17 individuals), the duration of stay at intermediate sites (subset of 19 sites from 16 individuals) and the arrival date at last sites (subset of 32 sites from 30 individuals) as response variables. 'Relative NDVI' and 'mean site NDVI' were included as fixed effects and 'siteID' nested in 'individual' as random effect. All model output is given in Table 1.

RESULTS

General description of strategy of itinerancy

The Montagu's Harriers we tracked from their West European breeding sites used wintering sites between 5.9°N and 18.1°N and between 17.1°W and 17.6°E (Figure 1A). During a winter, birds used on average 3.3 ± 1.1 (range: 1–6) different sites (for site use patterns see Figure 2). The average number of site visits was a bit higher (3.5 ± 1.3, range: 1–8) because 14 individuals out of 72 (19.4%) revisited sites during the same winter. In total, 23 sites were revisited, most of them only once (21 occurrences) and two of them twice. Revisits occurred in 13% of tracks (17 out of 129 tracks) where birds revisited a single site during a winter (11 tracks) or even revisited two sites (6 tracks). Use of a single wintering site occurred only in 3% of the tracks (4 out of 129), twice by an individual in two consecutive years, once by an individual tracked in a single year and once in an individual that had five sites in the next year. Consecutive sites were on average 229 ± 238 km apart (10–1434 km, median: 135 km, n = 321 movements between sites). The travel distance between sites did not change with date during the course of the winter (LMM: $t_{195} = -1.255$, $P = 0.211$). Mean direction between consecutive sites was 194° ± 73° (SbW, range: 5–359°, n = 321 movements between sites). Direction changed with date over the season (LMM: $t_{195} = -5.213$, $P < 0.001$). Movements between sites in the first half of the winter (before 15

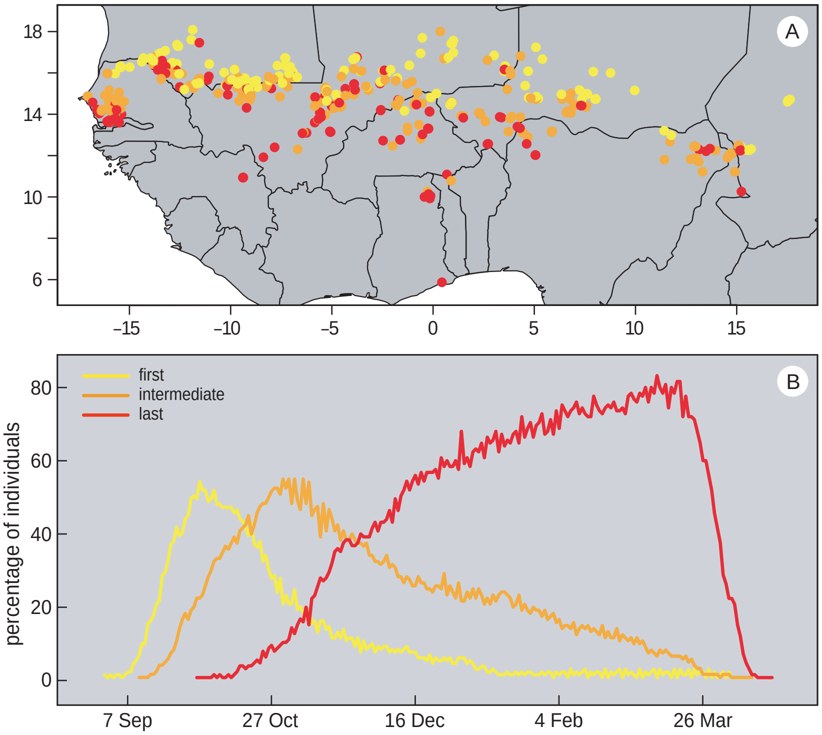

Figure 1. (A) Wintering sites of European GPS- and satellite-tracked Montagu's Harriers (129 winters). (B) Percentage of individuals at first, intermediate and last sites during the wintering season.

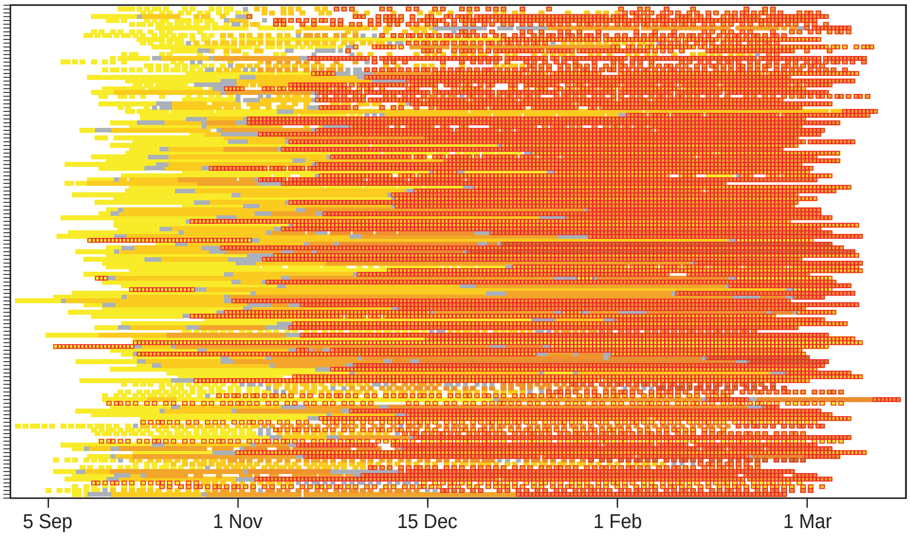

Figure 2. Site use pattern of European GPS- and satellite-tracked Montagu's Harriers (129 winters). Each row resembles one winter. For y-axis labels see Table S3. Colours indicate different sites: first sites yellow, consecutive sites in darkening orange colours. Days at last sites are marked with a red rectangle. Travel days between consecutive sites are indicated in grey. Days with no available data are visible as white rectangles.

December) were on average directed SSW (207 ± 57°) and movements between sites after 15 December were directed SSE with a wider spread (158 ± 97°; significant difference in frequencies, Pearson's Chi-squared test: $\chi^2_{15} = 86.6$, $P < 0.001$; Figure S5). Mean arrival date at the wintering grounds was 23 September ± 9 days (range: 30 August – 19 October, $n = 129$) and did not differ between the sexes (LMM: $t_{127} = -1.4$, $P = 0.164$). Spring departure was on average on 30 March ± 8 days (range: 5 March – 20 April, $n = 129$). Males departed on average 4.5 days earlier than females (LMM: $t_{127} = -3.25$, $P < 0.01$). The winter period had a total length of 188 ± 12 days (151–213 days, $n = 129$) of which 9 ± 7 days (0–37 days, $n = 125$) were days on which birds moved between wintering sites. Site visits lasted on average 52 ± 47 days (3–196 days, $n = 450$ visits). Length of stay at the last site of a wintering season (103 ± 49 days, 4–196 days, median = 113, $n = 129$) was significantly longer than at intermediate sites (33 ± 29 days, 3–153 days, median = 24 days, $n = 196$) or first sites (29 ± 23 days, 3–105 days, median = 25 days, $n = 125$; Pearson's Chi-squared test: $\chi^2_1 = -63.65$, $P < 0.001$; Figure 1B).

Habitat composition at wintering sites

Habitat composition varied greatly between wintering sites (Figure 3A and B). Sites ranged from being composed mostly of bare and sparsely vegetated habitat types to being exclusively located in agricultural habitats (Figure 3B). These are extremes on a continuum of possible habitat compositions, in which no clearly separated groups could be distinguished. Hence, we summarised habitat composition by grouping sites dominated by one of the main dominant habitat groups (Figure 3C). Of first sites, around 30% were dominated by sparsely vegetated habitats. This decreased to about 10% for intermediate and last sites. Sites dominated by agricultural habitats increased significantly from 20% for first sites to nearly 50% for intermediate and last sites. Sites dominated by natural habitat types were mostly found among first sites (46%), this decreased for intermediate and last sites to about 30%. Frequencies of dominant habitats differed significantly between the three subsets (Chi-squared test: $\chi^2_6 = 49.65$, $P < 0.001$). The frequencies differed significantly between first and intermediate sites (Chi-squared test: $\chi^2_3 = 36.26$, $P < 0.001$) as well as between first and last sites (Chi-squared test: $\chi^2_3 = 39.53$, $P < 0.001$), but not between intermediate and last sites (Chi-squared test: $\chi^2_3 = 1.19$, $P = 0.755$).

Site selection by harriers

Overall, sites used by Montagu's Harriers contained more grassland, mosaic vegetation/cropland, mosaic shrubland/grassland, sparse vegetation and cropland than expected from the average cover of these habitats at random sites within the whole wintering range (MCP-all). Habitats that occurred less than expected were bare area, mosaic cropland/vegetation, woodland and shrubland (Compositional analysis: $\lambda = 0.258$, $P =$

0.01; Figure S6). First sites used by harriers contained more grassland, sparse vegetation, bare area, mosaic shrubland/grassland and mosaic vegetation/cropland than random first sites (MCP-first). Habitats that occurred less than expected were woodland, cropland and mosaic cropland/vegetation (Compositional analysis: $\lambda = 0.057$, $P = 0.01$; Figure 4B). The picture was different for intermediate sites where the area of mosaic vegetation/cropland, grassland, cropland, mosaic shrubland/grassland, and sparse vegetation was larger than for the corresponding random sites (MCP-intermediate). Less abundant were mosaic cropland/vegetation, bare area, woodland and shrubland (Compositional analysis: $\lambda = 0.276$, $P = 0.01$; Figure 4B). Last sites consisted more than expected of cropland, mosaic vegetation/cropland, mosaic cropland/vegetation, mosaic shrubland/grassland, and sparse vegetation compared to random sites (MCP-last). Last sites consisted less than expected of grassland, bare area, shrubland and woodland (Compositional analysis: $\lambda = 0.166$, $P = 0.01$; Figure 4B).

Overall, habitat diversity was significantly higher at sites used by Montagu's Harriers compared to random sites (Figure S7; 450 harrier wintering sites, 3295 random sites; *t*-test: $t_{565.19} = -6.188$, $P < 0.001$). Habitat diversity was highest at last sites (mean: 0.96, n = 129), followed by intermediate sites (0.82, n = 196) and first sites (0.81, n = 125; Figure 4C). It differed significantly between first and last sites ($t_{248.68} = -2.794$, $P < 0.01$) as well as between intermediate and last sites ($t_{303.32} = -2.777$, $P < 0.01$) but not between first and intermediate sites ($t_{208.08} = -0.216$, $P = 0.829$). Habitat diversity at first and last sites, but not at intermediate sites, was significantly higher than at random sites within their respective MCPs (Figure 4A and 4C; first: $t_{10046} = 2.083$, $P = 0.037$; intermediate: $t_{218.5} = -0.939$, $P < 0.349$; last: $t_{139.82} = -3.772$, $P < 0.001$).

Overall, vegetation greenness (NDVI) was slightly lower at sites used by Montagu's Harriers compared to random sites (Figure S8; 5400 NDVI values at harrier wintering sites, mean 0.23; 17,556 NDVI values at

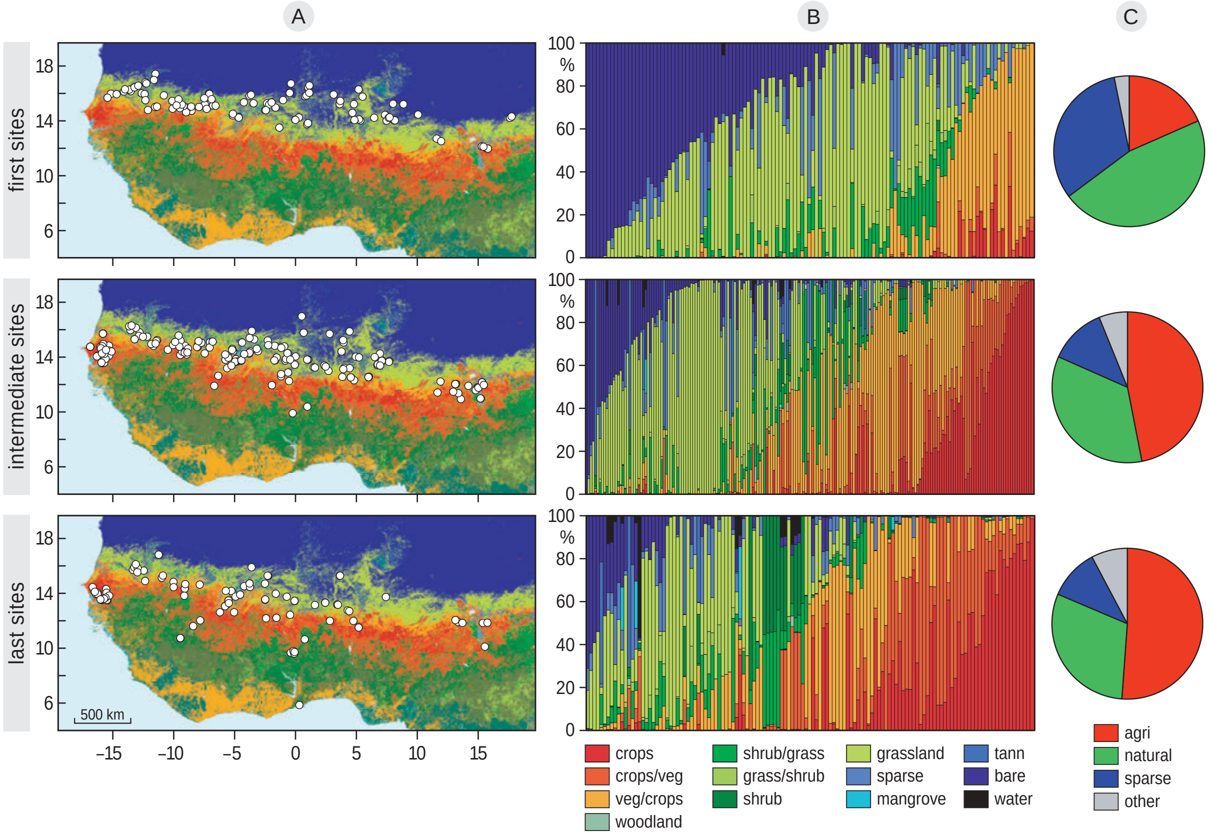

Figure 3. Habitat composition at wintering sites of GPS-tracked Montagu's Harriers for first (n = 57), intermediate (99) and last sites (59). (A) Location of wintering site centroids shown on GlobCover land use map. (B) Habitat use per site, each bar represents one site, ordered according to habitat score for graphical purposes. (C) Dominant habitats.

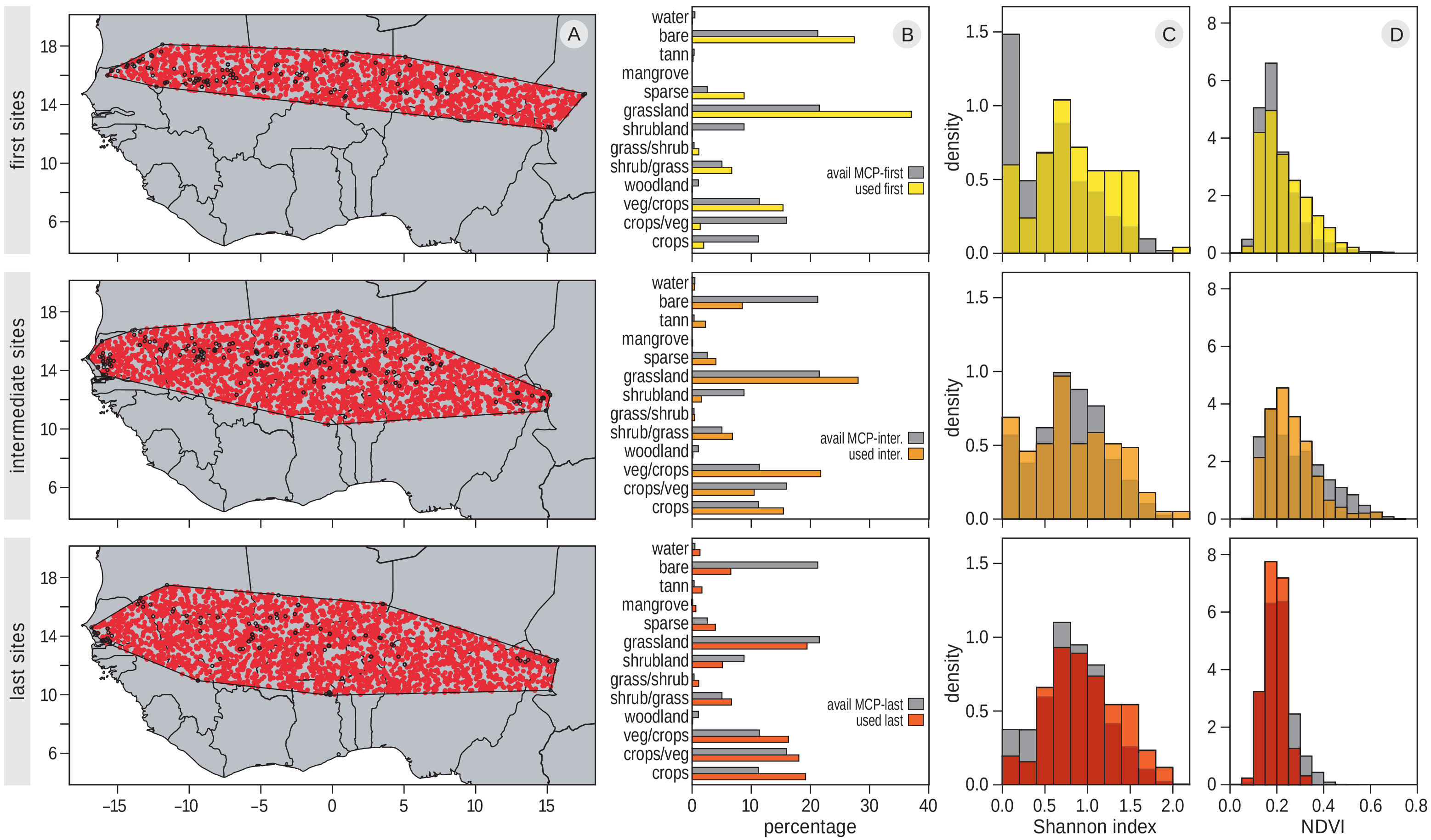

Figure 4. (A) Montagu's Harrier wintering sites (black points) and 100% MCP for first, intermediate and last sites. (B) Habitat used at harrier sites compared to wintering range MCPs. (C) Habitat diversity calculated as Shannon's diversity index for harrier wintering sites compared to random sites (grey bars). (D) NDVI (Normalized Difference Vegetation Index) at harrier wintering sites compared to random sites (grey bars).

random sites, mean = 0.24; *t*-test: $t_{565.2} = –6.19$, $P < 0.001$). Vegetation greenness was highest at intermediate sites (mean = 0.26, $n = 2352$), followed by first sites (0.23, $n = 1500$) and last sites (0.19, $n = 1548$; Figure 4D). It differed significantly between first and intermediate sites (*t*-test: $t_{3352.2} = –9.33$, $P < 0.001$), first and last sites ($t_{2096} = 14.38$, $P < 0.001$), as well as intermediate and last sites ($t_{3448.3} = 28.97$, $P < 0.001$). Vegetation greenness at first sites was significantly higher than at random sites within the respective MCP (Figure 4AD; 4142 NDVI values at random sites within MCP-first, mean: 0.20; $t_{2409.6} = –10.11$, $P < 0.001$). On the contrary, at intermediate and last sites vegetation greenness was lower compared to the corresponding random sites (intermediate: 6600 NDVI values at random sites within MCP-int, mean = 0.29; $t_{5205.2} = 9.59$, $P < 0.001$; last: 6804 NDVI values at random sites within MCP-last, mean = 0.21; $t_{2965.4} = 11.55$, $P < 0.001$).

Home range size and activity measures

Daily home range size was smallest at intermediate sites (mean = 25.7 km^2), slightly larger at first sites (28.6 km^2; LMM: first-intermediate: $\chi^2 = 1.52$, $P = 0.218$) and significantly larger at last sites (51.22 km^2; first-last: $\chi^2 = 13.62$, $P < 0.001$; intermediate-last: $\chi^2 = 30.47$, $P < 0.001$; Figure 5B). Montagu's Harriers flew least at first sites (mean = 3.86 hours per day),

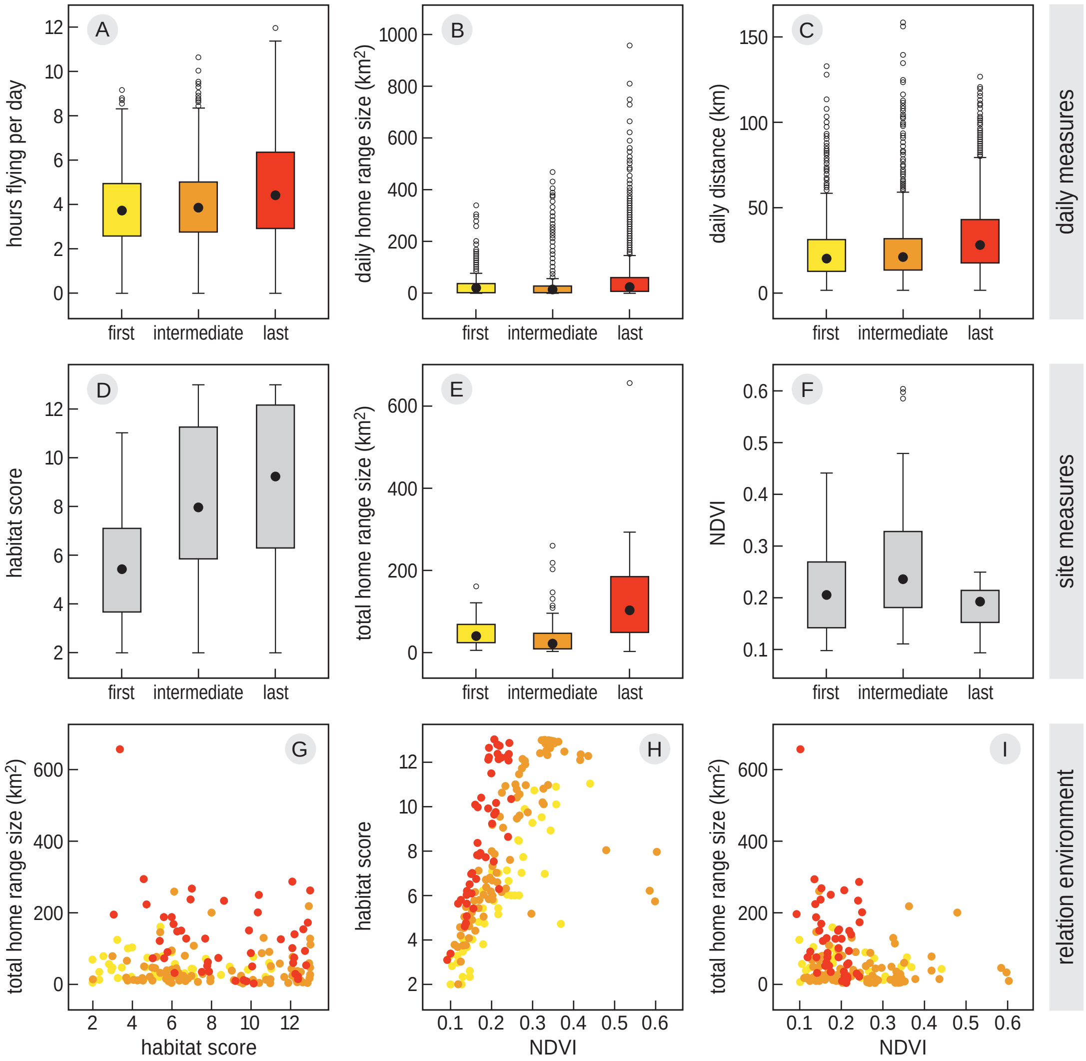

Figure 5. (A–C) Daily activity measures of GPS-tracked Montagu's Harriers, (D, F) environmental variables and (E) total site home ranges. (G, I) Relation between total home range and environmental variables, as well as (H) between environmental variables.

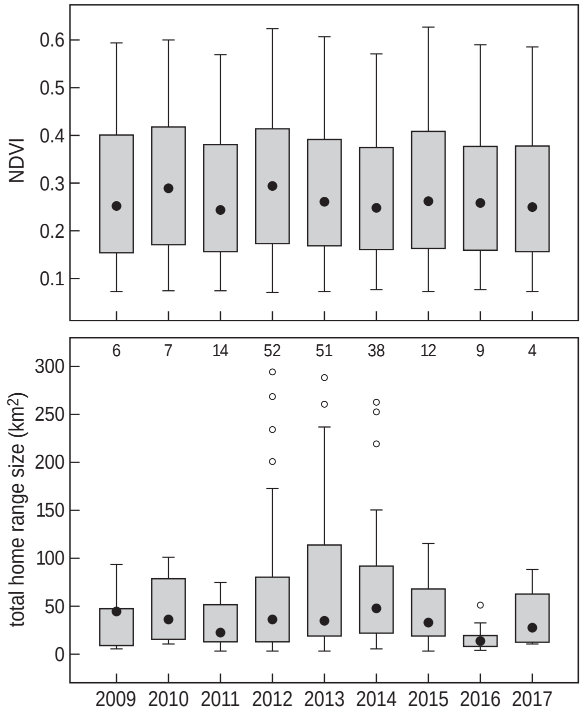

Figure 6. Yearly vegetation greenness (yearNDVI; top) and total home range size (bottom) for the years GPS-tracked Montagu's Harriers were followed. The number of site home ranges per year is given above the boxplots.

slightly more at intermediate sites (3.93; first-intermediate: $\chi^2 = 18.75$, $P < 0.001$) and much more at last sites (4.71; first-last: $\chi^2 = 6.02$, $P = 0.014$; intermediate-last: $\chi^2 = 52.93$, $P < 0.001$; Figure 5A). Daily distance covered was also shortest at first sites (mean = 25.1 km), slightly longer at intermediate sites (25.8 km; first-intermediate: $\chi^2 = 8.81$, $P < 0.01$) and was longest at last sites (33.1 km; first-last: $\chi^2 = 0.46$, $P = 0.50$; intermediate-last: $\chi^2 = 5.17$, $P = 0.046$; Figure 5C).

The median total home range size was 35 km^2 (mean = 63 km^2, range: 3–656 km^2, $n = 193$ sites; Figure S9). Total home range size for first sites (39.7 km^2) was only slightly larger than for intermediate sites (median = 21 km^2; first-intermediate: $\chi^2 = 0.85$, $P = 0.36$). Total home range size for last sites was much larger (101 km^2; first-last: $\chi^2 = 43.19$, $P < 0.001$; intermediate-last: $\chi^2 = 70.00$, $P < 0.001$; Figure 5E). Total home range size did not differ with latitude (LM: $t = -0.048$, $P = 0.962$) or longitude ($t = 0.421$, $P = 0.674$). However, total home range size did decrease significantly with increasing greenness values (LMM: $t_{187.54} = -3.83$, $P < 0.001$; Figure 5F and 5I). But total home range size did not differ with habitat score ($t_{138.63} = -0.72$, $P = 0.472$; Figure 5D and 5G), despite NDVI and habitat score being positively correlated (Figure 5H). Finally, total home range size did not differ with annual vegetation greenness (yearNDVI; LMM: $t_{2.23} = 0.93$, $P = 0.44$; Figure 6).

Site fidelity

Montagu's Harriers that were tracked in two years, reused 75% of their wintering sites visited in the first year (median = 75%, 1$^{\text{st}}$ Qu. = 50%, 3$^{\text{rd}}$ Qu. = 100%, $n = 57$ two-year comparisons). Reuse was 60% for first sites (60 two-year comparisons), 50% for intermediate sites ($n = 52$) and 91% for last sites ($n = 64$). For the 14 birds that were tracked in three years, we saw that first and intermediate sites were used once, twice or three times. Last sites, however, were almost always used in all the three years (Figure 7A).

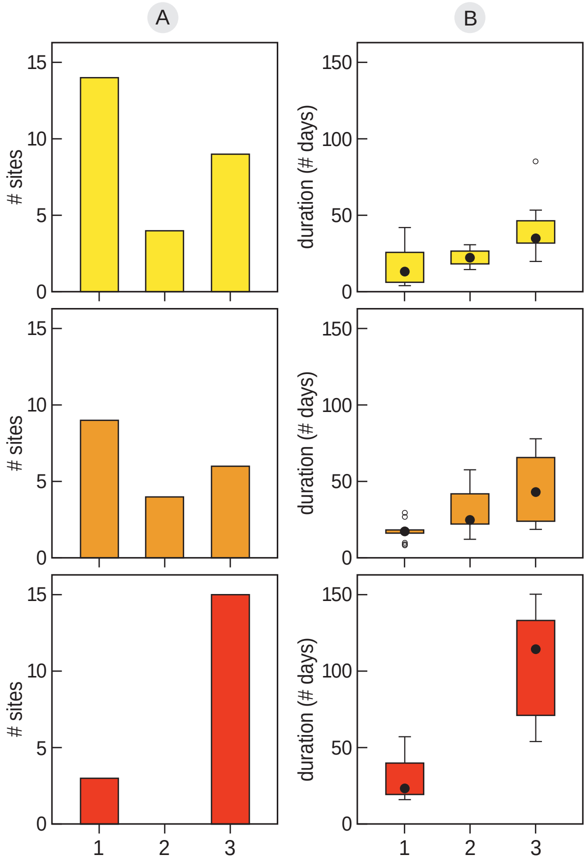

Figure 7. Reuse of geographical sites by individuals tracked in three consecutive years. (A) Sites reused once, twice or thrice during these three years for first (top), intermediate (middle) and last sites (bottom). (B) Length of stay at these sites according to reuse category and site category. Both significantly influenced length of stay (Linear Model: reuse category $F_2 = 39.5$, $P < 0.001$; site category $F_2 = 21.97$, $P < 0.001$).

Within-individual differences in relation to environmental conditions

Montagu's Harriers which were tracked in several years sometimes added or skipped one or more sites compared to the previous year. Neither drier nor wetter years (yearNDVI) explained within-individual or between-individual variation in the number of sites used (Table 1 (a)).

Home range size of harriers followed by GPS trackers did not correlate with annual variation in NDVI when present at these sites (within-individual comparisons). However, we found significant between-individual effects with individuals wintering in drier areas having larger home ranges (Table 1 (b), Figure 8A). The same was true for the time harriers spent flying; no within-individual effects were found but significant between-individual effects with individuals wintering in drier areas flying more (Table 1 (c), Figure 8B). A significant within-individual effect was only found for the mean daily distance flown at a site, with birds flying more kilometres at a site in a drier year, as well as between-individual effects with individuals wintering in drier areas flying more kilometres per day (Table 1 (d), Figure 8C).

Within-individual differences in the timing of movements between sites were mainly explained by local NDVI values. Harriers departed significantly earlier from a first site in a drier year than from the same site in a greener year (Table 1 (e), Figure 9A), and consequently also remained for a significantly shorter time at a first site when it was drier (Table 1 (f), Figure 9B). The duration of the stay at intermediate sites was not correlated to NDVI (Table 1 (g), Figure 9C). Timing of arrival at last sites tended to be later in a drier year compared to the arrival date at the same site in a greener year (Table 1 (h), Figure 9D). There were no between-individual effects in timing of movement (Table 1 (e–h)).

DISCUSSION

Itinerancy and other wintering strategies

Based on observations of (sudden) increases in bird numbers during ephemeral food peaks (such as migratory locust outbreaks), Moreau (1972) and Newton (2008) suspected that some migratory landbird species perform nomadic movements during the winter period. Nomadism was for example suspected in White Stork *Ciconia ciconia*, Lesser Spotted Eagle *Clanga pomarina* and Lesser Kestrel *Falco naumanni*. Later, tracking studies revealed that these species were itinerant instead (Berthold *et al.* 2001, Meyburg *et al.* 2015, Catry *et al.* 2011). A strategy of nomadism was also expected for Montagu's Harrier (García & Arroyo 1998). But as shown by Trierweiler *et al.* (2013) and in this study, the Montagu's Harrier joins the list of species that are itinerant. Importantly, we believe there remain no species that are nomadic during their non-breeding period in Africa. Instead, itinerancy seems to be the most common wintering strategy.

Residency, with birds using only a single site for the entire wintering period, is another possible wintering strategy. Examples include Osprey *Pandion haliaetus* (Kjellén *et al.* 1997, Alerstam *et al.* 2006), Common Redstart *Phoenicurus phoenicurus* (Kristensen *et al.* 2013), Northern Wheatear *Oenanthe oenanthe* (Schmaljohann *et al.* 2012) and Pied Flycatcher (Ouwehand *et al.* 2016). Importantly, residency often is part of a mixed strategy, with some individuals being resident and others being itinerant. This varies from most individuals being resident (10 out of 12 European Nightjars *Caprimulges europaeus* (Norevik *et al.* 2017), 17 out of 19 European Hoopoes *Upupa epops* (Bächler *et al.* 2010, van Wijk *et al.* 2016), 44 out of 66 Barn Swallows *Hirundo rustica* (Liechti *et al.* 2015) to most individuals being itinerant, e.g. 6 out of 9 Lesser

Table 1. Model output for several variables using within-subject centring in mixed models as described in van de Pol & Wright (2009).

	Within-individual effect NDVI					**Between-individual effect NDVI**				
	Estimate	SE	*df*	*t*-value	*P*-value	Estimate	SE	*df*	*t*-value	*P*-value
(a) Number of sites	–4.57	8.37	53	–0.55	0.590	–39.18	29.80	28	–1.31	0.200
(b) Home range size	–369.76	351.41	35	–1.05	0.300	–634.86	198.67	13	–3.20	**0.007**
(c) Hours flying	–3.81	3.83	35	–0.99	0.330	–9.88	2.42	13	–4.09	**0.001**
(d) Daily distance	–70.61	25.62	35	–2.76	**0.009**	–104.55	20.34	13	–5.14	**<0.001**
(e) Departure first	123.86	47.37	35	2.61	**0.013**	56.26	112.08	2	0.50	0.670
(f) Duration first	133.06	47.70	35	2.79	**0.009**	84.42	84.52	2	1.00	0.420
(g) Duration interm.	27.23	96.80	26	0.28	0.780	57.19	101.01	3	0.57	0.610
(h) Arrival last	–450.39	250.56	58	–1.80	0.070	–215.66	115.79	1	–1.86	0.310

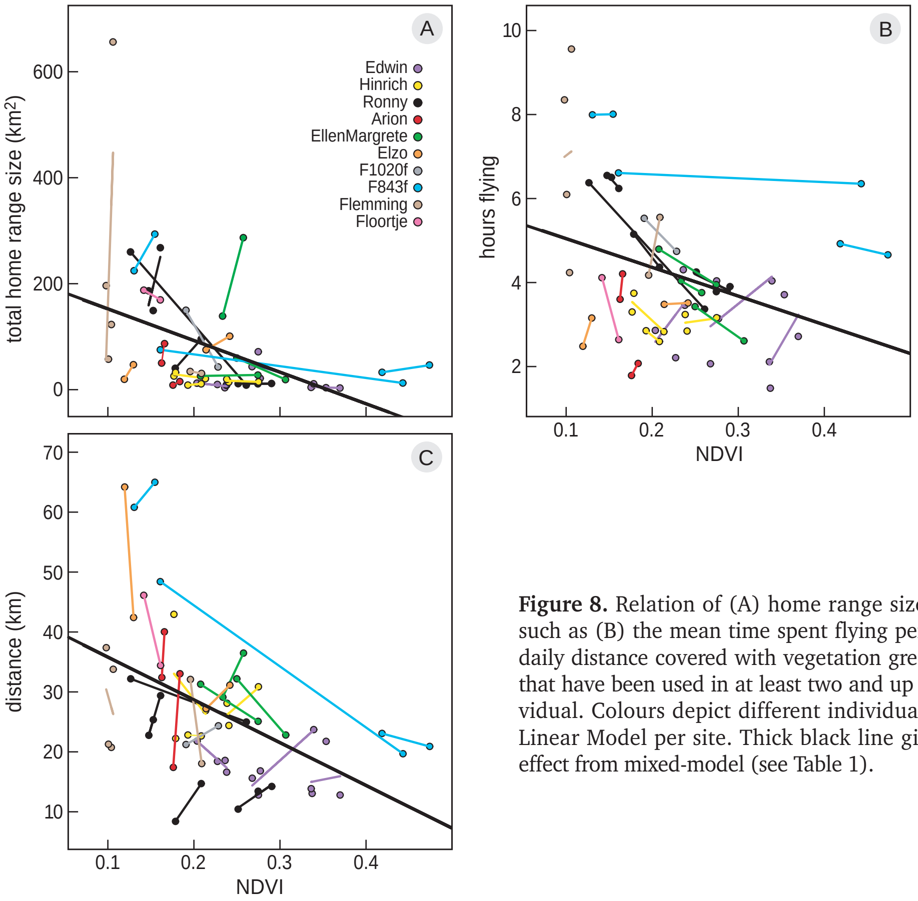

Figure 8. Relation of (A) home range size and activity measures such as (B) the mean time spent flying per day and (C) the mean daily distance covered with vegetation greenness (NDVI), for sites that have been used in at least two and up to four years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 1).

Kestrels (Catry *et al.* 2011, Limiñana *et al.* 2012a) and 11 out of 12 Northern Wheatears (Arlt *et al.* 2015). A mixed strategy also applies for the Montagu's Harrier, although the occurrence of residency is noticeably low; only in 3% of the cases (n = 129) a bird had a single wintering site. We conclude that in African-Palearctic migratory landbirds two main wintering strategies exist, itinerancy and residency, which are not a dichotomy of two distinct strategies but rather the extremes on a gradient of mixed strategies from full residency to complete itinerancy.

A factor that complicates the discussion about wintering strategies is that some authors consider part of the sites individuals use in their wintering range as migratory stopovers, especially in cases with large intra-African movements. For example, Tøttrup *et al.* (2012) consider the long stay of Red-backed Shrikes in the Sahel in autumn as a migratory stopover, rather than part of an itinerant wintering strategy. The question is whether this is the case, as the duration of this stay in the Sahel seems to be mainly determined by food availability in the Sahel and the timing of the late autumn rains in the Kalahari (the shrikes' final destination) rather than by the time required to fuel for the flight from the Sahel to Southern Africa (Thorup *et al.* 2017). One might even argue that the distinction between migration and wintering is artificial anyway, as migrants are animals tracking spatiotemporal variation in favourable conditions, including resources, around the globe throughout the year (Thorup *et al.* 2017). But such a generalisation does not help to understand wintering strategies. Instead, we propose to be explicit about the functions of the sites used by the animals, in particular the relative contribution to 'wintering' and 'fuelling for migration'. In the example of the Red-backed Shrike the function of the stay in the Sahel seems two-fold, with the birds first making use of the lush vegetation in the Sahel at the beginning of the winter and 'waiting' for the conditions in the Kalahari to improve as part of an itinerant wintering strategy, and second preparing (fuelling) for the long flight from the Sahel to southern Africa. In the Montagu's Harrier, fuelling before moving to the next site seems negligible as the distances between subsequent sites are relatively small (on average 229 km) and harriers travel to a large extent by energy-efficient soaring flight (Vansteelant *et al.* 2015). In addition, as fly-and-forage migrants Montagu's Harriers can forage on the way (Klaassen *et al.* 2017). Preparations for migration are only relevant at their last wintering site, from which they commence their long spring migration (Schlaich *et al.* 2016).

Variation in wintering behaviour

Itinerancy showed many faces among individuals. No two individuals behaved exactly in the same way. We found no overlap in sites used by different individuals during the winter. In fact, wintering sites were longitudinally distributed across a width of 3700 km. Directions and distances of movements between sites varied individually, as did the number of sites used during the winter (ranging from 1 to 6 sites) and

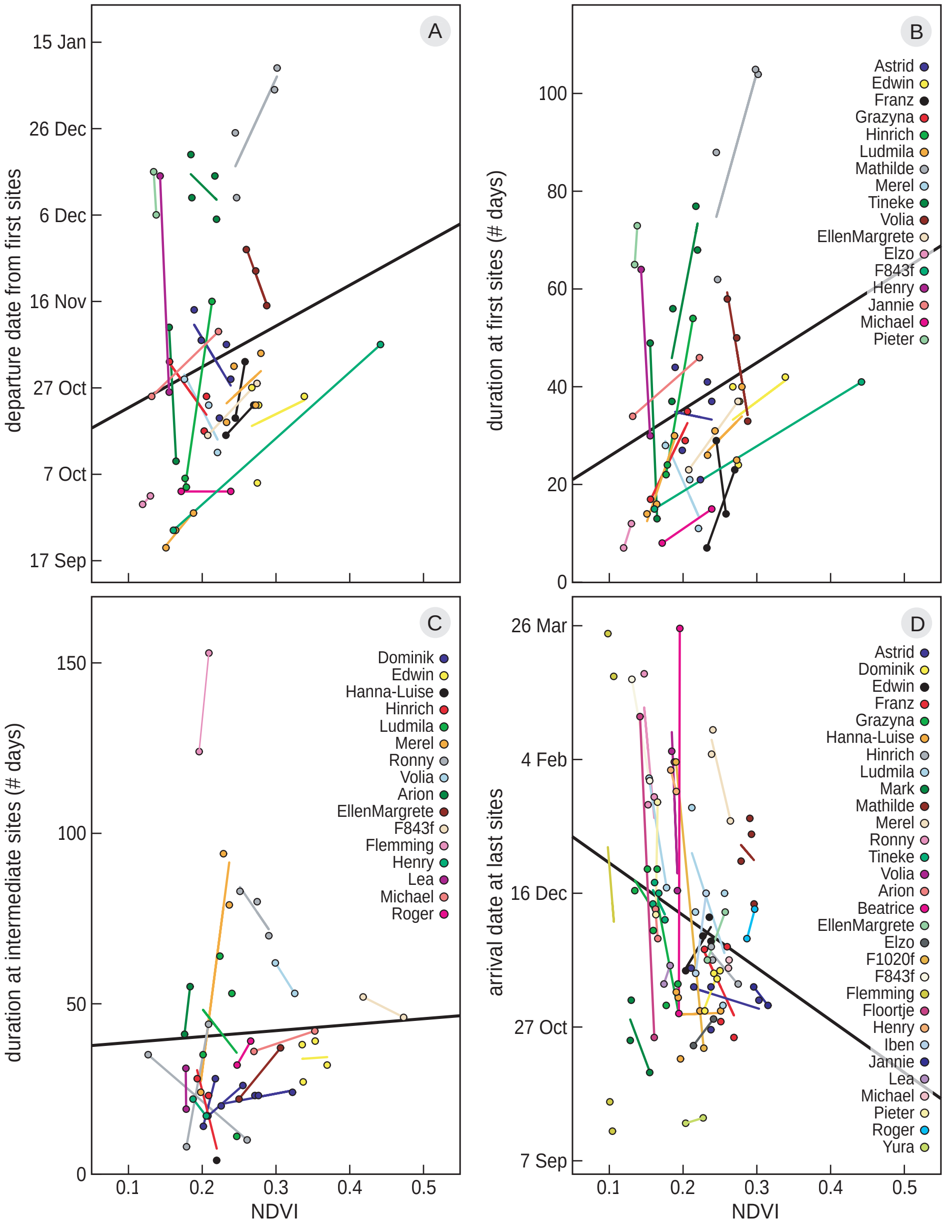

Figure 9. Relation of timing of movements between wintering sites with vegetation greenness (NDVI), for sites that have been used in at least two and up to five years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 1).

timing and duration of site visits (Figure 2). There is no 'average' bird. Instead, variation in behaviour is all important. The many different ways in which a strategy of itinerancy can be realised at the individual level suggest great flexibility of harriers to adjust to changes in spatiotemporal variation of environmental conditions. The remaining question is how these individual strategies develop, a question that can only be answered by tracking individuals from the first year of their lives (Sergio *et al.* 2014). The large number of tracked individuals allowed us some insight into this variation in behaviour and underlines the need to be careful when extrapolating from small sample sizes, an issue in many tracking studies.

Site fidelity of African-Palearctic migratory landbirds

Moreau (1969), and later Sauvage *et al.* (1998), Salewski *et al.* (2000) and King & Hutchinson (2001), compiled overviews of recaptures of ringed passerines and waders between years to check for winter site fidelity. They found evidence for winter site fidelity in 60 species, suggesting that site fidelity is common among African-Palearctic migrants. However, ringing is not particularly suitable to study site fidelity, especially as ringing operations typically are conducted each year at the same sites and the probability that a bird is recovered beyond its ringing site is extremely low. This results in a strong bias towards recaptures at the same site. On the basis of tracking data, Meyburg *et al.* (2015) reported strong winter site fidelity for Lesser Spotted Eagle, similar to Montagu's Harrier. Other tracking studies instead provided evidence for low site fidelity in White Stork (Berthold *et al.* 2002, 2004), European Hoopoe (van Wijk *et al.* 2016) and Common Redstart (Kristensen *et al.* 2013). Tracking is a strong method to study winter site fidelity, but hitherto studies that reported on repeated tracks are notably scarce. Consequently, we have an incomplete picture of winter site fidelity in African-Palearctic migratory landbirds, apart from the fact that both high and low winter site fidelity have been observed, irrespective of wintering strategy (residency versus itinerancy).

Our dataset included repeated journeys of 33 individuals tracked during multiple winters. With the data we are able to confirm the initial suggestion by Trierweiler *et al.* (2013) that Montagu's Harriers are to a large extent faithful to the sites they visit during the African dry season. Site fidelity has the advantage of local knowledge of the landscape, such as where to find food, where to find a place to drink, and where to find a safe place to roost (Trierweiler & Koks 2009). A disadvantage of site fidelity is that birds are less flexible in exploiting annual spatiotemporal variation in resources. Given the fact that Montagu's Harriers show strong site fidelity, we can conclude that local knowledge of the landscape apparently is more important than flexibility in site selection.

Habitat use

We found that wintering sites of Montagu's Harriers generally consisted of mosaics of grassland, cropland, shrubland, and sparse vegetation, as also reported by Limiñana *et al.* (2012b), Trierweiler *et al.* (2013) and Augiron *et al.* (2015). Importantly, sites used by harriers differed from random sites in having a higher habitat diversity. This preference might be related to food abundance, as diverse habitats generally host more biodiversity (Rosenzweig 1995) and therefore potentially more prey species. On the contrary, relatively high numbers of grasshoppers, the most important prey for Montagu's Harriers in Africa (Mullié 2009, Mullié & Guèye 2010), were found in the relative monotonous 'intensively' farmed area of Khelcom in Senegal (Mullié & Guèye 2010), an area also renowned for large communal harrier roosts (Augiron *et al.* 2015, own observations). Clearly, systematic field observations on prey abundance from sites varying in habitat diversity are needed to understand the selection of wintering sites by Montagu's Harriers.

Agricultural habitats stood out as one of the main habitats at the sites used by harriers, especially at intermediate and last sites. First wintering sites were generally located further to the north in the Sahel, where natural habitats dominate the landscape, which explains the lower occurrence of agricultural habitats at these sites rather than changes in habitat preferences (Figure 3). The importance of mixed agricultural habitats is not unique to Montagu's Harriers. Also species like Lesser Kestrel, Northern Wheatear and Whinchat *Saxicola rubetra* are frequently observed in agricultural habitats in the Sahel (Limiñana *et al.* 2012a, Wilson & Cresswell 2010, Blackburn & Cresswell 2015). The surface area of arable land with millet and sorghum has strongly increased in the Sahel in the second half of the previous century in order to feed the ever-growing human population (Brink & Eva 2009, Zwarts *et al.* 2009). This might benefit species that make use of agricultural habitats. On the other hand, the farming system itself has also changed, from an extensive system of shifting cultivation involving fallow land, to a more intensive system of permanent cultivation and a shortening of the crop-fallow cycle (Zwarts *et al.* 2023). Fallow land, representing natural habitat, might be of particular importance for wintering birds, but we cannot judge the impact of these changes as we have an insufficiently detailed picture of habitat use and habitat selection. The latter is the consequence of the coarseness of the available habitat maps for the Sahel.

We relied on the GlobCover land use dataset with a 300-m resolution. Ground-truthing revealed that the accuracy of this dataset is mediocre (73% for the Sahel; Defourny *et al.* 2009). Moreover, the habitat classification for this dataset is rather coarse. For example, the category 'crops' does not provide information on what crop type was grown or whether the land was left fallow. Similarly, the category 'sparse vegetation' described different habitat types at different sites. At some sites it described sparsely vegetated grassy savannah, but we also noticed via ground-truthing that laterite plateaus were included in this category. Laterite plateaus have been noticed as important landscape structures for harriers (own observations), since shrubs on these plateaus host grasshoppers and farming is limited due to barren soil. Unfortunately, as fallow land and laterite plateaus are not identifiable on the land use map we used, we cannot investigate the importance of these habitats and landscape structures, and thus cannot fully exploit the potential of the small spatiotemporal resolution the birds were tracked with. Higher resolution maps with detailed habitat categories allowed formal habitat use and habitat selection analyses, which would provide the important information relevant to conservation on what habitats and landscape elements are used for foraging, resting and roosting. Using detailed high-resolution land use information is the key to future habitat selection analyses of migrants wintering in the Sahel.

The role of the Sahel in the annual cycle of migratory landbirds

Although Montagu's Harriers use several sites during the winter, their strategy of itinerancy is performed rather strictly within the narrow latitudinal band of the Sahel region. This is believed to reflect habitat suitability, with the Sahara north of the Sahel being too dry, and the wooded savannah south of the Sahel being too forested (Montagu's Harriers generally prefer open landscapes (Clarke 1996; see also Figure 3). For landbirds that have a strategy of itinerancy, this restriction to the Sahel is rather unique. There are only few other examples of itinerant migrant landbird species remaining in the Sahel, e.g. the Tawny Pipit *Anthus campestris* (Briedis *et al.* 2016) and the Northern Wheatear (Arlt *et al.* 2015), also habitat specialists of open arid landscapes.

This does not mean that the Sahel is not used by other migrants. On the contrary, itinerant migrants commonly use the Sahel before they continue to more southerly sites outside the Sahel biome. These species typically use the Sahel in the beginning of the winter, just after the rainy season has ended and vegetation is still green and food aplenty (Morel 1973). Examples include the Common Nightingale *Luscinia megarhynchos* (Hahn *et al.* 2014), Thrush Nightingale *Luscinia luscinia* (Stach *et al.* 2012), Common Cuckoo *Cuculus canorus* (Willemoes *et al.* 2014), Common Swift *Apus apus* (Åkesson *et al.* 2012) and Red-backed Shrike (Tøttrup *et al.* 2012). In eastern Africa only, Montagu's Harriers commonly also winter south of the Sahel (Clarke 1996), but as tracking data for these eastern populations is lacking, we have no information about their wintering strategy.

Tracking resources and the effect of annual variation in environmental conditions

The strategy of itinerancy in Montagu's Harriers was first described by Trierweiler *et al.* (2013). Our analyses, based on a much larger dataset, confirm these results. By relating the movements of the birds to vegetation greenness (NDVI), Trierweiler *et al.* (2013) also showed that harriers track a shifting 'green belt' of vegetation greenness indicative of higher grasshopper abundance. In contrast to Trierweiler *et al.* (2013) our dataset included a large number of tracks from the same individual in different winters, which, uniquely, allowed us to analyse effects of annual variation in environmental conditions at the level of individual birds.

We found that individuals responded to variation in environmental conditions by adjusting the timing of their movements (and thus the duration of their stays at sites). When conditions were relatively dry (lower NDVI values), the birds left their first site earlier, but arrived slightly later at their last wintering site. The patterns for intermediate sites were unclear, presumably due to variation in the number of intermediate sites used. But the overall picture suggests that birds adjust the timing of their movements to the environmental conditions encountered. Thus, Montagu's Harriers are not static in the timing of their movements between sites (no fixed behavioural response), but itinerancy is a flexible adjustment to between-year variation in environmental conditions encountered at their different individual wintering sites (plastic behaviour). In other words, behavioural plasticity is the mechanism behind the 'green belt hypothesis' (Trierweiler *et al.* 2013) of how Montagu's Harriers stay within a certain range of NDVI values that indicate highest food abundance.

Several other studies correlated (the timing of) movements between wintering sites with environmental conditions (Red-backed Shrike, Thrush Nightingale and Common Cuckoo (Thorup *et al.* 2017); Pallid Swift *Apus pallidus* (Norevik *et al.* 2018); Great Reed Warbler *Acrocephalus arundinaceus* (Koleček *et al.* 2018); Willow Warbler *Phylloscopus trochilus* (Lerche-Jørgensen *et al.* 2017)). In all these examples, conditions encountered at consecutive wintering sites improved after midwinter movements, suggesting that tracking spatio-temporal 'blooms' in resources is common in migratory landbirds. However, these analyses were made at the population level, and to our best knowledge there are no other studies showing this response within individuals, as we do in the current study.

We used vegetation greenness as a proxy for food availability instead of using direct data on prey availability (as, obviously, the latter is not available at the scale of the Sahel). Although this is a common approach in migration studies (e.g. Thorup *et al.* 2017), we do realize that insectivorous landbirds do not eat vegetation but the insects that rely on it. We should be aware of the potential shortcomings of using a proxy. Since Montagu's Harriers mainly prey on grasshoppers during winter and grasshoppers depend on green vegetation, NDVI seems a valid proxy for food abundance (Trierweiler *et al.* 2013, Schlaich *et al.* 2016). But at the same time we know that some species of shrubs carry green leaves but host no grasshoppers. In addition, more factors than vegetation alone may influence grasshopper abundance. We therefore would like to stress the importance of backing-up remote sensing data with on-the-ground observations of prey abundance.

Future prospects

Recurrences of individual Great Reed Warblers at the same site in Congo but at different times in subsequent years led Moreau (1972) to the question: "How far, one wonders, is it the rule for these intra-tropical movements to be replicated in the successive seasons when they finally came to anchor in the same few square meters of African vegetation?". For the Montagu's Harrier we can now answer this question, profiting from the fact that we had data on repeated journeys. Confirming that they are itinerant and showing high site fidelity, we showed that these migrants indeed replicate their intra-tropical movements but adjust the timing to environmental conditions.

Many open questions remain. We do not yet know what the consequences of this strategy are for the rest of the annual cycle. Are there carry-over effects to migration or even breeding, and what about fitness consequences? The only hint we have for Montagu's Harriers is that individuals that departed later from drier last wintering sites also arrived later at the breeding grounds (Schlaich *et al.* 2016). How will this develop in the future in the light of further land use changes in the Sahel? Furthermore, we do not know whether conditions at the breeding sites or at the wintering sites are limiting populations of Montagu's Harriers and how this varies between populations. And finally, we do not yet understand how individuals' itinerary schedules originate.

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SAMENVATTING

Europese trekvogels gebruiken in Afrika een verscheidenheid aan strategieën om daar de winter door te komen. Individuen kunnen trouw zijn aan één overwinteringsplek, of individuen kunnen meerdere gebieden gebruiken tijdens de winter. Er werd verondersteld dat een deel van de soorten erratisch is, en opduikt op plekken met een tijdelijke overmaat aan voedsel. Zo zouden Grauwe Kiekendieven *Circus pygargus* bijvoorbeeld uitbraken van Afrikaanse treksprinkhanen *Locusta migratoria migratorioides* volgen. Zenderonderzoek heeft echter laten zien dat individuele Grauwe Kiekendieven weliswaar meerdere gebieden gebruiken, maar dat ieder individu tussen de jaren trouw is aan dat 'setje' gebieden. Zo'n strategie van wat je opeenvolgende plaatstrouw zou kunnen noemen ('itinerancy' in het Engels) blijkt bij veel landvogels voor te komen. Op deze manier lijken trekvogels in de winter variatie in ruimte en tijd in het voedselaanbod te benutten. Opvallend genoeg lijkt er geen soort te zijn waarvoor de strategie van rondzwerven van toepassing is. Als individuen plaatstrouw zijn aan hun opeenvolgende overwinteringsgebieden, hoe gaan ze dan om met variatie in het voedselaanbod tussen winters? Zijn ze star in de timing en duur van het gebruik van hun overwinteringsgebieden, of reageren ze op de voor de Sahel zo kenmerkende regenafhankelijke jaarlijkse fluctuaties in het voedselaanbod? Om dat te onderzoeken konden we putten uit de vliegbewegingen van 125 adulte Grauwe Kiekendieven die we tussen 2005 en 2018 in Europese broedgebieden van satelliet- of GPS-zenders hadden voorzien. Bij elkaar opgeteld leverden deze vogels gegevens voor 129 complete winterseizoenen, inclusief 33 individuen die in twee of meer winters konden worden gevolgd. De aankomst in de Sahel viel gemiddeld op 23 september (spreiding 30 augustus tot 19 oktober), zonder verschil tussen mannen en vrouwen. In het voorjaar vertrokken de kiekendieven gemiddeld op 30 maart (spreiding 5 maart tot 20 april), waarbij mannen 4,5 dagen eerder noordwaarts keerden dan vrouwen. De duur van het verblijf op de overwinteringsplekken in Afrika beliep gemiddeld 188 dagen, waarvan negen dagen werden gebruikt om van de ene naar de andere plek te vliegen. Gemiddeld gebruikten de Grauwe Kiekendieven 3,3 verschillende plekken als winterlocatie (met een individuele variatie van 1–6; gebruik van slechts één plek kwam maar in 4 op 129 winterseizoenen voor), waaraan ze in hoge mate plaatstrouw tussen de winters waren (75%). Opeenvolgende winterplekken lagen gemiddeld 229 km uit elkaar (mediane waarde 135 km), met een forse spreiding van 10 tot 1434 km. De verplaatsing in de loop van de winter was gemiddeld zuidwaarts gericht, waarbij de verplaatsingen na 15 december een meer zuidzuidoostwaartse component hadden. De laatste van de winterplekken werd het langst gebruikt (gemiddeld 103 dagen), de intermediaire en eerste plekken beduidend korter, namelijk respectievelijk 33 en 29 dagen. Bij elkaar bestreken de gezenderde vogels uit Europa (van Verenigd Koninkrijk tot en met Belarus) de westelijke en centrale Sahel over een breedte van 3700 km. Hoewel ze in uiteenlopende habitats voorkwamen, verschilde de habitatkeus naar seizoen (en dus winterplek): de noordelijkste plekken waren het meest natuurlijk en het schaarst begroeid (vooral savanne met kale plekken), de zuidelijker gelegen plekken waren gevarieerder met een groter aandeel landbouw. Grauwe Kiekendieven bevonden zich doorgaans in de meer gevarieerde landschappen binnen de regio. De kans is groot dat voedselaanbod daarin de sturende factor was. Het dagelijkse activiteitsgebied van de kiekendieven op de eerste winterplek omvatte gemiddeld 28,6 km^2; ze vlogen er per dag gemiddeld 3,86 uur, waarbij 25,1 km werd afgelegd. Dat verschilde nauwelijks van de intermediaire winterplekken, met respectievelijk 25,7 km^2, 3,93 dagelijkse vlieguren en een afgelegde afstand van 25,8 km. Op de laatste winterplek, waar ze, zoals gezegd, het langst verbleven, bestreken de kiekendieven een grotere oppervlakte (51,2 km^2), vlogen ze langer per dag (4,71 uur) en legden ze grotere afstanden af (33,1 km). Dat lijkt erop te wijzen dat de vogels het in die tijd van het jaar en op die plek niet makkelijk hadden om aan de kost te komen (meer vliegen over grotere afstanden). In relatief droge jaren legden de kiekendieven meer kilometers per dag af binnen hetzelfde gebied in vergelijking met relatief groene (natte) jaren. Bovenal pasten de kiekendieven hun timing aan; in drogere jaren bleven de vogels korter in hun eerste gebied en verplaatsten ze zich eerder naar het volgende gebied. In nattere jaren kwamen de vogels eerder in hun laatste gebied aan. We concluderen dat binnen een strategie

van opeenvolgende plaatstrouw de kiekendieven star zijn in welke gebieden ze gebruiken (ruimtelijke component) maar juist flexibel in de timing en duur van het gebruik van deze gebieden (temporele component). Dit is dus de manier hoe de kiekendieven binnen een strategie van opeenvolgende plaatstrouw omgaan met jaarlijkse fluctuaties in het voedselaanbod. Met dit zenderonderzoek hebben we dus een beter beeld gekregen over hoe de strategie van opeenvolgende plaatstrouw precies in elkaar steekt. En bovenal hebben we geleerd dat de gemiddelde Grauwe Kiekendief niet bestaat.

RÉSUMÉ

Les oiseaux migrateurs européens utilisent des stratégies variées lors de leur séjour en Afrique durant l'hiver boréal. Certains sont fidèles à un unique site d'hivernage, quand d'autres se déplacent entre plusieurs zones au sein d'un même hiver. On a pensé que certaines espèces sont erratiques et se déplacent à la recherche de secteurs où des pics de disponibilité alimentaire temporaires se produisent. Il a semblé par exemple que les Busards cendrés *Circus pygargus* suivent les invasions de Criquets pèlerins africains *Locusta migratoria migratorioides*. Cependant, des études utilisant des émetteurs suivis par satellite ont montré que, bien que les Busards cendrés utilisent plusieurs territoires, chaque individu est fidèle à cet ensemble de territoires d'une année sur l'autre. Cette stratégie d'itinérance entre des territoires hivernaux successifs semble répandue chez de nombreuses espèces terrestres. De cette manière, ces espèces migratrices semblent en mesure exploiter les variations spatio-temporelles de l'offre alimentaire en hiver. Mais si les individus sont fidèles à ces sites d'hivernage successifs, comment s'adaptent-ils aux variations interannuelles de la disponibilité alimentaire ? Le calendrier et la durée d'exploitation de leurs sites d'hivernage sont-ils figés ou répondent-ils aux fluctuations annuelles des ressources alimentaires, qui dépendent des pluies et sont caractéristiques du Sahel ? Pour étudier cette question, nous avons analysé les mouvements de 125 Busards cendrés adultes que nous avons équipés d'émetteurs satellites ou GPS dans les zones de reproduction européennes entre 2005 et 2018. Au total, ces oiseaux ont fourni des données correspondant à 129 saisons hivernales complètes et 33 individus ont pu être suivis sur deux hivers ou plus. L'arrivée au Sahel a eu lieu en moyenne le 23 septembre (entre le 30 août au 19 octobre), sans différence entre les mâles et les femelles. Au printemps, les busards sont partis en moyenne le 30 mars (entre le 5 mars au 20 avril), les mâles repartant vers le Nord en moyenne 4,5 jours plus tôt que les femelles. La durée du séjour sur les sites d'hivernage en Afrique a été en moyenne de 188 jours, dont 9 jours de déplacements d'un site à un autre. En moyenne, les Busards cendrés suivis ont utilisé de 1 à 6 sites différents pour leur hivernage, avec une moyenne de 3,3 sites et les individus étaient très fidèles d'un hiver à l'autre (75%). L'utilisation d'un unique site n'a été constaté que 4 fois sur 129 saisons hivernales. Les sites consécutifs étaient en moyenne distants de 229 km (valeur médiane de 135 km), avec une variation considérable de 10 à 1434 km. Les déplacements au cours de l'hiver étaient en moyenne dirigés vers le Sud, ceux réalisés après le 15 décembre ayant une composante orientale et étant orientés Sud-Sud-Est. Le dernier des sites d'hivernage a généralement été celui occupé le plus longtemps (103 jours en moyenne), tandis que les temps de séjour sur les sites intermédiaires et initiaux ont été nettement plus courts, avec 33 et 29 jours respectivement. Ces Busards cendrés provenant de longitudes variées, du Royaume-Uni à la Biélorussie, ont couvert le Sahel occidental et central sur une largeur de 3700 km. Bien qu'ils aient fréquenté des habitats divers, leur choix d'habitat a avant tout reflété la saison et donc de la localisation du site d'hivernage : les sites les plus septentrionaux étaient les plus naturels et occupés par une végétation clairsemée (principalement de la savane avec des parcelles dénudées), tandis que les sites plus méridionaux étaient plus variés avec une plus grande proportion d'agriculture. Les Busards cendrés ont montré une tendance à s'établir dans des paysages en moyenne plus variés que ceux disponibles aux alentours. Il est probable que l'approvisionnement en nourriture soit le facteur de choix déterminant. La zone d'activité quotidienne des busards sur leur site d'hivernage initial s'est élevée en moyenne à 28,6 km^2. Ils y ont volé en moyenne 3,86 heures par jour, couvrant 25,1 km. Les valeurs obtenues sur les sites d'hivernage intermédiaires sont proches, avec respectivement 25,7 km^2, 3,93 heures de vol par jour et une distance parcourue de 25,8 km. Sur le dernier site en revanche, où ils ont séjourné le plus longtemps, les busards ont couvert une plus grande surface (51,2 km^2), volé plus longtemps par jour (4,71 heures) et parcouru de plus grandes distances (33,1 km). Cela semble indiquer qu'à cette époque de l'année, les conditions de vie ont été plus difficiles (plus de vols effectués et sur de plus longues distances). Lors des années relativement sèches, les busards ont parcouru plus de kilomètres par jour dans la même zone que lors des années plus humides et verdoyantes. Et surtout, ils ont adapté leur calendrier : lors des années sèches, les oiseaux sont restés moins longtemps dans leur première zone et ont rejoint plus tôt la suivante. Et lors des années plus humides, les oiseaux sont arrivés plus tôt dans leur dernière zone. Cette étude nous permet de conclure que la stratégie d'itinérance des Busards cendrés entre des sites auxquels ils sont fidèles comporte une composante spatiale figée (fidélité aux sites) et une composante temporelle flexible (durée d'utilisation variable des sites). Cette itinérance entre des sites connus constitue donc la stratégie adoptée par le Busard cendré pour faire face aux fluctuations annuelles de la disponibilité alimentaire. L'utilisation d'émetteurs suivis par satellite nous a permis de mieux comprendre plus précisément comment celle-ci fonctionne, mais également d'observer que chaque individu l'applique de façon très personnelle.

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Experimental food supplementation at African wintering sites allows for earlier and faster fuelling and reveals large flexibility in spring migration departure in Pied Flycatchers

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By travelling vast distances, migratory birds take advantage of earth's seasonality. Afro-Palearctic migrants can profit from lush spring conditions in temperate regions for chick rearing, but must also gain sufficient energy reserves to cross the Sahara. Rainfall during the dry season in Africa may influence the food available to birds to accumulate reserves. Conflicts of interests in resource exploitation at locations thousands of kilometres apart may occur if migrants encounter poor food conditions during these migratory preparations. Studying how wild birds adjust their fuelling and migration decisions to dynamic environments allows us to understand how flexible migrants can be, which is particularly important in an era of rapid change. We performed supplemental feeding prior to migration in individual Pied Flycatcher *Ficedula hypoleuca* wintering territories in Ivory Coast and remotely monitored their body mass change until they started their spring migration flight over the Sahara. We tested how access to extra food causally affects fuelling, departure mass and departure date. Seasonal fluctuations in natural arthropod availability prior to migration were monitored in two years, to explore how natural resource dynamics alters fuel accumulation. Birds that fully accessed extra food in March–April put on weight earlier and faster than birds without extra food supply, and departed 12 days earlier. Birds accumulated fuel loads that were higher than required for the Sahara-crossing, regardless of their access to extra food. Fuelling rates fluctuated in synchrony with natural conditions, as non-supplemented birds achieved the highest body mass gains at the time that natural arthropod availability peaked in the study area. Fuelling rates were lower in 2020, i.e. the year when the first rains after the dry season started late, than in 2019. Our study showed that Pied Flycatchers modulated fuelling rates – but not departure fuel loads – to food dynamics in West Africa, causing flexibility in the timing of departure. This strategy probably enhances a safe Sahara crossing, but may limit the possibilities of migrants to anticipate advancing spring conditions at breeding sites.

Key words: pre-migratory fattening, seasonal interactions, food availability, climate warming, geolocator, non-breeding season, migration timing, annual cycle adaptation, ecological barrier, field experiment, Sub-Saharan Africa

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Migration behaviour is widespread across bird taxa and is considered an adaptation to exploit seasonality in resource abundance (Alerstam *et al.* 2003). It is still poorly known how annual-cycle decisions of migratory birds are shaped by seasonality within their tropical overwintering sites. Yet, most birds spend much of the year in the Tropics, where they prepare for their return journey to their temperate breeding grounds. Investigating how migrants respond to variability in tropical wintering resources is important to understand observed population declines in Afro-Palearctic birds and human-induced changes in both Africa and Europe (Both *et al.* 2006, 2010, Møller *et al.* 2008, Ockendon *et al.* 2012, Sanderson *et al.* 2006, Vickery *et al.* 2014). Insight into the ways in which migrants adjust their behaviours to tropical non-breeding resources can reveal critical constraints and pathways that determine how animals adjust to changes in Africa and at their breeding grounds.

A fundamental question is how migrants cope with seasonal dynamics in the tropics in order to optimize spring migration decisions and to be able to exploit food peaks during chick rearing. In Africa, seasonal dynamics is strongly linked to the annual arrival and retreat of the intertropical convergence zone that drives alternations between wet and dry seasons when moving from S(E) to N(W) and back again (Beresford *et al.* 2019). Decades ago, Moreau (1972) acknowledged how paradoxical it was that millions of Palearctic migrants choose to stay in Africa, where they experience seemingly deteriorating ecological conditions of the dry season during their stay. Although they arrive in lush and green conditions, they prepare their migration and leave before the start of the new rainy season.

Some species show migratory movements that seem to follow seasonal changes in vegetation greenness, which may possibly allow birds to circumvent resource limitation (Salewski *et al.* 2002a, Thorup *et al.* 2017). Yet, others remain in one area (Salewski 1999) or leave territories in late winter to fuel elsewhere (Risely *et al.* 2015). At locations where birds remain site-faithful over long periods and prepare their spring flights (Bayly *et al.* 2012, Ouwehand & Both 2016), birds must cope with the local conditions and dynamics. Birds that start migrating before the first rains may experience food shortage during the period when they fatten up for their energetically demanding flight across the Sahara, as was found for Montagu's Harriers *Circus pygargus* wintering in the Sahel (e.g. Schlaich *et al.* 2016). Species that start this barrier crossing later, especially when staying further south in more humid zones in West Africa, may take advantage of the onset of the upcoming rainy season, which triggers regreening of the environment and (presumably) increases food availability.

Correlational evidence suggests that wetter/greener conditions in late winter promote earlier timing in some Afro-Palearctic migrants resulting in earlier arrival or higher fitness (e.g. Balbontin *et al.* 2009, Both 2010, Finch *et al.* 2014, Goodenough *et al.* 2017, Robson & Barriocanal 2011). However, coarse environmental indices generally applied in correlative studies poorly and sometimes erroneously represent dynamics of food resources to which migrants are exposed (Beresford *et al.* 2019, Haest *et al.* 2020). Empirical and experimental studies are therefore needed to demonstrate the underlying pathways.

There are currently no studies on the causal links between food dynamics at tropical non-breeding sites and migration decisions in Afro-Palearctic migrants, but such studies are available for the Neotropical bird migration system. Poor rainfall conditions were found to delay the spring migration of individual birds in habitats where arthropod resources steeply declined, and this subsequently impacted fitness later in the annual cycle (Cooper *et al.* 2015, Marra *et al.* 1998, Studds & Marra 2007, 2011). Experimental reductions in late winter food led to poorer flight muscle condition, which was thought to be responsible for delayed departure (Cooper *et al.* 2015); however, since repeated measures of individuals during fuelling were not collected, the effect of food supply on pre-migration fattening could not be formally examined. It is unknown whether Afro-Palearctic migrants adjust their migration decisions in similar ways. The seasonal dynamics and ecological barriers unique to the Afro-Palearctic flyway may have resulted in different (hierarchy of) adaptations in the annual cycle.

Empirical data on how individual birds adjust pre-migration fuelling to conditions at their tropical wintering sites are rare (Bayly *et al.* 2020). Fuelling decisions during migration are much better documented (e.g. Schmaljohann & Eikenaar 2017), and indicate that food availability and body reserves affect migrants' decisions on when and where to replenish energy. The energetically demanding period of fuel accumulation makes up a large part of the whole spring migration process (Lindström *et al.* 2019). We expect that conditions during the pre-migration phase is a key factor in determining the outcome of barrier crossings and early arrival at breeding sites, especially for species that accumulate large fuel stores at their tropical overwintering sites (Alerstam 2011, Lindström *et al.* 2019).

We investigated the impact of food availability during the pre-migration period on fuelling and spring departure in European Pied Flycatchers *Ficedula hypoleuca*, an insectivorous songbird that overwinters in humid savanna in West Africa. This species has become a model system in organismal responses to climate change at the breeding grounds (e.g. Both & Visser 2001, Møller *et al.* 2010), but the phenological relations at their African wintering sites are poorly understood. Pied Flycatchers defend territories in winter (Salewski *et al.* 2000, 2002a), where they prepare for the long non-stop trans-Saharan flight at the end of the African dry season (Ouwehand 2016, Ouwehand & Both 2016). This allows us to experimentally test the causality between food dynamics and body mass increase, departure mass and departure date, by food supplementing free-living birds. Furthermore, we explore how natural fluctuations in arthropod resources alter fuelling of birds in two consecutive years, to provide insight into the extent and scale that food dynamics influence fuel accumulation and departure decisions under natural circumstances.

The arrival of Pied Flycatchers on breeding grounds is largely explained by departure date from wintering grounds (Ouwehand & Both 2017), and food availability in Africa may thereby potentially have a large impact on safe and timely migrations. Although Pied Flycatchers winter in the humid savanna zone in Sub-Saharan Africa, where they may profit from the onset of the first rainfall at the end of the dry season, we expect that birds will experience food shortage in dry years (in line with Both 2010) or when rains start late. Moreover, flycatchers have been shown to gain a selective advantage when laying early (Both & Visser 2001, Helm *et al.* 2019), and may therefore need to trade-off pre-migration fuelling and early arrival at their breeding sites. Departing with low reserves may entail large survival costs when crossing ecological barriers, while waiting for improved food conditions with the onset of the upcoming rainy season may delay migration and entail reproductive costs.

We hypothesize that improved food conditions during the pre-migration period influences the migration decisions of birds, by either allowing them to fuel and/or depart earlier, or, to do so with higher fuel stores (using departure mass as proxy). We expect that responses of non-supplemented birds to natural resource fluctuations mimic experimentally induced fluctuations, and impact birds especially in dry years or when rains are late and arthropod availability during fuelling is probably low. Fuelling and departure decisions may be further affected by age- and sex-specific differences in timing, experience or competitive ability, with potentially earlier timing in older birds and males, and/or a higher departure mass.

METHODS

Study system and general field methods

The European Pied Flycatcher (hereafter, Pied Flycatcher or flycatcher) is an insectivorous passerine that breeds in temperate and boreal forests in Eurasia, and occupies non-breeding residency sites (hereafter, wintering sites) in Sub-Saharan West Africa from September–March/April (Bell *et al.* 2022, Lundberg & Alatalo 1992, Ouwehand & Both 2017). Pied Flycatchers are generally considered to be site-faithful to wintering territories (Salewski *et al.* 2000, 2002a). In their African wintering sites, flycatchers undergo a pre-breeding moult, starting in February (Jenni & Winkler 1994, Salewski *et al.* 2004), and fatten-up prior to spring migration (Ouwehand & Both 2016, Salewski 1999). We studied Pied Flycatchers and ecological conditions in north-east Ivory Coast, in the centre of this species' range (Dowsett 2010), during the second half of their non-breeding season (i.e. from 7 December 2018 to 9 January 2019, from 28 February to 26 April 2019 and from 4 February to 15 April 2020). We followed the ethical standards for animal welfare as required in The Netherlands (e.g. Ouwehand & Both 2017) for data collection and sampling. No separate approval from animal experiments committee was required, but practices were covered by the permit provided by the Office Ivoirien des Parcs et Réserves.

The study site of approximately 1 km^2 is situated in close proximity to the Comoé River and the ecological research station in the southern part of Comoé National Park (8°45.875'N, 3°47.189'W; Figure S1), within the Guinean-Sudanian savanna zone. This part of the NP has high flycatcher densities and consists of a mixture of humid woodland, dry forests patches, tree and bush savanna and gallery forest. The climate is characterised by a distinct dry and rainy season, with an average annual amount of rainfall of c. 1000 mm. Most rainfall occurs between May and October, while drought conditions prevail from November until March (Figure S2).

Pied Flycatchers were caught using baited spring traps or 1–8 mist nets (individual length 3–6 m) with and without playback from 5:30–12:00 (sometimes 15:30–18:30). Individuals were fitted with an EURING inscription ring and one colour ring to improve recognition of birds based on an individuals' pre-breeding plumage characteristics (following Both *et al.* 2016).

Only one plastic or aluminium colour ring was placed respectively on top of the inscription ring (preventing direct foot contact with plastic) or on the opposite leg (preventing malformation of soft aluminium) to reduce the risk of leg problems (Pierce *et al.* 2007). Birds were measured (tarsus, wing length, p3), weighted (accuracy 0.1 g), aged (first winter or older) and sexed by plumage characteristics, and/or a blood sample taken for sexing (in case of unambiguous plumage; following Ouwehand 2016). To confirm that birds indeed departed directly on migration after fuelling in our study site, we mounted tracking devices with Rappole-Tipton leg-loop harness of elastane, using an Intigeo geolocator (n = 17 in 2019, n = 7 in 2020) with a 7-mm long light-stalk (P30Z11-7-Dip of Migrate technology, mass: 0.42 g, incl. harness) or solar-powered radio transmitter (n = 1 in 2020; LifeTag of Cellular Tracking Technologies; weight; 0.57 g incl. harness).

Experimental set-up

Birds were first habituated to food bowls (diameter: 12 cm, depth: 3 cm) from 7 December 2018 to 9 January 2019 and from 28 February to 14 March 2019 (Photo 1D-E). Bowls were pinned at c. 0.1 m high into the ground at a location regularly visited by a bird and provided with 3 (c. 0.35 g) Mealworms *Tenebrio molitor* a day. After habituation, birds were assigned to an experimental treatment and provided with either 4 g of living Mealworms per day, or 3 Mealworms (c. 0.35 g) per day. The latter was the minimum to still attract birds to bowls for weighing and is hereafter referred to as birds without additional food. Since we aimed to alter food conditions during the fuelling phase, the experimental treatment started by 16 March until birds departed, since catching data from earlier years indicated that fuelling started mid to late March (Ouwehand unpubl. data). In spring 2020, all birds received only 3 Mealworms a day (c. 0.35 g), starting on 9 February. Food was always provided during the relatively cool morning period (5:30–11:30) to prevent Mealworms from dying through overheating.

During habituation and weighing sessions, we recorded food bowls by means of a video camera, which allowed us to confirm the identity of birds, and provide additional insight into unintentional food consumption by non-target birds (Figure 1C). Recordings revealed that at three of nine locations the focal bird accessed the food supply of 4 g only moderately, while Mealworms were frequently (c. 50% of recording days) eaten by other bird species instead. Since this likely influenced the effectiveness of the treatment in 30% of our food supplied birds, the three birds that moderately accessed extra food were separated from those that fully accessed the extra food supply and we evaluated the causal effect of food on fuelling and departure by a 3-level factor reflecting the ‘access to additional food’ that birds showed (i.e. no, moderate, full).

Remote body mass measurements

Body mass of individual birds was repeatedly measured using autonomous weight loggers, with an accuracy of 0.1 g (developed by Feldbrugge Prototyping), hereafter called ‘balances’. Measurements in 2019 were taken from 17 March until all birds departed. Measurements in 2020 ranged from 27 February to 15 April, when the COVID pandemic forced termination of fieldwork. Consequently, measurements from 2020 only covered the full fuelling trajectory of one individual that departed before 15 April. The balances consisted of an external weighing platform (diameter: 15 cm) with a food bowl, which was connected to a datalogger with SD memory card in a water-resistant casing (Figure 1). Balances had a measurement range of 0–80 g, with a sampling interval of 90 milliseconds (c. 11 measures per second) which allowed short visits to be measured. Measurements were started when we provided the birds their daily mealworm supply in the food bowl attached to one of the eight (randomly chosen) balances. The very first visit of a bird to the balance within a day reflected therefore the body mass prior to food supplementation on that day, providing a comparable measure of mass changes between days for birds in different treatment groups. After a weighing session stopped, any remaining food was returned to the pinned bowl.

For each weighing session, the birds’ identity and the precise start and end time of visits were annotated. The birds’ body mass was inferred by subtracting the calculated median baseline mass during a 10-s period prior to the visit from the median calculated mass during the visit (i.e. the period in which a bird was stationary on the balance). To guarantee robust measurements we excluded (1) visits where birds dived into the bowl or touched the balance for less than 1 s, (2) measurements that were inconsistent within visits, and (3) weighing sessions with unstable baseline measurements. The latter was common in three specific balances in 2019, and these data and devices were removed from the study (causing data gaps at the start of some fuelling trajectories, e.g. bird */O). If a bird carried a tag, its body mass was corrected accordingly. The remaining data were used to construct individuals’ fuelling trajectories.

Photo 1. To measure fluctuations in natural insect availability during the period that birds prepare their migration, we repeatedly monitored arthropods (A–C) at fixed locations using one malaise trap and three pitfalls to target flying and ground-dwelling insects. (A) Malaise trap at point 3-N on 5 April 2019. (B) One pitfall in the front with a cover to protect it against rain and Wender emptying the pitfalls on 10 March 2018 at point 1-S in a forest island (points refer to map locations in Figure S1). (C) After four days of trapping, arthropod yields were collected, sorted and identified. Insect abundance was based on the number of items, while the body length measurement of each trapped item allowed us to estimate insect biomass from length-mass regressions for each taxonomic group. To obtain repeated body mass measurements of birds with autonomous balances (Figure 1C), (D) individuals were first extensively observed (here by Armel and Bronwyn) to find perches and locations that they often used during foraging and resting, and (E) that could provide a suitable spot to place a food bowl for habituation. Prior to the start of the supplementary feeding experiment, as many birds as possible were habituated by providing three mealworms per day in a food bowl in their territory, while a video camera was used to monitor if birds were successfully attracted to the food bowl.

Departure date and departure mass

Within the subset of birds that returned with geolocators in the next year, we investigated if the date a bird was last seen on a balance or food bowl could be used to approximate spring migration date. Raw light data of geolocators was used to infer the onset of Sahara crossing in spring, i.e. using the evening prior to the onset of diurnal flight in these (normally) nocturnal migrants (following Ouwehand & Both 2016). The date that birds started their spring migration across the Sahara was tightly correlated (Figure S3) to the date a bird was last seen on a balance or food bowl, and we therefore used the latter to approximate spring departure date across all birds, hereafter referred to as departure date.

The first measurement on the last day a bird was weighted was used to estimate departure mass. We did not correct for potential body size-related differences in body mass, as body mass has previously been reported to be independent of body size (wing length) in Pied Flycatchers (Kelsey *et al.* 2019). We calculated departure fuel load (fat and protein) and fuel deposition rate (FDR) from respectively departure mass and mass changes relative to 9.3 g, which is the structural body mass of living Pied Flycatchers without visible subcutaneous fat stores and with breast muscle score 0 (following Salewski *et al.* 2010)

$$\text{departure fuel load}_i = \text{(departure body mass}_i \text{ (g)} - \text{structural body mass}_i \text{ (g))} / \text{structural body mass}_i \text{ (g)} \quad (1)$$

$$\text{fuel deposition rate}_i \text{ (1/d)} = \text{mass change between two consecutive days (g)} / \text{structural body mass}_i \text{ (g)} \quad (2)$$

Arthropod sampling

We sampled arthropods repeatedly (trapping duration of 4 days per round) to provide a proxy of natural fluctuations in food resources for flycatchers during the pre-migration period (Photo 1A-C). Sampling locations covered a gradient from forest interior to open savanna inhabited by Pied Flycatchers (Figure S1). In 2019, eight locations were continuously sampled during March–April. The four northern locations (Figure S1) were resampled in 2020, when sampling occurred once every eight days. At each location, one malaise trap and three pitfall traps were used to estimate abundance and biomass (expressed per 96 h of trapping) of respectively flying and ground-dwelling arthropods. The yield of three pitfalls were combined into a single pitfall arthropod sample. Malaise traps were 150 cm long and 120 cm high with one standard tube, and an additional tube and extra bottle added to the collection circuit to improve effectiveness. Pitfalls consisted of plastic cups (diameter: 7.8 cm, depth: 11.3 cm, 5 m apart) with a cover to prevent rain from entering (petri-dish on three wooden stick). Arthropod samples were collected using a 1-mm sieve. Specimen were stored in 70–96% ethanol in the fridge until further processing. After collection malaise traps and pitfalls were (re-)filled with respectively ethanol and cooling liquid.

Each sampled specimen with a body length of at least 3 mm (from abdomen to head, but excluding antennae, legs and wings) was identified, counted and its body length measured with an accuracy of 1 mm using graph paper. Insecta, Crustacea and Arachnida were mostly identified to order level (exceptions were ticks and mites identified as Arachnida spec., and Formicidae were separated from other Hymenoptera), and specimens in the subphylum Myriapoda to class, using Picker *et al.* (2002). Body length measurements were used to calculate fresh body mass by means of taxonomy-specific regressions provided by Sohlström *et al.* (2018), which allowed us to estimate body mass for more than 99% of our captured arthropods (but did not include mass for scorpions or specimen identified to a higher then required taxonomic level).

Although small arthropods (<3 mm) are very common in the environment (Bibby & Green 1980, Ouwehand 2016), these small items are considered to be underrepresented in the diet of Pied Flycatchers (Marchetti *et al.* 1998). Items larger than 30 mm likely require a longer searching and handling time. We hence only included items within a (presumed) edible and profitable size range in our analysis, to prevent masking of trends in potential prey abundance and biomass by respectively highly abundant small items or heavy larger items. Such prey are probably rarely taken except when slender or soft-bodied like Lepidoptera, Myriapoda and Odonata (for which we excluded specimens larger than 40 mm). Regarding bulky arthropods with hard body parts, we excluded specimens with a body length exceeding 30 mm in Orthoptera and 20 mm in Coleoptera, Hemiptera, Isopoda, Arachnida, Hymenoptera, Diptera and cockroaches.

Some samples were affected by ant raids, notably red driver ant *Dorylus* sp., which may have masked trends in total arthropod abundance and biomass. Samples (n = 5) in which more than 100 ants in malaise sampling or in one (pooled) pitfall sample occurred were therefore excluded.

Statistical methods

Two linear models (LMs) were fitted to estimate the causal effects of ‘access to additional food’ in 2019 (3-levels: ‘no’, ‘moderate’, ‘full’) directly on (1) the date at which birds departed from our study area (date fitted as April day: 1 = 1 April), and (2) body mass at departure (g). Both LMs included fixed effects for sex and age class. A similar LM tested if treatment groups (i.e. ‘access to additional food’) showed initial differences in body mass before fuelling and experimental treatments started, and included fixed effects for sex and age class. For this purpose, we used the most recent (balance or catching) mass measurement of birds before 6 March, which was the date when the earliest bird in our population showed considerable gains in body mass.

Although all birds were expected to gain mass and depart, the process of fuel accumulation in the wild may show strong non-linearity, and may vary within and between individuals. To investigate this non-linear process of fuel accumulation, we used hierarchical additive models (HGAMs) on natural log-transformed body mass changes over the season in relation to different factors that may contribute to variation in fuelling trajectories, while the shape of nonlinear functions are allowed to vary between different grouping levels without making assumptions about the shape of these patterns (Pedersen *et al.* 2018, Wood 2017). Each HGAM was fitted with the ‘mgcv’ package in R using REML estimation (Wood 2011). First, we studied the causal effect of food on fuelling using the experimental setup in 2019 with an HGAM that included a general smooth for Julian day (1 = 1 January, hereafter ‘day’), factor-smooth interactions and intercepts for access to ‘additional food’ (levels: no, moderate or full), ‘age’ (first winter or older) and ‘sex’ (male or female), and individual-level random smooths to account for repeated measures and some additional degree of individuality in fuelling. Second, we investigated annual differences in fuelling between birds that received no additional food (beyond the 0.35 g), and thus most closely resembled natural conditions. The HGAM included a general smooth for ‘day’, factor-smooths interactions and intercepts for ‘year’, ‘age’ and ‘sex’, and individual-level random effects smooths. The maximum number of basis functions in both HGAMs were set to $k = 5$ to restrict the potential wiggliness of each smooth term. For model selection, we relied on an additional penalty to each term so that effects could be penalized to zero and which can effectively remove terms from the model (select = TRUE; Marra & Wood 2011). How well the HGAM captured patterns in the data is described by the total % deviance explained. Whether a smooth term significantly contributed to the model was inferred from the effective degrees of freedom (EDF); i.e. terms with EDF = c. 1 or <1 are equivalent to being linear terms, while a further increase in EDF indicates that more ‘wiggliness’ of terms is effective to improve the model. For each effective term, we discuss group-level factor differences using visual inspection of the whole fuelling trajectory and/or differences in smooth complexity (i.e. wiggliness).

To provide further insight into processes driving day-to-day modulations in fuelling rates, we fitted a third HGAM to the full dataset, optimized to best describe fine temporal scale fluctuations in body masses seen within individual trajectories. The HGAM included a general smooth for ‘day’, factor-smooths interactions and intercepts for ‘additional food’, ‘year’, ‘age’ and ‘sex’ (with $k = 5$), and ‘individual-by-year’ random effects smooths (with $k = 14$ to assure maximum flexibility within individual curves). High wiggliness in this model has higher potential to describe body mass changes even in individuals with irregular measures and strong inter-annual variation, and allow for stronger deviations of shared trends from other factor smooths. From the model predictions, we estimated daily mass changes (g/day) for each individual per year over the date range for which we had raw data measurements for that specific bird. We excluded one bird (individual */Y2) in subsequent analyses for which raw data measures were more than 25 days apart and for which HGAM predictions showed large uncertainty (dashed line in Figure S4B). A linear mixed model (LMM) was fitted to investigate if access to additional food (3-levels: ‘no’, ‘moderate’, ‘full’) created consistent differences in fuelling rates (i.e. HGAM-derived daily mass changes in g/day) of birds in 2019, and included fixed effects for ‘sex’ and ‘age’, and random intercepts for ‘individual’. Another LMM tested for year differences in daily mass changes in birds without additional food during the period when data were collected in both years (i.e. day 76–105), and included fixed effects for ‘sex’ and ‘age’, and ‘individual-within-year’ as random intercept.

Furthermore, we investigated if natural fluctuations in arthropod availability in the study site could explain fluctuations in fuelling rates in birds without additional food. For this we only considered daily body mass changes after 5 March, which represented the moment that the earliest bird in our population showed considerable gains in body mass. To match the 4-day arthropod sampling duration with HGAM-derived body mass change estimates, we first calculated a mean mass change per bird over each 4-day sampling period. Since mass change estimates did not always perfectly overlap with 4-day periods, i.e. periods can be shorter at the end and start of a fuelling trajectory, we only calculated mass means when the overlap with an arthropod sampling period was at least two days. To subsequently establish if arthropods sampled across the whole study sites could explain the fuelling rate at the flycatcher population level, we fitted four separate LMs to establish per arthropod proxy how well the mean yield across all sampling locations explained the (population) mean mass change across birds without extra food supply.

RESULTS

In 2019 we measured body mass of 17 individuals repeatedly until the birds had departed (8 females, 9 males, 12 first winter, 5 older birds). All 17 birds took part in a field experiment in which birds differed in their access to extra food supplements; i.e. 6 birds ‘full’, 3 ‘moderate’ and 8 ’no’ access to extra food supply. In 2020 eight birds, which received no additional food, were repeatedly measured for part of the fuelling period (3 females, 5 males, 2 first winter, 6 older birds). Four of the latter individuals had also been measured in 2019 (Table S1). COVID-19 restrictions in 2020 forced measurements to end on 15 April, before most birds departed on migration.

Birds that fully accessed extra food supply started fuelling earlier and increased body mass faster over time (Figure 1B, Table S3) compared to birds that received no additional food. Pied Flycatchers without access to additional food supply departed on average on 13 April, which was 12 days later than birds with full access to the extra food supply ($F_{2,12} = 17.75$, $P < 0.001$; Figure 1A, Table S2). If we consider the average departure date as the end of fuelling, and the start of the experiment (16 March) as the beginning, the fuelling duration of birds that only accessed natural resources was 29 days, compared to 17 days in birds with full access to the extra food supply. At locations where access to supplemented food was moderate and where (unintentional) consumption by (larger) heterospecific birds occurred, Pied Flycatchers showed

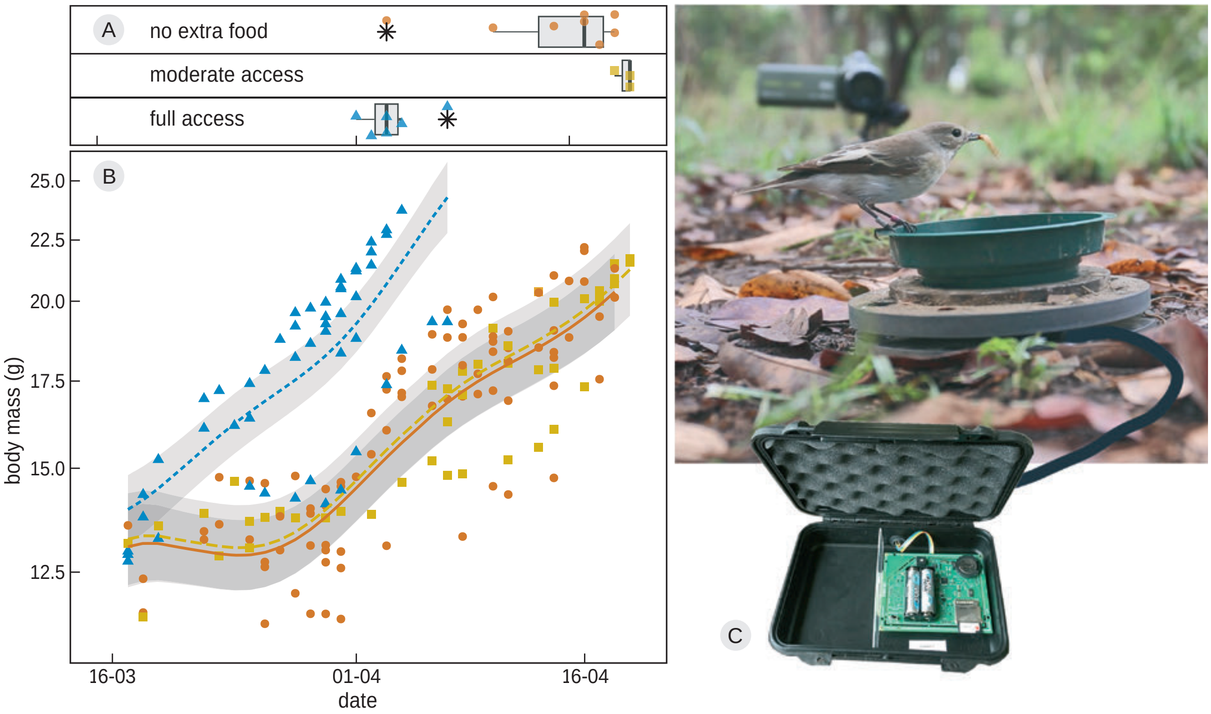

Figure 1. (A) Spring departure decisions and (B) fuelling trajectories in 2019 in Pied Flycatchers wintering in Ivory Coast in relation to access to experimental food supplementation with Mealworms. After birds were habituated to visit a food bowl, repeated body mass measures in the field were obtained by luring birds to a food bowl connected to an autonomous balance (C). Boxplots and (jittered) raw data in A show approximated spring departure dates of birds (incl. one bird of 13 g; i.e. */red dot) based on the date a bird was last seen at a balance (see Figure S3). Each point in B refers to the body mass in grams of a bird on a specific date. Lines and confidence intervals show the predicted fuelling trajectories per group (from models in Table S3).

fuelling trajectories that largely overlapped with birds that received no additional food. A positive effect of full access to food supplementation was also apparent within individuals (Figure 2), and allowed birds to achieve higher body mass at earlier dates than they did in the next year when no additional food was provided.

The extra food supply did not significantly affect the mass of birds when they departed for spring migration ($F_{2,12}$ = 0.8, P = 0.46; Table S4), and ranged from 17.5 to 23.6 g (i.e. excluding one outlier of a 13-g bird; Figure S5A). Nor did body mass of birds in different treatment groups differ significantly prior to fuelling ($F_{2,9}$ = 0.13, P = 0.88; Table S5, Figure S5A). Assuming the same structural body mass across Pied Flycatchers, the recorded mass range of 17.5–23.6 g corresponded to a fuel load of 88–154% of structural body mass. Birds equipped and returning with geolocators reached body masses of 20.2–22.6 g at the day (or day before) they start crossing the Sahara, corresponding to fuel loads of 117–143% of structural body mass. These results confirm that Pied Flycatchers commonly accumulate fuel stores at their wintering territories from where they start to cross the Sahara directly (see also Figure S3 and Ouwehand & Both 2016, 2017). However, we consider it likely that the early 'departing' individual without extra food in Figure 1A, which had a final mass of only 13 g, moved to another fuelling site or died, rather than having started migration, as this reflects energy stores that doesn't allow crossing the Sahara without refuelling.

Fuelling trajectories of non-supplemented birds varied clearly between years (Table S6), suggesting that birds flexibly adjusted fuelling prior to spring migration to perceived natural conditions in these years. In 2019 birds generally started to gain mass later but did so more rapidly than in 2020 (Figure 2, Figure S6). By comparing the (incomplete) predicted fuelling trajectories of flycatchers in 2020 with those in the previous year (Figure S6), we find that average body mass during the last observation date (which for most birds was not the departure date) in 2020 was already achieved a week earlier in 2019. The within-individual patterns recorded in four birds (Figure 2) illustrate that flexibility can result from various factors. For three of

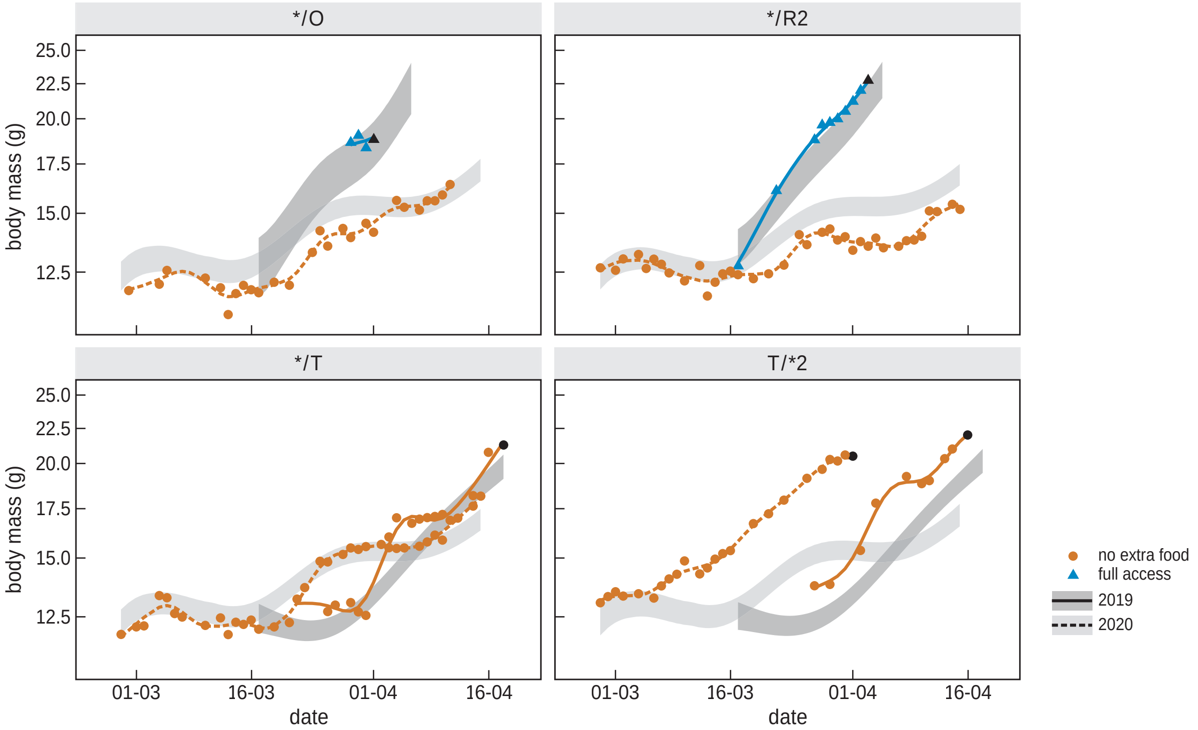

Figure 2. Body mass measurements over time in four birds that were repeatedly measured in 2019 and 2020. Birds differed in their access to experimental food supplementation in 2019. Points reflect body mass in grams and the associated lines show the predicted fuelling trajectories of individual birds (see Figure S4 for trajectories of other individuals). Black symbols indicate if birds were measured until departure (n = 1 in 2020, all in 2019). Grey ribbons depict confidence intervals of the predicted (population) trajectories in the age class, sex, year and experimental group to which an individual belonged (i.e. using model outputs of Table S3 for 'full access' and Table S6 for 'no extra food').

these birds (individuals */T, */O, */R2) the observed within-individual variation in fuelling seem to roughly be the same as the predicted fuelling trends arising from year and food treatment differences (Figure 1, Figure S6). In contrast, female T/*2 in 2020 clearly deviated from general trends (Figure 2); she steeply increased mass early in the season and was the first of all flycatchers to depart, in contrast to the other birds without access to food supplementation that fuelled slower and departed later, especially in 2020 (Figure S6).

We found no consistent sex and age differences in departure dates (Table S2), fuelling trajectories (Table S3, S6–S7, Figure S7), and mass prior to fuelling and mass at departure (Table S4–S5, Figure S5B–C).

We observed synchronous daily changes in body mass across birds without access to additional food (red lines in Figure 3A). Fuelling rates showed striking peaks in 2019 and daily rates were on average higher (0.28 ± 0.03 g/d, i.e. FDR of c. 3%) than during the same 29-day period in 2020 (0.13 ± 0.04 g/d, i.e. FDR c. 1%; year effect: $\chi^2_1 = 8.74$, $P < 0.005$). Synchronous mass gains (Figure 3A) in birds without extra food were particularly visible in 2019, and coincided with temporal peaks in 4-day arthropod sampling yields (Figure 3B). Under natural circumstances birds achieved higher fuelling rates when abundance and biomass of arthropods in our study area was higher (ground arthropods: biomass: $F_{1,11} = 17.1$, $P < 0.005$, $r^2 = 0.57$, abundance: $F_{1,11} = 3.9$, $P = 0.073$, $r^2 = 0.20$; flying arthropods: biomass: $F_{1,11} = 5.1$, $P < 0.05$, $r^2 = 0.26$, abundance: $F_{1,11} = 8.2$, $P < 0.05$, $r^2 = 0.37$; Figure 4).

The maximum mass gain observed in our study site was 1.28 ± 0.04 g/d (i.e. FDR c. 14%) in a bird in 2019 that had moderate access to additional food, at a time that most birds had already departed on migration. Fuelling rates larger than 0.8 g/d (i.e. FDR > 9%) were only recorded in 2019, and mostly after the majority of birds with full access to extra food had already departed (Figure 3A). Food supplementation in 2019 allowed birds to overcome low availability in natural arthropod resources, especially at the start of fuelling

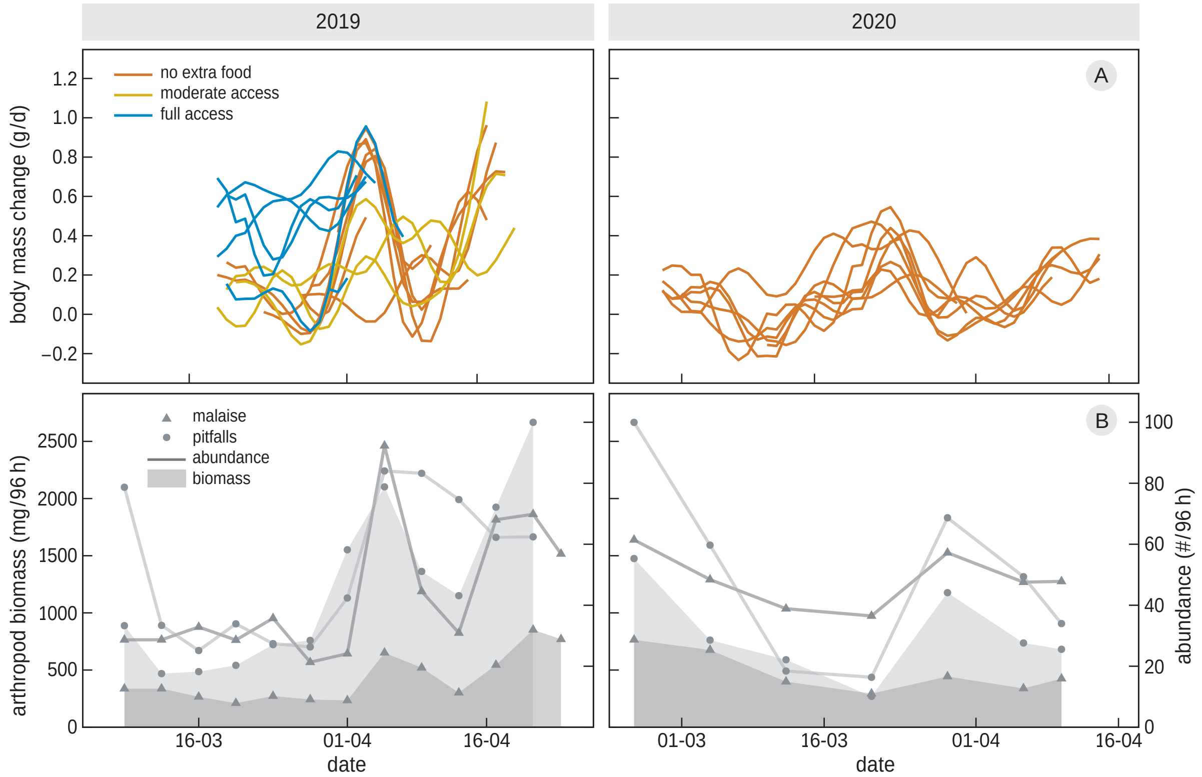

Figure 3. Seasonal fluctuations in daily body mass change of Pied Flycatchers in 2019 and 2020. Daily body mass change was calculated using the model predictions at individual level within seasons (Table S7, Figure S4). B shows fluctuations in natural arthropod resources during the same seasons. Arthropod yields reflect mean biomass in mg (shaded area) and mean abundance (lines) per 4-day sampling period, measured with malaise and pitfall traps to target respect. flying and ground-dwelling arthropods in eight (2019) or four (2020) sampling locations in the study site (see Figure S1, S8).

(blue lines in Figure 3A). This led to overall higher fuelling rates in birds with full access to additional food (0.46 ± 0.05 g/d, i.e. FDR around 5% of structural body mass) compared to birds with no or moderate access to additional food (respectively, 0.30 ± 0.03 g/d and 0.25 ± 0.04 g/d; FDR of c. 3%; $\chi^2_2 = 9.58$, $P < 0.01$).

DISCUSSION

How ecological conditions determine departure of long-distance migratory birds from African overwintering areas is poorly understood. We showed that Pied Flycatchers at their African wintering site, when preparing for a non-stop trans-Saharan flight, were strongly affected by food availability. Fuelling rates of flycatchers correlated positively with within-season fluctuations of arthropod abundance and biomass. Food supplementation revealed that effects of food availability on fuelling and timing of departure are causal. Individuals with full access to food supplements increased their body mass earlier in the season and departed 12 days earlier than non-supplemented birds. The fuelling trajectories of individuals recorded in two consecutive years revealed large individual flexibility in fuelling under different (food) conditions.

These findings confirm our hypothesis that food availability in Africa prior to migration modifies timing of spring departure in Afro-Palearctic migrants, as was previously described in Neotropical migrants (Cooper *et al.* 2015, Studds & Marra 2007, 2011). The ability of individuals to modify innate time schedules to ecological conditions may result from programmed flexibility (Åkesson & Helm 2020) that allows the fine-tuning of endogenous time keeping mechanisms. Although rigid endogenous rhythms and local photoperiodic conditions at non-breeding sites (Gwinner 1989, 1996) will determine when birds can start migratory preparations, the observed departure schedules may thus show considerable flexibility. When the potential time window over which fuelling can occur is large, not only the duration and rates of fuelling may be variable, as recorded for some Palearctic migrants (Bayly *et al.* 2012), but also the observed onset of fuelling can vary (this study). This may explain why males and females

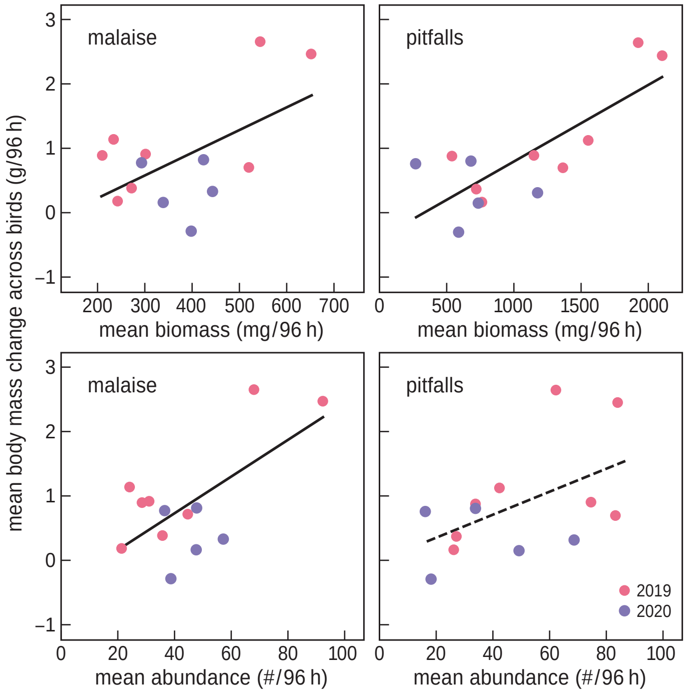

Figure 4. Fuelling rates of Pied Flycatchers at population level in relation to four proxies of natural food availability during migration preparations. The mean fuelling rate of each bird during a 4-day arthropod sampling period was first estimated, and included only birds without food supplementation and mass changes after 5 March (i.e. the earliest observed instance of fuelling), before expressing fuelling rates at population level. Each symbol shows the mean fuelling rate across birds during a 4-day arthropod sampling period. Lines indicate trends (dashed: $P = 0.05–0.10$) or significant (solid: $P < 0.05$) relationships from LMs.

showed – in contrast to our expectations – similar fuelling and departure decisions, despite previous findings that male Pied Flycatchers migrate approximately one or two weeks ahead of females in spring (Bell *et al.* 2022, Both *et al.* 2016, Ouwehand & Both 2017).

We found that effects of arthropod availability on fuelling rates generally acted throughout the (shared) local environment, as indicated by synchronous fuelling responses of site-faithful Pied Flycatchers across different territories. This resulted in stronger modulations in the fuelling rates in birds without access to extra food in comparison to the more constant and overall higher fuelling rates in birds that fully accessed food supplements. Differences in fuelling rates between experimental groups were most pronounced early in the season (Figure 3A). Later in the season when arthropod resources peaked in our study area (Figure 3B), birds without extra food accumulated fuel at faster rates (Figure 3A) than typically seen in birds with full access to 4 grams of Mealworms per day (respectively FDR around 9% vs. c. 5% of structural body mass). It seems likely that our food supplementation did not create *ab libitum* food conditions, although it did help birds to start earlier with fuelling. The shortest achievable fuelling duration is estimated at c. 10 days when circumstances were really good (i.e. assuming FDR of 9% and departure mass of 17.5 g). On the other hand, fuelling duration can be considerably longer when conditions are poor.

Fuelling was especially slow in the study year 2020, when rainfall started late. The period Jan–April 2020 was dryer than in 2019, with later onset of the rainy season, despite relatively large amounts of rainfall at the start of the dry season in October/November (Figure S2). The fact that fuelling of most birds was slower in 2020 than in 2019, suggests that particularly the onset and amount of rain in the second half of the non-breeding season in Africa (i.e. Jan–April) may be critical in determining fuelling conditions. Synchronous and steep peaks in arthropod yields and fuelling rates were very apparent in 2019 (Figure 3 and 4). Non-continuous (and less extensive) arthropod sampling in 2020 allowed only a partial description of arthropod fluctuations in 2020, and prevent a formal year comparison over the whole period. Visual inspection suggests less pronounced peaks in 2020, and larger overall arthropod availability in 2019 compared to 2020 during fuelling in the first half of April (Figure 3). Slower fuelling probably also resulted in later departure dates in 2020, as radio tracking in the study area revealed that Pied Flycatchers left the study area mostly in May (Bil *et al.* 2023), which is relatively late compared to previous years when birds departed between early and late April (Ouwehand unpubl. data 2017–2019).

Long-term arthropod and fuelling data are not available to indicate how often migrants modulate fuelling and departure timing to local food conditions at their wintering site, but rainfall data helps to place our findings in a wider perspective. The onset and amount of rainfall in 2019 at the end of the dry season was relatively normal compared to the 5-year averages in the study area (Figure S2), while conditions in 2020 were much dryer than average. Satellite-derived daily rainfall estimates (RFE2 of the U.S. Climate Prediction Centre) from NE Ivory Coast provide a reasonable predictor for the weekly Jan–April rainfall sums at Comoé station (data available for 2015–2020: $\beta = 0.65 \pm 0.11$, $r^2 = 0.24$). This suggests that local rainfall at Comoé station in Jan–April 2019 was also normal when compared to long-term average RFE2 rainfall Jan–April sum (2001–2020) in NE Ivory Coast. However a situation of local drought conditions occurred during Jan–April 2020 at our study site, since plentiful rain only fell at Comoé station during May, while RFE2 values for NE Ivory Coast in 2020 (compared to 2001–2020) indicate relatively wet conditions (elsewhere) during Jan–April. Given that rainfall conditions in 2019 were normal, we expect that birds in this region regularly modulate their departure timing, while even larger effects might be expected in years with late onset of rains such as in 2020.

The fact that local rainfall in 2020 deviated strongly from regional rainfall in NE Ivory Coast during the fuelling period, demonstrates the limitations of using coarse rainfall estimates. This is an even greater issue when using the Sahel rainfall index, a commonly used proxy of rainfall conditions affecting Afro-palearctic migrants. The Sahel rainfall index poorly predicted the annual rainfall sum measured in a weather station located c. 150 km SE of our study site (Bondoukou data available for 1920–2017: unpubl. analysis Zwarts). For example, Jan–April rainfall conditions in NE Ivory Coast were fairly good in the period of the Great Drought in the Sahel, during 1969–1991. Local rainfall conditions also deviated strongly from the Sahel rainfall index in our study years, since 2019 and 2020 are both considered relatively wet years according to the Sahel rainfall index (Figure S50 in Zwarts *et al.* 2023).

An important next step is to quantify more precisely which prey species allow flycatchers to sufficiently increase their body mass, and describe their relation to climatic drivers. Although we found that ground-dwelling and flying arthropod availability predicted fuelling rates, this does not mean that these specific groups are especially important. Pied Flycatchers forage on a wider range of substrates then we sampled (e.g. bark, tree canopies; Salewski *et al.* 2003, Zwarts & Bijlsma 2015). We observed flycatchers exploiting caterpillar outbreaks in freshly (de)foliated tree canopies of *Daniellia olivieri* during our study (Ouwehand unpubl. data). Tree canopy-dwelling arthropods were poorly quantified in our study, but were previously found to become more abundant in the study area when monthly rainfall during the non-breeding season increased (Salewski 1999). Such prey may thus have changed in synchrony with arthropod proxies. On the contrary, arthropod availability also fluctuates at finer spatial scale (Figure S8), and habitats and arthropod groups may differ considerably in their responses to climatic drivers (see also Bil *et al.* 2023). A better knowledge of diet preferences in relation to available resources within and between seasons will improve quantification of food availability for fuelling birds, by concentrating on the most relevant trapping techniques and insect groups.

Birds reached high body masses by the time they left the study site (Figure S5A), and did not need supplemented food *per se* to achieve this. Despite the ability of birds to fine-tune fuelling decisions to food, birds in our study did not use food supplements to reach a higher departure fuel load. When food was plentiful prior to departure, birds achieved higher fuelling rates and reached this threshold more quickly which allowed birds to depart earlier on migration. Birds may wait for suitable weather conditions to start migration (e.g. Deppe *et al.* 2015, Shamoun-Baranes *et al.* 2017), but our birds departed as soon as they had gained large fuel loads (Figure S4). Also, the flycatchers did not slow down fuel accumulation prior to departure (Figure 3A). The proximate mechanisms that determine how feeding conditions regulate decision-making at wintering sites might be similar to those operating during migration (e.g. Alerstam 2011, Biebach 1985, Hedenström 2008, Klinner *et al.* 2020, Schmaljohann & Eikenaar 2017). Klinner *et al.* (2020) proposed a critical 'fuel-threshold' below which the survival probability is higher when staying at the fuelling site and above which departing is the best option to reach the migratory destination in time. Pied Flycatchers probably need a specific fuel-threshold to depart on migration. Our results on flycatchers indicate that a fuel-threshold may correspond to a body mass of at least 17.5 g and a fuel load of 88%. When birds fly non-stop (Ouwehand & Both 2016) at speeds of 50 km/h (Schmaljohann *et al.* 2008), a fuel load of 88% would facilitate a flight of c. 3160 km (assuming 1%/h body mass decrease, following Delingat *et al.* 2008), which is under normal flight conditions more than sufficient to cover the distance of 2250 km over the Sahara.

Given the pressure on birds of arriving earlier to match chick rearing with warming spring conditions (Helm *et al.* 2019), it seems counterintuitive that Pied Flycatchers alter their departure timing in order to achieve a seemingly excessive fuel-load. A potential consequence could be that food shortage prior to departure delays the timing of arrival and breeding, since we previously found that breeding arrival in Dutch Pied Flycatchers was strongly determined by the date birds leave their wintering sites (Ouwehand & Both 2017). Our current study shows that differences in food conditions created large differences in departure, and did so already in a year when local rainfall conditions were normal. This may even imply that fuelling constraints that delay departure and carry over to impact on breeding arrival and laying, can slow down observed adaptation towards earlier migration schedules (Helm *et al.* 2019). Human induced change potentially increases the 'natural' conflict in resource exploitation of migrants that want to travel earlier to track advancing food resources at warming breeding sites. However, we lack sufficient data in our current study to make direct inferences that can support this interpretation about the consequences of later departure for subsequent annual cycle events. Whether poor rainfall conditions cause food constraints and places migrants in jeopardy will depend on a whole series of decisions that individuals make. Each individual makes decisions on wintering site selection, when to (re)fuel, how fast to migrate, and what to do when arriving at the breeding grounds.

Complex ecological interactions at the wintering sites may allow birds to compensate for negative rainfall effects. This may be particularly important because rainfall in the Guinea zone is highly unpredictable across years, as shown by large deviations around the average rainfall sum in Jan–April in NE Ivory Coast (unpubl. analysis Zwarts; Bondoukou data 1920–2017). Our observation of one female flycatcher in 2020 that fuelled and departed exceptionally early, despite slow fuelling seen in other flycatchers that year, nicely illustrate the potential of birds to overcome 'shared' environmental impacts. This may happen if individuals can access natural resources that occur heterogeneously. Our study site is a mosaic of habitats with considerable vegetation heterogeneity in space and time that sedentary Pied Flycatchers selectively use over the course of non-breeding season (Bil *et al.* 2023). Occupying high quality wintering habitats improved the ability of Neotropical songbirds to cope with dry-season conditions, and was especially important for timely departure in years with poor rainfall conditions (Studds & Marra 2011). Previously described earlier breeding and higher fitness in Pied Flycatchers that occupied wintering sites with more mesic isotope profiles (Goodenough *et al.* 2017) may reflect similar small-scale habitat mediating effects. Differences in territory quality or flexibility in how birds make use of spatial-temporal heterogeneity in their home range (Bil *et al.* 2023) may help birds to mitigate effects from the shared environment. This may directly arise from changes in the birds' diet or experienced food availability, or, act indirectly through effects of predation risk, competition or heat stress on foraging behaviour. High quality wintering habitats for flycatchers might be particularly located on the edge of forest and savanna, resulting in high densities of site-faithful flycatchers, from where birds can profit from the different dynamics associated with two different habitats (Figure S8 and Bil *et al.* 2023). Ongoing deforestation in Africa will likely reduce the availability of forests and thereby limit the possibilities of flycatchers to make use of seasonal dynamics, or, mitigate drought effects.

Factors such as habitat quality, predation pressure, competition and health may also exaggerate environmental impacts, or, influence birds in unexpected ways. The latter was apparent in the three Pied Flycatchers in our study that only moderately accessed food supplementation. Video recordings illuminated an unintended effect of food supplementation, where supplies were regularly eaten by larger African bird species. Rather than the anticipate positive effect of food supplementation in the flycatchers' territory, this may have enhanced competition for food or influenced how birds trade-off fuelling decisions.

The flexibility in fuelling behaviour may also be larger than apparent from our results of fuelling in site-faithful individuals. Although Pied Flycatchers are generally considered site-faithful, other wintering strategies reported in flycatchers involve 'floating' (i.e. not having a territory), and habitat-related territory switches (Salewski 1999, Ouwehand unpubl. data). Pied Flycatchers could potentially leave their wintering territories in search of better fuelling locations, albeit this strategy seems relatively rare (Salewski *et al.* 2002b, Smith 1966). Experiments in the Neotropics revealed that free-living territorial songbirds can respond to food shortage by becoming floaters (Cooper *et al.* 2015). Future research is needed to investigate if similar solutions occur in flycatchers and are suitable alternatives to cope with local food limitation in their unpredictable environments, or, that floating and occupying new fuelling sites is the less preferred strategy that involves high costs associated with switching (Cresswell 2014).

Mechanisms underlying the observed fuelling decisions likely evolved in such a way that birds depart at the time that maximizes fitness, presumably by reducing costs of migration and/or to match timing of reproduction with seasonality of food at the breeding site. It is well known that accumulating a fuel surplus enables birds to withstand unpredictable adverse conditions during barrier-crossing, which is especially sensible when risks during migration are high, or when conditions during barrier-crossings are difficult to predict (see Schmaljohann *et al.* 2013). Flexible fuelling decisions – in contrast to rigid time schedules – allow birds to immediately make use of seasonal peaks in food when available to achieve this fuel surplus. Flexible fuelling may even have evolved to allow birds to cope with unpredictable rainfall dynamics during the pre-migration phase in Africa. A potential consequence may be that birds can only leave timely on migration if the food conditions in winter allow them to do so. If suitable conditions for fuelling happen relatively early in the season, birds may not want to risk deteriorating conditions or wait with full fuel loads that are costly to carry. Yet, birds could use any left-over reserves after Sahara-crossing to flexibly adjust their migration pace on their way to the breeding sites (but see Ouwehand & Both 2017). Early departure of these individuals may thus not directly result in arriving too early at the breeding grounds if birds extend staging in southern Europe after crossing the Sahara, where conditions may be more predictable. Late departing birds may invest into continuing their flight directly towards their breeding sites to compensate for a delayed departure. The extent to which birds and populations can take advantage of this plasticity to compensate for delays likely varies and may depend on the phenology in a breeding population, the quality of wintering areas and conditions that birds encounter en route.

If poor fuelling conditions force flycatchers to delay departure and arrive late at the breeding grounds, birds could adjust their breeding decisions. Breeding opportunism has been found in Pied Flycatchers and could include active breeding dispersal strategies to match local resources, skipping breeding when conditions are not suitable (Both *et al.* 2017) or modulating breeding investment according to current conditions. Although breeding opportunism may seem counterintuitive for short-lived songbirds, this could be a viable option for birds like flycatchers that seem to favour fuelling strategies that promote safe migration (rather than early departure) and if the high food surplus at temperate breeding grounds provides good survival prospects.

Describing how migrants choose their environments and investigating the fitness consequences of these choices are thus key elements to better predict the abilities and limits of migrants to cope with ongoing environmental change. Integrated tracking studies of the annual cycle of individual birds are an essential step forward to achieve this. Even so, ground studies in Africa would be a fruitful avenue for future studies on the cost and benefits of different annual cycle strategies that are difficult to measure when studying birds only in breeding populations. Field studies at non-breeding residency areas are still under-represented, and especially so in Afro-Palearctic migrants. Ground studies in Africa provide the ground-truthing needed for interpreting the growing body of data from birds carrying tracking and geolocator devices. Our study highlights the need for such studies, as we found that fuelling and migration decisions in Pied Flycatchers are strongly shaped by local ecological conditions in Africa, which are difficult to describe by coarse rainfall estimates and geolocator devices. Tracking birds is one thing, learning what is going on *in situ* is quite something else.

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Data Accessibility

Data described in this article are available at
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SAMENVATTING

Door over grote afstanden te trekken kunnen vogels de seizoensveranderingen op aarde benutten. Vogels die in Afrika overwinteren maar in Europa broeden, kunnen zo profiteren van een groter maar tijdelijk beschikbaar voedselaanbod in gematigde streken om hun jongen groot te brengen. Om dit te kunnen doen moeten vogels daar op tijd arriveren, maar ook voldoende energiereserves aanleggen voordat ze de Sahara oversteken. Als de voedselomstandigheden in Afrika in het droge seizoen slecht zijn, kan dit leiden tot conflicten tussen deze belangen. Door te onderzoeken hoe vogels deze beslissingen maken in een dynamische en veranderende leefomgeving, kunnen we inzicht krijgen in hoe flexibel trekvogels hun gedrag aanpassen. Hiertoe vingen we Bonte Vliegenvangers *Ficedula hypoleuca* in hun winterterritoria in Ivoorkust en gaven hun een geolocator. Een deel van deze vogels werd experimenteel bijgevoerd, en alle werden tot aan het vertrek herhaaldelijk gewogen op autonome gewichtsloggers. Op die manier hoopten we inzicht te krijgen in het effect van (extra) voedsel voorafgaande aan de voorjaarstrek op het opvetproces, de vertrekdatum en het gewicht waarmee de vogels de voorjaarstrek over de Sahara beginnen. In beide jaren van het onderzoek (2019 en 2020) kwantificeerden we het natuurlijke aanbod van geleedpotigen gedurende de opvetfase, om te onderzoeken hoe de natuurlijke voedseldynamiek het opvetproces van vogels beïnvloedt. De vogels die in maart–april extra voedsel kregen en benutten, begonnen eerder met opvetten en deden dit sneller dan vogels zonder toegang tot extra voedsel, wat resulteerde in 12 dagen eerder vertrek naar het broedgebied. Vogels legden grotere vetreserves aan dan strikt noodzakelijk voor de Sahara-oversteek en dat deden ze onafhankelijk van het experimentele voedselaanbod. Opvetsnelheden van vogels veranderden mee met de natuurlijke omstandigheden binnen en tussen jaren. Vogels zonder extra voedsel bereikten de hoogste gewichtstoename op momenten dat het natuurlijke aanbod van geleedpotigen piekte. De gemiddeld geringere gewichtstoenames in 2020 in vergelijking met 2019 suggereren dat vogels trager opvetten in jaren met late regens. Het laat een grote flexibiliteit zien in de timing van de voorjaarstrek onder invloed van de voedseldynamiek op overwinteringslocaties in West-Afrika die de opvetsnelheid van trekvogels, maar niet hun streefgewicht bepaalt. Deze strategie bevordert waarschijnlijk een veilige oversteek over de Sahara, maar kan de mogelijkheden beperken om (vervroegde) voedselpieken in het broedgebied te blijven benutten.

RÉSUMÉ

En migrant sur de longues distances, les oiseaux mettent à profit l'alternance des saisons sur Terre. Ceux qui hivernent en Afrique et se reproduisent en Europe exploitent l'abondance de nourriture dans les régions tempérées au printemps et en été pour y élever leurs petits. Pour cela, ils doivent y arriver à temps, mais aussi constituer des réserves d'énergie suffisantes avant de traverser le Sahara. Si les conditions alimentaires en Afrique sont mauvaises pendant la saison hivernale qui correspond à la saison sèche au Sahel, ces deux exigences peuvent devenir contradictoires. En étudiant les choix qu'ils effectuent en fonction des changements trophiques survenant dans leurs habitats hivernaux, il est possible de comprendre comment les oiseaux migrateurs adaptent leur comportement. À cette fin, nous avons capturé des Gobemouches noirs *Ficedula hypoleuca* dans leurs territoires hivernaux en Côte d'Ivoire et les avons équipés d'un géolocalisateur. Certains de ces oiseaux ont reçu un complément d'alimentation et tous ont été pesés à plusieurs reprises avec des balances autonomes jusqu'à leur départ en migration. Cette expérience visait à étudier l'effet de la complémentation alimentaire sur le processus d'engraissement, la date de départ et le poids des oiseaux jusqu'au début de la migration prénuptiale à travers le Sahara. Au cours des deux années de l'étude (2019 et 2020), nous avons quantifié l'approvisionnement naturel en

arthropodes pendant la phase d'engraissement prémigratoire afin d'étudier comment la disponibilité alimentaire naturelle affecte ce processus. Les oiseaux qui ont reçu et consommé de la nourriture complémentaire en mars et avril ont commencé à grossir plus tôt et plus rapidement que les oiseaux qui n'y ont pas eu accès. Ils ont débuté leur migration vers les zones de reproduction en moyenne 12 jours plus tôt. Tous les oiseaux ont constitué des réserves de graisses plus importantes que celles strictement nécessaires à la traversée du Sahara et ce, indépendamment du nourrissage complémentaire. Leurs vitesses d'engraissement ont évolué en fonction des conditions trophiques naturelles que ce soit au cours d'une même année et d'une année à l'autre. La prise de poids des oiseaux non complémentés a culminé au moment où l'offre naturelle d'arthropodes a atteint son maximum. Elle a été moindre en 2020 qu'en 2019, ce qui suggère que les oiseaux engraissent plus lentement les années où les pluies sont tardives. L'étude démontre que la disponibilité alimentaire dans les sites d'hivernage en Afrique de l'Ouest détermine le taux d'engraissement des oiseaux migrateurs, mais pas leur poids de départ en migration : elle influence donc fortement le calendrier de la migration printanière. Cette stratégie semble privilégier la sûreté de la traversée du Sahara, au détriment de la capacité à exploiter efficacement les pics d'abondance alimentaire qui surviennent de plus en plus précocement sur les sites de reproduction.

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SUPPLEMENTARY MATERIAL

Table S1. Overview of individual birds (IDs) of which we measured pre-migratory fuelling (by means of body mass increase) at their wintering location in Comoé NP in Ivory Coast, and whether we were able to estimate their departure date by means of the last day a bird was seen on a bowl. Tag type and tag departure indicate how birds were tracked and if a departure date could be obtained from the tag. NA indicates that no data was available for the date a bird was last seen on a bowl, tag departure, or return of birds. Missing data resulted from closure of the field station that prevented collecting these data, tag failure, or birds not returning to the study area (i.e. return = 0).

Year	IDs	Age class	Sex	Food access	Last seen on bowl (1 = 1 April)	Return	Tag departure (1 = 1 April)	Tag type
2019	*/O	older	F	full	1	1	NA[1]	Geolocator
2019	*/R1	1st winter	F	no	17	0	NA	Geolocator
2019	*/R2	1st winter	M	full	3	1	3	Geolocator
2019	*/Rot	1st winter	F	moderate	19	0	NA	Geolocator
2019	*/T	1st winter	M	no	18	1	18	Geolocator
2019	*/Y1	1st winter	M	moderate	19	1	19	Geolocator
2019	*/Y2	1st winter	F	no	18	1	19	Geolocator
2019	*/Yr	1st winter	M	full	4	0	NA	Geolocator
2019	–/gw*	1st winter	M	full	2	0	NA	Geolocator
2019	–/pz*	older	M	no	16	1	NA[1]	Geolocator
2019	–/s*	1st winter	F	no	10	0	NA	Geolocator
2019	–/zy*	older	M	full	3	0	NA	Geolocator
2019	G/*1	1st winter	F	no	3	0	NA	Geolocator
2019	O/*	1st winter	F	moderate	18	0	NA	Geolocator
2019	Ob/*	older	M	no	14	0	NA	Geolocator
2019	T/*2	1st winter	F	no	16	1	16	Geolocator
2019	v*/–	older	M	full	7	0	NA	Geolocator
2020	*/O	older	F	no	NA	NA	NA	Geolocator
2020	*/R2	older	M	no	NA	NA	NA	Geolocator
2020	*/T	older	M	no	NA	NA	NA	Geolocator
2020	[SB]/O	1st winter	M	no	NA	NA	NA	Geolocator
2020	m*/–	older	F	no	NA	NA	33	Radio transmitter
2020	T/*	older	M	no	NA	NA	NA	Geolocator
2020	T/*2	older	F	no	0	NA	NA	Geolocator
2020	V/[SB]	1st winter	M	no	NA	NA	NA	Geolocator

[1] Bird returned with malfunctioning geolocator

Table S2. Model summary of a LM investigating the causal effect of food availability on approximated spring departure date from Africa in free-living Pied Flycatchers that took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with ‘full’ access to food supply, ‘moderate’ access, or ‘no’ access to additional food). Departure date was described as April day (1 = 1 April) and the model included sex and age class (first winter or older) and included all birds in 2019 regardless of their departure mass. The intercept reflect first winter females with ‘no’ access to additional food.

Parameter		**β**	**SE**	***t***	P_r
(Intercept)		12.98	1.650	7.859	**< 0.001**
Food	(full)	–11.89	2.363	–5.035	**< 0.001**
	(moderate)	4.864	2.720	1.788	**0.099**
Age (older)		0.379	2.334	0.162	0.87
Sex (male)		2.483	2.201	1.128	0.28

Table S3. Model summary of hierarchical additive mixed models (HGAM) investigating the causal role of food availability on $\log_e$-transformed body mass change during the premigration period in free-living Pied Flycatchers that took part in a supplementary feeding experimental in north Ivory Coast in 2019. In total 181 weight measures were taken from in total 17 birds, with measurements continuing until birds left the study site. Access to experimentally provided additional food was either ‘full’, ‘moderate’, or, ‘no’. The effective degrees of freedom (EDF) increases as the ‘wiggliness’ of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females with ‘no’ access to additional food. Total deviance explained by the model is 97.2%.

Parametric terms		**β**	**SE**	***t***	P_r
(Intercept)		2.717	0.034	79.7	**< 0.001**
Age (older)		–0.021	0.051	–0.41	0.683
Sex (male)		0.037	0.047	0.80	0.425
Food	(full)	0.292	0.065	4.49	**< 0.001**
	(moderate)	0.014	0.049	0.27	0.786

Smooth terms	**EDF**	**Ref *df***	***F***
ƒ(Day)	**2.53**	4	22.6
ƒ(Day : Age *older*)	**1.90**	4	0.88
ƒ(Day : Sex *male*)	**2.18**	4	1.12
ƒ(Day : Food *full*)	**2.56**	4	3.64
ƒ(Day : Food *moderate*)	0.0002	4	0.00
ƒ(Day, Individual)	**40.92**	79	12.6

Table S4. Model summary of a LM investigating the causal effect of food availability on approximated departure mass of free-living Pied Flycatchers at the moment that they left on spring migration departure. Birds took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with ‘full’ access to food supply, ‘moderate’ access, or ‘no’ access to additional food). The model included mass (g), sex and age class (first winter or older) and included all birds in 2019 regardless of their departure mass. The intercept reflect first winter females with ‘no’ access to additional food.

Parameter		**β**	**SE**	***t***	P_r
(Intercept)		18.78	0.99	18.82	**< 0.001**
Food	(full)	1.36	1.43	0.95	0.36
	(moderate)	1.80	1.65	1.09	0.30
Age (older)		–1.06	1.41	–0.75	0.47
Sex (male)		2.19	1.33	1.64	0.13

Table S5. Model summary of a LM investigating the initial differences in body mass prior to fuelling in free-living Pied Flycatchers that took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with 'full' access to food supply, 'moderate' access, or 'no' access to additional food). The model included mass (g), sex and age class (first winter or older). The intercept reflects first winter females with 'no' additional food.

Parameter	**β**	**SE**	***t***	P_r
(Intercept)	12.13	0.53	22.63	**< 0.001**
Food (full)	–0.29	0.69	–0.42	0.68
(moderate)	–0.11	0.75	0.15	0.88
Age (older)	0.39	0.67	0.58	0.57
Sex (male)	0.32	0.62	0.52	0.61

Table S6. Model summary of hierarchical additive mixed models (HGAM) investigating the effects of the natural environment by means of a year-effect on $\log_e$-transformed body mass change during the premigration period in free-living Pied Flycatchers in north Ivory Coast in 2019 ($n = 8$) and 2020 ($n = 8$) that receive no additional food supply (i.e. only a minimal amount of food, c. 0.35 g to still attract them to a balance). NB. In 2019 measurements continued until all birds left the study site for migration, but in 2020 measurements stopped at 15 April before most left the study site. In total 298 weight measures were taken. The effective degrees of freedom (EDF) increases as the 'wiggliness' of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females in 2019. Total deviance explained by the model is 95.6%.

Parametric terms	**β**	**SE**	***t***	P_r
(Intercept)	2.611	0.031	85.41	**< 0.001**
Year (2020)	–0.002	0.037	–0.045	0.964
Age (older)	0.065	0.033	1.98	**0.049**
Sex (male)	–0.005	0.033	–0.146	0.884

Smooth terms	**EDF**	**Ref *df***	***F***
ƒ(Day)	**3.825**	**4**	**51.6**
ƒ(Day : Year *2020*)	**3.772**	**4**	**30.3**
ƒ(Day : Age *older*)	0.742	4	0.23
ƒ(Day : Sex *male*)	1.170	4	0.40
ƒ(Day, Individual)	**37.74**	67	21.1

Table S7. Model summary of hierarchical additive mixed model (HGAM) describing fuelling in free-living Pied Flycatchers from $\log_e$-transformed body mass changes during the premigration period in north Ivory Coast, optimized to best fit 'individual-within-year' trajectories ($n = 25$), while accounting for effects of year, access to additional food supply, age class and sex. Access to additional food supply was either 'full', 'moderate', or 'no'. In 2019 measurements continued until all birds left the study site, but in 2020 measurements stopped at 15 April before most birds left on migration. In total 393 weight measures were taken. The effective degrees of freedom (EDF) increases as the 'wiggliness' of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females with 'no' access to additional food in 2019. Individual curves were fitted as individual-within-year level random effect smooth with high with wiggliness ($k = 14$) to allow deviations from factor smooths (see Methods). Total deviance explained by the model is 99.1%.

Parametric terms	**β**	**SE**	***t***	P_{r}
(Intercept)	2.639	0.036	72.91	**< 0.001**
Year (2020)	–0.000	0.048	–0.019	0.984
Age (older)	0.0458	0.036	1.264	0.207
Sex (male)	–0.0019	0.033	–0.057	0.954
Food (full)	0.234	0.060	3.878	**< 0.001**
(moderate)	0.030	0.054	0.549	0.584

Smooth terms	**EDF**	**Ref *df***	***F***
f(Day)	**3.067**	4	33.3
f(Day : Year *2020*)	**3.424**	4	6.86
f(Day : Age *older*)	0.0003	4	0.00
f(Day : Sex *male*)	0.0000	4	0.00
Food (full)	**2.289**	4	3.77
(moderate)	0.0007	4	0.00
f(Day, Individual-within-year)	**140.63**	271	25.2

Photo S1. Female Pied Flycatcher in Comoé National Park; 8 April 2018 (photo Sander Bot).

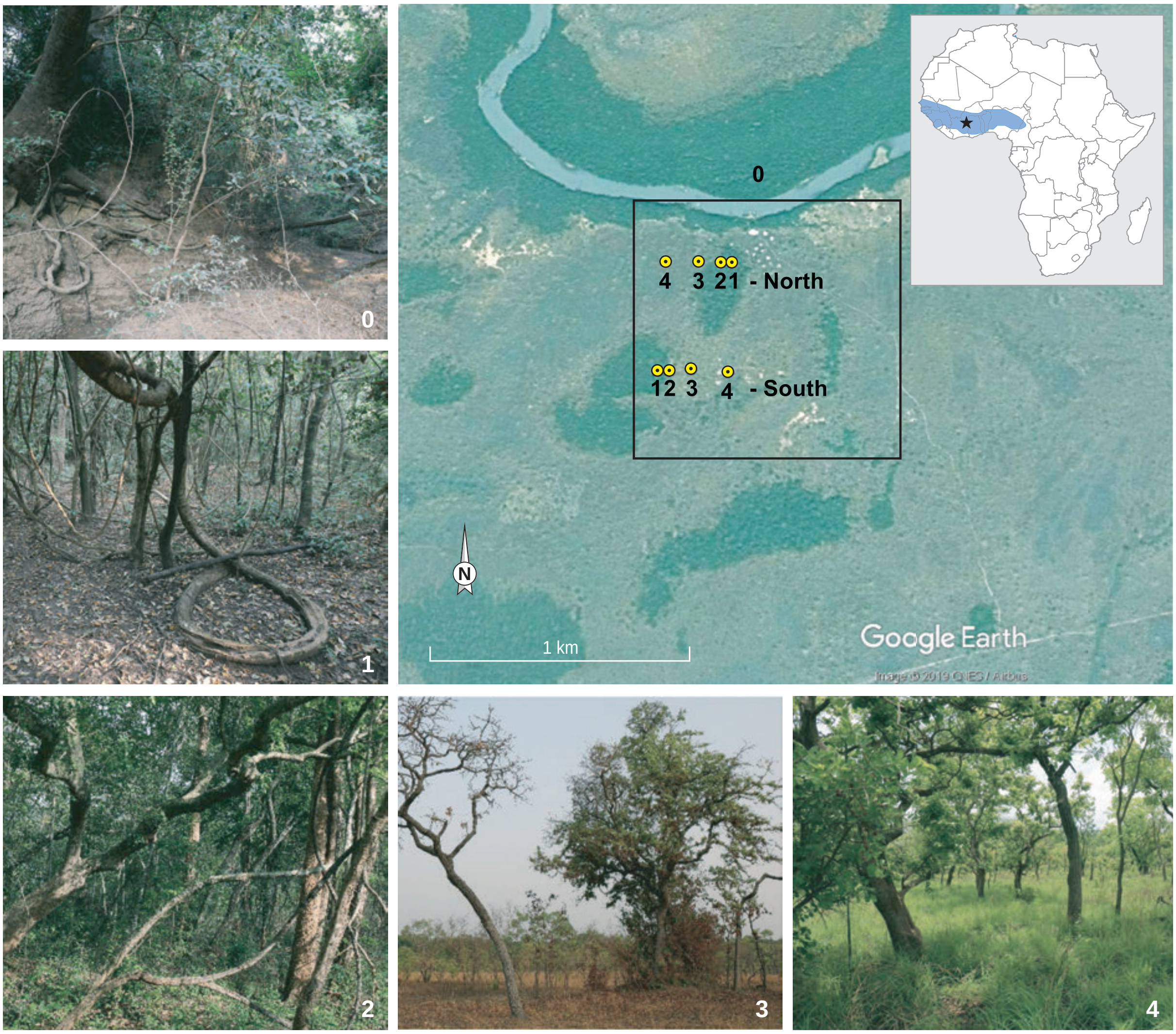

Figure S1. The study region in Comoé NP in northeastern Ivory Coast is located (indicated by a star) in the centre of the wintering range of Pied Flycatchers (range in blue; redrawn from Ouwehand 2016). The study site of c. 1 km^2, shown as the box in the google earth map, is dominated by savanna (picture and sampling locations 3–4). Other habitats commonly used by Pied Flycatchers during non-breeding are dry forest patches (pictures and sampling locations 1–2; forest interior and edge). Repeated arthropod sampling during the fuelling period was performed across these four habitats in four sampling locations in 2020 (1–4 North; yellow dots) and eight locations in 2019 (1–4 North and South). Gallery forests adjacent to the Comoé River (0) were not systematically sampled in this study, and were less used by flycatchers during the pre-migratory period.

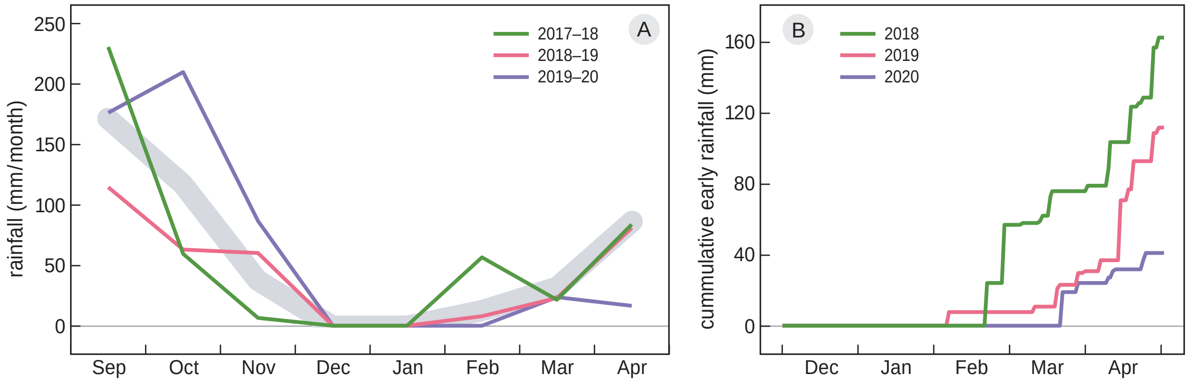

Figure S2. Local rainfall estimates in Comoé NP of (A) monthly rainfall sum (mm) for the wintering season in three different years, and the 5-year average from 2015–16 until 2019–20 (show as grey ribbon), and (B) cumulative daily rainfall (mm) during the second half of the dry season (i.e. 1 December – 30 April). Rainfall was measured at the study site (Comoé Research Station, Ivory Coast).

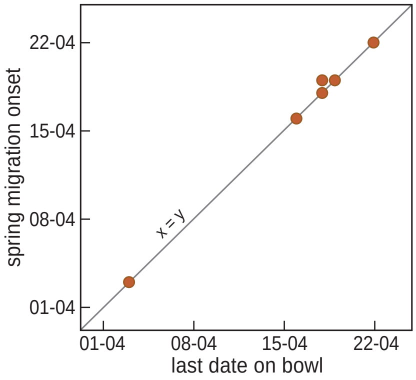

Figure S3. The spring migration onset of Pied flycatchers in relation to the date of departure as estimated from the last day a bird was seen accumulating fuel stores on the bowl in its wintering territory (with $x = y$ line). The onset of spring migration departure could only be confirmed for birds that successfully returned with geolocator loggers (5 birds from 2019 (Table S1) and 1 bird from a pilot in 2018) and for which raw geolocator data were available to estimate the moment that birds started their non-stop flights across the Sahara. All these birds had body masses between 20.2 and 22.6 g on the last measurement day, corresponding to fuel loads of 117–143% of structural body mass.

Photo S2. Pied Flycatchers in this study were all ringed and deployed with tags to track their migration. A colour ring allowed us to recognize individuals on the video footage. Knowing the identity of a bird was important to monitor if habituation and supplementary feeding was successful and to confirm that remote body mass measurements and observed departure belonged to the focal bird (see Figure 1C). In the subset of birds that returned the next year with their geolocator, we could show that the actual start of Sahara crossing was tightly linked to the last day a bird was seen and measured on the balance (Figure S3). The picture was taken on 8 April 2018, which was two days before this first winter female started with her flight over the Sahara Desert (photo Sander Bot).

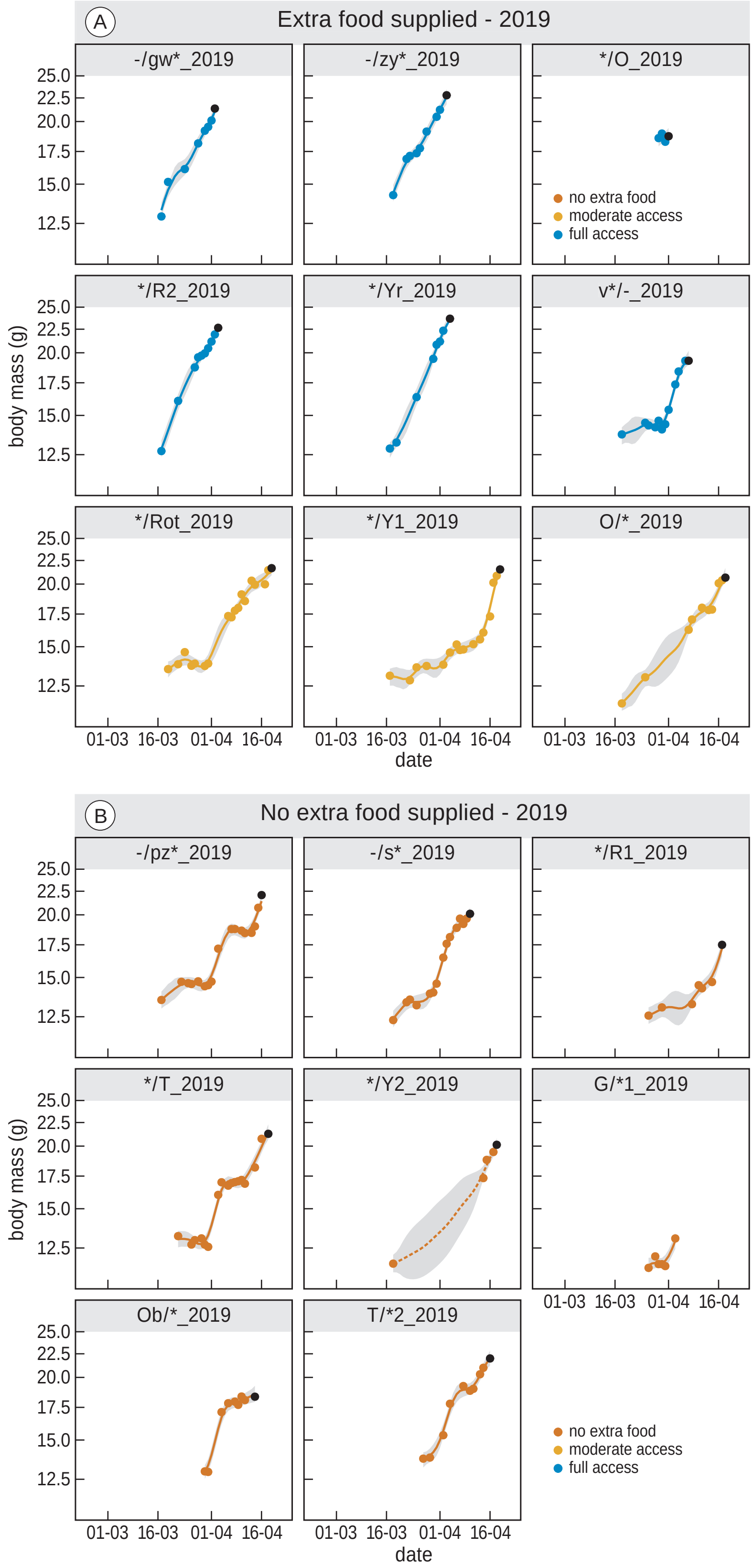
A
Extra food supplied - 2019
-/gw*_2019
-/zy*_2019
*/O_2019
*/R2_2019
*/Yr_2019
v*/-_2019
*/Rot_2019
*/Y1_2019
O/*_2019
no extra food
moderate access
full access
body mass (g)
25.0
22.5
20.0
17.5
15.0
12.5
01-03
16-03
01-04
16-04
date
B
No extra food supplied - 2019
-/pz*_2019
-/s*_2019
*/R1_2019
*/T_2019
*/Y2_2019
G/*1_2019
Ob/*_2019
T/*2_2019

Figure S4.

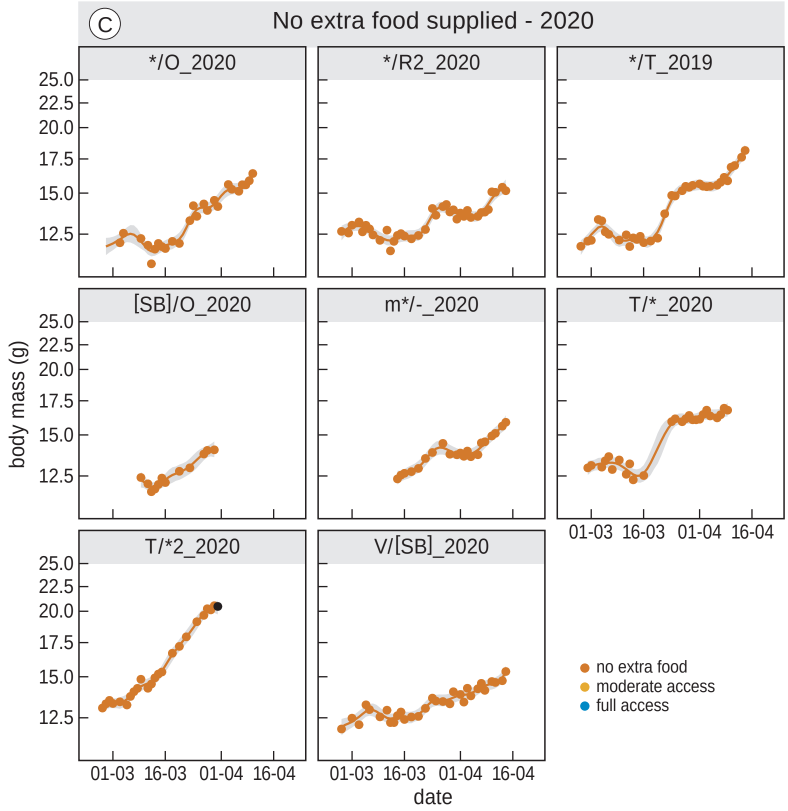

Figure S4. Change in body mass over time for each individual within a year during the premigration phase. In (A–B), birds were exposed to experimental food supplementation in 2019 in which birds showed full access to extra food (blue), moderate access (orange), or received no extra food (red). In 2020 (C), none of the birds received extra food. NB. In 2020 most fuelling trajectories were incomplete and only one bird, compared to all birds in 2019, could be measured until birds left on spring migration (black symbols). Shown are raw body mass measurements and the associated predicted line and confidence intervals from a HGAM model optimized to fit $\log_e$-transformed mass change trajectories of individual birds within years (see Table S7 and Methods). The dashed line depicts one bird where model interpolation between subsequent measures was more than 25 days.

Photo S3. Armel providing food and setting up the balance to measure the body weight of a flycatcher being faithful to this site.

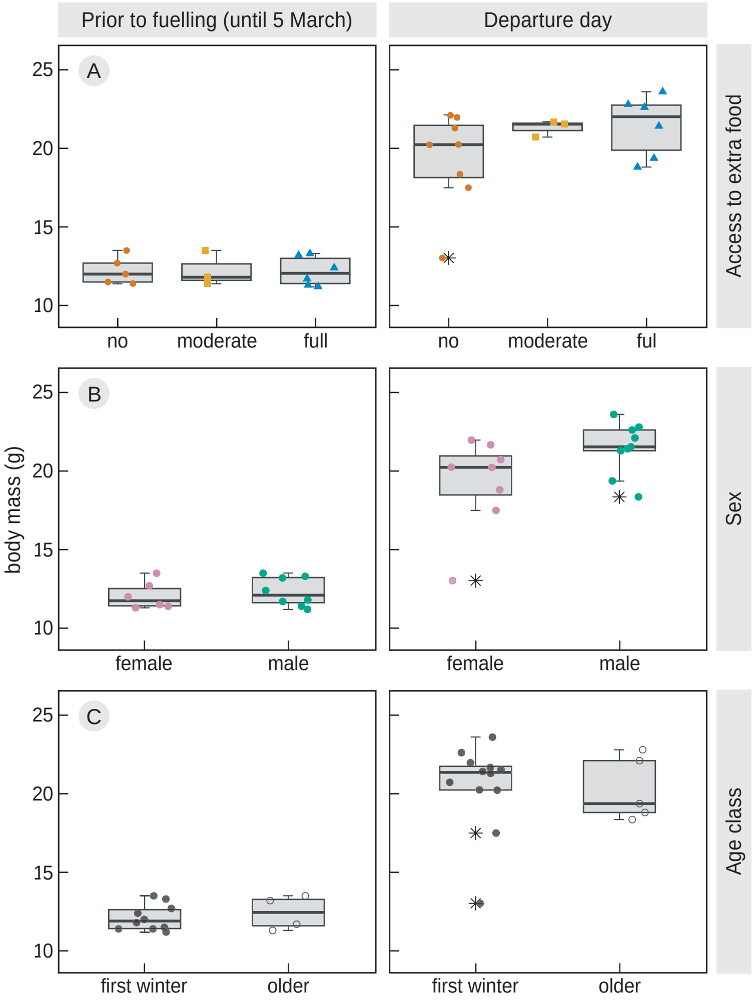

Figure S5. Body mass of Pied Flycatchers in 2019 in relation to (A) access to extra food, (B) sex and (C) age class. Body mass was measured prior to fuelling (left) and at departure using the last day a bird was measured (right). Masses in B–C are shown regardless of a birds' access to extra food. Each panel shows the boxplots and jittered raw data in each group.

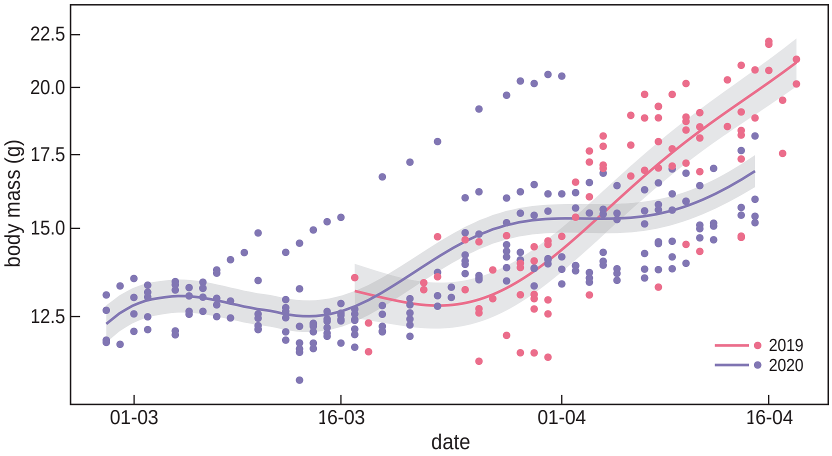

Figure S6. Natural variation in body mass increases over time of birds that receive no extra food, shown for two fuelling seasons in Ivory Coast. Shown are body mass measurements and the associated predicted lines and confidence intervals per year (from the model in Table S6).

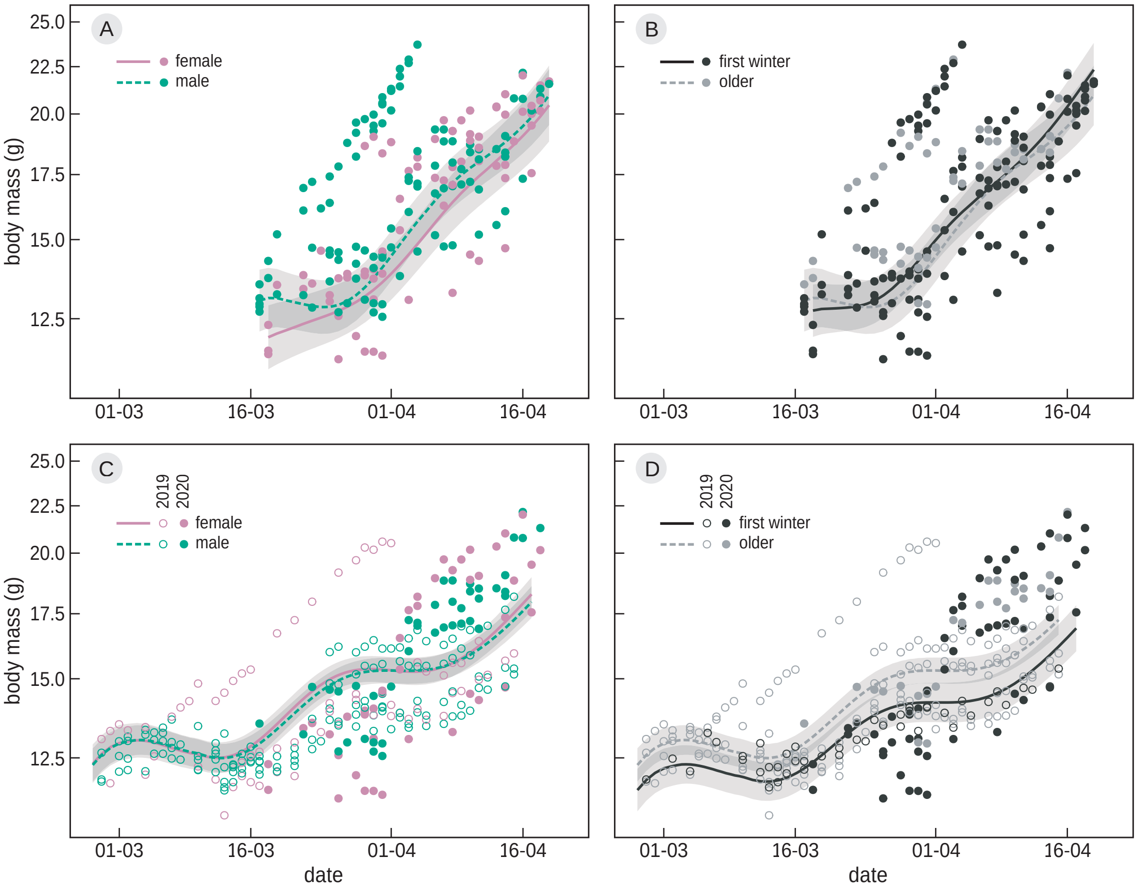

Figure S7. Body mass increase over time in Ivory Coast shown for Pied Flycatchers in different sex (A, C) and age classes (B, D). Birds in A–B were part of a supplementary feeding experiment in 2019 with varying access to extra food, while C–D show only birds with ‘no extra food’ in 2019 or 2020. Shown are body mass measurements and the associated predicted lines and confidence intervals per sex and age class (using models provided in Table S3 for A–B and Table S6 for C–D).

Figure S8. Spatio-temporal variation in arthropod biomass and abundance during the dry season in two years, shown per sampling location. Flying and ground-dwelling arthropods were repeatedly sampled by one malaise trap and three pitfall traps per sampling location (trapping duration of 96 h) for in total 4–8 sampling points. Sampling points were spread across the study site and covered a range of habitats used by Pied Flycatchers (Figure S1).

Living on the forest edge: flexible habitat use in sedentary Pied Flycatchers *Ficedula hypoleuca* during the non-breeding season

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Seasonality affects the availability of resources within the African non-breeding environment of migratory songbirds. We are generally unaware of how songbirds respond to such seasonal dynamics, especially at small spatial scales that are relevant for individual birds. In this study we focus on the question of how migratory songbirds use small scale variation in seasonality in their non-breeding environment. Therefore, we measured individual movements of European Pied Flycatchers *Ficedula hypoleuca* in relation to habitat differences in foliation in a non-breeding site in Comoé National Park, Ivory Coast. Through a combination of remote sensing and radio tracking we show that flycatchers change their habitat use during the second half of the non-breeding season, where at the start of this period flycatchers occupy both savannah and forest, whereas with progressing foliation, after savannah burning and with the onset of the first rainfall, they narrow their site use in favour of savannah. Further measurements of arthropod abundance show that this behaviour is related to increasing numbers of particular arthropod groups during foliation, which indicates that flycatchers might track seasonal changes in food availability by moving between habitats on a small spatial scale. We hypothesize that individuals reduce their susceptibility to seasonality by establishing territories on the forest edge, where they can access both savannah and forest habitat, and thereby explore a wider variety of resources under different circumstances. In conclusion, these findings indicate that small-scale heterogeneity likely plays a key role in the ability of flycatchers to cope with seasonal dynamics on a local scale.

Key words: Pied Flycatcher, non-breeding season, seasonality, arthropods, habitat use, radio-tracking, remote sensing, NDVI

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Non-breeding environments of Afro-Palearctic migratory passerines are characterized by pronounced seasonal changes. These are mainly driven by fluctuations in rainfall, which follow the cyclic movements of the Intertropical Convergence Zone, resulting in spatio-temporal variation in vegetation dynamics across the African continent (Beresford *et al.* 2019). As a result of this variation the specific seasonal dynamics that birds encounter during the non-breeding season depend on the timing and location of residency. Most Afro-Palearctic migrants spend the non-breeding period in the dry or humid regions north of the equator. Their subsequent residency coincides with the dry season which is generally characterized by wilting of the vegetation (Moreau 1972, Zwarts *et al.* 2023). Within the Sahel this dry season typically extends beyond the onset of spring migration, whereas a few hundred kilometres towards the south (in the Sudanian and Guinean regions) most migrants depart after the first rainfall, and consequently experience regrowth and foliation of the vegetation at the end of the non-breeding season (Zwarts *et al.* 2023).

Seasonal changes in vegetation conditions affect the availability of environmental resources that are important for the survival of migratory passerines. Most notably, food availability of insectivorous migrants is widely believed to be positively linked with vegetation greenness, as their prey species either directly (e.g. herbivores, detritivores) or indirectly (carnivores) rely on the consumption of plant material (Schaub *et al.* 2011. Kristensen *et al.* 2013, Thorup *et al.* 2017). Additionally, seasonal change in leaf cover might affect the risk of predation. Arboreal species in particular often rely on leaf cover to protect themselves against avian predators (Walther & Gosler 2001, Carrascal & Alonso 2006). Similarly, changes in foliage density also affect the availability of shade which plays a vital role in thermoregulation of songbirds in tropical environments (Wolf & Walsberg 1996, Cunningham *et al.* 2015, Martin *et al.* 2015). Given the variation in the resources that are affected, seasonal vegetation dynamics can differentially affect species, depending on their respective ecological traits.

One possible response of migratory songbirds to seasonality is tracking environmental shifts in resources. For example, various migrant species move along with shifts in plant growth within the African continent, and thereby visit multiple sites throughout the non-breeding period (e.g. Thorup *et al.* 2017, Koleček *et al.* 2018, Norevik *et al.* 2019). Although most studies on migrant species in Africa lack direct observations of environmental conditions, and the associated behavioural ecology during the non-breeding season (but see Schlaich *et al.* (2016) for an example in Montagu's Harriers *Circus pygargus*), these large-scale movements are widely interpreted as an adaptive behaviour by which birds track seasonally available resources. Despite the seeming advantage of avoiding local declines in resources, through large-scale movements, other species are known to remain (largely) sedentary throughout the non-breeding period (e.g. Salewski 1999, Kristensen *et al.* 2013). This reflects an ability of these birds to cope with seasonality within their local environment.

In order to determine how songbirds are able to cope with seasonality on a local scale, we need fine-

Photo 1. Savannah right after burning of the undergrowth during the dry season. Trees and shrubs are largely defoliated, and the soil is covered by ash litter (30 December 2018).

scale observations. However, most of our knowledge about the spatial behaviour of songbirds during the non-breeding season is based on imprecise tracking data from light-level geolocators (Rakhimberdiev *et al.* 2016). We are generally unaware of individual movements at fine levels, as would be described by radio-tracking studies (e.g. Stünzner-Karbe 1996, Willemoes *et al.* 2018). Additionally, many studies use remote-sensed indices such as the Normalised Difference Vegetation Index (NDVI) to measure environmental conditions on large spatial scales (e.g. Balbontín *et al.* 2009, Schaub *et al.* 2011, Kristensen *et al.* 2013) This is unsuitable for detecting variation on smaller scales, such as different seasonal patterns between tree species (Mahamane *et al.* 2007, Park *et al.* 2019, Fawcett *et al.* 2021). We also often lack detailed insight into the non-breeding ecology of species to interpret patterns in remote sensed datasets, such as relationships between NDVI and specific resources (Piersma 2020). Altogether, we are generally unaware of how songbirds respond to seasonal resource dynamics in the non-breeding area, especially at small spatial scales that are relevant for individual birds.

In this study we focus on the question of how migratory songbirds use small-scale heterogeneity in vegetation within the non-breeding environment. Therefore, we measured individual habitat use in relation to seasonal dynamics in foliation within a non-breeding site of the European Pied Flycatcher *Ficedula hypoleuca*, hereafter called flycatcher. Flycatchers are Afro-Palearctic migrants with a non-breeding range within the Guinean and Sudanian ecoregion of West Africa (Ouwehand *et al.* 2016). Previous observations from non-breeding sites suggested that flycatchers are territorial and occupy non-overlapping home-ranges (Stünzner-Karbe 1996, Salewski *et al.* 2002, Willemoes *et al.* 2018); also that individuals can use the same sites from arrival after mid-September until the onset of spring migration around April (Stünzner-Karbe 1996, Salewski *et al.* 2002). However, individuals have also been observed to shift between locations in forest and savannah habitats that were sometimes hundreds of meters apart (Stünzner-Karbe 1996). Based on this background we hypothesize that flycatchers respond to seasonality by tracking heterogeneity in the distribution of resources on small spatial scales.

To establish the relationship between site selection of flycatchers and small-scale variation in seasonality, we use a combined approach of remote sensing and radio tracking. Therefore we (1) investigate the possibility of using small-scale NDVI to quantify vegetation greenness in the environment, (2) describe how the site use of flycatchers is related to habitat and foliation and (3) describe the association between the observed patterns in site use and arthropod abundance.

METHODS

Study area

The study was conducted in Comoé National Park, Ivory Coast (8°45.875'N, 3°47.189'W) within a plot covering c. 69 ha in the immediate vicinity of the Comoé field station (for a description of the area see Ouwehand *et al.* 2023). Study site selection was based on high densities of flycatchers found in the national park during previous research (Salewski 1999). The vegetation within this plot mainly consists of savannah woodland, characterized by an open canopy of mostly deciduous trees and shrubs, with species such as *Terminalia macroptera*, *Daniellia olivieri* and *Combretum nigricans*, and a well-developed grass layer which is annually burned during the midst of the dry season (late December–January; Rüth 2008). During the year of this study the burning occurred around January 7 (determined by satellite imagery, Landsat-8, U.S. Geological Survey). The savannah is interspersed with forest patches, which are different from savannah woodland due to the absence of burning, and a denser shrub and canopy layer. Further heterogeneity also exists within these patches, where the edges are dominated by *Anogeissus leiocarpus*, a deciduous tree with a relatively open canopy, whereas the centre is characterized by a relatively dense canopy layer with a mixture of both deciduous and evergreen species (e.g. *Diospyros abyssinica*, *Cola cordifolia*). Another type of forest, hereafter called gallery forest, can be found along the border of the Comoé River, which somewhat resembles the vegetation in the forest patches, but with a more homogenous species composition and a higher dominance of evergreen shrubs and trees (e.g. *Diospyros abyssinica*).

General fieldwork

The data in this study was collected between 12 February and 15 April 2020. As part of ongoing research since 2017 we conducted regular surveys to collect observations of flycatchers in the study area (Ouwehand *et al.* 2023). We recorded the coordinates of each observation by means of a handheld GPS and tried to identify the individual if it had been colour-ringed. Based on these observations we selected specific individuals which we subsequently tried to catch by means of a mist net, or, occasionally, a baited spring-trap. We focused our catching efforts on individuals that had not been previously caught, and individuals that were carrying a geolocator from the previous season. Newly caught individuals were equipped with an aluminium colour ring for individual recognition. We established the age of individuals (1st winter/2nd calendar year or >2nd calendar year) by means of presence or absence of juvenile greater coverts and tertials, and wear and shape of tail feathers (Svensson 1992, Jenni & Winkler 1994). The sex was initially determined by the presence or absence of distinct male plumage characteristics, such as dark tail feathers and coverts, and after the onset of pre-breeding moult also by white forehead patches and dark coverts. In case birds lacked any of these distinctive male characteristics we collected a blood sample for molecular sexing (following Kahn *et al.* 1998), allowing us to distinguish between females and males with female-type plumage.

Remote sensing

In order to measure spatiotemporal changes in vegetation conditions we used UAV-derived aerial imagery, which allows for a high spatiotemporal sampling resolution (Park *et al.* 2019, Fawcett *et al.* 2021). We used a consumer-grade quadcopter (DJI Phantom 4 multispectral) with the software DJI GS Pro (DJI Technology, Shenzhen) to create an automated image acquisition plan for the study area and its immediate surroundings. The image angle was set at 90° with a frontal overlap of 70% and a side overlap of 60% between adjacent pictures, and pictures were taken at an altitude of 113 m yielding a resolution of 6.0 cm^2/pixel. Images were taken once every eight days during the period 12 February to 14 April. We used the program Pix4D v. 4.6.4 (Pix4D, Lausanne) to aggregate all images from the same date and bandwidth into a comprehensive raster file. The red and NIR rasters were subsequently used to calculate the NDVI of individual pixels and these values were finally stored in a new NDVI raster for each observation date.

NDVI and fresh foliage cover

In parallel with remote-sensing, we conducted a ground-truthing study to verify the biological basis of observed spatiotemporal differences in NDVI. Therefore, we specifically monitored fresh foliage cover within individual tree crowns and grass layer transects. For the tree monitoring we selected 14 of the most common species within the area, for each of which we located four trees on regular spaced locations throughout the study plot. We only selected trees in the upper canopy to ensure visibility on the aerial imagery. These trees were subsequently visited every eight days to

Photo 2. Savannah during foliation, with trees and shrubs including *Burkea africana*, *Piliostigma thonningii*, *Terminalia macroptera* and *Daniellia oliveri*. The soil is partly covered by fresh grown forbs and perennial grasses (6 March 2020).

Photo 3. The savannah after complete foliation of trees and shrubs, including *Crossopteryx febrifuga*, *Burkea africana* and *Terminalia macroptera*. The grass layer almost completely covers the soil (and thereby is further developed than during the study period) and will further develop during the rainy season (27 April 2018).

visually estimate the proportion of the crown circumference covered by fresh (i.e. green) leaves on a 10-point scale, which was done from a distance of c. 10–20 m from the trunk. These observations were initially collected by different observers in the field, but we also took pictures to compare estimations of different observers. After we detected a significant difference in estimates between observers, we used these pictures to get new estimates from a single observer (WB) which were used for the final analysis.

Additionally, we measured the amount of fresh plant material within grass layer transects by means of line-point interception. These sampling locations were selected within the vicinity of the arthropod sampling sites (see next paragraph) and consist of two 10-m line transects placed in perpendicular directions from a shared starting point. Following Herrick *et al.* (2005) we established the relative cover of fresh plant material (i.e. green leaves) within these transects by dropping a metal pin at each 20-cm interval along a reference rope that marked the transect. If this pin touched any green plant material it was scored as a 1, and in any other case (and also when the pin touched senescent plant material) it was scored as a 0. The relative cover of each 10-m transect was then calculated as the sum of scores divided by the total number of trials ($n = 50$). In total we sampled each transect three times during the period 26 February to 13 March. To analyse the relationship between grass coverage and remote sensed NDVI we then made a post-hoc selection of those transects which were directly visible on the aerial imagery, and not completely masked by trees. This resulted in a final sample of transects which were exclusively placed on the open savannah ($n = 8$). We also used the same interception to describe differences in habitat characteristics between sites that we classified as either forest or savannah. Therefore, we scored the relative cover of specific types of vegetation (sum of senescent and green plants) and litter on the first observation date. We specifically distinguished the categories shrubs (perennial woody plants), forbs (herbaceous plants), herbaceous litter (fallen non-woody plant material), woody litter (fallen branches and wood) and ash litter (burned plant material).

We used ArcGIS v. 10.8.1 (ESRI, Redlands, CA) to extract values of individual trees and transects from the remote sensed NDVI rasters. For this purpose, we initially plotted the coordinates of individual trees and transects on a true colour map. Next, we used reference pictures from the field to visually correct for any inaccuracies in the GPS location of these objects. Then we created a new shapefile that was used to draw polygons for the surface area of the individual canopies and transect. For trees we used the green rasters to outline the maximum expanse of the canopy (including leaves and branches) during the study period. For the transects we created a 0.5-m buffer polygon around the central axis of the transect, representing the ground-sampling area and its immediate surroundings. To confine these polygons to the vegetation of interest, we excluded all parts that were covered by overhanging branches on any date. The adjusted polygons for trees and transects were then used to derive the mean NDVI from the underlying raster cells for different dates. Next, these values were linked to the most recent ground-based observations of foliage cover for the same canopies or grass transects. On average the observation dates differed by 2.33 ± 0.48 days for transects and 0.78 ± 0.54 days for trees.

Radio tracking

We used radio tracking to quantify individual site-use of flycatchers and its relationship with vegetation conditions. Therefore, we randomly selected individuals (i.e. independent of age, sex and capture history) among our captured birds, which we subsequently equipped with a 0.53-g solar-powered radio transmitter (type CTT LifeTag, Cellular Tracking Technologies, Rio Grande, NJ) attached by means of an elastic leg-loop harness. The rechargeable nature of LifeTags enabled us to track individuals over longer periods than with conventional transmitters, although these tags only transmit signals when directly exposed to sunlight, resulting in zero pulses in dark or shaded habitats or if feathers cover the tag. For this reason, we modified the tags by adding a transparent plastic cap on top, which prevented feathers from covering the solar cell. Furthermore, to lessen the risk of entanglement we clipped the antenna down to 86.5 mm. In total we equipped 13 flycatchers with a radio transmitter (Table 1), for which we excluded four individuals with insufficient data from the analysis. In three cases this was likely due to a technical failure, including one instance where we could confirm that the plastic cap had disjoined from the tag, which was therefore covered by feathers (individual 61526652). The other excluded individual (61335200) was overall well detected, but with too few detections within approximately 50 m from receiver nodes (see next paragraph) to measure site selection over time.

To localize individuals, we made use of 21 solar-powered autonomous receivers (CTT Node, v. 1), hereafter called ‘nodes’, which we placed in an isometric grid at an individual distance of approximately 200 m. To maximize charging we placed the nodes in treetops, where the solar cells were exposed to full sunlight throughout the day. Nodes can receive LifeTags within a maximum range of c. 300 m, and each reception is stored in a data file with the tag-ID (an identification number based on the unique frequency of tags), date, time, and the strength (RSSI) of the signal. After initial storage the nodes retransmit this data to a central receiver (CTT SensorStation v. 2.0), which compiles the data including the node-ID (an unique identification number) into a single data file.

Location estimation

In our initial setup we aimed to estimate individual positions per time interval by triangulation of receptions from different nodes. Therefore, we created a habitat-specific calibration curve for RSSI as a function of distance, based on observations of tagged individuals with known locations in the field (6 individuals, 45 locations). Following the R-documentation ‘Localization.R’ (https://github.com/cellular-tracking-technologies/celltracktech) the curve was restricted to follow an asymptotic regression function, for which we calculated the parameter estimates by means of non-linear least squares. Next, we used this calibration curve to triangulate locations of tagged birds within the node-grid. However, based on unrealistic outcomes (which included unlikely shifts in subsequent locations, and cluttering of estimated locations at exact distances between nodes), which was likely due to the uncertainty of distance estimation at relatively low RSSI values (Figure S1), we concluded that this method would be unsuitable for our purpose. Instead, we opted for an alternative approach where we established spatial behaviour of tagged birds by determining presence within a radius of 50 m from each node (i.e. an area of 7854 m^2). Using this approach we avoided the uncertainty in position estimation at large distances (i.e. near the asymptote of the calibration curve), while the scale proved to be sufficiently small to detect within-individual shifts in site selection. For this approach we derived the predicted RSSI value at a distance of 50 m from the calibration model (Figure S1) and selected all detections for which the RSSI value was equal to or larger than the resulting value. Next, we grouped the observations per 5 minutes and selected only the cases where a bird was detected at least five times within the 50-m range of a node. This selection was made to reduce the influence of single detection errors, and thereby the probability of falsely considering a bird to be present. For each selected period we determined the site where a bird was most likely present, which in most cases was simply the only site in which a bird was detected ($n = 5641$). In alternative cases where birds were detected on multiple sites ($n = 527$), we assigned presence to the site with >50% of detections. Periods in which this condition was not met ($n = 75$) were removed from the analysis.

Arthropod sampling

In order to establish the relationship between vegetation conditions and food availability for flycatchers, we monitored the abundance of arthropods within the environment. Based on our own observations and a previous study of Salewski (1999) we knew that flycatchers in the study area were mainly insectivorous and foraged in a wide range of substrates using a range of foraging techniques. However, we lacked a priori insight into the relative importance of specific arthropod groups within the diet, as well as the relative intake from different strata of the vegetation. To capture a broad range of potential available arthropod food sources we used pitfalls and malaise traps, which capture ground-dwelling and aerial (but low flying) arthropods respectively. These trap types capture arthropods passively and therefore the number of captures depend on both the abundance and activity of arthropods, which are thus best described as measurements of 'activity-abundance' (McCravy 2018), although we will shortly refer to this as 'abundance'. In total we sampled at eight locations which were placed within the different vegetation types inhabited by flycatchers. These locations were placed near two separate woodland patches, along a vegetation gradient from closed canopy forest to open canopy savannah woodland. In addition, we selected a single trapping site within the gallery forest, which differs in its (spatial) characteristics from the forest patches.

Each location was sampled by means of three pitfall traps and one malaise trap (for dimensions of traps see Ouwehand *et al.* 2023: but note that sampling design differs from this study). The pitfalls were placed along a line at 5-m intervals, all within c. 10 m from the malaise trap. These traps were alternately opened and closed for four days, yielding an average sampling duration of 3.99 ± 0.16 days. Sampling was initiated on all sites on 23 February, but the total sampling period was unequal between sites, due to an unplanned reduction in personnel because of the Covid-19 pandemic. As a result, four sites were sampled until 10 March, and the other four until 8 April.

In each sampling round we collected two arthropod samples on each site: one sample from the malaise trap and a pooled sample from the three pitfall traps. The samples were conserved in ethanol and placed in a fridge for short-term storage. Captured arthropods were processed by measuring the body length excluding external body parts like antennae, legs and wings, and we removed arthropods with a body length <3 mm, which we expected not to be prominent food sources for flycatchers. We identified all other arthropods on taxonomic order level.

To analyse potential food abundance, we made a selection of items that we considered to be realistic prey

Table 1. Proportion of soil covered by specific types of vegetation and litter within forest ($n = 8/4$ distinct locations) and savannah ($n = 8/4$ distinct locations). Numbers show the proportion of times that a pin that was dropped along a 10-m line transect ($n = 50$, interval = 20 cm) touched the specified type of vegetation or litter (multiple categories possible), based on the estimated marginal means from a GLMM. Confidence intervals and significance of the difference between habitats are only given in case the variance is > 0 in both habitats.

	Forest		Savannah			
Variable	Proportion ± SE	95% CI	Proportion ± SE	95% CI	χ^2	p
Shrubs	0.03 ± 0.00	0.03 - 0.03	0.21 ± 0.08	0.10 - 0.45	14.03	< 0.001
Forbs	0.11 ± 0.04		0.00 ± 0.00		-	-
Grass	0.03 ± 0.00	0.03 - 0.03	0.21 ± 0.08	0.10 - 0.45	23.39	< 0.001
Herbaceous litter	0.94 ± 0.05	0.85 - 1.04	0.22 ± 0.02	0.18 - 0.27	152.61	< 0.001
Woody litter	0.06 ± 0.03	0.02 - 0.14	0.01 ± 0.01	0.00 - 0.04	5.18	0.020
Ash litter	0.00 ± 0.00		0.77 ± 0.04		-	-

for flycatchers. Since large arthropods are underrepresented in the flycatcher diet we used order-specific length criteria to remove unlikely prey items from the analysis (for details see Ouwehand *et al.* 2023). Our final measurement consists of the number of arthropods per order per sample, where we assume independence between the number of items from different orders. This assumption was violated in a few cases where we observed large numbers of driver ants *Dorylus* spp. in our traps, which saturated the collection bottle and presumably diminished the trapping rate of other arthropods. We tried to remove these events from our dataset by discarding samples with extremely high numbers of Hymenoptera, which were identified by having a probability of <0.01 given a Poisson distribution for all Hymenoptera samples from the same trap type (5.0% of malaise samples, $n = 2$; 15.8% of pitfall samples, $n = 6$).

Spatial and temporal NDVI

We use separate NDVI-based proxies for habitat and foliation to describe vegetation conditions in time and space. In general arthropods prefer to consume fresh leaves, whereas older leaves are better protected against herbivory (Aide 1993). In order to generate a proxy for the amount of fresh leaves, which is potentially linked to the abundance of arthropods that might serve as food for flycatchers, we calculated the difference in NDVI relative to the first observation date (12 February), hereafter called $\text{NDVI}_{\text{temp}}$. In addition, we used the (absolute) NDVI values from this first observation date (i.e. prior to most foliation of deciduous vegetation) to describe foliation characteristics that are also typical for habitats. These NDVI values, hereafter called $\text{NDVI}_{\text{habitat}}$, range between low values for vegetation that is completely defoliated during the dry season, and high values for vegetation that remains green. In describing the habitat use of flycatchers, we refer to the lower end of $\text{NDVI}_{\text{habitat}}$ values as savannah, and to higher end values as forest. This broad habitat classification captures an important part of the variation in $\text{NDVI}_{\text{habitat}}$ within the study area (ANOVA: $F_{1,14} = 487.35$, $P < 0.001$; forest: mean ± SE: 0.59 ± 0.01, savannah: 0.18 ± 0.01, data based on eight sites in both habitats with a radius of 20 m, of which we assigned the habitat in the field). However, by preserving the continuous variable $\text{NDVI}_{\text{habitat}}$ in our analysis, instead of classifying habitat into forest or savannah, we address the further heterogeneity of vegetation that exists as a continuum across these broad habitat classes (e.g. varying mixtures of evergreen and deciduous vegetation).

Analysis

All statistical analyses were done using R v. 4.1.2 (R Core Team 2022). We used linear mixed effect models (LMM) from the 'lme4' package (Bates *et al.* 2015) to analyse the relationship between NDVI and foliage cover. In the canopy models we fitted random intercepts for tree-ID (an identification number for individual trees) nested within species. Similarly, we fitted a random intercept for transect-ID (an identification number for individual transects) in the grass layer models. Additionally, we fitted a random intercept for Date (date of the drone footage as a categorical factor) in all models to account for the relatedness of data points from the same date (e.g. due to shared light conditions). We established the relationship between foliage cover and NDVI by adding foliage cover as a linear term to the model. We additionally explored the possibility for a quadratic relationship by adding a squared term of foliage cover, which we only retained if this model performed significantly better than the nested (linear) model, as established by means of a likelihood ratio test with a significance level of $P < 0.05$. We established model performance by calculating the marginal R^2 for the fixed effects, and the conditional R^2 for both fixed and random effects. Furthermore, we used a LMM to test for differences in foliation between habitats, where we modelled $\text{NDVI}_{\text{temp}}$ as response of the predictors date (numeric), $\text{NDVI}_{\text{habitat}}$ and their two-way interaction, where we fitted a random intercept for each level of location-ID to account for the relatedness of repeated measurements of the same locations. To compare site features between forest and savannah habitats, we used a generalized linear mixed model (GLMM) with a Poisson error distribution. In this model we also fitted a random intercept for each level of location-ID to account for the relatedness between the two transects that we considered per location. We used habitat (category) as a predictor and added an offset for the total number of trials per transect ($n = 50$), which thereby allowed us to extract the estimated marginal means of the response as a rate/ proportion of cover for the whole transect.

In order to establish the association between site selection and habitat, we follow a similar procedure as described by Holbrook *et al.* (2019). Therefore, we initially established the available habitat by calculating the arithmetic mean $\text{NDVI}_{\text{habitat}}$ of each individual home-range, subsequently called the 'available $\text{NDVI}_{\text{habitat}}$', which we define as all sites that were visited by an individual throughout the entire tracking period. Next, we established the used habitat within eight-day periods by calculating the mean $\mathrm{NDVI}_{\mathrm{habitat}}$ of used sites weighted for the proportion of visits, hereafter called the 'used $\mathrm{NDVI}_{\mathrm{habitat}}$' (see Figure 6 for a visual example of this procedure). We then used a LMM to establish the across-individual relationship between available and used habitats over time, where we modelled 'used $\mathrm{NDVI}_{\mathrm{habitat}}$' as a response variable, with the predictors 'available $\mathrm{NDVI}_{\mathrm{habitat}}$', Date (numeric) and their two-way interaction, and we added random intercepts for each level of 'individual' to account for the relatedness between repeated measurements of the same individuals. We additionally aimed to describe the relationship between the available habitat and the relative amount of foliation in sites that birds used over time, for which we used the same model terms with 'used $\mathrm{NDVI}_{\mathrm{temp}}$' as the response variable. This variable was also calculated as the mean $\mathrm{NDVI}_{\mathrm{temp}}$ of used sites weighted for the proportion of visits.

To allow for a further interpretation of patterns in habitat use in terms of spatial behaviour, we established the extent to which individuals revisited the same sites within their home-ranges over time. Therefore, we calculated the Shannon equitability index (E_h) for used sites, based on the occurrence of node-ID's across the different eight-day periods that individuals were tracked. This value ranges between 0 and 1, where a value of 1 would indicate that an individual visited the same sites every eight days during the entire tracking period, whereas low values represent a higher diversity in used sites over time. We then used a linear model to establish the between-individual relationship between habitat (within home-ranges) and home-range use, for which we treated the equitability of sites as a response variable, and available $\mathrm{NDVI}_{\mathrm{habitat}}$ as a linear predictor.

We performed two model selection analyses to explore the relationship between NDVI and the arthropod numbers within the pitfall and malaise traps. For this purpose, we used GLMM's with the number of arthropods (total count per order per catching event per site) as response variable with a negative binomial error distribution. In each model we included an offset for catching days, to account for differences in sampling duration, and random intercepts for round-ID and location-ID to account for the relatedness between samples from the same dates and locations. Additionally, we always included 'order' as a fixed factor in the model. We considered three potential relationships

Photo 4. Undergrowth of a forest patch during the dry season. The tree and shrub layers remain (partly) foliated (2 January 2019).

between arthropod numbers and NDVI: (1) no relationship, represented by a 'null model' without NDVI terms, (2) an overall log-linear relationship, represented by a model with main $\mathrm{NDVI}_{(x)}$ terms ($\mathrm{NDVI}_{\mathrm{habitat}}$ and $\mathrm{NDVI}_{\mathrm{temp}}$) and (3) a log-linear relationship that differs between orders, represented by a model with main $\mathrm{NDVI}_{(x)}$ terms and their two-way interactions with taxonomic order. In order to analyse the relationship between NDVI and arthropod abundance we acquired NDVI values by following the same procedure as described for the vegetation ground-truthing. The dates of these drone observation differed by 3.00 ± 1.23 (mean ± SD) days from the mid-date of the (four-day) sampling period. Since we possess no prior knowledge about the spatial scale at which our arthropods measurements are related to NDVI in the environment, we included scale as a variable in our analysis. Therefore, we created ten circular buffers ranging from 10 m to 100 m around the trapping sites to calculate the mean NDVI at different scales. These buffers were used to specify ten different sub-models for relationships 2 and 3, which we parametrized with $\mathrm{NDVI}_{(x)}$ values from each scale. We used AICc values to select a confidence set of best performing models, which included the minimum number of models with a cumulative AICc weight of >0.95. We used the model weight to calculate the weighted estimate and weighted standard error for the NDVI coefficients within this set of models (following Symonds & Moussalli 2011). To assess the model fit we also calculated the marginal R^2 and conditional R^2 of the best performing models. To compare the trends of different taxonomic orders within forest and savannah habitat we used the estimates of both the $\mathrm{NDVI}_{\mathrm{temp}}$ and arthropod models. Therefore, we first calculated the least-squared means for $\mathrm{NDVI}_{\mathrm{temp}}$ over time for the average $\mathrm{NDVI}_{\mathrm{habitat}}$ of forest (mean = 0.59) and savannah (mean = 0.18) sites, which we then supplied to the arthropod models to predict the number of arthropods in both habitats.

RESULTS

The study period in 2020 was relatively dry when compared to the foregoing years (Figure 1), where the timing of the first rainfall (21 March) was about a month later than the average for the period 2016–2019 (mean: 23 February, range: 5 February – 11 March). Also, the cumulative amount of rainfall for the study period was lower than in any of the previous four years, with a total of 32.0 mm by 15 April (2016–2019, mean: 103.4 mm, range: 93–114 mm).

NDVI ground-truthing

Despite the low amounts of rainfall, we observed considerable spatiotemporal change in NDVI during the study period, where overall patches of closed-canopy forest appeared to show high and stable NDVI values throughout the study period, whereas the NDVI in open savannah sites shifted from low to higher values later in the season (Figure 2).

When focusing on the (savannah) grass layer, the NDVI values were relatively low in the beginning of February, with minor temporal increase during the following period (Figure 3). Based on our ground-based measurements we find that only a minor part of the spatiotemporal variation in NDVI of grass layer transects could be attributed to grass cover (marginal

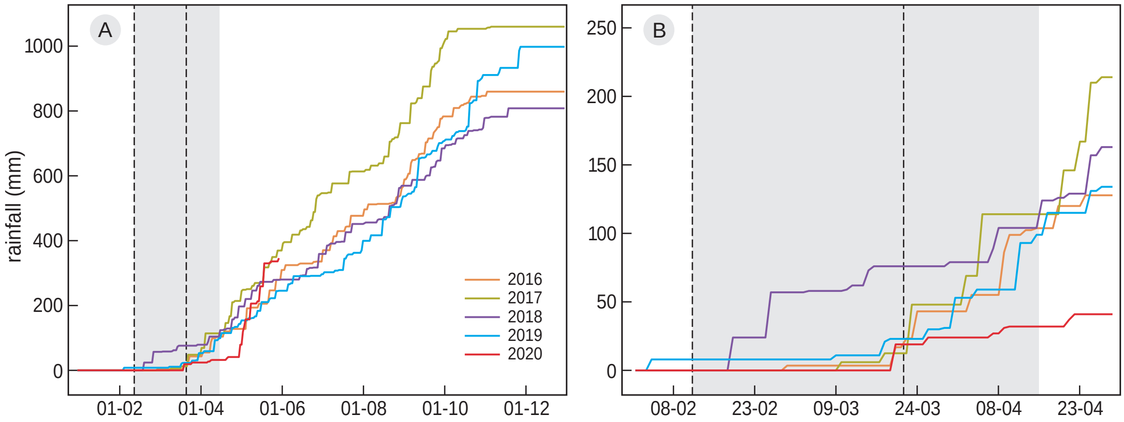

Figure 1. Cumulative amount of rainfall within the study area in Comoé National Park for the years 2016–2020. The grey area marks the period with NDVI and arthropod measurements, and dashed lines show the period in which Pied Flycatchers were tracked. Measurements were obtained on a daily basis by means of a rain gauge (data: Comoé Research Station, Ivory Coast).

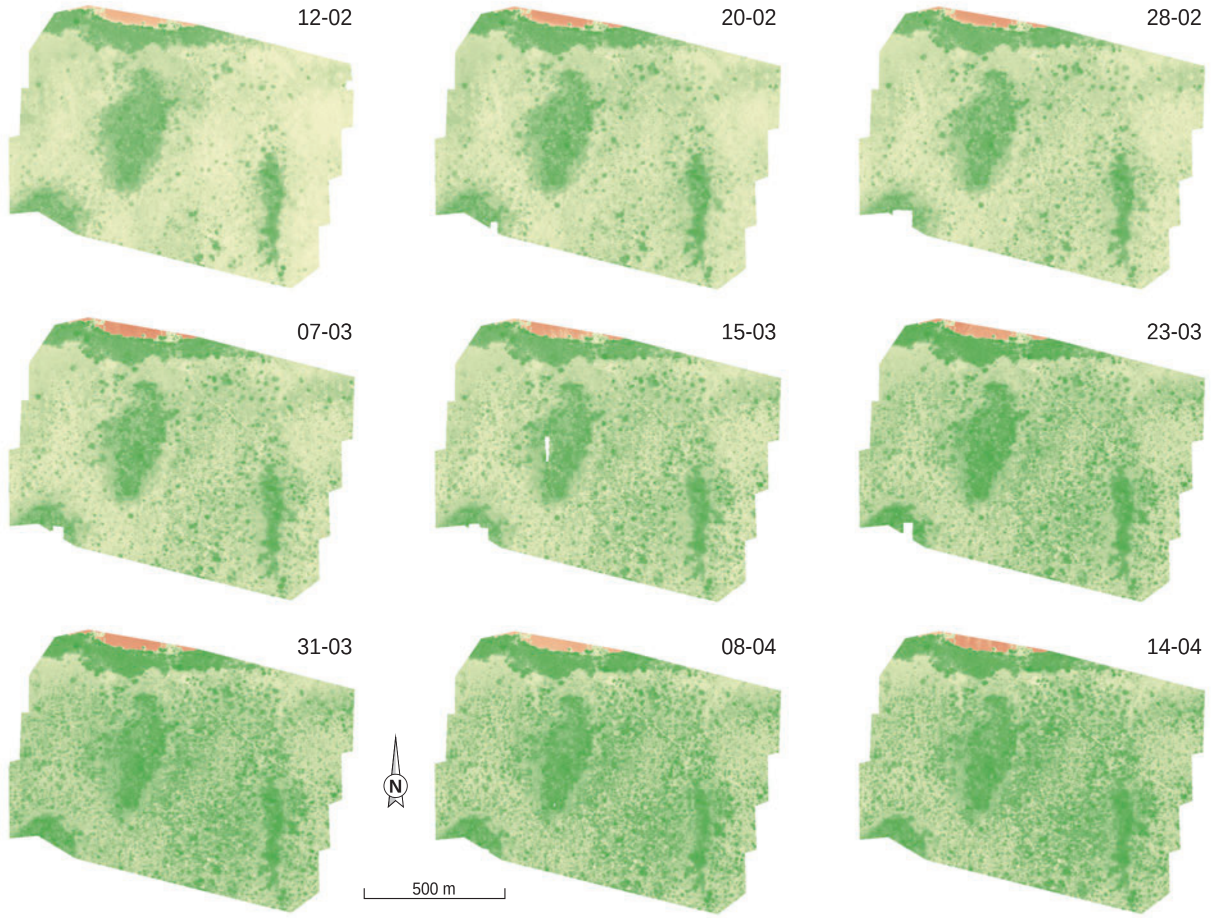

Figure 2. NDVI maps of the study area in Comoé National Park for the period 12 February to 14 April 2020. NDVI values are based on multispectral images that were collected every eight days by means of a drone.

$R^2 = 0.10$), which showed a positive linear effect on NDVI ($\chi^2_1 = 17.75$, $P < 0.001$, $\beta = 0.43 \pm 0.10$). Most of the remaining variance could be attributed to site and date specific influences that were captured by random effects within our model (conditional $R^2 = 0.94$; Table S1B).

For the canopy layer we observed large variation in temporal NDVI patterns between tree species. In some species NDVI increased steeply (e.g. *Burkea africana*) while for others it remained relatively constant over time, at either high (e.g. *Cola cardifolia*) or low (e.g. *Anogeissus leiocarpus*) values (Figure 3). Based on our ground-based measurements we found that these temporal patterns were largely attributable to changes in foliage cover (marginal $R^2 = 0.50$), for which we established a quadratic relationship with NDVI ($\chi^2_2 = 492.77$, $P < 0.001$; $\beta_{\text{linear}} = 0.53 \pm 0.05$, $\beta_{\text{quadratic}} = -0.18 \pm 0.06$). The remaining variance is largely explained by species, date and tree-specific characteristics that were captured by the random effects in the model (conditional $R^2 = 0.93$, Table S1A).

Although the relationship between foliage cover and NDVI for the canopy and grass layer was differently shaped, respectively quadratic and linear, the slopes of these relationships were similar within the range observed in both layers (Figure S3). The additional main difference in NDVI (canopy: estimate = 0.35 ± 0.03; grass layer: estimate = 0.22 ± 0.03) could be explained by the relative level of these layers in the vegetation. Aerial imagery of an open canopy might capture vegetation from underlying strata whereas an open grass layer will mostly reveal the soil surface, which might again differ in reflectance due to the presence or absence of (burned) litter (Table 1). Therefore, ground-truthing results supported the use of $\text{NDVI}_{\text{temp}}$ to describe changes in foliage cover (i.e. foliation) and $\text{NDVI}_{\text{habitat}}$ to express spatial differences that are mostly related to habitat.

General movement behaviour

In total we tracked the spatial behaviour of nine flycatchers for an average duration of 28 days (range: 14–40; Table 2, Figure S3A). During this period individuals visited on average 5.22 sites (range: 3–9). The number of detections were unequally distributed across the daylight period. The number of receptions peaked between 8:00 and 9:00 am., and subsequently decreased throughout the day with a slight rise around 16:00 (Figure S3B). During the tracking period three of the nine individuals remained undetected within the node grid for periods of one to six days (Figure S4). Given that these birds were still detected by the directional antenna's, this pattern likely arose from periods of residence beyond the detection range of the nodes. We also observed individual movements within the node grid, as apparent from the use of new sites and changes in relative presence at previously visited sites (Figure 4).

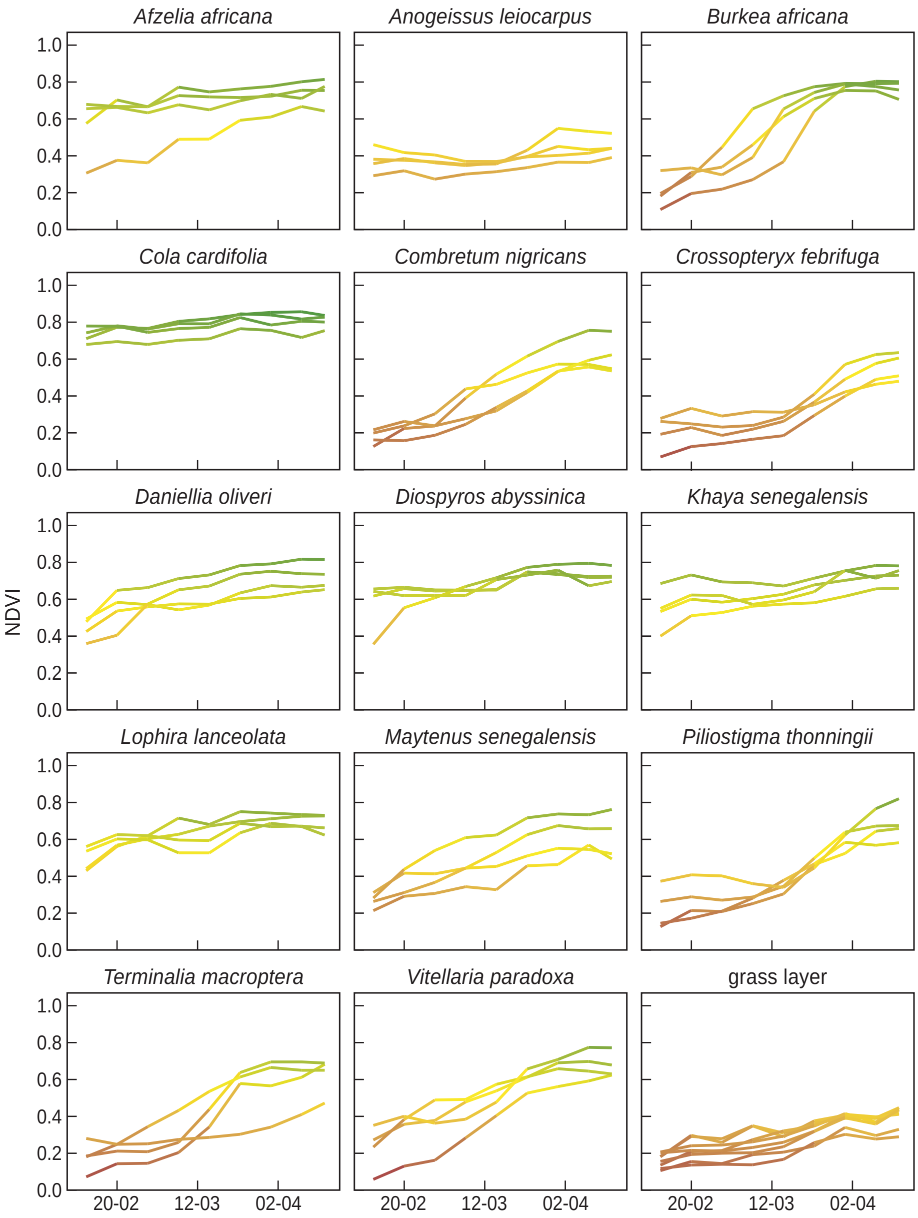

Figure 3. NDVI values for the canopy of individual trees and grass layer transects during the period 12 February to 14 April 2020. Lines show average NDVI values for individual tree crowns (n = 4 per species) and grass layer transects (n = 8) over time. Colour coding matches the y-axis.

Table 2. Meta-data of radio-tagged Pied Flycatchers captured between 10 February and 15 March 2020 ($n = 13$). Detailed site use data is shown for individuals that were included in the site use analysis ($n = 9$). The total number of detections are given for nodes (local receivers used in the site use analysis) and directional Yagi antennas (used for detecting presence or absence within a larger range); Age: 2 = second calendar year/first winter, >2 = after second calendar year; # presence = total number of 5-minute periods that a bird was located within 50 m from a node; # periods = number of 8-day periods during which a bird was tracked.

Tag-ID	Sex	Age	Start tracking	# detections (Nodes)	# detections (Yaggi)	Last seen (Yaggi)	Included	Tracking days	# presence used	# periods NDVI$_{habitat}$	# periods NDVI$_{temp}$	# nodes visited	# nodes/period (range)
61332A2D	Female	> 2	7 Mar	92.057	7.925	3 May	Yes	14	689	3	3	3	2–3
6133522A	Female	2	25 Feb	107.194	11.008	21 Apr	Yes	25	304	4	4	9	2–7
6133522D	Female	2	22 Feb	196.887	292.285	30 Apr	Yes	28	748	5	5	3	2–3
61520019	Male	2	13 Feb	153.205	36.641	18 Apr	Yes	37	375	3	2	7	4–7
6152002A	Male	> 2	14 Feb	350.043	545.483	5 May	Yes	36	2039	6	5	7	1–5
61520766	Female	> 2	24 Feb	104.717	122.829	6 May	Yes	26	513	4	4	4	4–4
61521978	Male	2	20 Feb	35.847	576	4 May	Yes	30	194	5	5	4	2–4
61524B66	Female	> 2	6 Mar	96.229	40.693	17 Apr	Yes	15	242	3	3	4	2–4
61611E2A	Male	2	10 Feb	94.334	1.474	2 May	Yes	40	516	6	5	6	1–6
61335200	Female	2	28 Feb	13.189	30.495	30 Apr	No	–	–	–	–	–	–
61347F00	Female	> 2	4 Mar	3.982	4.223	7 May	No	–	–	–	–	–	–
61523319	Female	> 2	15 Mar	0	0		No	–	–	–	–	–	–
61526652	Male	> 2	13 Feb	44.842	1.546	3 May	No	–	–	–	–	–	–

Photo 5. Edge of a forest patch with view towards the savannah. The undergrowth mostly consists of evergreen shrubs, whereas the canopy layer is dominated by *Anogeissus leiocarpus*, a deciduous tree species that typically occurs in forest edges (19 December 2018).

However, all flycatchers showed a high degree of within-individual overlap in site use over time (E_h used sites: mean: 0.95 ± 0.03, range: 0.90–1.00).

NDVI change

All sites showed an increase in NDVI during the tracking period (Figure 5A). However, the amount of foliation ($NDVI_{temp}$) differed between habitats (interaction $NDVI_{habitat}$ × date: $\chi^2_1 = 117.83$, $P < 0.001$). The savannah showed higher foliation rates than forest habitats (Figure 5B). The used $NDVI_{temp}$ of tracked flycatchers will thus increase during the tracking period, whereas the specific amount of increase can be influenced through habitat selection.

Habitat selection

On average, the tracked flycatchers increased their use of savannah towards the end of the tracking period, as demonstrated by a linear decrease in used $NDVI_{habitat}$ over time ($\chi^2_1 = 13.85$, $P < 0.001$, $\beta_{(10\ days)} = -0.02 \pm 0.01$; Figure 7A). During the same period the average amount of foliation across used sites increased at an accelerating rate (Figure 7B), as shown by a quadratic increase of $NDVI_{temp}$ over time ($\chi^2_2 = 512.59$, $P < 0.001$, $\beta_{linear} = 0.31 \pm 0.02$, $\beta_{quadratic} = 0.11 \pm 0.01$).

When considering site-use behaviour, there appeared to be a negative relationship between the available $NDVI_{habitat}$ within home-ranges and the degree to which

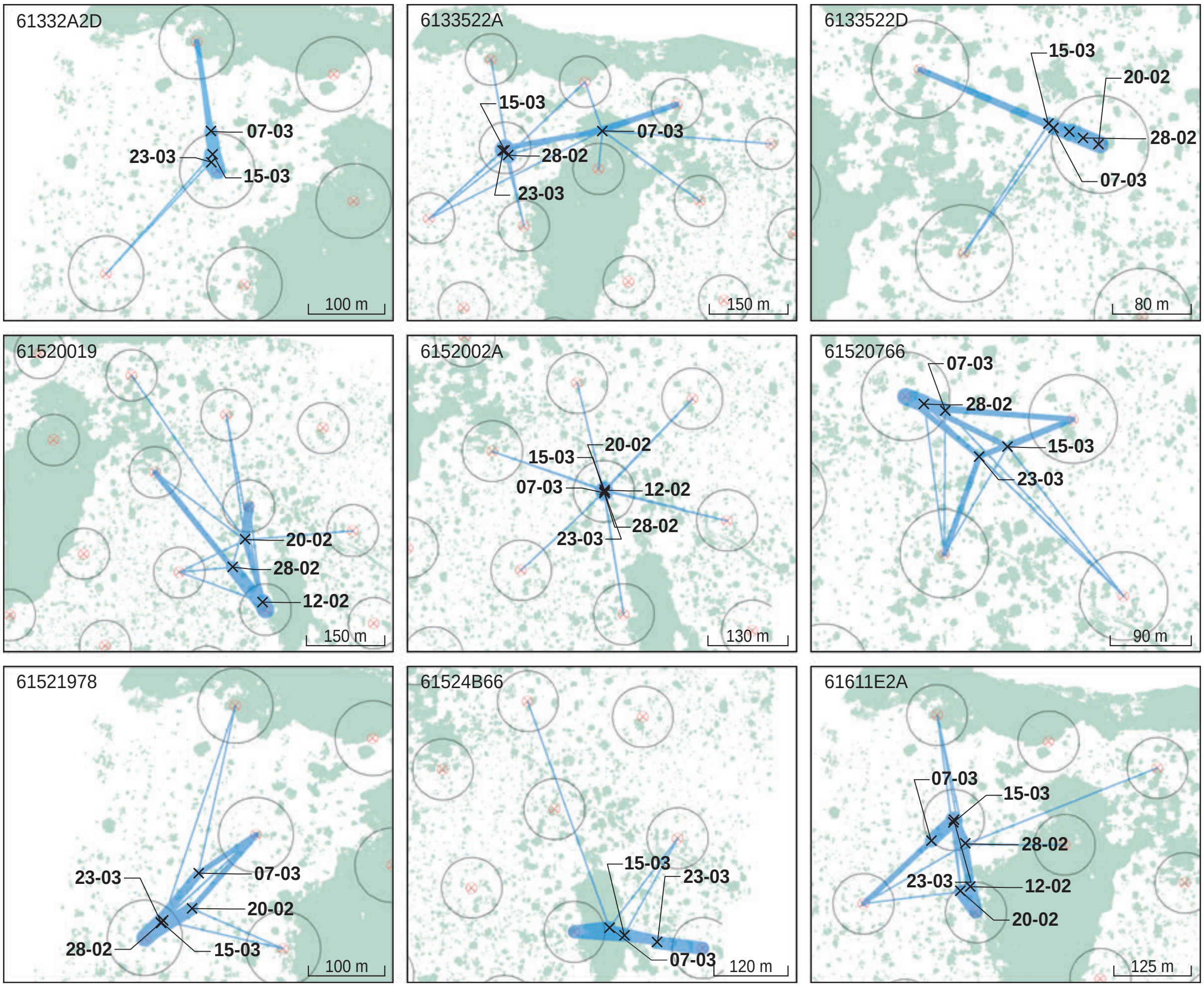

Figure 4. Individual movements of radio-tracked Pied Flycatchers based on presence near nodes. Red markers depict node locations, for which the circles mark the range (radius: 50 m) around nodes in which the presence of individuals was measured. For illustrative purposes the centre location is plotted per 8-day period (black cross), calculated as the mean location of all visited nodes weighted for the proportion of visits. Blue lines connect the centre locations to the associated nodes, where line width represents the proportion of visits (range: <0.01–1.00). The green areas in the background show the distribution of forest patches (large filled areas), and individual canopies in the savannah.

individuals visited the same sites over time ($\beta = -0.28 \pm 0.15$, $F_{1,7} = 3.67$, $P = 0.10$). This suggested a tendency of individuals with more forested home-ranges to visit fewer of the same sites over time. In accordance, individuals with more forested home-ranges showed a larger temporal decrease in used $\text{NDVI}_{\text{habitat}}$ (available $\text{NDVI}_{\text{habitat}}$ × date: $\chi^2_1 = 7.46$, $P < 0.01$). Consequently, the variation in used $\text{NDVI}_{\text{habitat}}$ between individuals decreased during the tracking period. All individuals used a narrower range of $\text{NDVI}_{\text{habitat}}$ values at the end of the tracking period, values that more closely resembled savannah (Figure 8B). Given the differences in foliation between the habitats we expected changes in habitat-use to result in a higher increase of $\text{NDVI}_{\text{temp}}$ over time for birds with more forested home-ranges. However, we did not find a significant interaction between $\text{NDVI}_{\text{habitat}}$ and date ($\chi^2_1 = 0.27$, $P = 0.60$). Instead, the outcomes showed a consistent difference over time, insofar that the used $\text{NDVI}_{\text{temp}}$ of birds within more forested home-ranges was relatively lower compared to birds with more savannah in their home-range ($\chi^2_1 = 11.61$, $P < 0.001$). At the same time the absolute values of used $\text{NDVI}_{\text{temp}}$ increased for all individuals as a result of overall foliation in the environment ($\chi^2_1 = 130.00$, $P < 0.001$, Figure 8B).

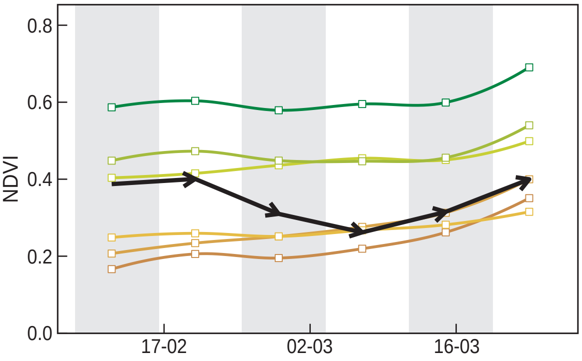

Figure 6. Example of individual site use for tag-ID '61611E2A'. To establish site selection we compared the weighted mean NDVI of visited sites (arrowed line) to the mean NDVI of the total home-range (coloured lines). These comparisons were done at the level of 8-day periods (marked by alternating grey and white areas), yielding repeated measurements of the same individuals over time.

NDVI and arthropod abundance

To further assess the potential role of food availability in the relationship between NDVI and site use of flycatchers, we explored the connection between NDVI and arthropod abundance, using the data of 3218 captured arthropods (malaise: $n = 1567$, pitfalls: $n = 1651$), belonging to eight taxonomic orders (malaise: $n = 7$, excluding Blattodea, pitfalls: $n = 7$, excluding Lepidoptera). The temporal variation in the numbers of captures between taxonomic orders and trap types was large (Figure 9).

A set of six models best explained the observed variance in the numbers of captured terrestrial arthropods (Table S2A). All these models include an interaction between $\text{NDVI}_{(x)}$ and order, with $\text{NDVI}_{(x)}$ measurements taken within a range between 10 m and 60 m from trap sites. The model-averaged estimates for $\text{NDVI}_{\text{habitat}}$ from these models reflect habitat-related

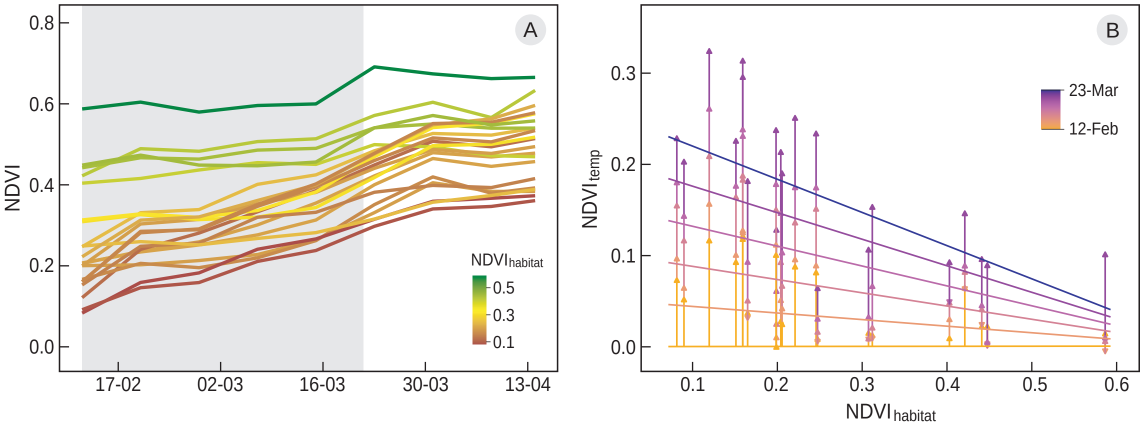

Figure 5. (A) Average NDVI for areas around nodes (radius: 50 m, $n = 21$) per 8-day period. Line colours are based on the NDVI on 12 February, which is used as a proxy for habitat ($\text{NDVI}_{\text{habitat}}$). (B) Interaction between $\text{NDVI}_{\text{habitat}}$ and the amount of foliation ($\text{NDVI}_{\text{temp}}$) for the same sites, measured as the difference in NDVI relative to 12 February. Arrows show the trajectories of the same sites over time. Lines represent the estimates marginal means for $\text{NDVI}_{\text{temp}}$, based on the interaction between the linear effects of Date and $\text{NDVI}_{\text{habitat}}$, which indicate a larger amount of foliation in savannah, i.e. low $\text{NDVI}_{\text{habitat}}$, compared to forest.

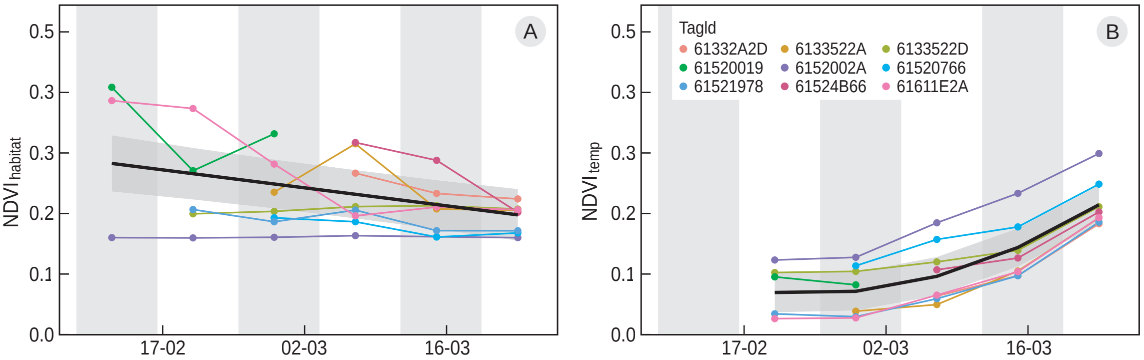

Figure 7. (A) Average $\mathrm{NDVI}_{\mathrm{habitat}}$ values of sites used by radio-tracked flycatchers ($n = 9$) over time. The black line gives the linear effect of date (± 95% CI) based on an LMM, which shows an average decrease in the use of forest over time. (B) Average $\mathrm{NDVI}_{\mathrm{temp}}$ based on the same used locations. The model prediction shows a quadratic increase in the amount of foliation within used sites over time. The alternating grey and white areas mark the 8-day periods that are used in the analysis.

differences in captures per order (Table 3). In the orders Hemiptera and Orthoptera the amount of forest habitat was positively associated with the number of captures, whereas this association was negative in Hymenoptera. For $\mathrm{NDVI}_{\mathrm{temp}}$ the confidence interval of the estimate only excludes zero in Hemiptera, where the number of captures were positively associated with the amount of foliation. For the malaise traps the number of captures were best explained by seven models that incorporate $\mathrm{NDVI}_{(x)}$ measurements from a radius of 30 m to 70 m (Table S2B). Similar to the pitfalls, all of these models included an interaction between $\mathrm{NDVI}_{(x)}$ and taxonomic order. The model-averaged estimate for $\mathrm{NDVI}_{\mathrm{habitat}}$ did not exclude zero in any of the orders, reflecting no effect of habitat on the captured numbers of flying arthropods, although for some orders there appeared to be a directional tendency (Table 3). For $\mathrm{NDVI}_{\mathrm{temp}}$ the model-averaged estimates did not include zero for Diptera and Lepidoptera, demonstrating a positive association between foliation and the number of captured Lepidoptera while the numbers of captured Diptera showed an opposite trend.

Based on these model outcomes we expected different dynamics in arthropod abundance between habitats (Figure 10). During the study period some

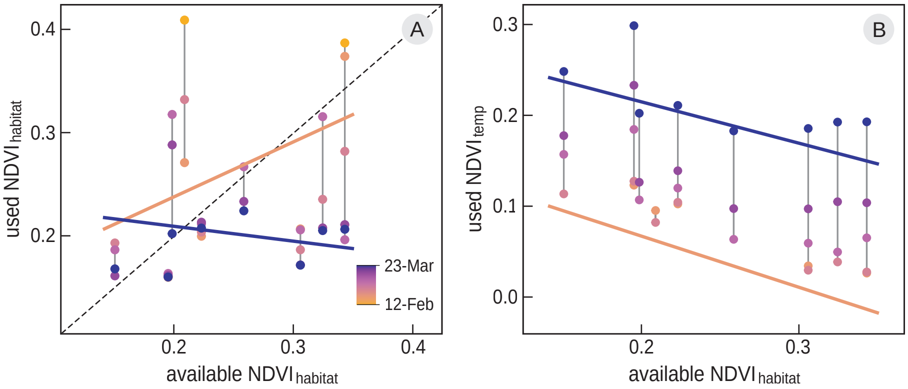

Figure 8. (A) Relationship between the average $\mathrm{NDVI}_{\mathrm{habitat}}$ within individual home ranges (available $\mathrm{NDVI}_{\mathrm{habitat}}$) and sites that were used by individuals (used $\mathrm{NDVI}_{\mathrm{habitat}}$) over time. Lines connect observations of the same individuals. The dashed line illustrates when birds use sites in proportion to their availability. The model predictions show that birds increased their use of savannah during the study period, where birds with more forested home-ranges show the change in habitat use over time. (B) Relationship between the average $\mathrm{NDVI}_{\mathrm{habitat}}$ within individual home-ranges (available $\mathrm{NDVI}_{\mathrm{habitat}}$) and the change in NDVI relative to 12 February ($\mathrm{NDVI}_{\mathrm{temp}}$), for sites that were used by individuals over time. The predictions show that, at any time during the study, birds with forested home-ranges used sites with lesser amounts of foliation compared to birds with savannah home-ranges. The predictions in both graphs are based on an LMM with an interaction between the linear predictors date and available $\mathrm{NDVI}_{\mathrm{habitat}}$, and given for 20 February (when $\mathrm{NDVI}_{\mathrm{temp}} > 0$) and 23 March.

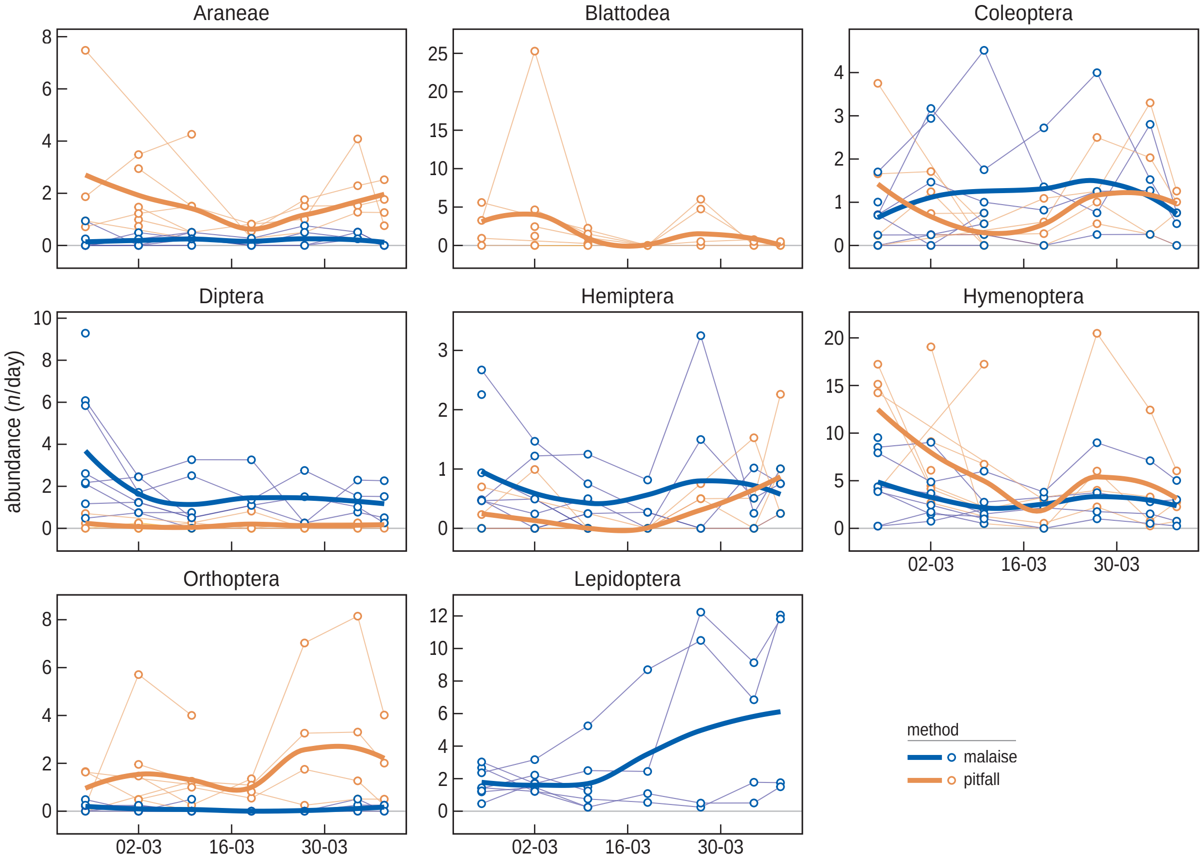

Figure 9. Average daily captures per 4-day trapping period for different orders. Lines connect datapoints from the same trapping locations and fattened lines show the overall smoothed means per trapping method. Note that the y-axis differs between taxonomic orders.

orders should become more abundant on the savannah (e.g. flying Lepidoptera and ground dwelling Hemiptera) whereas other orders should remain stable (e.g. ground-dwelling Orthoptera) or decrease (e.g. ground-welling and flying Hymenoptera). The predictions for forest habitat showed little variability over time, where in general arthropod abundance is predicted to remain stable throughout the study period.

DISCUSSION

Movement behaviour

By tracking small-scale movement behaviour, we show that flycatchers are flexible in their habitat use. In particular we show that flycatchers occupy both savannah and forest habitat and narrow their site use to savannah during the second half of the non-breeding season, where individuals with more forested home-ranges show the largest change over time. These changes involve adjustments in site use intensity of sites that were revisited over time, and the abandonment or use of new sites within home-ranges. Flexibility in site use of flycatchers is in accordance with previous findings of Stünzner-Karbe (1996) who also observed individual movements from forest to savannah during the second half of the non-breeding season, with more birds present in forest at the start of the non-breeding period. Our observations from previous seasons (based on colour-ringed individuals) confirm this pattern. These movements are likely typical for non-breeding flycatchers, and, for example, not a result of aberrant rainfall conditions during our study. Similar behaviour has been described in other species, for example by Brunner *et al.* (2022), who observed individual home-range adjustments between the wet and dry season in non-breeding Swainson's Warblers *Limnothlypis swainsonii* in the Neotropics. Brunner *et al.* (2022) found, as we did, that during the dry season some individuals already occupied home-ranges within the habitat that was later (during the wet season) also used by birds from other habitats, with the consequence that individuals differed in the degree to which they adjusted their site use over time.

Arthropods

Flycatchers influence their access to specific arthropod groups by moving between habitats that seasonally vary in arthropod abundance. We first show that the variation in NDVI due to habitat and foliation can have a different association with arthropod numbers, which also depends on taxonomic orders. These findings are in line with previous findings of taxa-specific numerical trends of arthropods in relation to seasonality in African environments (Nummelin & Nshubemuki 1998, Wagner 2001) as well as in the distribution of taxa across small-scale habitats (Blaum *et al.* 2009). Furthermore, we show that the relationship between vegetation conditions and arthropod numbers differs between our sampling techniques. This might be due to variation in this relationship among lower taxonomic levels, where our trap types (targeting either ground-dwelling or flying arthropods) will likely capture different species and life-stages that belong to the same orders (McCravy 2018). Altogether, these results do not support a simple relationship between NDVI and arthropod abundance, and therefore we require specific insight into the diet and behaviour of flycatchers to understand the implications for food availability.

A diet analysis by means of DNA meta-barcoding revealed that flycatchers in our study populations have a rather limited diet. Most of the consumed prey belong to two groups, namely Hymenoptera, and specifically the ant genus *Camponotus* (c. 40% of consumed biomass) and Lepidoptera (c. 20% of consumed biomass; Ouwehand, Verkuil & Both unpubl. data, based on two seasons in 2018–2019; see Verkuil *et al.* (2022) for methods). Our estimated trends for Hymenoptera from pitfall samples (which in contrast to flying Hymenoptera from malaise traps mostly concern ants, including the genus *Camponotus* as confirmed by DNA meta-barcoding of captured ants; Ouwehand, Verkuil & Both unpubl. data) show that ants are overall more abundant in the savannah than in forest, whereas their numbers are predicted to decrease during the time that flycatchers increase their use of this habitat (Figure 10). These opposing patterns contradict the notion that flycatchers track the availability of their most prominent prey group, *Camponotus* ants. The results do however show such a pattern for the second most prominent prey group, Lepidoptera, for which the predicted increase within savannah is in line with the increased use of this habitat by flycatchers. However, it is important to note that our estimated trend for Lepidoptera is solely based on adults caught in malaise traps, whereas our field observations indicate that the

Table 3. Model-averaged estimates and 95% confidence interval for the log-linear regression coefficients $NDVI_{habitat}$ and $NDVI_{temp}$, based on the best performing models for arthropod captures within pitfall and malaise traps (Table S2). Weighted estimates for which the confidence interval does not include zero are shown in bold.

		Pitfall		Malaise	
Parameter	**Taxonomic order**	Estimate ± SE	95% CI	Estimate ± SE	95% CI
(1) $NDVI_{habitat}$	Aranea	0.87 ± 1.36	–1.82 – 3.56	2.96 ± 2.03	–1.04 – 6.96
	Blattodea	2.37 ± 1.50	–0.58 – 5.32	– –	– –
	Coleoptera	–2.89 ± 1.60	–6.03 – 0.26	1.52 ± 1.66	–1.75 – 4.79
	Diptera	–0.56 ± 2.12	–4.75 – 3.62	1.86 ± 1.62	–1.32 – 5.05
	Hemiptera	**4.77 ± 2.09**	**0.65 – 8.89**	**2.39 ± 1.73**	**1.02 – 5.79**
	Hymenoptera	**–3.05 ± 1.36**	**–0.57 – –0.36**	–0.73 ± 1.59	–3.87 – 2.41
	Lepidoptera	– –	– –	–0.50 ± 1.63	–3.71 – 2.70
	Orthoptera	**4.03 ± 1.42**	**1.22 – 6.83**	4.54 ± 2.40	–0.19 – 9.26
(2) $NDVI_{temp}$	Aranea	–0.12 ± 2.69	–5.42 – 5.19	2.35 ± 3.21	–3.98 – 8.68
	Blattodea	–2.56 ± 3.07	–8.61 – 3.48	– –	– –
	Coleoptera	3.07 ± 3.10	–3.04 – 9.18	–0.26 ± 1.97	–4.15 – 3.62
	Diptera	–0.05 ± 4.22	–8.36 – 8.27	**–4.12 ± 1.93**	**–7.92 – –0.32**
	Hemiptera	**12.09 ± 4.03**	**4.15 – 20.03**	2.14 ± 2.24	–2.26 – 6.55
	Hymenoptera	–1.95 ± 2.97	–7.81 – 3.91	–1.75 ± 1.71	–5.11 – 1.62
	Lepidoptera	– –	– –	**5.78 ± 1.77**	**2.29 – 9.27**
	Orthoptera	0.73 ± 3.09	–5.37 – 6.82	1.96 ± 4.38	–6.66 – 10.59

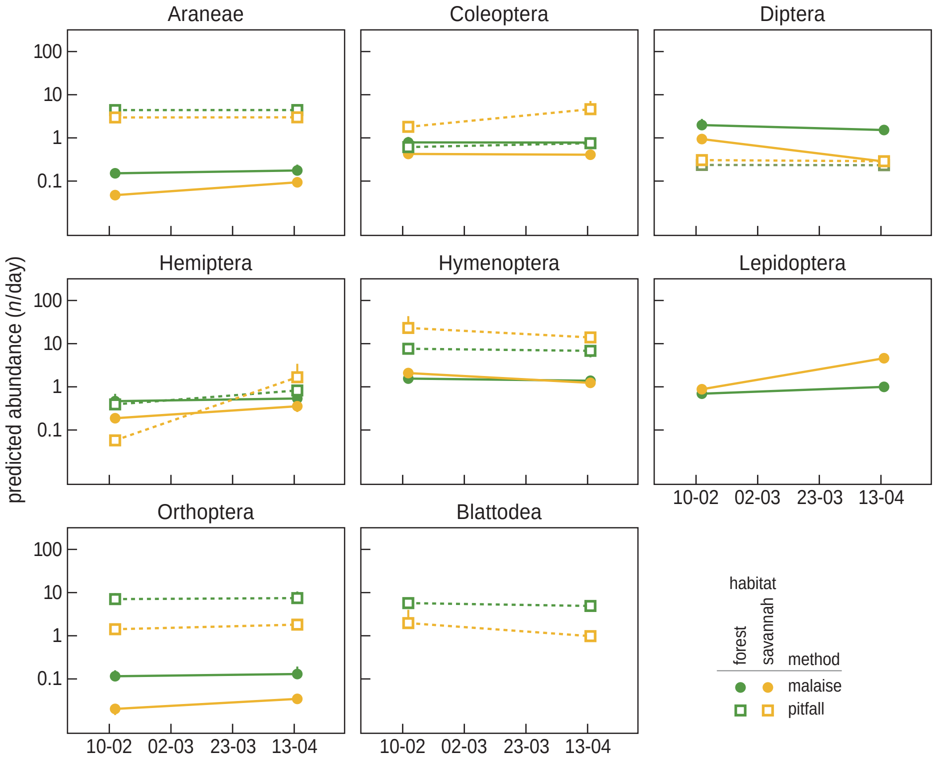

Figure 10. Estimated abundance for different arthropod orders within savannah and forest habitats over time. Predictions are based on the average $\text{NDVI}_{\text{habitat}}$ and $\text{NDVI}_{\text{temp}}$ of each habitat and their effects on arthropod abundance based on the model selection for malaise traps and pitfalls. Estimates are given for 12 February and 14 April, where error bars give the range of predictions from all selected models (Table S2).

Lepidoptera consumed by flycatchers also includes caterpillars. The absence of this prey group from our samples is likely due to the fact that caterpillars occur within canopies, whereas pitfall and malaise traps are designed to capture arthropods that move on or near the ground (McCravy 2018). Similarly, other arthropods groups that occur higher in the vegetation are likely underrepresented in our sampling, whereas foraging observations during our study show that the majority of foraging attempts of flycatchers were directed at leaves or branches within trees (85.7% on a total of 77 foraging attempts from 6 individuals), which is similar to that found by other studies (Stünzner-Karbe 1996, Salewski *et al.* 2002). Therefore, our findings might only have partially disclosed the dynamics of those arthropods that are relevant for foraging flycatchers. Despite these caveats, our results support the possibility that flycatchers use small-scale habitat heterogeneity to track seasonal changes in food availability.

We acknowledge that by only considering (log-) linear relationships with vegetation greenness, our models are unable to account for the short-term fluctuations in arthropod abundance that we observed (Figure 9, also see Ouwehand *et al.* 2023). Our field observations also confirm that flycatchers often exploit ephemeral food sources. This includes the previously described cases where we observed flycatchers foraging on temporal outbursts of caterpillars in canopies of *Daniellia olliveri* with fresh-grown leaves (February 2020) and in one occasion on berries in fruiting *Gymnosporia senegalensis* bushes (February 2018). Furthermore, we observed individuals that specifically foraged in flowering trees, for example in *Khaya senegalensis*, *Crossopteryx febrifuga* and *Terminalia macroptera*, where they might profit from concentrations of flower-visiting arthropods. In these examples the occurrence of food sources is associated with particular leafing and flowering stages of specific tree species. We recognize that such fine-scale dynamics are not addressed in our analysis, although they are relevant for explaining short-term behaviour. This is also indicated by Ouwehand *et al.* (2023) who found that individuals attained a higher body mass on days with higher numbers of arthropods. Despite the existence of such short-term dynamics, we are confident that the average trends in arthropod abundance are still useful for understanding the changes in flycatcher behaviour over a longer timescale (i.e. the duration of our study period).

Our findings are a demonstration of the need for restraints in using NDVI as a general proxy for food conditions of insectivorous migrants. By showing that the relationship between arthropod abundance and vegetation greenness depends on the specific taxa and sampling methods we challenge the validity of the common use of NDVI as a proxy for food availability, especially within studies that have no insight into the diet and foraging behaviour of species during the non-breeding season (e.g. Schaub *et al.* 2011, Kristensen *et al.* 2013, Thorup *et al.* 2017, Knight *et al.* 2019). We acknowledge that the small-scale dynamics in our study might differ from the dynamics that occur on the large scales that are considered in most tracking studies, however the applicability of large-scale simplified measurements will equally depend on the specific (small-scale) ecology of species. In addition, the applicability of large-scale NDVI as a resource proxy might be further hampered since such measurements discount small-scale heterogeneity in vegetation conditions, which we show plays a key role in the availability of resources during various parts of the season. In conclusion, we consider insight into the food sources of species and their relationship with vegetation conditions is a precondition for using remote sensing-derived proxies of food availability in studies on insectivorous songbirds. For most migratory species this will require investment in ecological fieldwork in situ.

Potential resources

Next to changes in the abundance of food resources, the observed changes in habitat use might also be influenced by an increase in food requirements over time. Our study period coincides with the period that flycatchers replace their tertials and a proportion of the body feathers, which on average starts around halfway through February and continues until the end of March (Salewski *et al.* 2004). During this period individuals experience rising energetic costs due to feather growth (Lindström *et al.* 1993). Furthermore, the end of our study period overlaps with pre-migratory fuelling, starting around 5 March within our population (Ouwehand *et al.* 2023). This period is characterized by hyperphagia and a steep increase in body weight (Ouwehand *et al.* 2023). Given the importance of successful fuelling for the timing of migration and survival and the role of plumage quality on sexual selection (Sirkiä & Laaksonen 2009), the fitness benefits of access to food resources will increase during these phases. As a result, individuals might favour access to food over other factors that might negatively affect (short-term) fitness, such as predation risk, during these stages. Such a shifting trade-off might already by itself (i.e. regardless of any change in food availability between habitats) initiate a change in habitat use over time, for example if predation risk is higher on the savannah. Although we lack insight into the role of predation, our observations suggest that movements towards the savannah coincide with increasing food sources, and are therefore unlikely to be solely driven by changes in risk-taking behaviour.

Photo 6. Flycatcher with radio-transmitter (7 March 2020).

The habitat shift that we observed near the end of the non-breeding period is an important part of individual movement strategies that unfold throughout the whole non-breeding season. As described by Stünzner-Karbe (1996), flycatchers are generally absent on the savannah during the first half of the non-breeding season, but start to settle in this habitat after (human-induced) burning in December-January. Colour-ring observations show that these settlers come from nearby forest patches where they occupy territories during the first part of the non-breeding season (Stünzner-Karbe 1996, Ouwehand & Bil unpubl. data). Based on these findings it is likely that those individuals that were already present within (homogenous) savannah sites at the start of our study (February) may have moved in from other places during the preceding months. These individuals probably express different movement behaviour to those birds that occupy home ranges on the boundary between forest and savannah habitat (i.e. the individuals with more heterogeneous territories in this study), for which (colour ring) observations indicate that they are more likely to stay within the same home-range throughout the non-breeding period (Ouwehand & Bil unpubl. data, Stünzner-Karbe 1996). The tendency of birds in savannah habitats showing a more consistent use of their home-range during the period of our study, might therefore differ from the site-use consistency of these birds during the entire non-breeding season.

We hypothesize that flycatchers can influence their susceptibility to seasonality through settlement decisions. Flycatchers are territorial during the non-breeding season (Stünzner-Karbe 1996, Salewski 1999, Willemoes *et al.* 2018), and individuals are therefore limited in their ability to access sites that are already occupied by conspecifics (Krebs 1982). Given this competition individuals might occupy sites that are temporarily unexploited, in order to ensure access to future (ephemeral) resources. This is in line with our finding that individuals did not often abandon sites, despite the changes in site use intensity. In this scenario, individuals with territories that include both forest and savannah habitat might explore a wider variety of resources under different circumstances, i.e. a more stable food supply in forest habitats during the dry season, and additional food in the more dynamic savannah during moult and fuelling. Alternatively, birds that do not occupy edge territories can relocate their territories from forest to the savannah when conditions improve in the latter. However, these individuals are thereby more reliant on resources in either habitat. Such benefits of heterogeneous territories are in accordance with the distribution of flycatchers in our study area, with highest densities of territories along the edges between forest and savannah habitat (see also Stünzner-Karbe 1996).

In conclusion, our findings indicate that small-scale heterogeneity likely plays a key role in the ability of flycatchers to cope with seasonal dynamics on a local scale. We do need further insight into the fitness benefits and existence of alternative movement strategies to determine the degree to which flycatcher populations rely on sedentary behaviour and small-scale habitat heterogeneity.

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SAMENVATTING

Het is vaak onduidelijk hoe trekkende zangvogels omgaan met seizoensveranderingen in Afrika, met name bij soorten die gedurende de winterperiode gebruikmaken van dezelfde verblijfplaats. In dit onderzoek richten we ons specifiek op de vraag of zangvogels zich aan seizoensveranderingen kunnen aanpassen door gebruik te maken van kleinschalige variatie in hun omgeving. Hiervoor hebben we naar overwinterende Bonte Vliegenvangers *Ficedula hypoleuca* in het nationaal park Comoé, Ivoorkust, gekeken. Met behulp van radiozenders laten we zien dat er halverwege de verblijfperiode van de vliegenvangers, in begin februari, relatief veel variatie bestaat in de mate waarin verschillende individuen het bos en de savanne gebruiken. In de daaropvolgende periode gaan individuen uit het bos meer gebruikmaken van plekken op de savanne, waarbij uiteindelijk alle individuen hoofdzakelijk dit habitat gebruiken. Deze verandering vindt plaats gedurende een periode van vergroening van de savanne, die gepaard gaat met een toename in het aanbod van specifieke insectengroepen. De verschuiving in het habitatgebruik van de vliegenvangers is daarmee mogelijk een reactie op een verbeterde voedselbeschikbaarheid in de savanne vergeleken met het eerste deel van de verblijfsperiode, waarin het bos waarschijnlijk betere voedselcondities biedt. Op basis van deze uitkomsten vermoeden we dat de vliegenvangers bij voorkeur territoria in bosranden vestigen, waardoor ze zowel toegang tot het bos als de savanne hebben, en zo beter in staat zijn om onder verschillende omstandigheden (voedsel)bronnen te vinden. Deze bevindingen bevestigen het belang van kleinschalige heterogeniteit voor de mate waarin de vliegenvangers gedurende de winterperiode op dezelfde plek kunnen verblijven.

RÉSUMÉ

Il est difficile de savoir comment les passereaux migrateurs font face aux changements saisonniers en Afrique, notamment les espèces qui sont fidèles à leurs territoires hivernaux. Nous avons donc spécifiquement cherché à savoir si ces espèces peuvent s'adapter en exploitant la diversité des habitats présents au sein de leur territoire. Pour cela, nous avons étudié des Gobemouches noirs *Ficedula hypoleuca* hivernant dans le Parc National de la Comoé, en Côte d'Ivoire. En utilisant des émetteurs radio, nous avons montré que début février, à la moitié de la période d'hivernage, il existe une importante variation individuelle dans les taux d'utilisation des habitats forestiers et de savane. Par la suite, les individus qui privilégiaient la forêt commencent à exploiter davantage la savane, jusqu'à ce qu'en fin d'hiver tous utilisent principalement cet habitat. Cette modification se produit pendant la période de verdissement de la savane, qui s'accompagne d'une augmentation de l'abondance de certaines espèces d'insectes. Ce changement dans l'utilisation des habitats est donc probablement une réponse à une augmentation de la disponibilité alimentaire dans la savane par rapport à la première partie de l'hiver, pendant laquelle la forêt est probablement plus nourricière. Sur la base de ces résultats, nous soupçonnons que les Gobemouches noirs établissent de préférence des territoires en lisière de forêt, ce qui leur donne accès à la fois à la forêt et à la savane. Ils sont donc plus à même de trouver suffisamment de nourriture tout au long de leur séjour. Ces résultats confirment l'importance de l'hétérogénéité des habitats à petite échelle, qui permet aux gobemouches d'occuper un même territoire pendant toute la période hivernale.

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SUPPLEMENTARY MATERIAL

Table S1. Regression coefficients and random effects of the linear mixed models for foliage cover and NDVI within the canopy layer and grass layer. The significance of the fixed effects is based on a type II Wald Chi-square test.

Model	**Fixed effect**	**Estimate**	**SE**	**χ^2**	***P***
(1) Canopy layer	Intercept	0.35	0.03		
	Foliage cover	0.53	0.05	113.34	<0.001
	Foliage cover (squared)	–0.18	0.06	10.46	0.001
	Random effect	**Variance**			
	Tree-ID	0.003			
	Species	0.003			
	Date (factor)	0.004			
	Residual	0.002			

Model	**Fixed effect**	**Estimate**	**SE**	**χ^2**	***P***
(2) Grass layer	Intercept	0.22	0.03		
	Foliage cover	0.43	0.10	17.75	<0.001
	Random effect	**Variance**			
	Transect ID	0.003			
	Date (factor)	0.001			
	Residual	0.000			

Table S2. Model selection results for the number of arthropods as function of NVDI for both malaise and pitfall trap samples. Only the best performing models with a cumulative AICc weight of >0.95, are shown. Models are ranked from lowest to highest AICc. OR = taxonomic order.

Model	NDVI Radius (m)	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Marginal R^2	Conditional R^2
(1) Pitfall traps								
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	30	24	1147.6	0.00	0.31	0.31	0.53	0.61
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	50	24	1148.5	0.85	0.20	0.51	0.53	0.61
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	40	24	1149.0	1.33	0.16	0.66	0.52	0.61
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	20	24	1149.0	1.34	0.16	0.82	0.52	0.60
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	60	24	1150.5	2.87	0.07	0.89	0.52	0.61
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	70	24	1152.0	4.38	0.03	0.93	0.52	0.61
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	80	24	1152.5	4.93	0.03	0.95	0.51	0.61
(2) Malaise traps								
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	50	24	1204.6	0.00	0.22	0.22	0.63	0.83
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	30	24	1205.1	0.49	0.17	0.39	0.63	0.83
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	60	24	1205.4	0.73	0.15	0.55	0.63	0.83
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	40	24	1205.5	0.82	0.15	0.69	0.62	0.83
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	80	24	1205.7	1.06	0.13	0.82	0.63	0.83
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	70	24	1206.0	1.36	0.11	0.93	0.63	0.82
OR × NDVI$_{habitat}$ + OR × NDVI$_{temp}$	90	24	1207.7	3.05	0.05	0.98	0.63	0.82

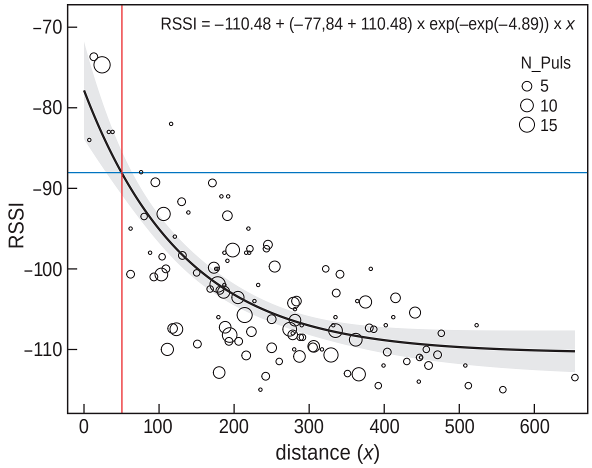

Figure S1. Relationship between received signal strength indicator (RSSI) and distance, based on node-receptions of tagged individuals that were simultaneously located in the field ($n = 115/5$ individuals, data collected between 26 February and 12 March). Each point represents at least one received signal from a known distance. In case a node received multiple pulses from a stationary bird, we considered it as one observation for which we calculated the mean RSSI. Dot size represents the pooled number of receptions per observation (average n/data point = 3.97, range 1–18). The plotted curve represents the best model fit based on an asymptotic regression function (±95% CI), for which the equation is given. The blue line shows the value of RSSI = –88.05, which was used as a cut-off to select observations within a threshold of 50 m (red line) from the nodes.

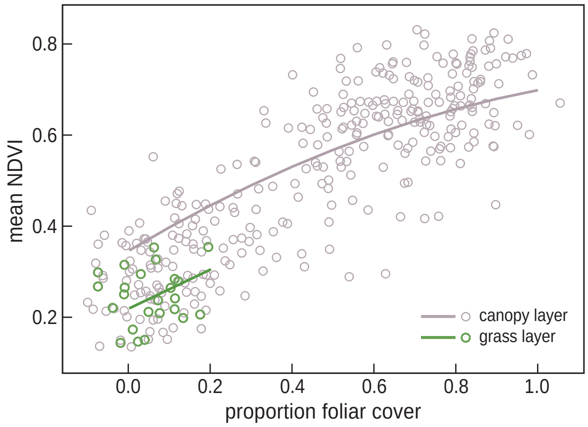

Figure S2. Relationship between NDVI and foliage cover for the canopy and grass layer. Points represent (repeated) observations of 48 individual trees within the canopy layer (total $n = 276$), and eight transects within the grass layer (total $n = 24$). Lines show the predictions from the linear mixed models for foliage cover and NDVI (Table S1).

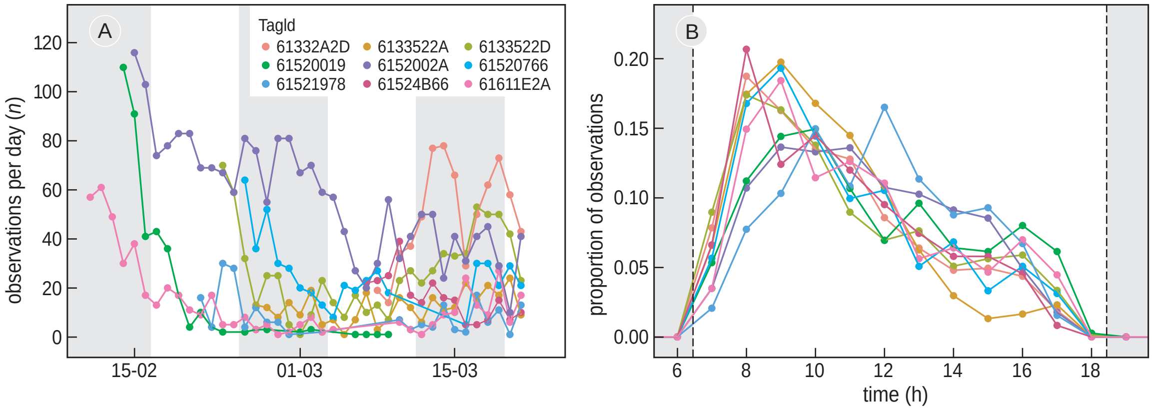

Figure S3. (A) Number of daily site-use observations for individuals included in the analysis (n = 9). The alternating grey and white areas mark the 8-day periods that are used in the analysis. (B) Distribution of observations throughout the day for the same site-use observations, calculated as the proportion of observations per hour. Dashed lines show the time of sunrise and sunset within the study area on 3 March 2020.

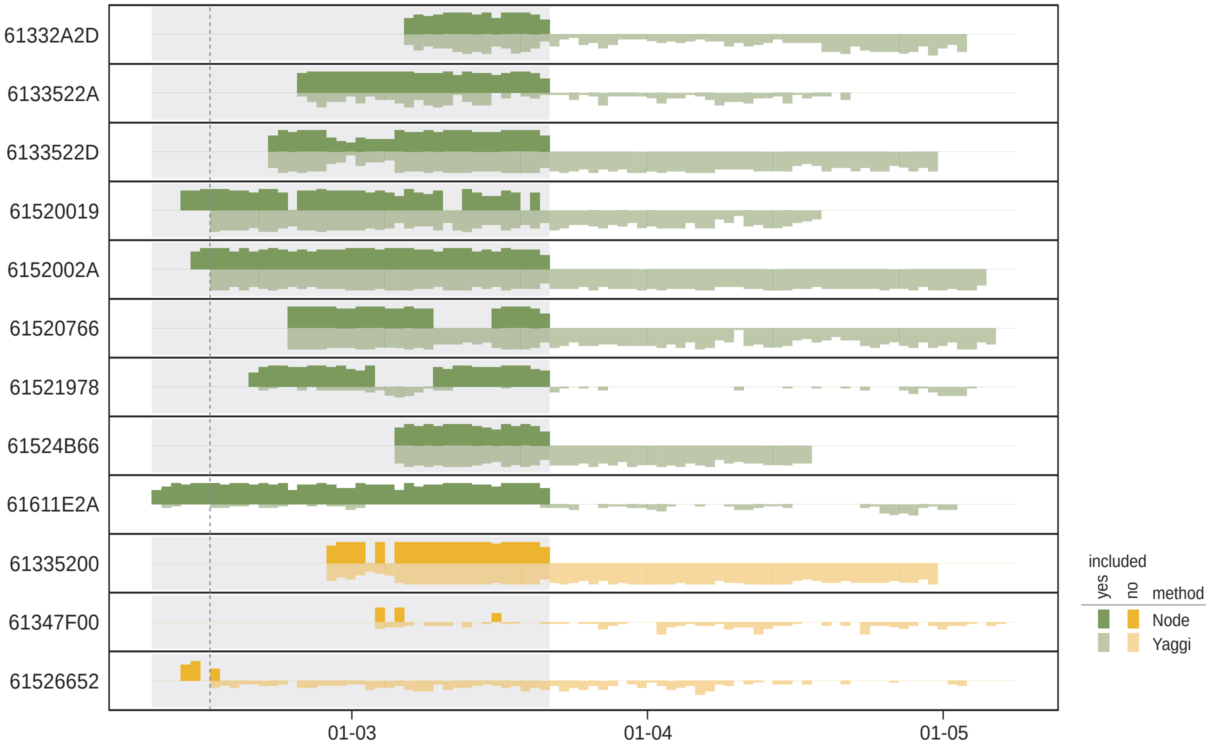

Figure S4. Daily presence of tagged individuals based on detections by nodes (dark coloured/upper bars) and directional Yaggi antenna's (light coloured/lower bars). The height of the bar shows the number of hours per day during which an individual was observed at least once (max = 12 h). The dashed line shows the start of the period during which Yaggi antennas were activated. Note that this figure is based on unfiltered data, including detections estimated at >50 m from nodes that are not included in the site selection analysis.

The fortunes of migratory birds from Eurasia: being on a tightrope in the Sahel

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Many studies have shown that rainfall in the Sahel has a great influence on population trends of European bird species that spend the northern winter there. African bird species living in the Sahel, notably those that forage on the ground, have also shown significant declines, but independent of rainfall. This paper summarises the results of field data gathered in the entire Sahel and evaluates the many factors that play a role in the fortunes of birds. (1) Rainfall determines the extent of open water in the Sahel, and by default the fortunes of waterbirds. In recent decades the surface area of open water has increased because water tables have risen. (2) Rainfall south of the Sahel determines river discharge and therefore the surface of floodplains in the Sahel. Rainfall has a cumulative effect: discharges disproportionally decrease after a number of years with little rain, and *vice versa*. During the dry season (October–May), floodplains gradually dry out. In wet years, water – and hence food – is available for birds up to their departure, but in dry years birds become concentrated at the few remaining pools and so present an easy target for bird-trappers. Further desiccation leads to starvation. (3) After a year with heavy rainfall, seed is available in abundance, but a dry year results in a shift in the plant community and a low seed supply. Mortality among seedeaters increases under dry conditions. (4) In dry years, trees lose their leaves early on, forcing arboreal birds into a diminishing number of trees that retain leaves. In extremely dry years trees die on a massive scale and it takes many years before tree coverage is restored. When droughts occur in quick succession, as in 1972/73 and again in 1984/85, tree recovery is slow and populations of arboreal birds will continue to decline, or recover slowly or only partly (as for Eurasian Wryneck *Jynx torquilla* and Common Redstart *Phoenicurus phoenicurus*, whose numbers remain reduced by tenfold when compared to the 1950s, despite a slight recovery). Rainfall in the Sahel gradually recovered after 1990, as did the woody vegetation albeit with a delay, and many migratory bird species responded accordingly. Subalpine Warblers *Curruca subalpina* and Western Orphean Warblers *Curruca hortensis* have increased as much as threefold to fivefold since 1990. Southern European bird species, wintering in the arid parts of southern Sahara and Sahel, were hit the hardest during the Great Drought in 1969–1992, but also recovered the fastest, particularly strongly once rainfall had significantly recovered.

Despite clear links between migratory birds and rainfall-related variables in their wintering areas, a migrant's world is more complicated than exclusively being constrained by rainfall. In the past century, the human population in sub-Saharan Africa has increased tenfold, with far-reaching consequences. (1) Cattle numbers boomed and grazing pressure increased greatly. Heavy grazing means lower grass seed production, especially of seeds that birds prefer. The steep decline of granivorous birds over the past several decades is therefore no surprise. (2) Every year, 2% of the savannah is converted into farmland. This is unfavourable for most, but not all, bird species. Farmers selectively favour particular tree species on their land (and remove the rest), by which the resulting tree species composition differs from the typical variety found in savannah. The shift in tree composition particularly disfavours birds wintering in both the more arid and more humid vegetation zones. Arboreal birds wintering in the intermediate zone have benefitted from the expansion of farming, because their preferred tree (White Thorn *Faidherbia albida*) is favoured by farmers and has

become more abundant. (3) The expansion of agriculture is most obvious in the low-lying, slightly more humid and more fertile soils, much to the detriment of flooded forests, which being important refuges during droughts are particularly rich in birds. Most flooded forests have disappeared from the Sahel. (4) Millions of hectares of humid woody savannah have been converted into Cashew *Anacardium occidentale* plantations since 1980. Cashew plantations are almost completely devoid of birds and so constitute a significant loss of a once highly diverse wooded habitat. (5) The proliferation of *Prosopis juliflora*, an exotic tree species resembling an acacia, has locally and regionally displaced indigenous acacia species. *Prosopis* attracts few birds in comparison with acacias. (6) Irrigation and dam construction have decimated the size of floodplains in Senegal, Mali, Nigeria and Chad, with corresponding effects on many bird species, especially waterbirds, that concentrate in these areas. (7) Massive bird catches, such as those in the Inner Niger Delta after about 1990, did not occur in the past when cheap nylon nets (initially used for fishing) were not yet available. Furthermore, storage and transportation of trapped birds were impossible until ice and vehicles became available. (8) Large bird species have virtually disappeared from the Sahel due to human predation, especially in the densely populated western part. As a wintering area for most migratory Eurasian birds, the Sahel has become less attractive. Far fewer migratory birds now use the Sahel than half a century ago, not least because many populations have substantially declined in numbers. Furthermore, several European migrant species increasingly are wintering north of the Sahara, which may relate to impoverished conditions in the Sahel, but as likely to significant habitat changes in Europe and the pace of climate change.

Key words: Sahel, drought, land use, trends in bird populations

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Africa has long been a ‘black box’ in the study of migratory birds. Wolda (1915) wondered why Eurasian Wrynecks *Jynx torquilla* in his Dutch study plot showed such steep population fluctuations. Was it excessive rainfall during the breeding season, resulting in high mortality among nestlings and fledglings, a supposition that might explain the unexpected lack of a further increase following four consecutive years of doubling numbers? He made no mention of Africa, where most Wrynecks spend half of their lives and where his birds in 1913 had coped with an extreme drought such as occurs only a few times in a century. In the late 1960s, when standardized monitoring of breeding birds had just started in some European countries, another sudden drop in numbers of a long-distance migrants was noted. At least for Common Whitethroat *Curruca communis*, the startling decline in Britain (Batten 1971) was consistent with reported declines of the same magnitude in Germany (–87%), Denmark (–68%) and France (–69%; Berthold 1973). In accordance with the ‘Zeitgeist’ – the negative impact of organo-chlorines on birds was only just proven and the talk of the town – Berthold (1973, 1974) tended to blame the use of persistent pesticides in wintering areas and/or along the way from wintering to breeding areas. As pointed out by Winstanley *et al.* (1974), exposure to toxic chemicals during migration and on the wintering grounds, although plausible, was not enough to explain that the Common Whitethroat was declining over large areas without any sign of recovery. For such a wide-ranging phenomenon, high mortality in its Sahel wintering range due to lack of rainfall, was a far likelier scenario. Since then, the link between rainfall in the sub-Sahara and the fortunes of Palearctic migrants wintering in the Sahel became established in many studies (listed in Table S1).

It was precisely this variation in rainfall that Hulme (2001) emphasised as crucial in the sub-Saharan ecosystem: “the African Sahel provides the most dramatic example worldwide of climate variability that has been directly and quantitatively measured. There is no such thing as *normal* rainfall in the Sahel. What is *normal* to the Sahel is not some annual rainfall total averaged over 10, 50 or 100 years, but variability of the rainfall supply in space and from year-to-year and from decade-to-decade." The drought in 1968, which caused the collapse of the European breeding population of the Common Whitethroat, was followed by several, even more disastrous dry years in the Sahel in the 1970s and 1980s, a period known in West Africa as *la Grande Sécheresse*, or the Great Drought. The consequences were far-reaching for many long-distance migrants from Europe, such as for Sand Martin *Riparia riparia* (Cowley 1979), Purple Heron *Ardea purpurea* (Den Held 1981) and Sedge Warbler A*crocephalus schoenobaenus* (Peach *et al.* 1991).

Still, were the declines of migrant birds from 1969 onwards due only to dry years in the Sahel? This was not evident in the view of Sinclair & Fryxell (1985) who stressed that the problem in the Sahel was not a temporary lack of rain but human-induced overgrazing and, consequently, desertification where soil denudation might have caused climatic changes towards aridity. If true, the future would look bleak for the many European bird species wintering in sub-Saharan Africa. However, even if Sinclair & Fryxell's vision proved to be too gloomy, it is unlikely that rainfall would be the only variable determining the fortunes of migrant birds in Africa. With a 640% increase of the human population over the period 1950–2022, and an accompanying increase in the exploitation of natural resources, it is clear that major changes have been underway in the Sahel for a long time.

Half a century has passed since the famine years in the Sahel shocked the world in the 1970s and early 1980s. Rainfall in the Sahel has gradually recovered from 1994 to the present (2022). We are now in a better position to distinguish the impact of rainfall from long-term changes in human land-use. But the question of what is going on in the Sahel has remained as compelling as ever, the main reason being the scarcity of actual field data. In the Sahel, we cannot rely on long-term bird monitoring systems (but see Ishong *et al.* 2022). One of the alternatives is to revisit sites where bird counts have been performed in the past, as applied in Nigeria. No differences over short time intervals were found in northern Nigeria, where 16 sites had been counted in 2002 (Wilson & Cresswell 2006) and again in 2007 (Stevens *et al.* 2010). Cresswell *et al.* (2007), also in northern Nigeria, repeated the counts of Jones *et al.* (1996) from 1993/1994 in 2001/2002, and found no changes in bird densities on farmland but much lower densities in a forest reserve where tree density had declined by 82%, correlating with an 88% decline of Western Subalpine Warblers *Curruca iberiae*. In 2004, Thiollay (2006) repeated his road counts from 1971–1973 and concluded that the once common large bird species in Mali and Niger were extinct or had become extremely rare (see also Ogada & Buij 2011, Mullié *et al.* 2017). For NW Senegal, bird densities based on counts in 1960–1962 (Morel 1968a), 1969–1976 (Morel & Morel 1974, 1992) and 1993–1994 (Tréca *et al.* 1996) were compared to counts in the same plots in 2014–2015 (Zwarts *et al.* 2018). Most birds had declined (by –37 to –97%). Thus, the few available data suggest a large decline of the birds in the Sahel between 1960–1970 and 2010.

Monitoring schemes on the European breeding grounds can be used to follow the fluctuating numbers of migrant birds wintering in the Sahel from year to year (e.g. Vickery *et al.* 2014), but resident African birds in the Sahel, being much commoner than migrants, are omitted from this equation. Population changes as measured by European bird surveys include the effects of environmental conditions in the European breeding areas in addition to carry-over effects from the wintering grounds and incurred *en route*. For European Turtle Dove *Streptopelia turtur* (Brown & Aebischer 2004), Eurasian Wryneck (Coudrain *et al.* 2010), Northern Wheatear *Oenanthe oenanthe* (Arlt & Pärt 2017) and Whinchat *Saxicola rubetra* (Fay *et al.* 2021), the emphasis on variables explaining declines has been increasingly focused on habitat fragmentation and destruction on the breeding grounds. As most of these species spend a larger part of their lives in Africa than in Europe, and fare worse than bird species remaining in Europe in winter (Berthold *et al.* 1998, Sanderson *et al.* 2006, Heldbjerg & Fox 2008, Kamp *et al.* 2020, Bowler *et al.* 2021), the chances are that Africa is a leading actor in the weal and woe of long-distance migrants. However, the declining species cover an enormous range of habitats within their African wintering areas, from wetlands to drylands and from deserts to humid forests, using a similarly wide range of foraging niches, feeding in trees and water, on the ground and in the air. What then is the common denominator for so many species in decline, if there is any?

Newton (2008), reviewing the available studies on the Palearctic-Afrotropical Migration System, concluded that the conditions in Africa obviously affect the breeding population in Europe, but also that this conclusion is based on correlative analyses only. His remark that more field work in Africa is needed to understand the mechanisms remains valid. In the interim, some field studies in Africa have seen the light of day, but on-the-ground studies are still outpaced by correlative desk studies, and by a wide margin. The lack of basic data collected in the field in African wintering areas is monumental in scope, notably (1) where do birds occur, (2) in what densities and (3) in what habitats? In 2011, we set out to systematically collect these data over the entire Sahel, an area about the size of the European continent (10 million km^2). We use the word Sahel as a catch-all term for the more than 1000 km-wide transient zone from the hyper-arid Sahara (<100 mm rain/year) south to the hyper-humid zone (>1200 mm rain/year). A series of papers is testimony to the results, which mostly refer to the distribution of migrant and resident bird species across the wider Sahel (Zwarts *et al.* 2023 in series). They include habitat selection by foraging birds, educated estimates of population sizes and within- and between-year variations therein relative to dry and wet years. This basic information is used to quantify the impacts on birds of the increasing grazing pressure by livestock and the current conversion of savannah into farmland (Zwarts *et al.* 2023h,i). The present paper synthesises and elaborates this information in an attempt to answer the question why so many migrants are in decline. Obviously, the impact of the highly variable Sahelian rainfall is an important covariable in our analysis, and much attention is paid to the annual variation in rainfall and associated variables, such as extent of riverine floodplains (Zwarts *et al.* 2009), seed production of herbaceous vegetation (mainly annual grasses; Bille 1977, Le Houérou 1989: 96–103, Hegazy & Lovett-Doust 2016: 179–201), density of arthropods (Gillon 1983) and availability of foliage, flowers and fruit of trees and shrubs (Poupon & Bille 1974, Hiernaux *et al.* 1994, Brandt *et al.* 2019). To complicate matters, the effect of rainfall on these variables is often delayed and may accumulate over the years, becoming visible in fewer areas of open water following reduced groundwater level and long-term effects on tree mortality and subsequent regeneration.

Although the present paper will present some correlative analyses, our first aim is to summarise the (limited) field data from Africa and use it in our search for explanations on why so many Eurasian long-distance migrants are in long-term decline. The partial increases of some migrant species concomitant to the recovery of rainfall in the Sahel since the mid-1990s (and notably in the 2010s) are put in perspective.

METHODS

Monitoring schemes for breeding birds are now available for most European countries (https://pecbms.info/country/), but only nine out of 35 schemes started as early as the 1970s (3) or 1980s (6). The British scheme started in 1962 (territory mapping in farmland, ditto in woodland from 1964 onwards). This non-random census was superseded by the BBS, using random line transects, in 2000, with both schemes running in parallel between 1994 and 2000; Freeman *et al.* 2007). The CBC/BBS is the only monitoring scheme covering a short period before the Great Drought started in the late 1960s. For our purposes we used the joint CBC/BBS indices for the UK since 1966 (Woodward *et al.* 2020, www.bto.org/birdtrends), as well as the schemes initiated in Denmark in 1975 (Eskildsen *et al.* 2021, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet), Sweden in 1976 (www.fageltaxering.lu.se/resultat/trender), The Netherlands in 1984 (Boele *et al.* 2022, www.sovon.nl) and Germany in 1990 (Kamp *et al.* 2021). For bird species with restricted, often southern European, breeding ranges, the combined trends are used, based on a shorter time span (PECBMS 2020, www.pecbms.info). Additional sources were used to calculate pre-1984 population trends for some species (e.g. Purple Heron, Eurasian Wryneck, Common Redstart *Phoenicurus phoenicurus* and Sand Martin; Zwarts *et al.* 2009).

We will mostly use the 'lumped names' of species that recently have been split, i.e. Bonelli's Warbler for Western and Eastern Bonelli's Warbler *Phylloscopus bonelli* and *P. orientalis*, Orphean Warbler for Western and Eastern Orphean Warbler *Curruca hortensis* and *C. crassirostris*, Subalpine Warbler for Western and Eastern Subalpine Warbler and Moltoni's Warbler *Curruca iberiae*, *C. cantillans* and *C. subalpine* and Black-eared Wheatear for Western and Eastern Black-eared Wheatear *Oenanthe hispanica* and *O. melanoleuca.*

RESULTS

Population trends during and after the prolonged Sahel drought

The rainfall in the Sahel declined between 1969 and 1984 and slowly – with alternating positive and negative changes – improved thereafter, reaching the 20th century's mean by 2010 (Figure S4A). If rainfall were the main determinant of population size of birds spending the winter in the Sahel, populations should have declined between the late 1960s and the mid-1980s, followed by recoveries in the decades to follow. Taking 1984 as the tipping point, trends before and after the drought's nadir were compared to test the prediction whether Sahel rainfall indeed governs trends of birds depending on the Sahel in winter. Only the British monitoring series – referring to peripheral populations of which wintering areas are mostly confined to coastal west-Africa (Wernham *et al.* 2002) – was sufficiently long to cover the entire period (Table 1).

The half century of monitoring in Britain revealed a plethora of contrasting trends among long-distance migrants. The expected decline during the Sahel Drought and subsequent increase concomitant to improving rainfall was found, for example, in Common Whitethroat and Common Redstart, two species wintering in the core regions of the Sahel, but another species from the wetlands in the same region, Sedge Warbler, declined during the drought without a subsequent recovery during the years with improved rainfall. Three other Sahelian species even continued their decline after the drought-related crash in the 1970s and 1980s, namely European Turtle Dove, Lesser Whitethroat *Curruca curruca* and Western Yellow Wagtail *Motacilla flava*. Species wintering in the more humid zones south of the Sahel also declined during the Great Drought (such as Garden Warbler *Sylvia borin*, Common Nightingale *Luscinia megarhynchos*) and also did not recover in the years of improved rainfall. Surprisingly, several species wintering in climate zones with >1000 mm rainfall per year showed their steepest declines in more recent years, including Common Cuckoo *Cuculus canorus*, Common House Martin *Delichon urbicum*, Willow Warbler and Spotted Flycatcher *Muscicapa striata*. By far the strongest increase after the 1984-nadir was recorded in species wintering mainly north of the Sahara, notably Common Chiffchaff *Phylloscopus collybita* and Eurasian Blackcap *Sylvia atricapilla* (Table 1). Thus, although the expected effect of Sahel rainfall on population changes was found in some species, a majority of species wintering in the sub-Sahara continued their drought-related decline from the 1970s–1980s in subsequent years, even with much improved rainfall.

Table 1. The average annual change in the population index (%) of 17 migrant species in the UK during the Sahel Drought between 1966 and 1984 ('dry') and between 1984 and 2019, during a period of gradually increasing – but still below long-term average – rainfall in the Sahel ('humid'). Arboreal species marked light green, wetland species dark green and aerial feeders blue. Rain refers to the species-specific average annual rainfall (mm) in the main distribution areas in Africa (from Zwarts *et al.* 2023a,b and unpubl. data); two species (marked N) stay mainly north of the Sahara and two species winter in Africa further south (marked S). Bird data from Woodward *et al.* 2020 (www.bto.org/birdtrends).

Rain	Migrant species	Dry	Humid
S	Common Cuckoo	–0.1	–2.2
407	European Turtle Dove	–0.7	–2.8
S	Barn Swallow	–0.1	0.2
900	House Martin	0.7	–2.1
>1000	Willow Warbler	–0.2	–1.8
N	Common Chiffchaff	–2.6	7.8
500	Sedge Warbler	–2.0	0.0
>1000	Reed Warbler	0.5	2.3
N	Eurasian Blackcap	0.8	7.5
>1000	Garden Warbler	–1.9	0.2
318	Lesser Whitethroat	0.7	–0.3
466	Common Whitethroat	–4.7	2.3
>1000	Spotted Flycatcher	–1.8	–2.4
>1000	Common Nightingale	–3.6	–2.2
608	Common Redstart	–2.7	2.4
413	Western Yellow Wagtail	–0.7	–2.0
926	Tree Pipit	0.1	2.5

Shorter time series, starting in the 1980s, are available for populations on the European continent that are less peripheral than the British one (Table 2). Trends were consistent across species and countries, with but few anomalies. Species in decline did so in all the four above countries and elsewhere in Europe (e.g. Eurasian Wryneck, Willow Warbler, Spotted Flycatcher, Northern Wheatear, Ortolan Bunting *Emberiza hortulana*), as did species on the increase (Common Chiffchaff, Eurasian Blackcap, Common Whitethroat, Common Redstart). Divergent trends were found, for instance, in Common Grasshopper Warbler *Locustella naevia*, European Pied Flycatcher *Ficedula hypoleuca* and Tree Pipit *Anthus trivialis* which increased in The Netherlands but declined in surrounding countries.

Despite the recovery of the rainfall in the Sahel, many migratory species that had declined during the Great Drought continued their downward trend, except species wintering mainly north of the Sahara and in southern Europe, several southern European warblers and some species confined to wetlands. Of the species spending the winter in sub-Saharan Africa, 18 feed on the ground. Most ground-foraging species are in decline, often by >1% or even >2% per year, irrespective of the climate zones of wintering areas (European Turtle Dove, Eurasian Wryneck, Whinchat, Ortolan Bunting). Decline was also the overriding trend in 22 arboreal species, with a preponderance of species wintering south of the Sahel in humid forests (Eurasian Golden Oriole *Oriolus oriolus*, Wood Warbler *Phylloscopus sibilatrix*, Willow Warbler, Icterine Warbler *Hippolais icterina*, Garden Warbler, Barred Warbler *Curruca nisoria*, Spotted Flycatcher, Thrush Nightingale *Luscinia luscinia*, Common Nightingale, European Pied

Table 2. Change in population size (%/year) of 51 migratory bird species in the United Kingdom (UK), The Netherlands (NL), Germany (D), Denmark (DK), Sweden (SU) and Europe (EU) between 1976–1985 and 2012–2021, of which 22 species are foraging in Africa in trees and shrubs, 6 in the air, 5 in wetlands and 18 in drylands on the ground. The series is shorter for some species in England (after 1994), The Netherlands (after 1989) and Europe (after 1991 or 1998) (marked with a *italic* font). The series for Germany runs from 1990 to 2018. Rain refers to the average annual rainfall (mm) in the main distribution area of the species in Africa (from Zwarts et al. 2023a,b and unpubl. data); two species (marked N in the first column) mainly stay north of the Sahara and nine species winter in central, eastern and southern Africa (marked S). Annual declines of ≥1% are marked orange and increases of ≥1% blue. Sources: UK (Woodward *et al.* 2020, www.bto.org/birdtrends), The Netherlands (Boele *et al.* 2022, www.sovon.nl), Germany (Kamp *et al.* 2021), Denmark (Eskildsen *et al.* 2021, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet), Sweden (www.fageltaxering.lu.se/resultat/trender), Europe (PECBMS 2020, www.pecbms.info/).

Rain	Migrant species	UK	NL	D	DK	SU	EU
300	Common Quail			1.8			
S	Common Swift	*–1.7*		–1.0	–0.6	–1.9	–0.5
400	Great Spotted Cuckoo						*1.6*
S	Common Cuckoo	–2.2	–0.8		–1.0	–1.2	–1.2
407	European Turtle Dove	–2.8	–2.9	–2.2			–2.3
600	White Stork						1.5
500	Western Marsh Harrier		–1.1		8.3	4.7	10.8
449	Eurasian Hoopoe						*–0.6*
S	European Bee–eater						*1.1*
518	Eurasian Wryneck		–1.7	–2.7		–1.7	–1.6
S	Red-backed Shrike			0.4	–1.9	–1.1	*–0.1*
S	Lesser Grey Shrike						*–2.5*
419	Woodchat Shrike						–1.9
S	Eurasian Golden Oriole		–1.1	–0.2	0.3	–2.1	0.2
161	Greater Short-toed Lark						*1.0*
400	Sand Martin	0.6	8.5	–2.3	0.0	–1.8	
S	Barn Swallow	0.2	0.8	–0.5		–1.8	–0.3
900	Common House Martin	–2.1	*1.7*	–1.7	–0.0	–1.7	–1.3
>1000	Red-rumped Swallow						*1.5*
>1000	Wood Warbler	*–2.1*	–0.6	–1.5	–2.4	–0.5	–1.1
451	Bonelli’s Warbler (W+E)						*–0.2*
>1000	Willow Warbler	–1.8	–0.6	–2.0	–3.0	–0.9	–1.0
N	Common Chiffchaff	7.8	1.0	0.8	4.2	7.7	2.7
>1000	Great Reed Warbler		*–3.6*				1.7
500	Sedge Warbler	0.0	7.7	19.0	–1.2	–1.4	–0.2
>1000	Eurasian Reed Warbler	2.3	1.1	1.2	–0.2	–0.9	–0.7
S	Marsh Warbler		–0.1	–1.5	0.0	1.6	–0.7
874	Melodious Warbler						*–0.5*
S	Icterine Warbler		–1.2	–1.6	–3.2	–0.5	–1.2
500	Savi’s Warbler		1.4				
500	Grasshopper Warbler		6.6	–2.2	–1.9	–1.6	–1.8
N	Eurasian Blackcap	7.5	7.2	4.4	2.6	3.4	4.3
S	Garden Warbler	0.2	–0.3	–0.8	–1.2	–0.1	–0.6
S	Barred Warbler						–0.8
318	Lesser Whitethroat	–0.3	–0.8	–0.4	–1.3	–0.9	–0.1
267	Orphean Warbler (W+E)						*10.2*
368	Subalpine Warbler						*6.3*
466	Common Whitethroat	2.3	7.0	4.2	0.2	0.2	0.8
S	Spotted Flycatcher	–2.4	–1.5	–1.3	–0.7	–1.3	–1.4
>1000	Thrush Nightingale				–3.0	–1.4	–0.8
>1000	Common Nightingale	–2.2	0.8	3.0		–1.4	–1.6
>1000	European Pied Flycatcher	*–1.5*	1.0	–1.3	–3.9	–1.0	–0.8
S	Collared Flycatcher					1.6	3.5
608	Common Redstart	2.4	1.5	3.4	2.6	0.3	0.9
>1000	Whinchat	*–1.9*	*–2.5*	–2.4	–4.0	–1.1	–2.1
407	Northern Wheatear	*–0.7*	*–3.8*		–1.9	–1.3	–1.7
332	Black-eared Wheatear (W+E)						*–2.5*
413	Western Yellow Wagtail	–2.0	0.7	0.0	–4.3	–1.8	–2.2
106	Tawny Pipit		*–3.1*				*–2.9*
926	Tree Pipit	–2.5	3.4	–2.1		–1.6	–1.5
>1000	Ortolan Bunting		–3.1			–2.4	–2.6

Flycatcher; but see Collared Flycatcher *Ficedula albicollis*). No such decline was apparent in Eurasian Reed Warbler *Acrocephalus scirpaceus*, classified here as arboreal since many birds in West Africa winter in mangrove (Zwarts *et al.* 2014). Of the arboreal Sahelian species just one showed a small decline (Lesser Whitethroat), two species were more or less stable (Bonelli's Warbler, Melodious Warbler *Hippolais polyglotta*) and four prominently increased within the time slot of 1980/1990–2020 (Orphean Warbler, Subalpine Warbler, Common Whitethroat, Common Redstart, the first two from the arid climate zone, and by +10% and +6% per year respectively; Figure 1). A large increase was found for two species concentrated during winter in Sahelian wetlands, albeit with substantial differences between countries: Western Marsh Harrier *Circus aeruginosus* (+11%/year in Europe) and Sand Martin in The Netherlands (+8%/year, an anomaly within Europe).

Population changes related to rainfall in the Sahel

Rainfall in the Sahel is pulling the strings in migratory bird populations, but the outcome is far from uniform given the large deviations in trends within and between species and regions. The population fluctuations of Common Whitethroat and Common Redstart seem to closely track the year-on-year variation in Sahelian rainfall, suggesting that population size is to a large extent governed by winter mortality (Figure 2). The relationship is, however, less simple than it looks. Take, for instance, Common Whitethroat in Britain, which declined by 73% in 1969 when, after 18 wet years, the rainfall had been just 10% below average. But in 1973 and 1974, two extremely dry years with a rainfall index 26% and 27% below average (Figure S4A), Whitethroats declined by just 22 and 11%, respectively. In the following eight dry years Whitethroats declined, on average, by 8%, but the year-on-year fluctuation ranged from –34% to +26%. An analysis of this variation (Table 3) showed that population decline in dry years was large at a high population level and small at a low population level, indicating density-dependent winter mortality.

The year-on-year changes in the population index of Common Whitethroats and Common Redstarts in four countries were related to rainfall and population size (Table 3). Rainfall in the Sahel had a positive effect on population change (but not statistically significant in Common Redstart in three of the four countries). Population size had a negative effect on population change, in most cases highly significantly so. Overall, a wet year resulted in an increase, a dry year in decline. When population size was large, an increase in wet years was always less and a decline in dry years always larger. If living conditions in breeding or wintering areas had systematically deteriorated over the years, year-on-year population changes were expected to be less often positive and more often negative. This was investigated by including year as an additional (linear) variable in the multiple regressions: year appeared to be not, or weakly, significant in both species (Table 3).

Rainfall and flood extent

Concentrating in floodplains is something else than wintering in Sahelian drylands, not least because there are so few available. All together floodplains cover less than 1% of the Sahel (Table S2). For wetland species,

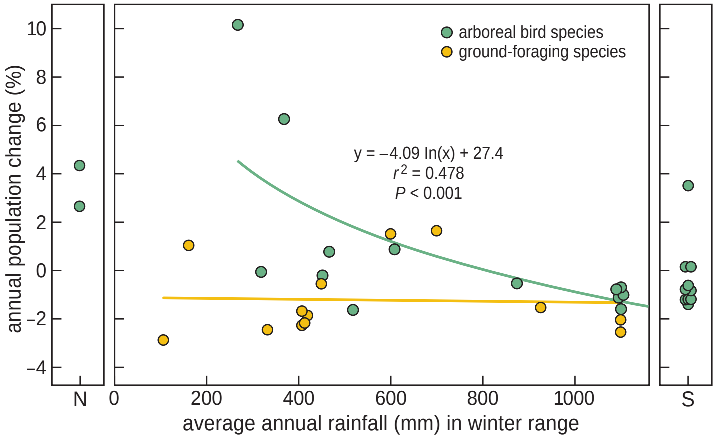

Figure 1. Annual population change in Europe of 14 ground-foraging and 16 arboreal species as a function of the average annual rainfall within the range of occurrence in the Sahel and adjacent vegetation zones; all data from the first and last column of Table 2. The population changes of two species wintering mainly north of the Sahara (marked N in Table 2) or seven in central and southern Africa (marked S) are shown left and right of the graph.

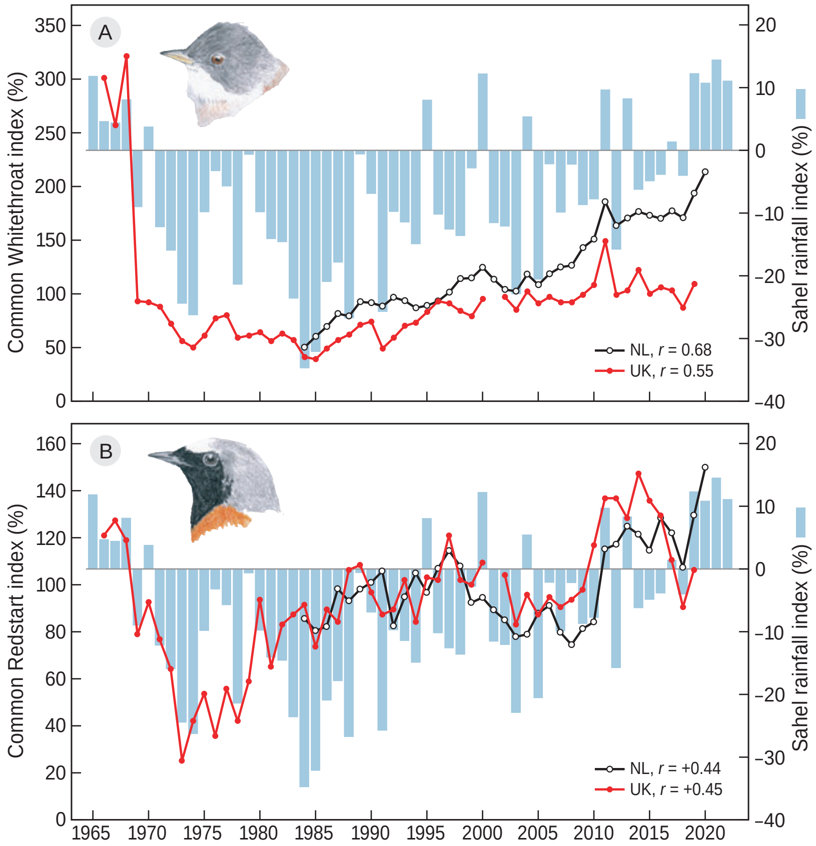

Figure 2. Population index (relative abundance) of (A) Common Whitethroat and (B) Common Redstart in United Kingdom (UK) and The Netherlands (NL) compared to Sahel rainfall index in the preceding year between 1965 and 2022. The correlation (r) between bird index and Sahel rainfall (given in the legends) is in all four cases significantly positive (NL Redstart $P = 0.003$, all others $P < 0.001$). Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends; The Netherlands: Boele *et al.* (2022), www.sovon.nl. The Dutch index of Common Whitethroat was divided by two to facilitate comparison with the British series.

Table 3. Results of 16 multiple regression analyses to investigate whether the change from year to year in the relative abundance of Common Whitethroat and Common Redstart in the UK, The Netherlands (NL), Denmark (DK) or Sweden (SU) is related to Sahel rainfall index, population size (i.e. population index) in the previous year, and trend over years. β is the standardised coefficient, r^2 the explained variance. Analyses based on the data shown in Figure 2 for UK and The Netherlands, and similar data for Denmark and Sweden. Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends, The Netherlands: Boele *et al.* (2022), www.sovon.nl, Denmark: Eskildsen *et al.* (2021), www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet; Sweden: www.fageltaxering.lu.se/resultat/trender.

Bird species	Country	Rainfall		Population		Year		All variables		
		β	P	β	P	β	P	r^2	n	P
Common Whitethroat	UK	0.645	<0.001	–1.265	<0.001	0.815	0.017	0.541	51	<0.001
	NL	0.481	0.011	–1.153	0.019	0.684	0.165	0.317	36	<0.001
	DK	0.382	0.013	–0.628	<0.001	–0.315	0.039	0.519	44	<0.001
	SU	0.200	0.120	–0.705	<0.001	–0.045	0.724	0.523	46	<0.001
Common Redstart	UK	0.396	0.039	–0.494	0.014	0.032	0.885	0.314	33	<0.001
	NL	0.256	0.205	–0.352	0.065	0.152	0.482	0.391	36	<0.001
	DK	0.163	0.357	–0.563	0.023	0.467	0.063	0.140	44	0.106
	SU	0.505	0.002	–0.359	0.010	–0.231	0.143	0.274	46	0.004

floodplain size is more relevant than rainfall although the two are highly correlated (Figures S4A and S4B) and numbers of wetland birds would be expected to fluctuate in line with both rainfall index and flood extent. Impact of flood extent on numbers in The Netherlands was larger than of rainfall index for Sedge Warbler (*r* = +0.61 with rainfall, *r* = +0.75 with flood extent of the Inner Niger Delta; Figure 3A), Sand Martin (*r* = +0.63 vs. *r* = +0.70; Figure 3B) and Purple Heron (*r* = +0.56 vs. *r* = +0.70; Figure 3C).

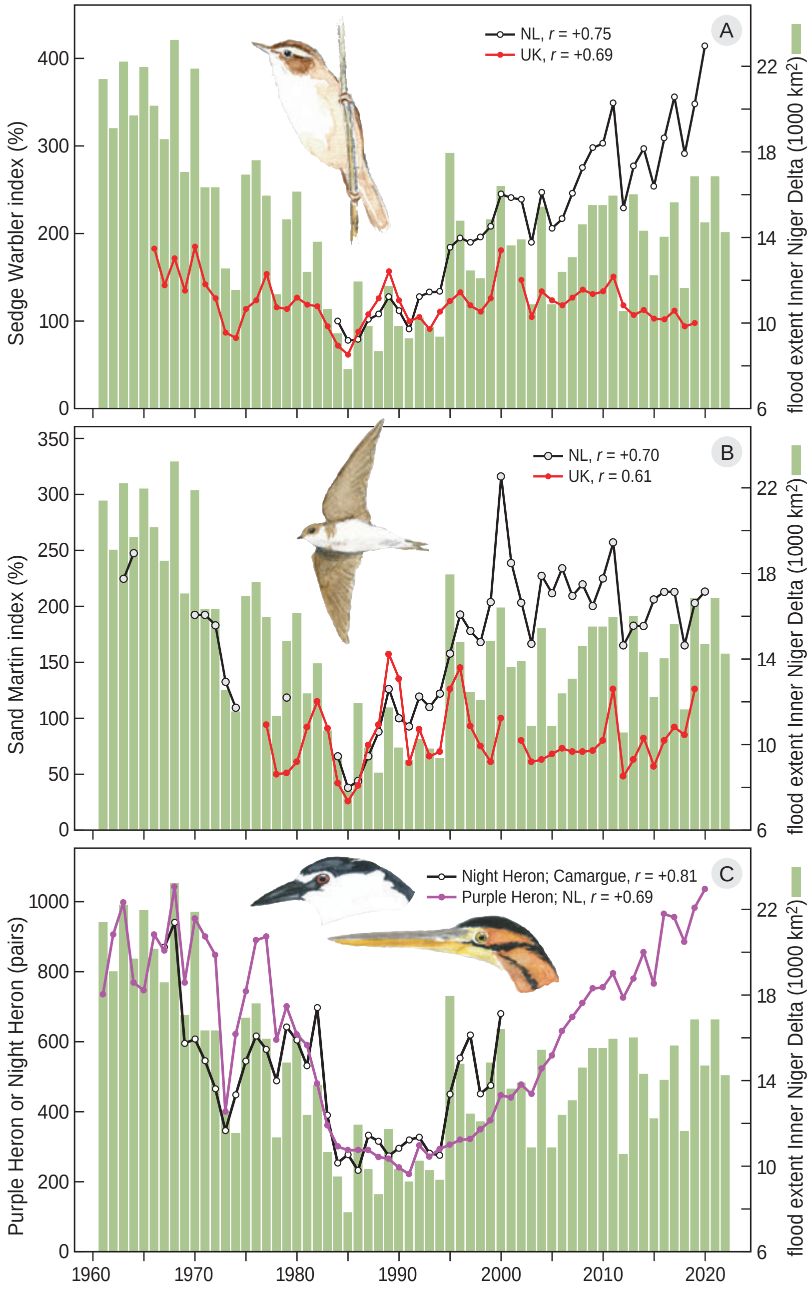

Figure 3. Population index (relative abundance) of (A) Sedge Warbler and (B) Sand Martin in United Kingdom (UK) and The Netherlands (NL), and (C) number of breeding pairs of Purple Heron in The Netherlands and Black-crowned Heron in the Camargue (France) compared to flood extent of the Inner Niger Delta in the preceding year. The correlation (*r*) between bird number and flood extent is significantly positive in all trends shown ($P < 0.0001$). Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends; The Netherlands: Boele *et al.* (2022), www.sovon.nl, Zwarts *et al.* (2009); France: Kayser *et al.* (2003), Zwarts *et al.* (2009).

For Black-crowned Night Heron *Nycticorax nycticorax* breeding in the Camargue (France), the difference was even larger: $r = +0.62$ with rainfall vs. $r = +0.81$ with flood extent (Figure 3C, but notice the shorter timeline). Annual population change in four wetland-dependent bird species was always positively correlated with flood extent (7 out of the 10 correlations significantly so). Conversely, population change was significantly negatively correlated with population size. The annual population change in Sedge Warbler and Sand Martin has become significantly more negative in recent years in Sweden, but more positive in The Netherlands (Table 4).

Longer-term changes

When nestbox monitoring started in The Netherlands in the early 1900s, the Common Redstart was, after the Great Tit *Parus major*, the most common occupant, using 30% of the boxes (Wolda 1918). During the 20th century the Redstart's share gradually decreased to less than 1% since 1970. Concomitant changes in the breeding habitat may have played a subsidiary role in this decline (Gatter 2007, Martinez *et al.* 2010), but similar trends were found in farmland, orchards, gardens and forests in The Netherlands, as in Switzerland and Germany. Based on ten long time series from West and Central Europe, the Redstart declined by 95% between 1940 and 1980 (Zwarts *et al.* 2009), but slightly recovered between 1980 and 2020 (Figure 4). Using nestbox studies, the population trend of the Wryneck could be reconstructed for almost 70 years, during which there was a long-lasting decline between the 1950s and the early 2010s, and a small upturn in the ten following years (Figure 4). In both species, the population was about ten times larger in the 1950s than in the 1980s (Redstart) or in the 2010s (Wryneck). Rainfall had a significant positive impact on population change from year to year; significant negative effects were found for population size and year (Table 5).

Table 4. Year-on-year changes in the breeding population of two passerines and two herons in several European countries are related to the extent of floodplains (here exemplified by the Inner Niger Delta), to the size of the breeding population in the previous year, and trend over years (multiple regressions, using the same data as Figure 3; β is the standardised coefficient, r^2 the explained variance).

Bird species	Country	Flood extent		Population		Year		All variables		
		β	*P*	β	*P*	β	*P*	r^2	*n*	*P*
Sand Martin	UK	0.396	0.011	–0.426	0.003	–0.124	0.391	0.391	40	<0.001
	NL	0.642	<0.001	–0.791	<0.001	0.268	0.046	0.486	40	<0.001
	DK	0.257	0.109	–0.639	<0.001	–0.254	0.114	0.460	44	<0.001
	SU	0.242	0.029	–1.082	<0.001	–0.960	<0.001	0.563	46	<0.001
Sedge Warbler	UK	0.665	<0.001	–0.418	0.003	–0.505	0.003	0.534	33	<0.001
	NL	0.673	<0.001	–1.594	<0.001	1.127	0.001	0.697	36	<0.001
	DK	0.257	0.109	–0.639	<0.001	–0.254	0.114	0.460	35	<0.001
	SU	0.735	<0.001	–0.757	<0.001	–0.736	<0.001	0.563	46	<0.001
Purple Heron	NL	0.706	<0.001	–0.567	<0.001	0.312	0.014	0.312	60	0.001
Night Heron	FR	0.740	<0.001	–0.842	<0.001	0.111	0.767	0.524	35	<0.001

Table 5. Results of two multiple regression analyses to investigate whether the change from year to year in the relative abundance of Common Redstart and Eurasian Wryneck in NW Europe is related to the Sahel rainfall index, population size (i.e. population index) in the previous year, and trend over years; same data as in Figure 4. β is the standardised coefficient, r^2 the explained variance.

Bird species	Rainfall		Population		Year		All variables		
	β	*P*	β	*P*	β	*P*	r^2	*n*	*P*
Common Redstart	0.465	0.002	–1.027	<0.001	–0.576	0.010	0.281	81	<0.001
Wryneck	0.362	0.007	–1.274	<0.001	–1.023	0.001	0.492	68	0.001

DISCUSSION

Trends and fluctuations in populations of migrants

RAINFALL AND ADVERSE CONDITIONS IN GENERAL

Many studies have shown correlations between rainfall in the Sahel and survival of wintering birds, ranging from ducks, storks and raptors to doves and passerines (Table S1). Drought years in the Sahel causing high mortality and plummeting bird numbers is the received wisdom. Even so, very few data are available to show what is actually happening in the field. Is mortality caused by disease, starvation or predation, or an admixture which varies per climate zone or habitat? Where does most mortality occur, on the wintering grounds (and when) or during the return migration? Does mortality differ according to age and sex? And how flexible are birds in employing strategies to survive the perils of drought: is there a shift in habitat choice or do they move to more humid climate zones? Eye-witness accounts are available of mortality and survival strategies of resident and migratory birds in deserts (Haas & Beck 1979, Salewski *et al.* 2010, Gutiérrez *et al.* 2022), albeit much less so for the sub-Saharan zone (but a host of studies – including experiments – is available for the New World migration system; e.g. Holmes 2007, Faaborg *et al.* 2010, Rappole 2022).

Take for example Ruff *Calidris pugnax* and Garganey *Spatula querquedula* in the Inner Niger Delta (Mali), both of which are rarely captured by local people during wet years when the birds are (too) widely distributed over the available feeding grounds to make the effort worthwhile, whereas in drought years they become easy prey when foraging on the last remaining wet spots (Zwarts *et al.* 2009). Higher mortality during drought years is due not only to human predation, but also to starvation. In normal years, Garganey in Africa are concentrated in huge roosts by day and feed more dispersed by night. During a drought year Garganey had to resort to feeding during daytime when the birds could be approached to within few metres (Tréca 1981), illustrating how desperate and weakened they were. Ruff normally start increasing their body mass about five weeks prior to their return flight, eventually by some 40%, but in dry years they are unable to fatten up. In March during a drought year, birds still showed a mass as low as their mid-winter body mass or even lower (Figure 215 in Zwarts *et al.* 2009). Obviously, birds in this poor a body condition are unable to return to their breeding grounds; indeed, many died on the spot (Wymenga *et al.* 2002). High mortality is reflected in the number of recoveries of wetland-dependent European migrants. From EURING data, on average 1% of the annual total number of Ruff recoveries originated from sub-Saharan Africa during wet years, compared to 24% in dry years in the Sahel. Large differences were also apparent in Garganey (1% recovered from Africa in

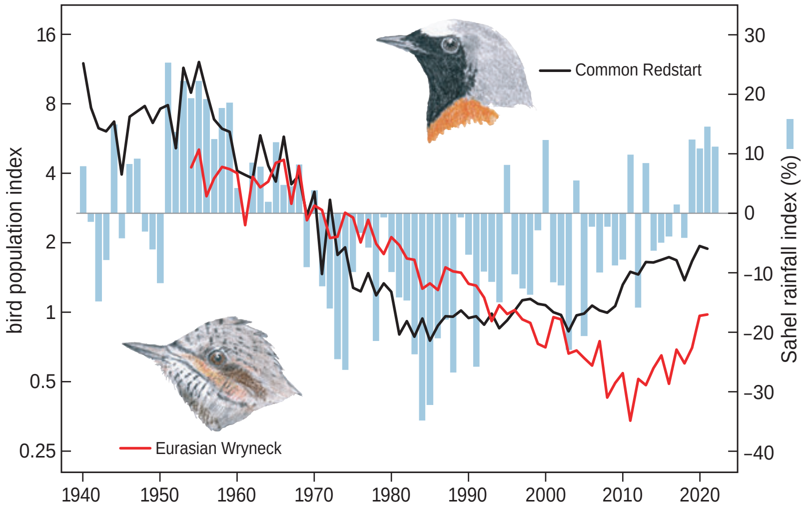

Figure 4. Rainfall in the Sahel in the preceding year (blue bars; right-hand axis) and population trends of Common Redstart and Eurasian Wryneck breeding in NW Europe (left-hand axis), based on 10 and 19 studies, respectively; from Zwarts *et al.* (2009), updated with the British, Danish, Dutch and Swedish indices to complete the series for the period 2005–2021 (www.bto.org/birdtrends, www.sovon.nl, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet, www.fageltaxering.lu.se/resultat/trender). The average in 1990–2000 is set at 1, the other years are indexed relative to 1990–2000. NB: population index on the left-hand axis is presented on a logarithmic scale.

wet years, 12% in dry years), Purple Heron (3% in wet years, 50% in dry years) and Wood Sandpiper *Tringa glareola* (no recoveries in wet years, 9% in dry years) (Zwarts *et al.* 2009, see Table S1).

Drought often works its way indirectly in the unforgiving African arena, as illustrated in Barn Swallows *Hirundo rustica* captured in drylands near the Okavango Delta (Botswana) during three consecutive years in which the local rainfall in December and January varied between 33.6 and 446.9 mm (van den Brink *et al.* 1997, 2000). In the wet year, flying termites were abundant, but in the dry year distinctly rare. The moult of primaries took 120 to 150 days in the wet and normal year, but increased to 155 to 190 days during the dry year when many birds were emaciated. Adult body mass in the dry winter was, on average, 8% lower than during the wet year, in juveniles even 16% less; of the latter, some were in fact dying upon capture. The dying of Barn Swallows as recorded in the field under drought conditions is reflected in the ring recoveries. On average, 3.3% of British Swallows were recovered from their wintering areas in the southern third of Africa (208 out of 6136; EURING-data, in Figure 242A in Zwarts *et al.* 2009), but least often in years with much rain in S Africa and most (some 9%) in relatively dry years. During the northward flight British Barn Swallows pass the Sahel and Sahara in March, a perilous undertaking in years with little rainfall when the Sahel is even more desiccated than is usual at the end of the dry season. On average, 2.5% of the British recoveries are from the Sahel plus Sahara, varying between 0% in wet Sahel years and about 7% in dry Sahel years (Figure 242B in Zwarts *et al.* 2009).

It is not just Barn Swallows that suffer during the crossing of the desert during their return flight, especially in a year with few rains in the Sahel. Other species emerge from an analysis of EURING data that show similar mortality patterns, including White Stork, Yellow Wagtail, European Reed Warbler and Pied Flycatcher (but not Common Redstart and Willow Warbler; Figure 144 & 244, Table 31 in Zwarts *et al.* 2009). It would therefore be expected that fewer birds are able to build up sufficient body reserves in a dry Sahel year to survive the rigours of the Sahara, independent of species-specific strategies of refuelling and foraging (Smith 1966, Jenni-Eiermann *et al.* 2010). If so, it is to be expected that Sahel drought brings carry-over effects on reproduction, as was recorded for White Stork (Dallinga & Schoenmakers 1989), Barn Swallow (Loske 1989; Figure 262 in Zwarts *et al.* 2009), Sand Martin (Norman & Peach 2013) and Common Redstart (Finch *et al.* 2014), although, averaged for 19 migrant species, the impact appeared to be relatively small compared to those related to the conditions on the breeding grounds (but the last-named study was restricted to Britain; Ockendon *et al.* 2013).

Capture-mark-recapture studies have been used to investigate the correlation between Sahel rainfall and annual survival (Table S1). No such correlations were found for three migrant species that spend the winter mainly outside the Sahel: Willow Warbler (Peach *et al.* 1995), European Reed Warbler (Thaxter *et al.* 2006) and Whinchat (Blackburn & Cresswell 2016a,b). For White Stork and Lesser Kestrel *Falco naumanni* spending the winter in the Western Sahel, survival was correlated with Sahel rainfall, but only in juveniles, not in adults (Barbraud *et al.* 1999, Mihoub *et al.* 2010). In White Storks from central Europe wintering in eastern and southern Africa, annual survival appeared to be unrelated to the Normalized Difference Vegetation Index of their wintering grounds but to the NDVI of the eastern Sahel where they stay in October and November (Schaub *et al.* 2005). Unfortunately, using annual survival rate, it is not possible to distinguish mortality during migration from mortality rates on the wintering grounds (e.g. Leyrer *et al.* 2013 for a successful attempt to separate the two in Red Knot *Calidris canutus*). To what degree the annual survival actually reflects winter mortality is difficult to say. How formidable the spring crossing of the Sahel and Sahara can be, is demonstrated by satellite-tracked raptor species like Osprey *Pandion haliaetus*, European Honey Buzzard *Pernis apivorus* and Western Marsh Harrier, in which half of the annual mortality (at least in juveniles) is incurred during this passage (Strandberg *et al.* 2009). Resightings of colour-banded Eurasian Spoonbill *Platalea leucorodia* showed that mortality was 18% higher for birds crossing the Sahara than for birds staying in Iberia and France during winter (Lok *et al.* 2015), whereas satellite-tracked Black-tailed Godwits *Limosa limosa* suffered fatalities mostly when encountering adverse wind conditions in the Sahara during their flight from W Africa to NW Europe (Loonstra *et al.* 2019).

DENSITY-DEPENDENCE AND COMPETITION

For Common Redstarts in Finland density-dependent mortality outside the breeding season was held responsible for the observed annual fluctuations in breeding numbers in 1969–1982 (Järvinen 1987). Reanalysing these data, a negative correlation between mortality and population index was indeed apparent ($r = -0.42$, $n = 13$, $P = 0.04$) but there was an even higher correlation of population index with Sahel rainfall index

($r = -0.71$, $n = 13$, $P = 0.004$). Population index and rainfall, both taken from Figure 4, were correlated for the 13 years of study in Finland ($r = +0.55$), and their respective impact could not be separated in this particular study. On the other hand, density-dependent mortality, independent of the impact of Sahelian rainfall, was found for Sedge Warbler (Peach *et al.* 1991), Common Whitethroat (Baillie & Peach 1992) and Sand Martin (Norman & Peach 2013). The annual survival of British Sand Martins in 1981–2003 varied between 0.11 and 0.66. The highest survival of Sand Martins occurred in 1985/1986, a relatively dry year in the Sahel, when the population size had dropped to an exceptionally low level in the foregoing two drought years (see also Figure 3B), suggesting that relatively many birds can survive a dry year in the Sahel when numbers are low. The opposite occurred in 1969 when, for the first time for 18 years, the rainfall in the Sahel was below-average and the thriving Common Whitethroat population in the UK crashed (Figure 2A), as elsewhere in Europe (Berthold 1973, 1974). The strongly diminished population must have had better chances of survival in the subsequent drier years in the Sahel. The trends of selected species (Figure 2–4) showed a negative density-dependent impact on population change, in most species – except Common Redstart – highly significantly so (Table 3–5). This suggests that winter mortality is density-dependent, unless the estimates of the annual indices are imprecise. A large error in the estimates of indices is likely to result in an overestimate of density-dependence based on two consecutive annual indices.

Density-dependent winter mortality is not to be expected if all birds are hit equally hard in a drought year, for instance when all wetlands dry up, or all trees drop their leaves early. Extreme adverse events do occur in the Sahel, but normally floodplains and water bodies will get smaller in dry years, forcing the birds to concentrate in the last remaining feeding sites and relatively more birds will die of starvation, especially when the initial population is large. The same applies to dryland birds, but in a more diffuse way. In dry years, more tree species than usual shed their leaves and become unattractive to arboreal birds. In the Sahel many birds have the option to switch to 'refuge trees', such as the widespread Winter Thorn *Faidherbia albida* and trees in seasonal wetlands that remain in full leaf (Zwarts *et al.* 2023g). Density-dependent mortality may still occur when depletion of the remaining food resources leads to starvation, aggravated by interference competition which sometimes differentially affects sexes and age groups (Stutchbury 1994, Marra & Holmes 2001; but see Rappole 2022: 194 for another view). Several migrant species are known to defend territories, e.g. Pied Flycatcher (Salewski *et al.* 2003), Whinchat (Blackburn & Cresswell 2016b) and Northern Wheatear (Blackburn & Cresswell 2016c). Other migrant species have individually overlapping home ranges (Willemoes *et al.* 2017, Mostafa *et al.* 2021) but feed on their own and do not tolerate congeners or other species nearby, particularly species with a lower body mass (Salewski *et al.* 2007, Zwarts *et al.* 2023e).

LONG-TERM TRENDS

After a decline of 20 years into the nadir of the mid-1980s, Purple Heron and Sand Martin took 30 years to regain the population levels from before the Great Drought in the Sahel (Figure 3), as did Wryneck and Common Redstart (Figure 4). The recovery of populations of long-distance migrants differed per country, exemplified for The Netherlands (in general faster and steeper), Great Britain, Sweden and Denmark (Figure 2–4, Table 4). Between-country differences are to be expected because changes in landscape and climate differ substantially within Europe. For instance, the steep increase of some, but not all, marshland birds in The Netherlands originates from large-scale conversion of farmland into marshland, on top of natural succession and changes in water regimes in existing marshland (van Turnhout *et al.* 2010). The decline of farmland birds, although in progress all over Europe, differs equally substantially per country depending on the degree of agricultural intensification (e.g. Donald *et al.* 2006, Bowler *et al.* 2021). Regional differences in population trends may also be explained by variations in productivity of the birds involved (Morrison *et al.* 2013). Unequivocally attributing population changes to conditions in either the wintering or breeding areas is therefore doomed to failure; the growing body of evidence points at an intricate and nuanced interplay of factors operating in ever-changing breeding and wintering regions, further complicated by conditions on stopover sites (Moore 2018).

The common denominator of bird trends based on systematic bird surveys and ringing, however, is the overall better performance of bird species wintering in the Sahel compared to those wintering in the more humid climate zone south of the Sahel (Ockendon *et al.* 2012, Johnston *et al.* 2016). Both studies used data starting between 1983 and 1994 and ending in 2008, a period during which rainfall in the Sahel recovered. Of the species wintering in the most arid zone, Orphean Warbler (average rainfall in their Sahelian distribution area: 267 mm) even quadrupled in 26 years (Table 2).

Bird monitoring in southern Europe started as late as 1996 (Spain) or in the 2000s (Italy, Portugal, Greece), i.e. long after the stamp of the Great Drought (1972–1992). Data are therefore lacking to substantiate the idea that southern European warblers (like Orphean and Subalpine Warbler, wintering in the arid southern Sahara and northern Sahel) declined even more strongly than bird species ranging across a much wider climate zone in the Sahel and Sudan vegetation zone, such as Common Whitethroat (wintering on average at 466 mm rainfall) and Common Redstart (608 mm rainfall). Given the more irregular rainfall in an arid climate, with steeper ups and downs (Figure S1, S2), both the negative effect of drought and the positive effect of wet years are supposedly much more marked for birds wintering in the most arid regions of the Sahel. The inference can be drawn that during a wet period birds wintering in the arid Sahel fare relatively better than species wintering further south in the more humid climate zone, and vice versa during a drought (see also Thaxter *et al.* 2010, Ockendon *et al.* 2012).

Birds and dust storms

The Sahel can be extremely dusty during the dry season, with far-reaching consequences both regionally and globally. The impact of dust radiation on vegetation growth in the Sahel is enormous (Evans *et al.* 2019). The contribution of the Sahara and the Sahel to the worldwide dust emission to the atmospheres is as large as of all other deserts and drylands in the world together (Kok *et al.* 2021). Most dust is produced in the second half of the dry season (January–May), a period during which there is often a strong Monsoon wind from the NE, known as the Harmattan. Crossing the Sahara is therefore risky for migrants during their return flight (Haas & Beck 1979, Loonstra *et al.* 2019), but what effect does it have on birds wintering in the Sahel? It can be nothing but huge, as anyone can attest who has experienced a heavy dust storm: foraging birds seem to have vanished from the earth, no insects to be seen and afterwards everything covered by a thick blanket of fine dust (thunderstorms have the opposite effect; Sinclair 1978). Very little evidence is available

Photo 1. Very few foraging birds were recorded during the harsh conditions of a dust storm, presumably because the birds waited till the storm subsided and feeding could be resumed. Lingering dust in the air and the thick layer of dust on leaves probably reduces insect availability for longer than the duration of the dust storm (Senegal, 16.363°N, 15.314°W, 26 February 2015).

on direct effects of dust storms on birds, such as a lower body mass of Sand Martins during and after dust storms (David Norman quoted in Norman & Peach 2013). The number of 'dust days' in the Sahel was close to zero during the wet 1950s, but the Great Drought was almost daily accompanied by dust during the dry season (Middleton 2019); this fact alone must have had dire consequences for insectivorous birds.

The relation between cumulative rainfall and the occurrence of dust storms has changed recently. After the recovery of the rainfall in the Sahel, a decline of the annual number of dust storms was expected. In fact, the opposite happened and the number of extreme Sahelian dust storms became three times more common between 1982 and 2016 (Taylor *et al.* 2017). The Sahara has warmed, causing global and regional anomalies in the atmospheric circulation, including more often strong winds from the Sahara and more days with extreme rainfall intensity, especially in the eastern Sahel (Panthou *et al.* 2018, Biasutti 2019). The frequency of dust storms also has a link with the expansion of agriculture since about 1700, which triggered an increasing exposure of the Sahelian soil to wind erosion. An analysis of offshore deposit sediments from the West African dust plume of the past 3200 years showed that until about the year 1700 dust deposition was related to precipitation in tropical West Africa. The advent of commercial agriculture at the beginning of the nineteenth century was paralleled by a sharp increase in dust deposition (Mulitza *et al.* 2010). The impact of the increase in African dust flux has severe consequences for the local human population, as evidenced by a plethora of studies, but should be equally damaging for birds wintering in the Sahel (despite an apparent lack of studies).

Birds and waterbodies

Waterbirds feeding in shallow water, such as Little Egret *Egretta garzetta* and Black-winged Stilt *Himantopus himantopus*, depend in the dry Sahel on the seasonal ponds and riverine floodplains which come into existence during the short rainy season (July–September) and which gradually evaporate during the long, dry season. The distribution of waterbirds can be predicted from the occurrence of open waterbodies using remote-sensing data (Suet *et al.* 2021). With little rain, wetlands will be scarce and small (Kaptué *et al.* 2013) and most will have vanished before the migrants start to leave the Sahel in March or April. It is likely, though not yet quantified on any scale, that the extent of surface water in March–April is crucial to waterbird survival in the Sahel during winter, the suggested explanation for the collapse of the Black-winged Stilt population in the extremely dry year of 1984 (Dubois 1992).

The ground water table in the Sahel varies seasonally and depends not only on the rainfall during a single year, but also on the rainfall during previous years. The relation between the surface of water bodies and cumulative rainfall has changed since the 1970s, because, in spite of the decline of the annual rainfall, there was a seemingly paradoxical rise in the ground water table. There are three explanations for this anomaly. First, due to the expansion of agricultural land, bare ground became more common, increasing surface runoff and hence water volume of temporary ponds and rivers (Leblanc *et al.* 2008). Second, a rise of the water table during the Great Drought was detected in areas without any farmland nearby, for instance in the Gourma, E Mali, with a doubling of the surface area of ponds between 1975 and 2002 (Gardelle *et al.* 2010, Gal *et al.* 2016). Here, in savannah, the larger surface runoff since the Great Drought followed a decline of the woody vegetation and an increase of bare land on shallow soils (rocks covered by a thin layer of sand). Third, rainfall intensity has increased, in the form of short-lived heavy downpours (Panthou *et al.* 2018), which favours groundwater replenishment (Descroix *et al.* 2018). The larger runoff enhanced the discharge of rivers in the semi-arid Sahel (Descroix *et al.* 2009). As a result, larger expanses of temporary flooded areas are available at present. To what degree waterbirds have profited from these developments is unknown, but it suffices to note that the living conditions of waterbirds in the Sahel are not exclusively governed by annual rainfall as such.

Birds and riverine floodplains

The large floodplains in the dry belt of the northern half of Africa cover some 40 to 100 thousand km^2 (Table S2) and are thronged by huge numbers of birds which share the region with millions of fishermen, pastoralists and farmers, probably not different from past centuries but not a guarantee for the future either. The variation in the total flood extent over the last 100 years is large. This variation has no bearing on variable rainfall in the Sahel itself, but rather on the discharge of rivers. It is the rain that fell during the same and previous year(s) in the catchment areas south of the Sahel zone that eventually determines the extent of floodplains downstream. Having a different catchment area, the annual variation in the size of the Sudd, fed by the White Nile (Figure S8), is not related to those of floodplains in the western Sahel (Figure S4). Tropical, seasonal floodplains are threatened by the regulation of the river flow with dams. The river water is stored in huge reservoirs during the short rainy season, thus lowering the flood level and reducing the downstream floodplain, to be released in the dry season. The 'regulation' of the natural river flow reduces the extent of the seasonal floodplain and changes the lower part into permanent marshland. In this way the Senegal Delta has lost nearly all of its floodplain and Hadija-Nguru half of it (Table S2). Bird counts clearly show that larger waterbird species declined after the loss of floodplain (summarised in Zwarts *et al.* 2009), but the impact on smaller bird species is unknown. Waterbirds may search for other wetlands, but how successfully? The close relationship between flood extent and population change suggests no respite from floodplain loss (Figure 3, Table 4). Regulation of waterbird populations via floodplain size in the wintering areas follows various pathways depending on bird species, as explained below (and in more detail in Zwarts *et al.* 2009).

Black-crowned Night Heron and Purple Heron winter in large numbers in the Sahel, with concentrations in the few extensive marshlands in floodplains. In the Inner Niger Delta, an estimated 50,000 Purple Herons and 12,000 Black-crowned Night Herons are present. Breeding populations of both species in Europe fluctuated in parallel with the extent of the floodplains in the Inner Niger Delta (Figure 3). The feeding ecology of these herons during their stay in the Inner Niger Delta is unknown, but the daily fish auction in Mopti showed that the annual fish trade differed by a factor of five between a dry and a wet year (Figure 47 in Zwarts *et al.* 2005). This suggests more food for fish-eating birds in wet years. The same fish auction data showed that most fish were captured during the deflooding stage of the floodplain, when fish become concentrated in the last remaining waters. Field observations confirm that fish-eating birds follow the same routine, with serious consequences. First, fishermen use hooklines and snares to catch herons and other waterbirds, which is particularly successful during the deflooding when birds flock at food bonanzas. In dry years this concentration occurs earlier in the dry season, exposing the birds to a longer period of depredation by man. In extremely dry years, when floodplains dry out before the birds' departure in early March, many waterbirds die of starvation. We assume, but lack quantitative data, that the last month of their stay in the area is crucial to the survival of Purple and Black-crowned Night Heron and, for the same reasons, of Squacco Heron *Ardeola ralloides* and Caspian Tern *Hydroprogne caspia*. Species like Whiskered and White-winged Tern *Chlidonias hybrida* and *C. leucopterus* are also influenced by floodplain desiccation, but to a lesser extent than herons and Caspian Tern because they are captured less often by local people and are able to catch fish from the rivers (deep water) after the floodplains have dried out.

Most birds captured by fishermen in the Inner Niger Delta are locally consumed, but the numbers of captured Ruff and Garganey are so large that it is worthwhile bringing them to the market. This bird trade was registered by Wetlands International Mali during two dry years (1999 and 2005) and two wet years (2000 and 2004; summarised in Zwarts *et al.* 2009). In the early dry season, Ruffs have a very scattered distribution, depending on where they can feed in shallow water and along the water's edge, but some months later they become concentrated by the thousands in the last remaining wet floodplains and shallow waters. As soon as birds gather in larger flocks, people in the Inner Niger Delta start trapping them during dark, moonless nights. Under the same circumstances, Garganey are even easier to catch because they fly in the late evening from their daytime roost to Water Lily fields to feed. Up to a thousand ducks can be caught in a single night with a small team and a limited number of nets. Catching such numbers is possible only when the flood level is so low that floodplains, apart from the deep Water Lily ponds, are dry. In wet years, Garganey run no such risk because the floodplains are still flooded at the time of their departure in late February/early March (Figure 164 in Zwarts *et al.* 2009). The annual number of Garganey captured henceforth varied between 0 in years with a high flood to 50,000 in years with a low flood. Aerial bird counts showed that Garganey numbers in the Inner Niger Delta varied between 100 and 800 thousand (16 winter counts; 1972–2007), thus a capture of 50,000 birds in dry years is substantial and likely represents additional mortality which might contribute to the ongoing decline of the West-European population due to the loss of breeding habitat.

The number of Ruff captured annually is more difficult to estimate because their low price (0.17 euro on the market in the 2010s compared to one euro for a Garganey) is not conducive to trade. The estimated total catch of 9 to 41 thousand Ruffs in 1999–2005 is certainly too low, but anyway substantial compared to the numbers present in the Inner Niger Delta (100 to 200 thousand in wet years, and 30,000 in extremely dry years; 17 counts in 1972–2007). Most birds are captured in February and March, mainly females because many males have already departed to Europe. The impact on the population level must be serious. During dry years, Ruffs move from desiccated floodplains to riverbeds and lake sites, but many do not survive a drought year given the extremely low body weight of captured birds. As for Garganey, many Ruff do not survive a dry year in the Sahel due to human predation, but in an extremely dry year even more birds die of starvation (Zwarts *et al.* 2009).

There is no detailed information how many Ruff and other waterbirds are captured in other Sahelian wetlands, but it is probably less than in the Inner Niger Delta; see Deniau *et al.* (2022) for a recent survey, but note that the high number of killed Black-tailed Godwit reported for the Inner Niger Delta must refer to Ruff, probably due to a mistaken interpretation of its local name: *kalla kalla* for Ruff and *kalla* for Godwit (besides, Godwits are near-impossible to catch with standing nets, unlike Ruff).

The flood extent has a distinct impact on the population size of the Sand Martin (Figure 2, Table 3) which are present in the millions in all large Sahelian floodplains. During deflooding Sand Martins congregate above recently emerged but still wet floodplains where insects abound in, and around, shallow waters. At Lake Chad, midges could be so abundant as to resemble swirling green mist, but relatively few chironomids were extracted from gizzards of collected specimens of Sand Martins (probably a sampling error; Fry *et al.* 1970). The diversity and biomass of chironomids at Lake Chad are impressive, as are the seasonal and annual variations in abundance with successive species-specific waves of emergence (Dejoux 1976). Midges and their larvae represent a near-constant and superabundant food supply to fish and birds. Furthermore, fields of *Echinochloa stagnina*, a tall grass standing in water on floodplains, function as roosts, facilitating roosting close to feeding areas. Given the high numbers in floodplains, a close relationship between population size and flood extent is not surprising.

Sedge Warblers in the Sahel are concentrated in the few marshes with a lush vegetation and reach highest densities on floating vegetation in floodplains and stagnant lakes. For the Inner Niger Delta alone, the wintering population was estimated at one million birds, which represents 5 to 10% of the estimated total winter population of 10 to 20 million birds which mostly breed in Eastern Europe and Russia and spend the winter in the eastern Sahel and farther south (Keller *et al.* 2020). The birds in the western Sahel originate from W Europe, possibly about one million birds (240,000 pairs in the UK (https://app.bto.org/birdfacts/results/bob12430.htm), 33 to 41 thousand pairs in The Netherlands (https://stats.sovon.nl/stats/soort/12430) and smaller numbers elsewhere in W Europe (Keller *et al.* 2020)). The Dutch (Figure 3A) and German populations (Kamp *et al.* 2021) quadrupled during the relatively wet Sahel years between 1990 and 2010, but not so the British population (Figure 3A). A high fraction of foreign-ringed Sedge Warblers in the Senegal Delta originated from breeding sites in the UK. Although considerable numbers are still present in the artificially flooded Djoudj N.P. (Flade 2008), most floodplains were lost since the water level in the lower Senegal was kept constant after the construction of the Diama (1986) and Manantali (1988) Dams. British Sedge Warblers seem to have suffered a much greater loss of wintering habitat than the continental birds from West Europe (the latter facing a loss of 30% of floodplains along the Niger after upstream dams had been built, not nearly as much as the 95% loss in the Senegal Delta; Table S2).

The large impact of flood extent in the Inner Niger Delta on population size of West-European Sedge Warblers hinges on the dense vegetation of wild and cultivated rice (water depth 1–2 m) and two grass species, *Vossia cuspidata* (2–3 m) and *Echinochloa stagnina* (>3 m). The surface area of this vegetation type declines disproportionately in years when the flood extent is small, reducing feeding opportunities. Dry floodplains, a state attained in dry years long before Sedge Warblers prepare their return flight to the breeding areas, are deserted by Sedge Warblers. Starvation is avoided partly by using an alternative elsewhere, i.e. floating vegetation of *Polygonum senegalensis* and *Ludwigia stolonifera*, water plants not found on seasonal floodplains but covering an estimated 56 km^2 in Lac Horo, a lake annually replenished when the water level of the Niger River is at its maximum. At Lac Horo an extremely high density of 103 birds/ha was recorded, giving a total of 390 to 760 thousand birds (95% confidence interval). Density counts were done during a wet (2004) and dry year (2005), both in March, for a substantial part probably referring to birds having left the nearby desiccated floodplains (Zwarts *et al.* 2009). Lac Horo is connected to the Niger River, and the water level is managed to allow farmers to grow crops on the emerging grounds within the lake. During 2004 and 2005, Sedge Warblers profited from the temporary floating vegetation, the lake facilitating an equivalent of half of the West European population. We lack information whether this was normal at the time; about the present state we can only speculate. Wetland birds in the Sahel are clearly vulnerable in their coexistence with farmers, cattle breeders and fishermen who heavily exploit the available natural resources. Any relationship between flood extent and population size (Figure 3) might have been different in the past or change in the future.

Other changes may, or may not, have a lasting impact on wintering bird numbers. For example, an increasing fraction of the floodplains of the Inner Niger Delta is used to grow floating rice and *Echinochloa* is planted in deep water to provide fodder for cattle. These developments most likely have no direct negative impact on birds foraging on floating vegetation, as far as could be discerned from density counts in the early 2000s. Another development may turn out differently. In 1960, the fishermen in the Inner Niger Delta used nets with a mesh width of 50 mm, compared to nets with a mesh width of 33–41 mm in 1985. Since 2005, fishermen started using plastic nets with a mesh width of only 10 mm. Large fish of 50 cm and more have become scarce in the course of the past decades. For fish-eating birds, this trend has not yet had harmful consequences, since the decrease in average fish size meant a boost in the supply of smaller fish. The increased fishing, on the other hand, has also a direct negative impact on birds, because each year many birds perish in fyke nets or due to hooklines. The number of captured birds has increased over the years, a combination of an increase in the human population and the introduction and prolific use of nylon nets, not available before 1960. The trade in trapped birds has boomed since storing on ice was introduced around the year 2000, improving storage life and enabling transportation to far away markets (Zwarts *et al.* 2009). These developments do not bode well for Ruff and Garganey.

Birds foraging on the ground

An estimated 130 million granivorous migrant bird species spend the winter in the Sahel, together with four billion granivorous Afro-tropical birds (Zwarts *et al.* 2023a). These numbers must have been much larger more than half a century ago. In the 1960s, the total population in Africa of the Red-billed Quelea *Quelea quelea* was roughly estimated at between 1 and 100 billion birds, an estimate based on reported numbers of birds killed by control teams (Crook & Ward 1968). An educated guess of Quelea numbers was based on reported colony densities in one-degree squares of occurrence (and assuming average densities in surveyed and unsurveyed areas being about the same) and two chicks per pair. The data were obtained mainly during the 1970s, thus before the Great Drought, and gave an estimate of some 1500 million birds (Elliott 1989). Some 60% of these numbers referred to the Sahel, viz. Senegal, Mali (Inner Niger Delta), Lake Chad Basin, Sudan and Ethiopia (see also Morel 1968b, Fry & Keith 2004). Our estimate for the Sahel in the 2010s, i.e. 180–480 million Red-billed Queleas (Figure S35 in Zwarts *et al.* 2023a), suggests a very large decline (47–80%) compared to the pre-drought level, even considering the fact that previous estimates were perforce make-do. Other seed-eating birds have declined as much. Systematic bird counts in plots in NW Senegal in 1960–1962 (Morel 1968a), 1969–1976 (Morel & Morel 1974, 1992) and 1993/1994 (Tréca *et al.* 1996) were repeated in 2014–2015 and showed losses of 39–97% of common seed-eating bird species and an equally large decline of insectivorous ground-foraging birds (61–91%; Zwarts *et al.* 2018). Sharp declines of ground-foraging birds are typical for the Sahel, as exemplified by Common Quail *Coturnix coturnix* in N Senegal (from 2.6/km^2 in the 1960s to 0.1/km^2 in the 2010s; Zwarts *et al.* 2023a) and European Turtle Dove along the Senegal River and in the Inner Niger Delta in Mali, where present-day numbers are a pitiful reminder of the untold millions reported in the 1960s and 1970s (Curry & Sayer 1979, Morel & Morel 1987). How can this widespread collapse of ground-foraging bird populations be explained?

The most parsimonious explanation would be the increasing grazing pressure from livestock, cattle by 2.3%/year and goats and sheep by 3.78%/year (www.fao.org/faostat/en/#data/TP). The consequent number of cattle has become 3.8 times larger within 60 years, the number of goats and sheep 6.9 times. Under intensive grazing fewer plants flower, seed production falters (Sternberg *et al.* 2003) and the soil seed-bank is reduced. The seed loss for seed-eating birds is larger still because sustained grazing leads to a shift in plant composition, grasses with seeds preferred by birds being replaced by grasses thriving under grazing but whose seeds are difficult for birds to handle and therefore largely ignored (Pol *et al.* 2014, Zwarts *et al.* 2023j). The number of seedeaters during the dry season in grazed areas was 84% lower than in nearby exclosures without livestock (Figure 14 in Zwarts *et al.* 2015). The impact of the grazer-induced vegetation shift was also found in insectivorous birds, with 64% fewer birds in grazed than in ungrazed area, probably due to a decline of insects under high grazing pressure (Seymour & Dean 1999, DeBano 2006, Kaiser *et al.* 2015, Zhu *et al.* 2015, Ma *et al.* 2017).

The feeding conditions for granivorous birds in the Sahel have gradually worsened in the footsteps of a decline of savannah and mounting livestock numbers, but nonetheless variable rainfall accounts for large differences in food supply between years. Seed supply in wet years may still be bountiful, but the annual seed production is much lower in dry years (Bille 1977). Prolonged drought disproportionally and negatively affects grasses whose seeds are preferred by granivorous birds (Zwarts *et al.* 2023j); drought makes drinking spots increasingly scarce, a circumstance crucial to birds with a seed diet (Morel 1975). In drought years, many seed-eating birds die, surviving birds being in poor condition (Morel & Morel 1974).

The impact of the expansion of agricultural land at the expense of savannah (annually 2%; CILSS 2016) and wetlands is variable. Some species of granivores at first profited from the increasing acreage of cropland, not least Red-billed Queleas (Bruggers & Elliott 1989), but our density counts in the 2010s showed that of the 33 common granivorous bird species, 25 were more abundant on savannah than on farmland, 14 even being twice as abundant. Among the 24 insectivorous ground foraging species, 19 were more abundant on savannah, 10 of them being twice as much so (Zwarts *et al.* 2023h). Some species may show more resilience to habitat changes than others (as suggested for Whinchats wintering in variously degraded farmland on the Jos Plateau in central Nigeria in the early 2010s; Blackburn & Cresswell 2015), but any intensification of farmland use is likely to eventually bring trouble to birds (clearly evident from surveys in Europe; Newton 2017). Our large-scale surveys covering the full width of the Sahel leaves no doubt that the gradual shift in land use negatively affected most ground-foraging birds, including three species of wheatear, although not (yet) Western Yellow Wagtail.

Despite an improvement of Sahelian rainfall since the 1990s, ground-foraging migrants continued to decline (Table 2, Figure 1). The deteriorating food supply in the Sahel is not the only explanation for their decline, and indeed habitat degradation on the breeding grounds plays a decisive role too, as reported for European Turtle Dove (Browne & Aebischer 2003, Moreno-Zarate *et al.* 2019, Dunn 2021), Whinchat (Fay *et al.* 2021), Northern Wheatear (Arlt & Pärt 2017) and Ortolan Bunting (Stolt 1993, Vepsäläinen *et al.* 2005, Berg 2008). Population declines in general have been larger in long-distance migrants from western than from eastern Europe, e.g. in European Turtle Dove, Greater Short-toed Lark, Northern Wheatear, Whinchat, Tawny Pipit and Ortolan Bunting (Keller *et al.* 2020), often being attributed to larger land degradation and habitat losses in W Europe (Donald *et al.* 2006, Bowler *et al.* 2021). However, the same argument can be deployed for the wintering habitat in sub-Saharan Africa. The grazing pressure from livestock in the western Sahel is much larger than in the eastern Sahel, and the larger bird declines in the west are in concordance with a more intensive human stamp on the land (Zwarts *et al.* 2023i). The majority of the birds from eastern Europe spend the winter in the eastern Sahel (and southward to South-Africa), whereas most birds from western Europe end up in the western Sahel. Accordingly, we should expect that granivorous long-distance migrants in western Europe will fare worse than those in eastern Europe. As Newton (2008) so succinctly put it, these are birds in double jeopardy.

Birds in shrubs and trees

Annual rainfall in the Sahel has a large impact on arboreal birds, in the short- as well as in the long-term. The short-term impact is obvious. In dry years, Sahelian trees have fewer leaves and shed them earlier during the dry season; they also produce fewer if any flowers and the flowering period is reduced (Poupon & Bille 1974, Hiernaux *et al.* 1994). With flowers and leaves diminished less food and feeding opportunities would remain for tree-dwelling birds, but this relationship has not yet been quantified in a Sahelian context. It is telling, however, that during the dry season birds concentrate in trees with a dense canopy and ignore trees without leaves (Figures 15 and 16 in Zwarts & Bijlsma 2015), which goes a long way to explain the concentration of birds in fewer tree species in dry years than in wet years; and the smaller numbers of birds (Zwarts *et al.* 2023f). The suggestion is that mortality among birds in the dry season in years with little rainfall is higher than in wet years. Poor survival in drought years is reflected in the year-on-year fluctuation of the breeding population in Europe, as illustrated for the Common Whitethroat and Common Redstart (Figure 2).

The impact of rainfall on population change from year to year may seem less drastic in arboreal bird species than in species bound to floodplains (Table 3 and 4), but in the long run a drought year has a much larger impact on arboreal birds because trees may die. Floodplain vegetation recovers quickly from a drought when it is followed by a wet year, even after a series of (extremely) dry years (Hiernaux *et al.* 2021), but it takes many more years before woody vegetation has recovered after a drought year causing mass mortality of trees. In Australian drylands, a drought can offset tree regeneration and growth for at least fifty, relatively wet, years (Fensham *et al.* 2009). Trees in the Sahel have experienced a double die-off in the past half century, first during the drought of 1972–1973, then again during the drought in 1982–1987. Loss of woody cover in NW Senegal, with an average annual rainfall of 300 mm, was variously estimated at 22% in 1954–1989 (Gonzalez 2012), 20% in 1965–2009 (Dendoncker *et al.* 2020) and 35% in 1971–1995 (of which 13% in 1972 and 22% thereafter; Poupon & Bille 1974, Vincke *et al.* 2010)). Local differences in tree mortality can be large, however, partly related to terrain morphology, soil, ground water table and grazing pressure.

The resolution of satellite imagery before 2002 was still too low to discriminate scattered trees in savannahs and farmland. More recent high resolution satellite images have instead been compared to aerial photographs, available since the 1940s, and satellite photos, available for the period 1965–1972, to show the decline of woody cover during the Great Drought (Tappan *et al.* 2004, Brandt *et al.* 2014, Spiekermann *et al.* 2015, CILSS 2016, Zwarts *et al.* 2018). Thanks to (very) high resolution satellite images available since 2002, the opportunities to quantify the gradual increase of the woody cover in the past few decades in relation to human population density, land use, soil and average rainfall are unprecedented (Brandt *et al.* 2017 & 2018, Hiernaux *et al.* 2022). Ground surveys have added much detail to satellite imagery, or indeed were the only sources of information at a time when satellites were just entering the scene.

The loss of woody vegetation in the Sahel was largest in grazed areas. For example, tree mortality in 1972 amounted to 22% in Dahra (Senegal; 400 mm rain/year) where there was no grazing, but 48% in a site with normal grazing pressure. The grazing-related discrepancy in tree loss was even larger in Ndoli (Senegal; 560 mm rain/year), i.e. 8% in an ungrazed and 41% in a grazed site (Bille 1992). Tree mortality in the Gourma in E Mali (average rainfall 300 mm) was lower in (clayey) valleys than on (sandy) hill slopes; the local decline in woody cover by 50 to 70% was attributed to soil rather than grazing (Poupon & Bille 1974, Hiernaux *et al.* 2009, Vincke *et al.* 2010). The largest declines were noted on sandy dunes in S Mauritania (average rainfall 150 mm), with a 90% loss of vegetation (Niang *et al.* 2008). In contrast, we found no reports on drought-related tree mortality in the hyper-humid zone. These data suggest that tree mortality during droughts is extremely high in the hyper-arid zone, (nearly) absent in the hyper-humid zone and intermediate in the arid and humid zones. Arboreal species restricted in their winter distribution to the arid zones will henceforth suffer more from tree loss than bird species from the humid zones.

Arboreal birds are highly selective in their choice of foraging substrate, resulting in half of the birds congregating in trees and shrubs which represent 6.7% of the woody cover. Furthermore, tree selection differs per bird species with, for instance, Western Bonelli's Warbler mainly in White Thorn *Faidherbia albida* and Western Orphean Warbler mainly in Umbrella Acacia *Acacia tortilis* (Zwarts *et al.* 2023d). To quantify the actual impact of Sahelian drought on arboreal birds, we need to know whether tree mortality differed for preferred and non-preferred woody species. Tree mortality during droughts was less for drought-tolerant species, but high for species from more humid zones which were planted in the Sahel, such as edible fruit-yielding taxa from the Sudan vegetation zone (Bille 1992, Maranz 2009). Generally speaking, the overall result of drought was a large decline in the number of tree species (Wezel & Lykke 2006, Gonzalez *et al.* 2012). On the other hand, some common, and for birds important, tree species, such as the drought-resistant Sahelian species *Acacia tortilis* and *Balanites aegyptica*, declined less sharply. Other species completely disappeared from the arid zone (Bille 1992, Maranz 2009, Hiernaux *et al.* 2009, Vincke *et al.* 2010, Dendoncker *et al.* 2020). Most of the latter were rarely visited by birds, although the decline of *Acacia senegal* (sensitive to grazing) must have been a serious loss to tree-dwelling birds (Zwarts *et al.* 2023d,g).

After the drought-related shift in the woody vegetation towards more drought-resistant woody species, a reverse trend was to be expected after the gradual recovery of rainfall. No such development has (as yet) occurred, due to the large, and increasing, human impact. In the Ferlo (savannah in NW Senegal) and in central Senegal (mainly farmland) the decline of trees continued in the second half of the 20th century, accompanied by a parallel increase of shrubs (Herrmann & Tappan 2013, Dendoncker *et al.* 2022). Local variations on this theme are rife, though. In western Niger in 1996–2017, for example, loss of woody plants was the common denominator in farmland and savannah, but especially of shrubs (not trees) and much more so in savannah (shrubs declined from 1567 to 250/ha) than in cropland (from 342 to 155/ha). The ongoing depletion of woody vegetation was caused by the expansion of the cropped area, a shortening of the crop-fallow cycle and increasing pressure on wood resources (fuel, construction material). During these two decades neither rainfall nor soil moisture had significantly changed (Hiernaux *et al.* 2022).

Outcomes of local and regional studies have a large decline of tree diversity in common (Table 6), which does not augur well for arboreal birds. However, tree species attractive to birds are doing relatively well: *Acacia tortilis* and *Balanites aegyptiaca* in the arid and semi-arid savannah zone and *Faidherbia albida* in the semi-humid agroforestry zone. Obviously, apart from rainfall, farmers and pastoralists have had, and still have, in many ways a large impact on woody cover and species composition of the woody vegetation. Some specific examples will be given, particularly with regards to the effects on birds.

Table 6. Change in the woody vegetation in Senegal (SN) and Mali (ML) in four rainfall zones (mm rainfall/year) between the 1960s and 2010s (but 1980–2010 for SN 650); increase (↑), stable (→) or decline (↓) shown for 39 woody species, ranked according to the average bird density per ha of canopy (bar in second column; from Zwarts *et al.* 2023d). Sources: Herrmann & Tappan 2013 (SN 550), Brandt *et al.* 2014 (SN 400, ML 500), Dendoncker et *al.* 2020 (SN 300).

Woody species	Birds/ha	SN 300	SN 400	ML 500	SN 650
Maerua crassifolia				↓	
Faidherbia albida			↓	↑	
Ziziphus mauritiana		↓	↓	↓	↑
Acacia tortilis		↑	↑		
Balanites aegyptiaca		→	↑	↑	
Acacia nilotica			↓	→	
Bombax costatum					↓
Piliostigma reticulatum			↓	↓	↑
Diospyros mespiliformis				↓	
Acacia senegal		↓	↓		
Tamarindus indica			↓	↓	→
Pterocarpus erinaceus					↓
Cordyla pinnata					↓
Acacia seyal		↓	↓	↓	
Combretum glutinosum		↓	↓	↓	→
Acacia macrostachya					↓
Combretum nigricans			↓		↓
Combretum micranthum			↓	↓	
Sclerocarya birrea		↓	↓	↓	
Dichrostachys cinerea		↓			
Vitellaria paradoxa				↓	
Boscia senegalensis		→	↑	→	
Commiphora africana		↓	↓		
Prosopis africana				↓	
Acacia gourmaensis				↓	
Pterocarpus lucens			↑	↓	
Terminalia avicennioides		↓	↓	↓	
Lannea acida			↓	↓	↓
Anogeissus leiocarpus			↓	↓	↓
Eucalyptus camaldulensis				→	
Sterculia setigera		↓	↓		↓
Leptadenia pyrotechnica		→			
Grewia bicolor		↓	↓	↓	
Calotropis procera		→			↑
Guiera senegalensis		↓	↓		↑
Hymenocardia acida			↓		
Detarium microcarpum				↑	
Adansonia digitata		→	↓	↑	→
Borassus aethiopum				↓	

Prosopis juliflora is native to the Americas and introduced in West Africa to combat desertification. It has spread rapidly into fertile areas since the 1970s (Shackleton *et al.* 2014, Hussain 2021). Based on our random sites from the zone between 7°N and 22°N, we estimated the total woody cover of *Prosopis* within this region at 28,000 ha, which does not include the extensive pure stands in the former lakebed of Lac Faquibine in Mali (Djoudi *et al.* 2011) and the northern half of Lake Chad (Batello *et al.* 2004). In South Africa, *Prosopis* forests are poor in birds compared to original acacia forests, the latter in danger of being outcompeted by the invasive *Prosopis* (Dean *et al.* 2002). In the Sahel zone, the average density of 4.67 migrants and 4.41 residents per ha of canopy may not give the impression of a bird-poor tree species, but this hinges on outliers, as Iberian Chiffchaffs *Phylloscopus ibericus* attracted by *Prosopis* standing in water and, in Sudan, by Nile Valley Sunbirds *Hedydipna metallica* visiting the trees when in blossom. Apart from these exceptional visits *Prosopis* is very poor in foraging birds. Average bird densities in acacias in the same regions were 3 to 6 times higher (Zwarts *et al.* 2023d). Further expansion of *Prosopis* at the expense of acacias will inevitably be a loss to birds, especially in flooded forests (see below).

Since about the 1990s, many villages in West Africa now have their own *Eucalyptus camaldulensis* woodlot, usually some ha in extent. Few birds foraged in this tree species. The average density was 3.0 birds per ha of canopy, mostly migrants (2.6/ha), of which Western Bonelli's Warbler (0.7/ha) was the most common. Since the total surface of the plantations is small and the woodlots are planted on bare ground, its overall impact on birds must be limited except for the Ethiopian highlands where some 200,000 ha were planted with *C. camaldulensis* and *C. globulus* (Edwards 2010). The average density in Ethiopia was 3.5 arboreal birds per ha of canopy, among which 1.8 migrants per ha of canopy. This compares poorly with other tree species in the same rainfall zone (500–1100 mm rainfall/year): 47.2 birds per ha of canopy, of which 17.7 migrants per ha canopy (Figure 5). Planting *Eucalyptus* has a negative impact on birds when the original woody vegetation is being replaced.

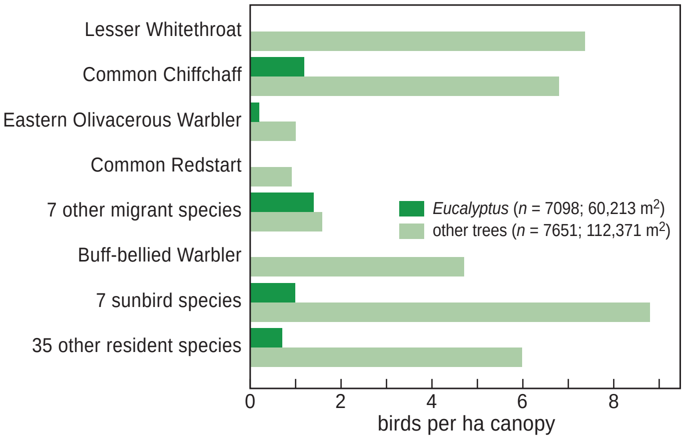

Figure 5. Density (*n* per ha canopy) of arboreal birds in Ethiopia given separately for *Eucalyptus* and all other tree species (>2 m high) together occurring in the same rainfall zone (500–1100 mm). Number of surveyed trees (*n*) and the total surface of all tree canopies; m^2) are given (based on data given in Zwarts *et al.* 2023b,d).

Cashew *Anacardium occidentale* is native to Brazil but has become a popular cultivation in the hyper-humid zone of West Africa since the 1980s. The surface area of these single-species plantations has gradually increased to 3.4 million ha in 2020 (www.fao.org/faostat/en/#data/QCL). In Guinea-Bissau, half of the woody cover presently consists of cashew plantations (Zwarts *et al.* 2023d). The cultivation of cashew has come at the expense of a varied woody vegetation including several tree species rich in birds. The negative impact is considered substantial because cashew trees are largely avoided by birds (only 0.2 migrants and 2.0 residents per ha canopy, on average), whereas arboreal birds in the hyper-humid zone were recorded at a density of 5 to 20 birds per ha of canopy (Zwarts *et al.* 2023b,d). Among migrant species, four suffered most: European Pied Flycatcher, Melodious, Wood and Willow Warblers.

Teak *Tectonia grandis* is native to SE Asia and introduced in the hyper-humid zone of West Africa in the early 20th century where monocultures amounted to 436,000 ha in 2010 (Kollert & Cherubini 2012). No migrants were recorded in Teak, and few resident insectivores (4.49/ha canopy). This tree may attract sunbirds when flowering (Zwarts *et al.* 2023d), but the large-scale planting of Teak must have brought about avifaunistic impoverishment of the hyper-humid zone.

Flooded acacia forests are extremely rich in birds with 60 arboreal birds/ha of canopy in *Acacia nilotica*, 80/ha in *A. seyal* and 140/ha in *A. kirkii*. Even more important is the function of flood forests as a refuge for millions of migrants late in the dry season, especially in dry years (Zwarts *et al.* 2023g). During the Great Drought, most flooded forests in the Inner Niger Delta of Mali and in the Senegal valley disappeared (Beintema *et al.* 2007, Tappan *et al.* 2004, Niang *et al.* 2008). Some recovery was recently recorded after a series of relatively wet years, unless floodplains had been converted into irrigated rice fields. Loss of flooded forests on this scale will be equivalent to a loss of several millions of migrants, or about 1% of the number of arboreal migrants present in Africa between 7°N and 22°N. The negative impact will be particularly substantial for Iberian Chiffchaffs which are concentrated in flood forests in the western Sahel.

The mounting grazing pressure by livestock in the Sahel caused non-thorny trees and shrubs to decline; thorny trees and shrubs became even more dominant. The overall number of woody species has declined, but food supply for insectivorous birds was not affected because thorny trees and shrubs are rich in insects (Zwarts *et al.* 2015). With a high density of livestock, such as near deep wells, thorny trees preferred by birds will also disappear, to be replaced by inedible woody vegetation like Sodom Apple *Calotropis procera* (Vincke *et al.* 2010). High grazing pressure is responsible for the removal of ground vegetation beneath trees and shrubs, effectively reducing insect food supply of bird species foraging on and near the ground in the vicinity of low bushes (Zwarts *et al.* 2023k). Such habitat loss affects species like Common Whitethroat and sit-and-wait foragers as Common Redstart which uses low branches to pounce on ground-dwelling insects.

In the arid and semi-arid zone (<600 mm rainfall/year), expansion of farmland at the expense of savannahs, even when it goes with but a small loss of the woody vegetation (Brandt *et al.* 2018), usually brings about a large shift in species composition. Such a shift may initially constitute a loss for arboreal birds in the arid zone but a gain for birds in the semi-arid zone (Zwarts *et al.* 2023g), but future developments may work out differently (Wittig *et al.* 2000).

In the humid zone (>600 mm rainfall/year), expansion of farmland at the expense of woody savannahs means a gradual, but in the long term large, loss of woody cover (Tappan *et al.* 2004, Brandt *et al.* 2018). The total loss of woody vegetation has been so great that it can account for the steep decline in species as Common Redstart and Eurasian Wryneck (wintering in this rainfall zone, except the short-winged central European Wryneck populations that winter in Iberia and Morocco; van Wijk *et al.* 2014) during the second half of the 20th century (Figure 4). The loss of woody cover increases when selective clear-cutting is practised in humid forests to create farmland plots. In contrast to the semi-arid zone, where farmers created a bird-rich *Faidherbia* agroforestry zone, farmland in the humid zone is poor in arboreal birds, because it is dominated by bird-poor Shea Trees *Vitellaria paradoxa* and further south by African Locust Bean Tree *Parkia biglobosa* (Zwarts *et al.* 2023d). Logging and deforestation cause forest birds to decline, but some bird species, including migrants such as Melodious and Wood Warblers, may inhabit – at least in the short term – forest gaps and 'derived savannah', a more open landscape with scattered trees (Waltert *et al.* 2005, Arcilla *et al.* 2015, Dowsett-Lemaire & Dowsett 2014 & 2019, Gatter 2016, Mallord *et al.* 2018, Kühnert *et al.* 2019). Whether such habitat constitutes a viable alternative to the original habitat, is difficult to say.

Trees are less attractive to birds after people have shaken, cut and clipped branches and twigs to feed livestock with fresh leaves, flowers and pods (Photo 3; Zwarts & Bijlsma 2015). The practice is usually confined to the second half of the dry season, and to acacia trees and particularly *Faidherbia*. The negative impact is large because (1) people prune trees species that are most important to birds, (2) the timing of pruning coincides with the period when birds are most dependent on the few tree species still in leaf (in other words the trees that are specifically targeted by herders), and (3) pruning is more widespread in dry years when birds have difficulty in staying alive. Quantitative data are lacking, but it is likely that pruning nowadays occurs more often than in the past due to the steady increase of livestock. Tree pruning is

Photo 2. *Eucalyptus* plantations dominate much of the woody vegetation in the Ethiopian highlands. As building material it enjoys high popularity (12 February 2019, 11.90°N, 39.34°E, Ethiopia).

widespread in the densely populated part of the Sahel, as in Senegal and Mali, but not (yet) elsewhere in the Sahel where grazing pressure of livestock is lower (Zwarts *et al.* 2023f,i).

A century and longer of changes against a backdrop of environmental turmoil

Moreau (1972) was convinced that the European migrants spending the winter in Africa had declined in the course of his lifetime. In fact, he surmised that woodland migrants must have reached their lowest ebb during the last glaciation, then expanded tenfold to a heyday some 5000 years ago, and declined again to one quarter of this (Moreau 1952, 1972: 30). Fifty years after the publication of his 'magnum opus', we face a steady decline of many migrant species, reinforced by the exceptionally dry 1970s and 1980s in the Sahel. With the advent of improved rainfall in the Sahel in recent decades, and particularly in the 2010s, several migrant species showed a recovery to 1970 levels. This may not last even if future predictions, that on average, the Sahel is going to receive more rain due to the higher level of greenhouse gases, come true (Dong & Sutton 2015). Nonetheless, it should be kept in mind that rainfall remains unpredictable in the Sahel. The present series of wet years will be interrupted at some point by a new Great Drought and thus, inevitably, trigger another crash in bird species wintering in the Sahel, notably those in the arid zone and in the riverine floodplains. It is also important to remember that the increase of several migrant species between 1990 and 2020 in response to the recovery of rainfall in the Sahel masks ongoing processes in the region at large which, in general, are irreversible in the face of the growing human population (especially in the more humid regions; Brandt *et al.* 2017), and ultimately will have an enduring negative impact on the birds.

Birds frequently surprise us by showing high adaptability to changing conditions. All the world's a stage, and all the migratory birds merely players. But what will happen when the climate of the Sahel enters another series of droughts? How are migratory birds, and African residents for that matter, going to cope with wintering grounds under increasing anthropogenic stress? Some changes are already in force, be it recognised or not (see below). Many migratory bird

Photo 3. Twigs and branches are torn off from *Faidherbia* trees to provide livestock with fresh leaves during the dry season. The photo is taken in Sudan (13.500°N, 30.334°E, 12 January 2019), where this practice occurs on a small scale compared to the western Sahel where most *Faidherbia* are heavily pruned during the second half of the dry season.

species have shown a northward shift in wintering areas, not a few swapping sub-Saharan wintering grounds for southern European ones (Morganti 2014), mostly storks, herons, raptors (especially Black Kite *Milvus migrans migrans* & *M. m. lineatus* and Booted Eagle *Aquila pennatus*; Biricik & Karakas 2011, Literák *et al.* 2017, Panter *et al.* 2020, Baghino *et al.* 2007) and waders (Black-tailed Godwit partly shifting from wintering in West Africa to Iberia; Lourenço & Piersma 2008) but increasingly also passerines, such as Barn Swallow (van Nus & Neto 2017), Daurian Swallow *Cecropis daurica* (Dufour *et al.* 2020) and Pallid Swift *Apus pallidus* (J. Solana & G. Bruno in Gibson 2021: 236–237), to name a few. This pattern of shifting wintering grounds northwards is not restricted to Afro-Palearctic migrants, but also discernible among migrants within Europe (Sutherland 1998), within Africa (Ambrosini *et al.* 2011) and in the Americas (Curley *et al.* 2020). Shortening of migration distances accrued survival benefits in juvenile White Storks: all 6 juveniles that overwintered in Europe survived their first year, compared to only 18 out of 48 juveniles that overwintered on the traditional wintering grounds in Africa (Rotics *et al.* 2017). But contrary to expectations, Black-tailed Godwits wintering in West Africa (Senegal and Guinee-Bissau) arrived two days earlier on the breeding sites in The Netherlands, and initiated their clutch six days earlier, than godwits wintering in Spain and Portugal. Neither quality of breeding habitat nor nest survival in this species were associated with wintering location (Kentie *et al.* 2017). The return flight of Godwits to the breeding grounds across the Sahara is, however, hazardous and associated with high mortality (Loonstra *et al.* 2019).

Of great changes going unnoticed in the Sahel, the one involving Eurasian Blackcaps and Common Chiffchaff is perhaps the most telling. Both species are recorded historically as largely spending the winter in the Mediterranean and in sub-Saharan Africa (Cramp 1992, Urban *et al.* 1997), but during our surveys in the 2010s were recorded only rarely in Africa between 7 and 22°N except in Ethiopia where numbers were substantial (Figure 8 and 14 in Zwarts *et al.* 2023c). Small numbers were captured in The Gambia (King 2000, King & Hutchinson 2001) and the Djoudj, Senegal (Ottosson *et al.* 2001) in the 1990s, but both species are at present decidedly scarce across the Sahel except Ethiopia (Zwarts *et al.* 2023b), and are rare in winter in the hyper-humid zone in West Africa (Dowsett-Lemaire & Dowsett 2014, 2019, Languy 2019). Since the 1970s, an increasing number of Blackcaps remained during the winter in W Europe (Berthold *et al.* 1992), where they have become a common garden bird (Plummer *et al.* 2015). In fact, the much-publicised wintering of central European Blackcaps in Britain has found its counterpart in much of western Europe and in Scandinavia (Bengtsson *et al.* 2009), where wintering has become widespread in recent decades. Ringing recoveries and geolocator data also suggest high plasticity and consistent changes in migratory behaviour of Blackcaps (Mokwa 2009, Hiemer *et al.* 2018, Delmore *et al.* 2020), but the disappearance of this species and Common Chiffchaff as common wintering birds in the Sahel (except western- and easternmost) went completely unnoticed. What such changes impart on the life histories of the birds involved is as yet unclear (Delmore *et al.* 2020). A northward shift of wintering areas to the Mediterranean Basin may perhaps bypass drought-related problems in the Sahel, but not if the predicted decline of the rainfall in the Mediterranean materialises in the near future (Giorgi & Lionello 2007).

When trying to unravel the backgrounds of population fluctuations, particularly those of long-distance migrants, it is clearly counterproductive to resort to either/or explanations. Naturally, populations face changes on the wintering grounds, just as they do in their breeding areas and in between whilst migrating, sometimes in concert, at other times with opposite effects. It is equally obvious that the relative importance of each of these factors varies constantly over time, either structurally under the aegis of man-caused land and climate change, or temporarily in the wake of weather cycles or variations in food supply. We have refrained from firm conclusions as to which factor has been the most decisive in the last half century's ups and downs in long-distance migrants, but rather we have focussed on the African side of the story and mainly in descriptive fashion at that. By casting as wide a net as possible (within the restrictions imposed by time and set-up of the study), we have tried to look beyond mere birds, particularly because distributions nor habitats of arboreal birds make sense without identification of trees at the species level. The devil is in the detail. At the same time, an important caveat remains, namely food supply (abundance, diversity, variations across habitats, seasons and years), for which the lack of recent hard data from the Sahel is monumental. Even so, if one conclusion can be made after years of tramping across the wider Sahel, it is that the world changes rapidly, and that the birds' numbers and behaviour change accordingly. Indeed, an open door, but no less true and partly quantified in this and other studies summarised in this special volume of Ardea.

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SAMENVATTING

Veel onderzoeken hebben aangetoond dat regenval in de Sahel grote invloed heeft op de populatieontwikkeling van vogelsoorten die daar de noordelijke winter doorbrengen. Daarentegen zijn er ook Sahelgangers, vooral vogels die op de grond foerageren, die sterk achteruit gingen onafhankelijk van de regenval in de Sahel. Dat wordt hier opnieuw bevestigd. Maar om te achterhalen wat er echt gaande is, zijn veldgegevens nodig. Daartoe werden in 2011–2019 over de volle breedte van de Sahel systematische tellingen uitgevoerd. Zoals te verwachten spelen vele factoren een rol: (1) Regenval bepaalt hoeveel open water er is in de Sahel. Water is een noodzaak voor vogels die daar gebruik van maken. Er is de laatste decennia veel open water bijgekomen, omdat regenwater – door allerlei omstandigheden – tegenwoordig gelijk in de bodem verdwijnt waardoor de grondwaterspiegel is gestegen. (2) De frequentie en intensiteit van stofstormen wordt deels bepaald door regenval. Er zijn nu veel meer stofstormen dan vroeger, omdat er meer open grond is (landbouw) en regen vaker in de vorm van zware buien valt (effect opwarming van de Sahara). Vogels kunnen tijdens stofstormen niet naar voedsel zoeken, maar hoe nadelig dat uitpakt voor vogels is onbekend. (3) Regenval ten zuiden van de Sahel bepaalt de rivierafvoer en daardoor ook de omvang van de overstromingsvlakten in de Sahel. Daarbij treedt een cumulatief effect op: na een aantal regenarme jaren neemt de rivierafvoer sterk af, en andersom. Tijdens de droge tijd (oktober–mei) vallen de vloedvlaktes droog. In natte jaren hebben trekvogels tot aan hun vertrek nog genoeg plekken tot hun beschikking om voedsel te zoeken, maar in droge jaren raken ze geconcentreerd op de weinige natte plekken die resteren. Daar zijn ze een makkelijke prooi voor vogelvangers. Als ook de laatste natte plekken zijn opgedroogd, zoals in extreem droge jaren gebeurt, sterven ze de hongerdood. (4) In regenarme jaren ligt er minder zaad op de grond en dat zijn ook nog eens overwegend voor vogels marginale zaden. De sterfte onder zaadeters neemt dan sterk toe. (5) In droge jaren verliezen bomen eerder hun blad en wijken vogels uit naar de weinige boomsoorten die nog wel blad hebben. Daarvan zijn er niet voldoende en veel vogels overleven het daarom niet. In extreem droge jaren, zoals in de jaren zeventig en tachtig, gaan bomen bovendien massaal dood. Het kan jaren duren voordat herstel is opgetreden. Als droge ramp-

jaren kort achter elkaar gebeuren, bijvoorbeeld in 1972–1973 en in 1984–1985, kan de boomvegetatie zich onvoldoende herstellen en nemen de vogelaantallen nog verder af. Dat verklaart waarom de populaties van Draaihals *Jynx torquilla* en Gekraagde Roodstaart *Phoenicurus phoenicurus* tien keer kleiner zijn geworden ten opzichte van de natte jaren vijftig en zestig. Na de 'Grote Droogte' (1972–1985) zijn er tot nu toe (2022) geen nieuwe droge rampjaren geweest. De bomen op de aride and semi-aride savanne hebben zich hersteld en vogels konden weer toenemen. De aantallen van bijvoorbeeld Draaihalzen en Gekraagde Roodstaarten zijn de afgelopen 30 jaar verdubbeld. Zuid-Europese soorten als Baardgrasmus *Curruca iberiae + subalpina + cantillans* en Westelijke Orpheusgrasmus *Curruca hortensis* zijn zelfs drie tot vijf keer zo talrijk geworden, beide overwinterend in aride gebieden waar bomen masssaal waren afgestorven en na de Grote Droogte even massaal zijn teruggekomen.

Toch kunnen we niet alles verklaren met variabelen die aan regenval zijn gekoppeld. De menselijke bevolking in de Sahel is binnen een eeuw vertienvoudigd en dat heeft consequenties: (1) De graasdruk van het vee neemt jaarlijks toe met 3 tot 4%, waardoor er veel minder (gras)zaad wordt geproduceerd, vooral zaden waar de vogels een voorkeur voor hebben. Zaadeters zijn daarom de afgelopen decennia sterk afgenomen. (2) Elk jaar wordt 2% van de savanne omgezet in boerenland. Dat is ongunstig voor de meeste, maar niet alle vogelsoorten. Boeren laten op hun land weliswaar veel bomen staan, maar dat zijn andere soorten dan kenmerkend voor de savanne. Vooral de boomvogels die in de aride en humide zone verblijven, worden getroffen maar de vogelsoorten die overwinteren in een brede zone daar tussenin profiteren zelfs (mogelijk tijdelijk) van de uitbreiding van het landbouwgebied omdat hun voorkeursboom (*Faidherbia albida*) daar veel voorkomt en door de boeren wordt beschermd. (3) Door de toename van het landbouwareaal zijn in de Sahel relatief veel natte, buitengewoon vogelrijke, bossen verdwenen. Deze bossen stonden op de rijkere gronden en waren een magneet voor overwinterende vogels en een refugium voor vogels in tijden van extreme droogte. (4) Miljoenen ha in de humide boomsavanne zijn sinds 1980 omgezet in cashewplantage. Veel vogels hebben daardoor habitat verloren want Cashew *Anacardium occidentale* is buitengewoon vogelarm. (5) *Prosopis juliflora*, een exotische boomsoort, verdringt lokaal de inheemse acacia's. Dat is een verlies want *Prosopis* is vogelarm vergeleken met acacia's. (6) Door irrigatie en de aanleg van dammen zijn vloedvlaktes in Senegal, Mali, Nigeria en Tsjaad gedecimeerd, met navenante effecten op de vele vogelsoorten die zich in deze gebieden concentreren. (7) Massale vogelvangst, zoals die na ca. 1990 in de Binnendelta usance werd, vond vroeger niet in die omvang plaats omdat de mensen nog geen nylonnetten hadden en geen ijs (waarmee vogels en vis gekoeld naar verder weg gelegen markten kunnen worden getransporteerd). (8) Grote vogelsoorten als gieren en trappen zijn door menselijke ingrijpen (vrijwel) verdwenen uit de Sahel, vooral in het dichtbevolkte westelijke deel. Al met al is de Sahel voor de meeste trekvogels minder aantrekkelijk geworden als overwinteringsgebied. Er verblijven nu veel minder trekvogels in de Sahel dan een halve eeuw geleden. Verschillende Europese vogelsoorten overwinteren in toenemende mate ten noorden van de Sahara, maar of dat te maken heeft met de slechtere omstandigheden in de Sahel, of bijvoorbeeld de mildere winters in Europa, is niet te zeggen.

RÉSUMÉ

De nombreuses études ont montré que les précipitations au Sahel ont un impact majeur sur l'état des populations d'oiseaux qui y passent l'hiver septentrional. En revanche, le déclin significatif des espèces sahéliennes, en particulier de celles qui se nourrissent au sol, est indépendant des précipitations. Cet article fait le bilan des résultats des inventaires systématiques réalisés dans la totalité du Sahel entre 2011 et 2019 et évalue le rôle des multiples facteurs qui influencent l'évolution des populations : (1) Les précipitations déterminent la quantité d'eau libre dans le Sahel, indispensable à la survie des espèces aquatiques. L'étendue des eaux libres a augmenté considérablement au cours des dernières décennies, car pour des raisons variées, l'eau de pluie s'infiltre aujourd'hui plus rapidement dans le sol, ce qui fait monter les nappes phréatiques. (2) La fréquence et l'intensité des tempêtes de poussières sont largement déterminées par les précipitations. Ces tempêtes sont beaucoup plus nombreuses aujourd'hui qu'auparavant, car il y a plus de terres dénudées pour l'agriculture et car l'intensité des précipitations augmente en raison du réchauffement du Sahara. Les oiseaux ne peuvent pas chercher de nourriture pendant ces phénomènes, mais on ignore dans quelle mesure cela leur est préjudiciable. (3) Les quantités de précipitations au Sud du Sahel déterminent le débit des rivières et donc l'étendue des plaines inondées dans la zone sahélienne. Les conséquences peuvent s'amplifier avec les années : ainsi, après plusieurs saisons sans pluie, le débit des rivières diminue fortement. Pendant la saison sèche (octobre–mai), les plaines inondées s'assèchent. Lors des années humides, les oiseaux migrateurs ont encore beaucoup d'endroits à leur disposition pour chercher de la nourriture jusqu'à leur départ, mais lors des années sèches, ils se concentrent sur les rares secteurs inondés qui subsistent. Ils y sont des proies faciles pour les piégeurs. Et lorsque même leurs derniers refuges s'assèchent, comme c'est le cas lors des années extrêmement sèches, ils meurent de faim. (4) Lors des années sans pluie, la quantité de graines au sol est faible et composée pour une bonne partie de graines à faible valeur nutritive. La mortalité des oiseaux granivores augmente alors fortement. (5) Lors des années sèches, les arbres perdent leurs feuilles plus tôt et les oiseaux se concentrent sur les quelques essences d'arbres qui ont encore des feuilles. Leur nombre étant insuffisant, de nombreux individus périssent. Lors des années extrêmement sèches, comme dans les années 1970 et 1980, les arbres meurent en masse. Il faut alors des années pour que les habitats soient restaurés. Lorsque des sécheresses catastrophiques se succèdent rapidement, comme par exemple en 1972/1973 et en 1984/1985, la végétation arborée n'a pas le temps de se rétablir suffisamment et les populations d'oiseaux s'effondrent encore plus. C'est ainsi que les populations du Torcol fourmilier *Jynx torquilla* et du Rougequeue à front blanc *Phoenicurus phoenicurus* ont été réduites à dix pourcent de leurs niveaux des années humides 1950 et 1960. Depuis la Grande Sécheresse des années 1970 et 1980, il n'y a toutefois pas eu de nouvelles années catastrophiques jusqu'à aujourd'hui (2022). La forêt s'est rétablie et les populations d'oiseaux ont rebondi. Le nombre de Torcols fourmiliers et de Rougequeues à front blanc, par exemple, a doublé au cours des 30 dernières années. Des espèces d'Europe du Sud comme la Fauvette passerinette et la Fauvette orphée sont même devenues trois à cinq fois plus abondantes. Toutes deux hivernent dans des zones arides où les arbres avaient en bonne partie disparu, mais ont repoussé après la Grande Sécheresse.

Mais tout ne peut pas s'expliquer par des variables liées aux précipitations. La population humaine du Sahel a été multipliée par dix en un siècle, ce qui n'est pas sans conséquences : (1) La pression de pâturage est devenue beaucoup plus forte, ce qui entraîne une production beaucoup plus faible de graines de graminées, en particulier de celles appréciées par les oiseaux. Les espèces granivores ont donc fortement diminué au cours des dernières décennies. (2) Chaque année, 2% de la savane est convertie en terres agricoles. Cette situation est défavorable à la plupart des espèces d'oiseaux, mais pas à toutes. Les agriculteurs laissent certes de nombreux arbres sur leurs terres, mais il s'agit d'essences différentes de celles qui sont typiques de la savane. Les espèces arboricoles qui fréquentent les parties les plus sèches et humides du Sahel sont particulièrement touchées, alors que les espèces qui hivernent dans la large zone intermédiaire profitent (peut-être temporairement) de l'expansion de la zone agricole, car leur arbre préféré (*Faidherbia albida*) y est commun. (3) L'augmentation des surfaces agricoles au Sahel a entraîné la disparition de grandes superficies de forêts humides exceptionnellement riches en oiseaux. (4) Des millions d'hectares de savane arborée humide ont été convertis en plantations d'anacardiers *Anacardium occidentale* depuis 1980. De nombreuses espèces ont perdu leur habitat dans ces opérations, car cette essence, qui produit la noix de cajou, est exceptionnellement pauvre en oiseaux. (5) *Prosopis juliflora*, une essence d'arbre exotique, remplace localement les acacias. Il en résulte une perte d'habitat pour les oiseaux, car le *Prosopis* leur est moins favorable que les acacias. (6) L'irrigation et la construction de barrages ont décimé les plaines inondables au Sénégal, au Mali, au Nigéria et au Tchad et entraîné des conséquences négatives sur les nombreuses espèces d'oiseaux concentrées dans ces zones. (7) Le piégeage massif des oiseaux s'est fortement développé dans le Delta Intérieur du fleuve Niger depuis 1990 environ. Il n'avait pas lieu à cette échelle auparavant car les piégeurs ne disposaient pas de filets en nylon et de glace pour transporter leurs prises vers des marchés plus éloignés. (8) Les plus grandes espèces d'oiseaux tels les vautours et les outardes ont quasiment disparu du Sahel en raison des persécutions humaines, surtout dans la partie occidentale plus densément peuplée. En tant que zone d'hivernage pour la plupart des oiseaux migrateurs d'Europe et d'Asie, le Sahel est donc devenu moins attrayant. La quantité d'oiseaux migrateurs qui le fréquente est bien moindre qu'il y a un demi-siècle, principalement en raison de la réduction considérable de la taille des populations. Par ailleurs, plusieurs espèces migratrices d'origine européenne hivernent de plus en plus au Nord du Sahara. Les raisons de ce déplacement de l'aire d'hivernage sont plus probablement à rechercher dans les modifications des habitats en Europe ou les changements climatiques que dans les conditions d'accueil dégradées au Sahel, mais elles restent à ce jour largement incomprises.

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SUPPLEMENTARY MATERIAL 1: Size of bird populations related to conditions in the Sahel

Table S1. Studies showing the impact of environmental conditions in the African wintering area on the breeding population in Europe. Impacting factors were measured in four ways: annual rainfall (selection of rainfall stations or overall Sahel rainfall index), flooding (size of large Sahelian floodplains measured directly or estimated using the annual or peak discharge of rivers), NDVI and total cereal harvest. The impact of these factors on birds was also measured via population size, percent change of the population relative to the previous year, percent ring recoveries from sub-Saharan Africa (EURING data) and survival. Carry-over effects were shown for migration (timing, mortality) and breeding (fraction non-breeding birds, breeding success).

	Impact				Parameter				Carry over		
Bird species	Rainfall	Flooding	NDVI	Harvest	Population	% Change	Recoveries	Survival	Migration	Breeding	**Source**
Garganey		F			P		R				Zwarts *et al.* 2009
Pintail		F					R				Zwarts *et al.* 2009
European Turtle Dove	R		N	H				S			Eraud 2009
Montagu's Harrier	R	F						S			Millon *et al.* 2019
Lesser Kestrel	R							S			Mihoub *et al.* 2010
Black-winged Stilt	R					C					Dubois 1992
Black-tailed Godwit	R						R				Zwarts *et al.* 2009
Ruff		F				C	R		M		Zwarts *et al.* 2009
Wood Sandpiper		F					R				Zwarts *et al.* 2009
Caspian Tern		F					R				Zwarts *et al.* 2009
White Stork		F				C			M	B	Dallinga & Schoenmakers 1989
White Stork	R							S			Kanyamibwa *et al.* 1993
White Stork	R							S			Barbraud *et al.*1999
White Stork			N					S			Schaub *et al.* 2005
White Stork	R				P	C	R			B	Zwarts *et al.* 2009
Glossy Ibis		F			P		R				Zwarts *et al.* 2009
Black-crowned Night Heron		F			P						Den Held 1981
Black-crowned Night Heron	R	F									Fasola *et al.* 2000
Black-crowned Night Heron	R	F			P	C					Zwarts *et al.* 2009
Squacco Heron	R	F									Fasola *et al.* 2000
Squacco Heron	R	F			P						Zwarts *et al.* 2009
Grey Heron		F					R				Zwarts *et al.* 2009
Purple Heron		F			P						Den Held 1981
Purple Heron		F						S			Cavé 1983
Purple Heron	R	F									Zwarts *et al.* 2009
Purple Heron		F			P		R				Zwarts *et al.* 2009
Western Marsh Harrier		F			P		R				Zwarts *et al.* 2009
Eurasian Wryneck	R				P	C					Zwarts *et al.* 2009
Sand Martin	R				P	C					Cowley 1979
Sand Martin	R				P						Bryant & Jones 1995
Sand Martin	R	F						S			Szép 1995
Sand Martin	R				P						Cowley & Siriwardena 2005
Sand Martin					P	C					Zwarts *et al.* 2009
Sand Martin	R				P			S			Norman & Peach 2013
Sand Martin	R							S			Masoero *et al.* 2016
Barn Swallow								S			Robinson *et al.* 2008
Barn Swallow	R						R		M	B	Zwarts *et al.* 2009
Common House Martin								S			Robinson *et al.* 2008
Common Chiffchaff									M		Zwarts *et al.* 2009
Sedge Warbler					P			S			Peach *et al.* 1991
Sedge Warbler	R					C					Foppen *et al.* 1999
Sedge Warbler		F			P	C				B	Zwarts *et al.* 2009
Eurasian Reed Warbler	R				P			S			Thaxter *et al.* 2006
Eurasian Reed Warbler	R								M		Zwarts *et al.* 2009
Eurasian Blackcap	R								M		Zwarts *et al.* 2009
Lesser Whitethroat								S			Boddy 1994
Lesser Whitethroat					P			S		B	Zwarts *et al.* 2009
Common Whitethroat											Winstanley *et al.* 1974
Common Whitethroat		F			P						Hjort & Lindholm 1978
Common Whitethroat								S			Boddy 1993
Common Whitethroat					P	C					Zwarts *et al.* 2009
Common Nightingale	R							S			Boano *et al.* 2004
European Pied Flycatcher									M		Zwarts *et al.* 2009
Common Redstart	R				P						Zwarts *et al.* 2009
Western Yellow Wagtail	R						R		M		Zwarts *et al.* 2009
Tree Pipit						C					Ockendon *et al.* 2014

SUPPLEMENTARY MATERIAL 2: Rainfall and flood extent in the Sahel

Rainfall

When migrants start arriving in the Sahel in September the rainy season is coming to an end, but not in the hyper-humid zone where the rainy season extends into November (Figure S1). The next rainy season will not begin until July and migrants staying in the Sahel between rainy seasons thus have to cope with an increasingly dry environment, even if they depart as late as May. The condition of migrants in this region is largely determined by rainfall during the preceding rainy season, but the birds remaining in the 10–12°N zone can take advantage of the first rains in April and its concomitant increase in food supply (Moreau 1972, Bell 2009). Further south, some rain might already have fallen in March, in years when the rainy season is not delayed.

The year-on-year fluctuation in rainfall runs parallel across all latitudinal bands in sub-Saharan Africa, from desert to humid forest, albeit at widely different levels (Figure S2A). The similarity in latitudinal rainfall patterns is particularly striking when rainfall is converted into departure from the long-term average (Figure S2B). The year-on-year match in rainfall greatly simplifies our analysis of the impact of rainfall on birds, notwithstanding the fact that rainfall is much more erratic in the drier regions. In Nouadhibou (Mauritania), for instance, the annual rainfall, measured over more than 100 years, amounts to 25 mm, on average. Several years were without any rain, but some years received over 100 mm (maximum 195); the standard deviation (32) is 1.26 times larger than the average. In contrast, the annual rainfall in Lungi (Sierra-Leone) varied between 2295 and 5056 mm during the 20th century, with an average of 3339 mm. The standard deviation was 557 mm, or 17% relative to the long-term average. The rainfall stations across the Sahel fit the overall trend that annual rainfall follows synchronous patterns among latitudinal zones on top of being less predictable in the more arid zone (Figure S3).

Since the spatial variation in annual rainfall does not vary systematically across the Sahel (Figure S2), a single index may be used to show the year-on-year variation in rainfall (Figure 4A). The Sahel rainfall index used here is based on 148 rainfall stations between 8°N and 22°N, excluding Ethiopia and Eritrea where annual rainfall patterns deviate from the Sahel at large. Most stations in the Sahel, especially in the western part, were highly correlated with the Sahel rainfall index (up to $r = +0.77$). This implies that the Sahel rainfall index better represents the western than the eastern Sahel.

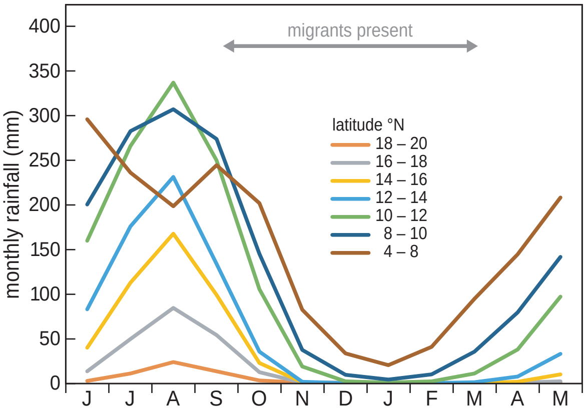

Figure S1. (A) Average monthly rainfall (mm) in northern sub-Saharan Africa between June and May in six latudinal bands, based on daily registrations between 1920 and 2020 for 161 stations situated between 17.5°W and 37.7°E; location of the stations in Supplementary Material 4 in Zwarts *et al.* (2023a). Most migrants are present between mid-September and mid-March.

Unfortunately, the number of rainfall stations in the eastern Sahel is insufficient to calculate a separate rainfall index for this section of the Sahel. The standard error of the rainfall index shown in Figure S4A is 2.5%, but accuracy would be less when the data were split longitudinally. More background information about the Sahel rainfall index is given in Appendix 4 in Zwarts *et al.* (2023a).

Flooding

Rainfall alters the Sahel temporarily from a desert-like landscape into a green plain with larger and smaller pools in depressions. During the dry season the water level in the ponds drops by some 10 mm per day (Gal *et al.* 2016), so that one after the other dries out until only lakes with deeper water remain by the end of the migrants' stay. Most rain in Africa north of the equator is caught in watersheds and drained directly or indirectly – via rivers running through the Sahel, i.e. the Senegal and Niger rivers in West Africa, and the Blue Nile and the White Nile (having its headwater south of the equator) in East Africa – into the sea. The Chari and Logone River in the central part of West Africa empty into Lake Chad. These rivers feed the large floodplains and other wetlands in the Sahel (Figure S5), but their upstream origins are situated in the humid zone south of the Sahel, except Lake Fitri (Chad) which is fed from a catchment area in the Sahel itself. The water level in

Lake Fitri starts to rise in June but is already declining by September, unlike the other Sahelian floodplains where the water level reaches its peak after the rainy season in September–October (Senegal, Waza-Logone, Hadejia-Ngure) or even later, in November–December (Inner Niger Delta, Lake Chad; Table S2). Sahelian floodplains are important for birds and especially for migrants, many millions of which concentrate here after the rainy season when ponds elsewhere become desiccated during the dry season (Brouwer & Mullié 2001).

The water level in rivers varies seasonally. In a wet year, the Niger River, for instance, rises to a water column of 6 m, flooding an area of 36,000 km^2 of the Inner Niger Delta in central Mali, first in the SW and reaching the NW 1–2 months later. Satellite images show that a maximum 25,000 km^2 can be flooded at any one time, but in a dry year with a reduced inflow, the water level only rises 4 m and at most 6000 km^2 is flooded (Figure S6). The maximal flood extent in a wet year may be four times larger than in a dry year, but the variation is much larger during the deflooding. In a wet year, the flood extent of the Inner Niger Delta declines from a maximum of 20–25 thousand km^2 to 8–10 thousand km^2 in early March. With a maximal flood extent of 10,000 km^2 or less, all floodplains will be dry in March. The difference between dry and wet years is even larger than shown in Figure S6, because at a high flood, depressions north and east of the Inner Niger Delta are filled by river water (e.g. Lac Faguibine, 590 km^2) and retain this water for months or even years.

The maximal flood extent of the Inner Niger Delta (Figure S4B) is closely related to the Sahel rainfall index in the same year (Figure S4A; $r = 0.91$), as visible from the synchronous year-on-year variation in annual rainfall in the catchment area of the Niger River and rainfall in the Sahel (Figure S2). There are some systematic differences, however. The Niger River, Senegal River, Chari, Logone and Nile lose a lot of water during their passage across the Sahel, due to evaporation and seepage. This is most evident in dry Sahel years. After a series of dry years the ground

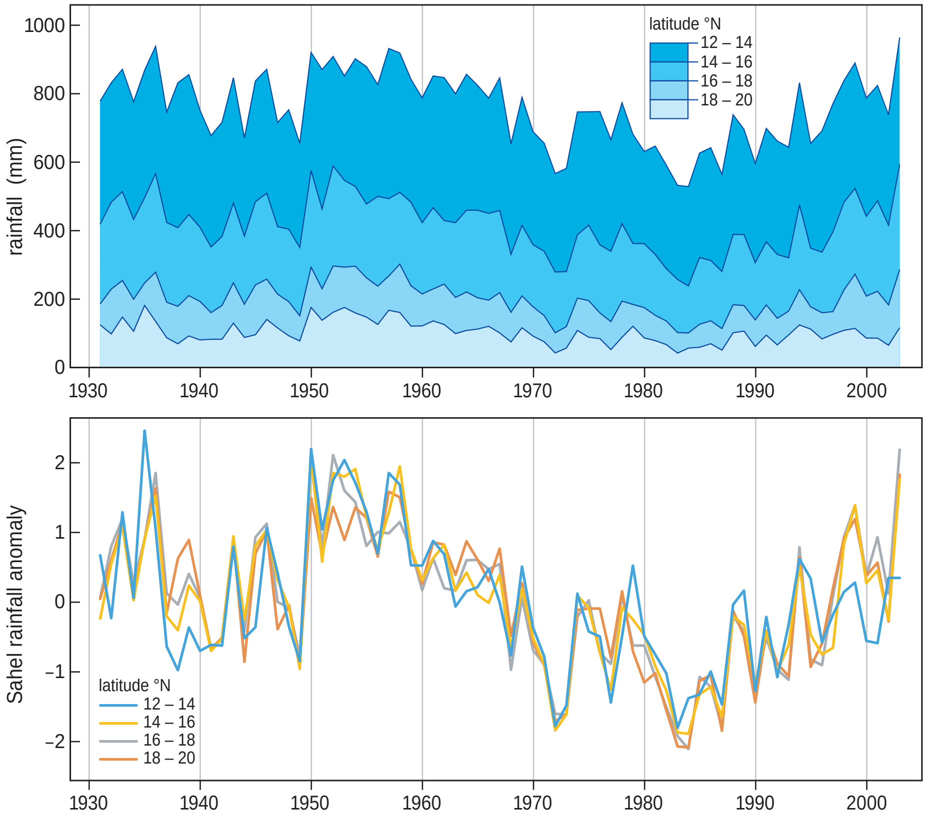

Figure S2. Year-on-year variation in annual rainfall in the western Sahel (17°W–15°E), shown for four longitudinal bands. The rainfall, shown in mm in panel A, is converted into rainfall anomaly (deviation from the long-term average divided by the standard deviation) in panel B. The six correlations between the average annual rainfall in the four zones between 1931 and 2003 varied between $r = +0.79$ and $+0.96$, being higher for contiguous zones ($n = 73$, $P < 0.001$). Source: Nicholson 2005.

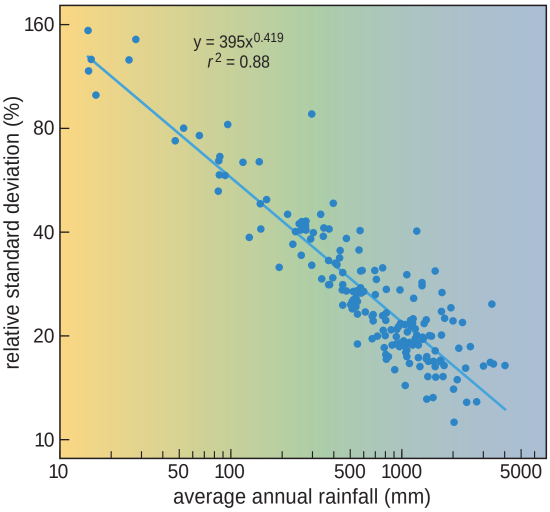

Figure S3. Standard deviation of annual rainfall (given as percent relative to the average) as a function of average annual rainfall, calculated over a period of 26 years (1949–1974) for 178 rainfall stations in Africa between 4.4° and 22.8°N and 17.5°W and 37.7°E; note log-scale on the *x*-axis.

water table recedes and the rivers consequently lose even more water. River flows in the Sahel thus not only depend on rainfall in the preceding months, but, to a large extent, to rainfall in earlier seasons (Gardelle *et al.* 2010). For example, in the Upper Senegal the rainfall declined by 29% between 1950 and 1985, from 1550 to 1100 mm, but the annual peak flow of the river in September declined by 60%, from 4500 to 1800 m^3/s. An even larger difference was found for wet and dry periods in the Chari River (1960–1971 versus 1982–1997): rainfall –15% and flow –75% (Nour *et al.* 2021).

Most Sahel rivers had a natural flow until about 1980, but this state has changed dramatically. Due to the construction of the Manantali Dam in the Upper Senegal River, a huge reservoir of 11 km^3 came into being. During the rainy period a large part of the inflow is stored in the lake and gradually released in the following dry months. The current water management reduces the flooding of the Middle Valley by, on average, 23% and the flooding of the Senegal Delta by 97% (Figure S4C). Similarly, the Sélingué Dam and a large irrigation scheme (Office du Niger) have reduced the flood extent of the Inner Niger Delta by 3000 km^2, on average (Figure S4B).

In NE Nigeria, N Cameroon and W Chad dams and irrigation schemes have also affected the river flow, with serious consequences downstream for seasonal floodplains (Hadejia-Nguru, Logone; Table S2). For the same reason Lake Chad is much smaller than in the past (Figure S7). From 1870 to 1970, Lake Chad was very large, varying in size between 15,000 and 25,000 km^2. Lake size declined to 5000–10,000 km^2 after 1980. Between June and December, the water level increases, due to rainfall and to the inflow of the Chari and Logone Rivers and declines thereafter due to evaporation. Before 1973, Lake Chad was a large, shallow lake with 90% open water. The rest was covered with aquatic plants (reed, cattail, papyrus and grasses). The northern half of Lake Chad dried out after 1973 and became partly covered by *Prosopis juliflora*, an exotic tree species. The southern half covers 1500 km^2 of open water and 3500 km^2 of seasonal floodplains with a grassy vegetation. Although Lake Chad was reduced in size, the extent of floodplains increased.

The Sudd is a huge floodplain along the White Nile in South Sudan. The flow of the White Nile into the Sudd depends mainly on the water level of Lake

Table S2. The variation in the extent of the flooded area at maximal flooding (peak; month) in eight sub-Saharan floodplains (Figure 5). The large annual variation in flood extent is due to differences in quantity of river flows, which in turn depends on rainfall in the catchment areas. Flood extent has been seriously reduced by dams and irrigation schemes upstream of the floodplains, exemplified by flood extent before and after large water management schemes were implemented in Senegal (Manantali Dam, 1988), Mali (Sélingué Dam, 1982), Nigeria (Tiga Dam, 1974, Challawa Gorge Dam, 1992) and in Cameroon/Chad (irrigation schemes). The irrigation schemes along the Logone and Chari Rivers are partly responsible for the decrease of Lake Chad, but have also reduced the floodplains along the Logone and Chari Rivers. The overall impact of these schemes could not be sufficiently quantified (but see Scholte 2006). Main sources: Zwarts *et al.* 2009, updated with daily water level measurements by ORSTOM and DNH for Senegal and Inner Niger Delta, respectively, and Hydroweb for Chad, Logone, Fitri and Sudd (www.theia-land.fr/en/product/water-levels-of-rivers-and-lakes-hydroweb). Other sources: Senegal (Mettrop *et al.* 2009), Lake Chad (Bader *et al.* 2011, Zhu *et al.* 2019, Pham-Duc *et al.* 2020), Logone (Vassalo *et al.* 2016, Nour *et al.* 2021, Jung *et al.* 2022), Lake Fitri (Yalikun *et al.* 2019), Sudd (Rebelo *et al.* 2012, Wilusz *et al.* 2017, Di Vittorio & Georgakakos 2018, 2021).

Area	**Peak month**	**Flooded**, 1000 km^2		**Loss** %
		Past	Present	
Senegal Delta	X	0.1–3.4	0.04–0.1	97
Senegal valley	X	0.3–5.1	0.3–4.3	23
Inner Niger Delta	X–XII	12–25	7–18	31
Hadejia-Nguru	IX	1.0–3.6	0.3–1.8	48
Lake Chad	XI–XII	20–25	8–12	55
Logone	IX–X	3.3–9.4		>25
Lake Fitri	IX	0–1.3		
Sudd	X–XII	6–36		

Victoria (Sutcliffe & Parks 1999). This relationship is used to estimate the total flood extent of the Sudd (Figure 8). In the wet year of 1964 35,000 km^2 of the Sudd was flooded. The flooded area gradually declined in later years to some 10,000 km^2 in the early 21st century. Since then, it has increased again and reached the same level as in the 1960s after a sudden rise of the water level in Lake Victoria in 2020. About 54% of the area is permanently covered by water and overgrown with dense vegetations of reed, papyrus and cattail. The temporary flooded area (46%) consists of wet grasslands (30%) and flooded forests (16%; Howell

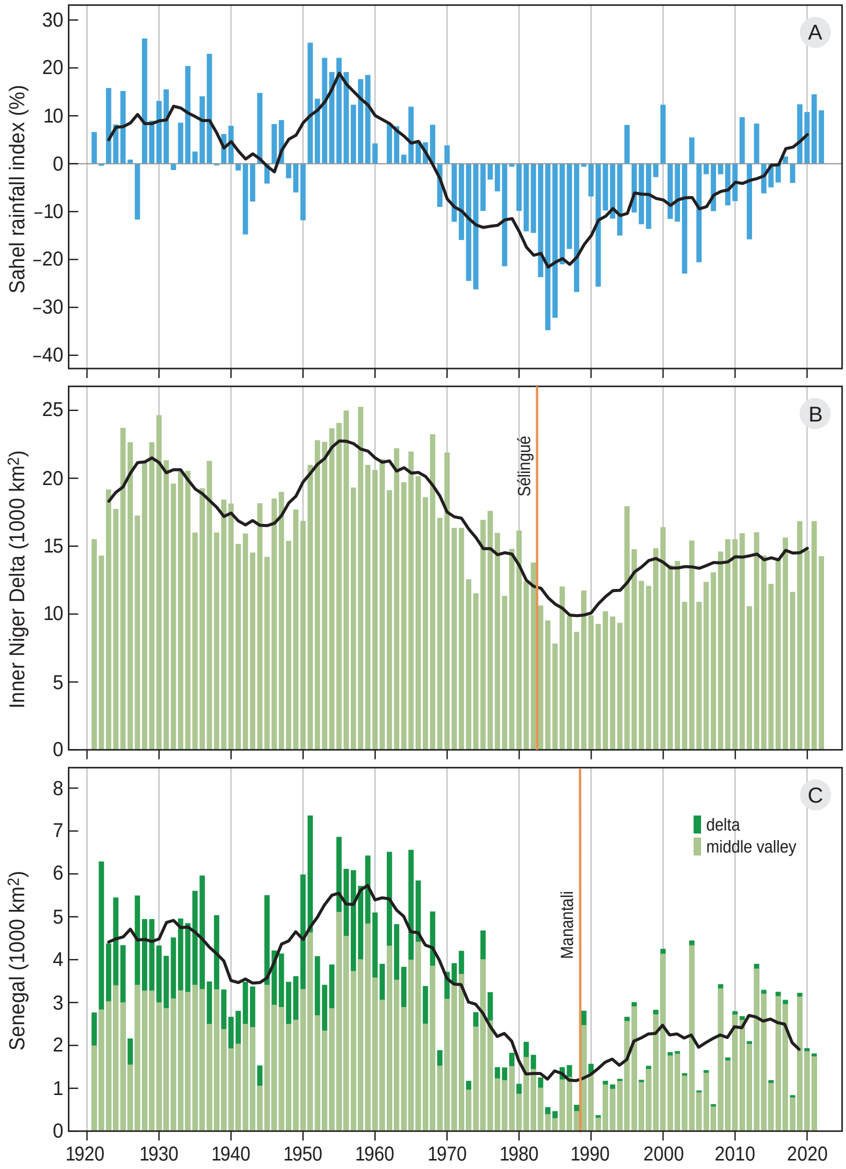

Figure S4. (A) The Sahel rainfall index from 1921 to 2021, given as percentage departure from the average calculated over the 20th century, based on 148 rainfall stations in Africa between 8 and 22°N and 17.5°W and 37°E (details in Supplementary Material 4 in Zwarts *et al.* 2023a). (B) Maximal flood extent (× 1000 km^2) of the Inner Niger Delta (based on Zwarts *et al.* 2005; updated for recent years) and (C) the delta and the middle valley of the Senegal River (× 1000 km^2; Mettrop *et al.* 2019, Zwarts *et al.* 2009; updated). The smooth curves give the 9-year running mean. The Manantali reservoir (1988) in the Senegal River and the Sélingué reservoir (1982) in the Niger River have reduced the river discharge during the wet season as well as the size of the seasonal floodplains. Since rainfall and flood extent are linked to bird numbers in the next summer, the horizontal axis has been shifted one year to the right to facilitate comparison with the bird data. For instance, the collapse of Common Whitethroat numbers noted in Europe in the summer of 1969 (year noted on the *x*-axis), found its nemesis in 1968, the first dry year in the Sahel after 19 wet years.

et al. 1988, Sutcliffe & Parks 1999, Di Vittorio & Georgakakos 2018). Rainfall in June–October temporarily floods another 2 to 18 thousand km^2 (Rebelo *et al.* 2012, Wilusz *et al.* 2017, Di Vittorio & Georgakakos 2018). The Sudd is the largest floodplain in Africa and presumably a very important wetland for migratory birds (but actual bird counts are lacking, apart from some aerial counts around 1980; Howell *et al.* 1988).

Figure S5. The eight most important wetlands in sub-Saharan Africa north of the Equator.

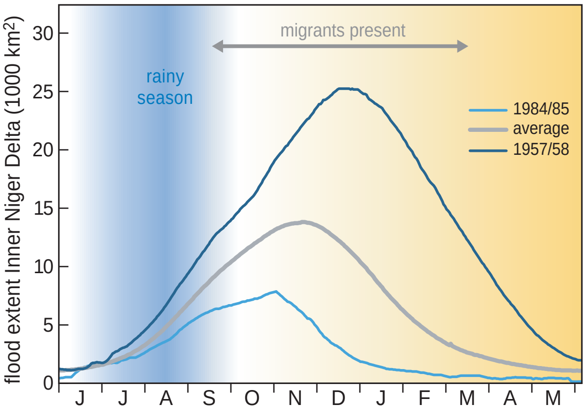

Figure S6. Seasonal variation in the extent of the floodplains in the Inner Niger Delta (Figure S2) during a year with an average river discharge and during an extremely dry (photo below) and extremely wet (photo right) year, based on daily measurements of the water level in Akka, 1956–2020 (source: Direction Nationale de l'Hydraulique, Mali), converted into flood extent using detailed water maps based on satellite images (Zwarts *et al.* 2005; updated).

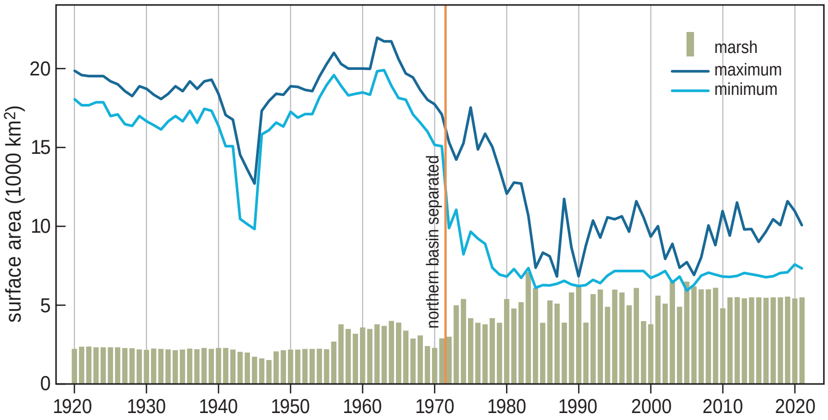

Figure S7. The annual variation in the surface area of Lake Chad (× 1000 km^2) at highest and lowest annual water level. From Zwarts *et al.* (2009; updated using Hydroweb (https://www.theia-land.fr/en/product/water-levels-of-rivers-and-lakes-hydroweb). The surface area of the marsh vegetation is based on Lemoalle (2014) and estimated at 5000 km^2, on average, for the 2010s. The horizontal axis has been shifted one year to the right to facilitate comparison with the bird data.

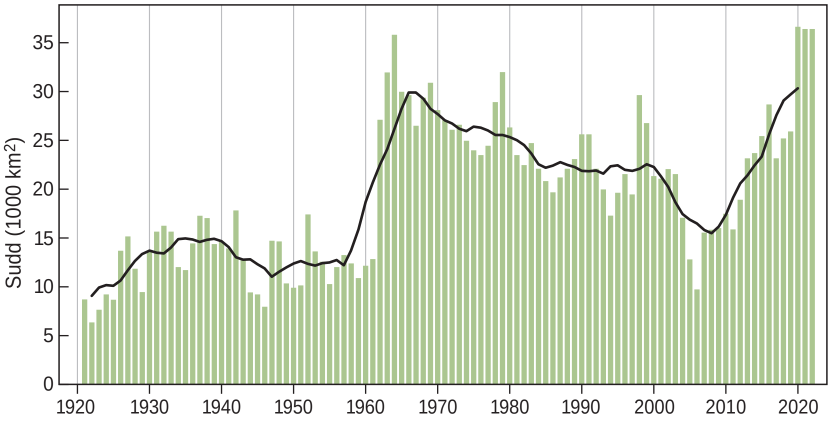

Figure S8. The maximally flooded area of the Sudd as derived from the relationship between flooded area (based on the hydrological model of Sutcliffe & Parks 1989) and water level of Lake Victoria (Zwarts *et al.* 2009, updated, using satellite radar altimetry for Lake Victoria and the Sudd; https://hydroweb.theia-land.fr/hydroweb/). The smooth curve gives the 9-year running mean. The horizontal axis has been shifted one year to the right to facilitate comparison with the bird data.