Moreau's paradox reversed, or why insectivorous birds reach high densities in savanna trees

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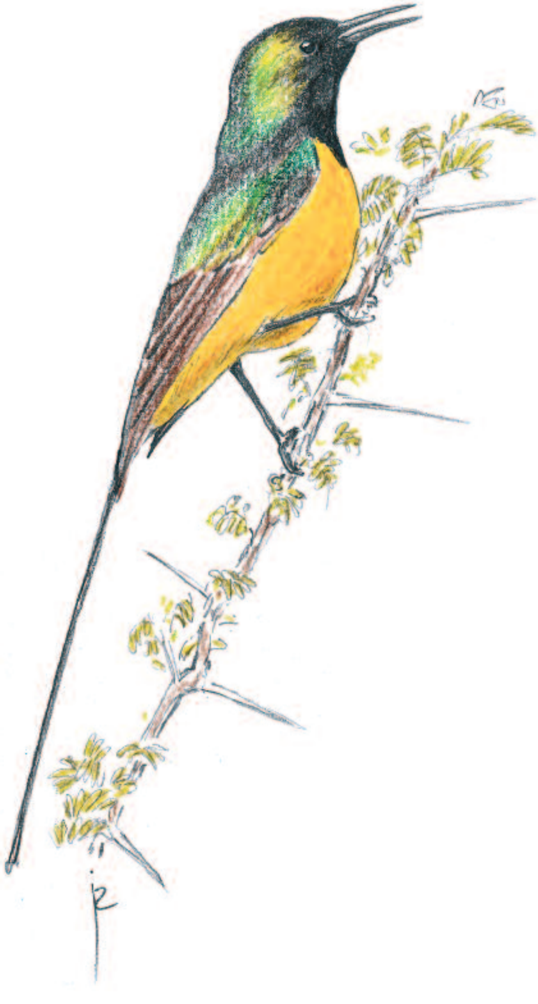

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In West Africa, tree preferences of wintering migratory birds (and African residents) were quantified in order to assess the importance of wintering conditions on distribution, abundance and trends of insectivorous woodland birds. This study encompassed 2000 plots between 10–18°N and 0–17°W, visited in October–March 2007–2015, and covered 183 woody species and 59 bird species. Canopy surface (measured in a horizontal plane) and birds present were determined in 308,000 trees and shrubs. Absolute bird density amounted to 13 birds/ha canopy, on average, varying for the different woody species between 0 and 130 birds/ha canopy. Birds were highly selective in their tree choice, with no insectivorous birds at all in 65% of the woody species. Bird density was four times higher in acacias and other thorny species than in non-thorny trees, and seven times higher in trees with leaves having a low crude fibre content than in trees with high crude fibre foliage. *Salvadora persica* shrubs, but only when carrying berries, were even more attractive. Overall, densities of migratory woodland birds were highest in the (thorny) trees of the Sahelian vegetation zone. This counterintuitive finding, with highest numbers of wintering birds in the driest and most desiccated parts of West Africa (short of the Sahara), also known as Moreau's Paradox, can be explained by the foliage palatability hypothesis. The Sahelian vegetation zone has always been subject to heavy grazing from large herbivores, and as a consequence woody species have evolved mechanical defences (thorns) to withstand grazing of large herbivores, at the expense of chemical defence against arthropods. South of the Sahel, with a much lower grazing pressure, thorny trees (rich in arthropods) are replaced by (usually non-thorny) trees with less palatable foliage and a higher crude fibre content, and hence with less arthropod food for insectivorous birds.

Key words: insectivorous birds, tree preference, Acacia, Sahel, migrants, Moreau's Paradox

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"...to all appearances far less food is available for migrants north of the equator than south of it. Yet somehow many more migrant species maintain themselves in the belt just south of the Sahara than anywhere further south and they do so in what are apparently continually deteriorating conditions." This conundrum was formulated by Moreau (1972: 70) in his final work on the Palearctic-African migration systems, and has become known as Moreau's Paradox. Gérard Morel, with 20 years of experience in the lower Senegal valley, tried to resolve this paradox by pointing out that (1) precisely because the belt just south of the Sahara is arid, with a single rainy season, the abrupt alternation of dry and wet season results in a sharp seasonal increase in plants and invertebrates (which cannot be fully exploited by resident birds alone, whose populations are adjusted to the period when food is scarcest), (2) the arrival of Eurasian birds in the Sahel is synchronised with the end of the wet season (lush vegetation), (3) despite the subsequent desiccation, there are always trees at every stage of leaf, flower and fruit production, and (4) potential African competitors are largely absent (Morel 1973). In short, Morel argued that Moreau's Paradox was an apparent paradox. Both authors, however, were quick to point out that many questions remained, not least those pertaining habitat choice and food. Moreover, Morel's sensible suggestions have not yet been tested in the field, nor do they solve the riddle of why the lusher vegetation belts south of the Sahel and Sudan vegetation zone are not as attractive to Eurasian birds as the more arid regions to the north.

Following in the footsteps of Moreau and Morel, we set out to explore the habitat selection of migratory tree-dwelling birds in the Sahel and adjoining vegetation zones. We presume that tree choice by migratory birds is pivotal to their survival, especially when habitat change occurs and is directional, as evident in the Sahel (Zwarts *et al.* 2009). We therefore systematically surveyed habitats across the western Sahel to record and identify all individual trees and shrubs within stratified plots, and their use by birds. We assumed that migratory birds would be highly selective in their tree choices based on the following expectations:

1. Bird species restricted to the dry Sahelian savanna (e.g. Orphean Warbler *Sylvia hortensis*) or to more humid woodland 600 km further south (e.g. Willow Warbler *Phylloscopus trochilus*) will encounter different tree species, as the composition of woody communities is related to annual rainfall. Hence, we expect latitudinal constraints set by tree and bird distributions.
2. Tree species usually found on seasonal floodplains should attract more birds since there are many more insects in wetlands than in drylands (e.g. Vafidis *et al.* 2014).
3. Tall trees should attract more birds than small trees due to the larger canopy volume per surface unit. The composition of bird communities should also differ according to tree height.
4. Tree species should be more attractive to birds when fruiting, provided the fruit is harvestable by birds.
5. Flowers attract pollinating and nectar-feeding insects and flowering trees should therefore be more attractive to birds than non-flowering ones (Hogg *et al.* 1984, Salewski *et al.* 2009). Even when flowers are nectarless, as in *Acacia tortilis* and *A. senegal*, flowers still attract large number of insects (Tybirk 1987).
6. Leaf-gleaning insectivorous birds should prefer tree species which retain or grow leaves in the dry season.
7. Acacias (and probably other thorny trees as well) invest in mechanical defence (thorns or spines) against mammalian herbivores rather than in chemical defence. Consequently, the foliage of thorny trees is more attractive to arthropods. Thorny and spiny trees (hereafter referred to as 'thorny') should therefore be preferred over non-thorny ones (Greenberg & Bichier 2005).
8. For insects, the nutritional value of leaves declines with increasing content of crude fibre (indigestible carbohydrates, like cellulose and lignin; Coley & Barone 1996). Leaf-gleaning insectivorous birds should prefer tree species with leaves having a lower crude fibre content.
9. Tough, hard or stiff leaves are less profitable for (insectivorous) herbivores (Choong *et al.* 1992, Hanley *et al.* 2007). Birds should avoid tree species with coriaceous leaves.
10. Some trees exude latex as defence against herbivorous insects (Agrawal & Konno 2009), so birds should prefer trees without latex.

These data will provide the groundwork for a future analysis of the distribution, abundance and trends of Palearctic woodland birds wintering in the Sahel and the Sudan vegetation zone. In this paper we provide empirical evidence on the tree preferences of birds and speculate why so many migrants winter in the dry savanna rather than in the more humid south.

METHODS

All data were collected in West Africa, between 10° and 18°N and 0° and 17°W, in nine years (2007–2015) during the dry season, in October–March. Study plots of 300 × 50 m (usually three per site, in a triangular configuration) were selected beforehand, using three criteria: (1) availability of high resolution satellite images on which individual trees are detectable, (2) roads or tracks should intersect latitudes at exactly 15.000°N, 15.050°N, 15.100°N and so on (successive distances between sites at least 5.5 km), and (3) avoidance of no-go areas. Along these routes, plots were situated alternately to the left or right side of the track or road. In addition to 1733 pre-selected plots, we visited 321 other sites that were selected because of a specific habitat or the presence of specific tree species (Figure 1). The average annual rainfall recorded at the different sites varied between 110 and 2200 mm with a gradual transition from desert and heavily grazed grassland with shrubs and sparse trees (Figure 2A–E) into cropland with scattered trees, scrubland and a mosaic of crop- and woodland (Figure 2F–J).

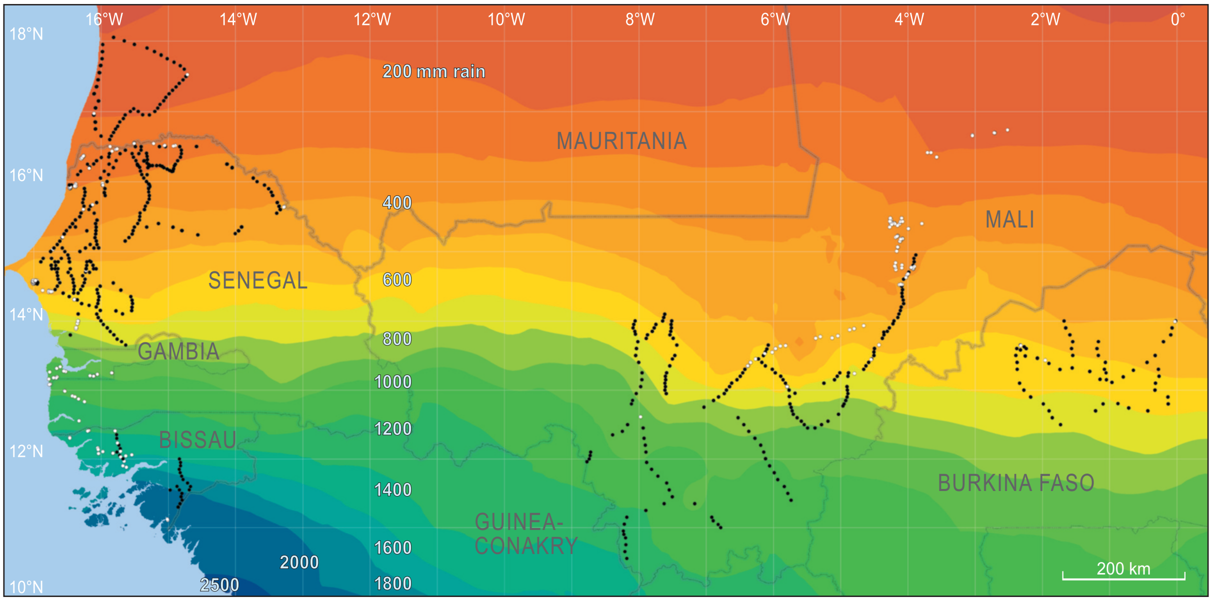


Figure 1. The location of stratified random (black dot) and non-random (white dot) sampling sites in West Africa, with average annual rainfall (in mm) as background.

Trees and shrubs (hereafter referred to as 'trees') in the plots were identified, measured and searched for birds. Methods are described in detail in Zwarts & Bijlsma (2015). We identified 183 tree species (Arbonnier 2007, Bonnet *et al.* 2008). Tree height and crown width were measured in all 307,914 trees[i]. Crown width was used to calculate canopy surface, i.e. the area in m^2 of ground vertically shaded by the tree (Zwarts & Bijlsma 2015). The distribution of birds across tree species was strongly biased. Many tree species were devoid of birds (Figure 3A), but bird density was not related to total canopy surveyed (Figure 3B). Even so, the less common tree species often contained no birds. In 58 tree species with less than 100 m^2 canopy surveyed, we saw no birds in 90% of the species. This percent declined to 74%, 50% and 17% of the tree species of which 101–1000 m^2 (n = 53), 1001–2000 m^2 (n = 14) and >2000 m^2 (n = 58) were investigated, respectively. The present analysis is based on tree species with at least 2000 m^2 of canopy surveyed. This choice obviates the chance that trees were classified as lacking birds when in fact sample size was just too small. Similarly, we decided to select tree species of which we measured canopy surface in at least 100 trees. Hence this paper analyses bird density in 56 tree species, which are, with only a few exceptions, the common and widespread species in the region (see Appendix).

To test the expectations mentioned in the introduction, we used Arbonnier (2007) and our own data to categorize the selected tree species according to distribution (1–2) and traits (tree morphology and phenology; 3–10). It should be kept in mind that tree properties are often interrelated.

1. Using the position of plots depicted in Figure 1, we calculated for each woody species the average annual rainfall within its distributional range (calculations based on all individual trees in the data set). We compare bird densities in tree species found in the driest and most humid habitat (40% <590 mm and 40% >700 mm rain per year).
2. Tree species usually (n = 4) or never (n = 52) found in seasonal floodplains.
3. Average height of woody species, calculated from our own data set, varied between 1.5 and 15.5 m. In the analysis we compare the 23 smallest and 22 largest tree species (average height <4.0 m and >5.7 m, respectively). The bird species were ranked according to their average position in the canopy (Figure 4) and this information is used to analyse whether bird species prefer large or small tree species.
4. Among the selected trees, *Salvadora persica* is the only one with berries eaten by insectivorous birds during the dry season.
5. Tree species flowering during the dry season (n = 28) or not (n = 28).
6. Tree species with or without leaves in the dry season. The dichotomy is, however, not clear-cut.

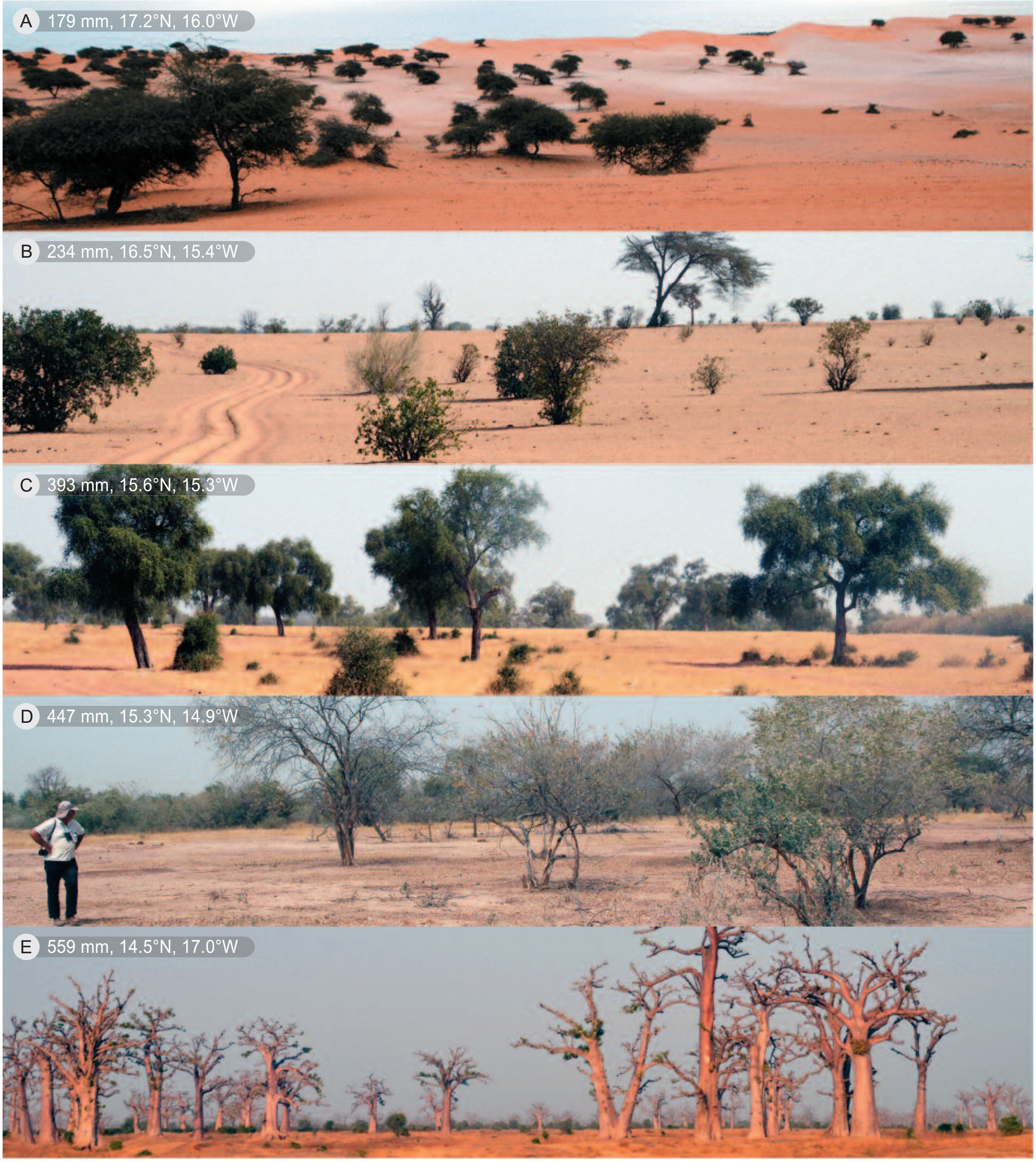


Figure 2. West African landscapes (11.9–17.2°N) in the dry season (December–February) ranked according to annual rainfall (179–1646 mm). (A) *Acacia tortilis raddiana* in sandy dunes; (B) heavily grazed *Boscia senegalensis* with some *Leptadenia pyrotechnica* shrubs and a single *A. tortilis*; (C) pasture land with *Balanites aegyptiaca*, (D) bare, stony laterite soil with *Pterocarpus erinaeus* trees and *Guiera senegalensis* shrubs; (E) former state forest turned into pasture with Baobabs *Adansonia digitata*; (F) cropland in fallow with *Guiera senegalensis*; (G) cropland with *Faidherbia albida*; (H) cropland with monoculture of Shea *Vitellaria paradoxa* where farmers systematically remove all other woody vegetation (note the many bunches); (I) cropland with African Locust Bean Tree *Parkia biglobosa* and *V. paradoxa* in the background; (J) woodland with African Oil Palm *Elaeis guineensis* and a dense woody understorey.


F 628 mm, 14.3°N, 16.0°W
G 642 mm, 13.3°N, 1.5°W
H 896 mm, 12.4°N, 6.4°W
I 1117 mm, 11.1°N, 6.9°W
J 1646 mm, 11.9°N, 14.8°W

Seven woody species have no leaves at all in the dry season, but the remaining 49 tree species vary substantially in whether their leaves do wither and are retained, or not (de Bie *et al.* 1998; Seghieri *et al.* 2012).

7. Tree species with ($n = 13$) and without ($n = 36$) thorns or spines (selecting trees with leaves in the dry season). Species with few thorns (*Commiphora africana*) or with thorns on the trunk (*Bombax costatum*) are considered to be non-thorny.
8. The crude fibre content of the foliage of 45 of the 56 selected tree species is based on the compilation in Le Houérou (1980), supplemented with 8 other studies (see endnote [ii]). Five of the 45 tree species are leafless in the dry period and were therefore disregarded in the analysis. A comparison is made between 20 tree species with the lowest and 20 with the highest crude fibre content (<19.6 and >20.7%, respectively). We used crude fibre rather than neutral detergent fibre (NDF), acid detergent fibre (ADF) or acid detergent lignin (ADL), as values of the latter three were rarely available for the tree species concerned.
9. Tree species with ($n = 9$) and without ($n = 40$) coriaceous leaves (selecting trees with leaves in the dry season).
10. Tree species having leaves with ($n = 2$) and without ($n = 47$) latex (selecting trees with leaves in the dry season).

All trees within plots were carefully searched for birds, the latter noted per individual tree. As explained in Zwarts & Bijlsma (2015), our search effort was high and sufficiently validated to confidently equate bird density with absolute bird density. In this paper all densities are given as bird numbers per canopy surface, i.e. surface area of the crown in a horizontal plane. Bird densities differ between and within tree species, partly in synchrony with time of year. To reduce this source of variation, we averaged bird density per tree species for the period of December to mid-March and omitted the data collected in October and November. In the selected data, the seasonal variation in bird densities is very small since most field work was done in January and the first half of February (a period with few bird movements). However, the full data set was used to construct Figures 4 and 7.

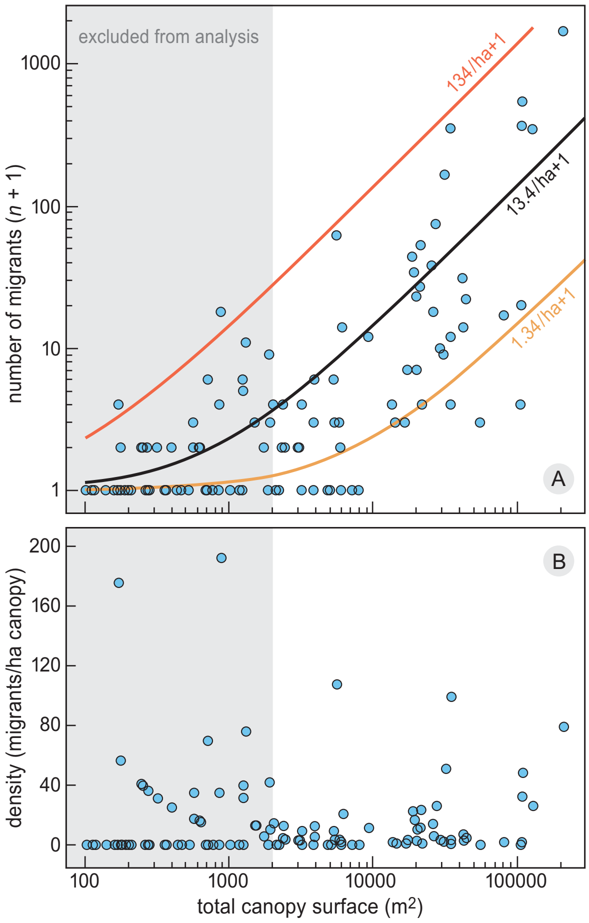


Figure 3. (A) The number of migrants detected in 125 tree species (excluding 58 species with <100 m^2 canopy surveyed) as a function of canopy surface investigated, using log-scales and $n+1$ on the y-axis to account for zeros. The black line shows the expected number at an average density of 13.4 birds/ha, the red and orange lines the expected number if density would have been 10 times larger or smaller. (B) Same data, expressed as migrants per ha canopy, to show the lack of relationship between bird density and total canopy cover ($r = 0.00$). The analysis is restricted to trees of which >2000 m^2 canopy was investigated in the dry season (December–March); the shaded section refers to 67 tree species with canopy surfaces of 101–2000 m^2.

For the present analysis we selected insectivorous birds feeding in trees, including sunbirds and Little Weaver *Ploceus luteolus*, the only weaver we recorded eating insects in trees between December and March. Doves, weavers and other ground-feeding birds using trees as a roost are ignored in the present study. We sum densities separately for Palearctic, long-distance migrants (hereafter referred to as migrants) and African species (hereafter referred to as residents, disregarding the fact that some may move short distances in response to rainfall and desiccation), and on the species level for the nine and six most common migrants and residents, respectively. Unlike migrants, which were routinely recorded from the beginning of the study, residents were disregarded during the first years of observation, hence the smaller (on average 15%) sample sizes than for migrants.

We refrained from collecting data on prey choice, because time-consuming dietary studies did not fit into our schedule and also because most prey taken by the birds were too small to be identified. However, if during the standard count we noted birds handling large prey (>1 cm), usually a caterpillar or a moth, this was noted systematically from October 2012 onwards (but not always in the years before).

Tree names are used according to Arbonnier (2007) and bird names according to the BirdLife Checklist version 7.0. Scientific names of all birds mentioned in this paper are given in endnote[iv]. We were unable to always identify Chiffchaffs as either Iberian *Phylloscopus ibericus* or Common *P. collybita*, but the few Chiffchaffs we heard and the many we could observe well were all Iberian Chiffchaffs, so the species is noted as (Iberian) Chiffchaff. Of the birds recognized as Olivaceous Warbler, 6 were noted as Eastern Olivaceous Warbler *Hippolais pallida* and 95 as Western Olivaceous Warbler *Hippolais opaca*, depending on whether they were regularly dipping their tail while feeding or not. Since we usually did not pay attention to this behaviour, they are lumped as Olivaceous Warbler.

SPSS v. 22 was used for statistical analyses; statistical details are given in the endnotes. The paper presents average bird densities per tree species (given in the Appendix). We performed multiple regression analyses, one-way analyses of variance and covariance analyses on these averages to analyse the variation in bird densities for the selected tree species. Were the analyses to be performed on the raw data (the more usual procedure), we would have faced the problem that birds were absent in more than 98% of the individual trees, and, if present, usually with one bird per tree. We refrained from testing the difference between average densities but rather used the fraction of individual trees in which birds were present, using logistic regression analyses; these analyses were done on all trees, including those without birds (Figures 7 and 9).

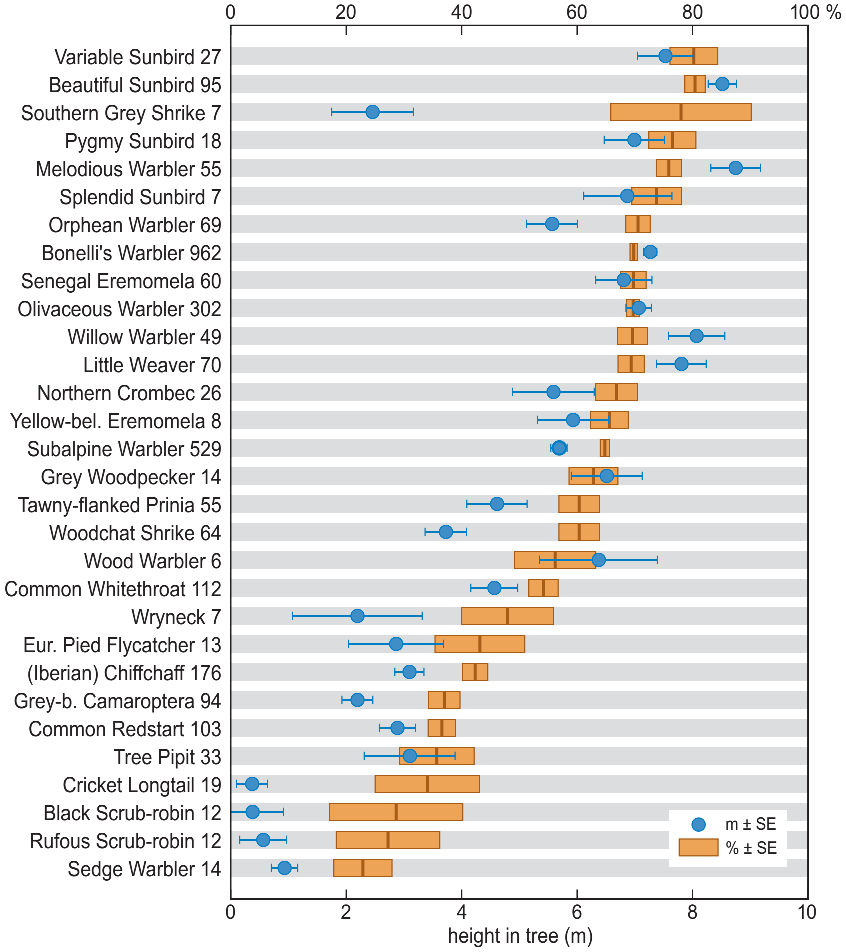
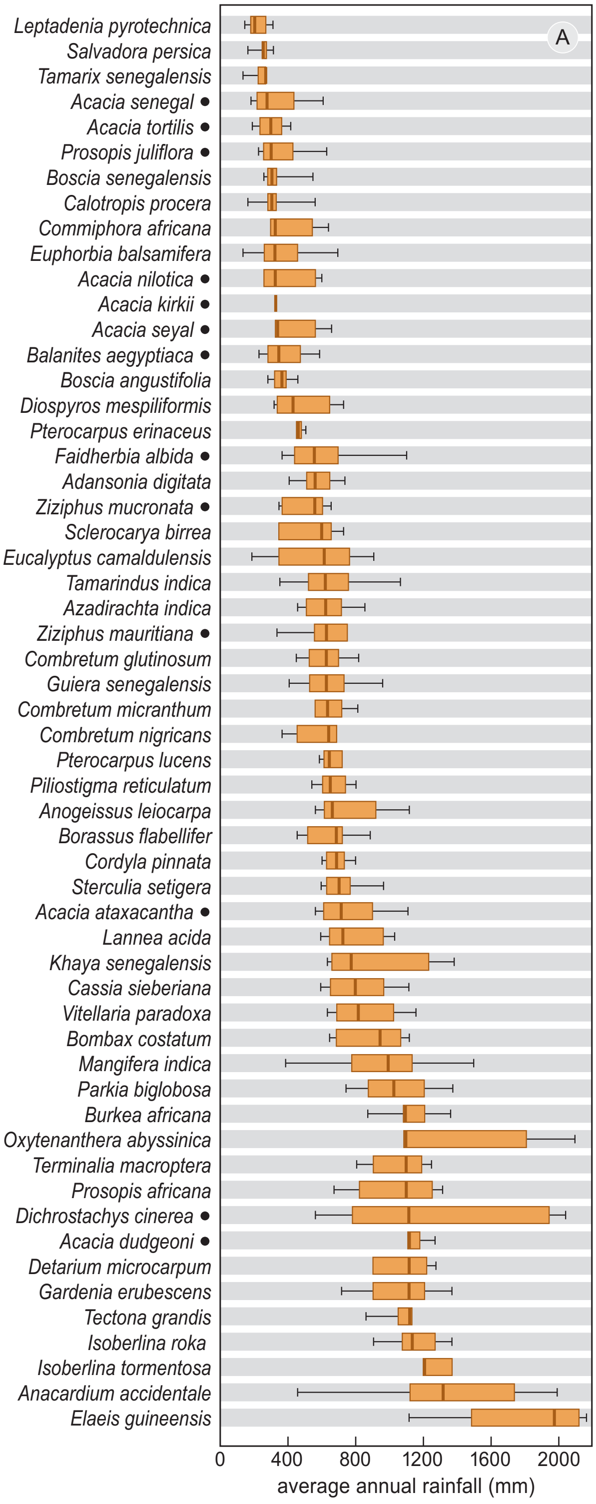


Figure 4. The average height (±SE) at which birds were recorded in trees and shrubs, calculated as absolute height (m; dots) and as relative height (% relative to height of tree or shrub in which the bird was seen; bars). Number of observations is given. Sunbirds feed high in the crown and are mostly found in high trees. In contrast, Cricket Longtails, scrub-robins and Sedge Warblers stay close to the ground and are usually found in shrubs. Statistical details in[iii].



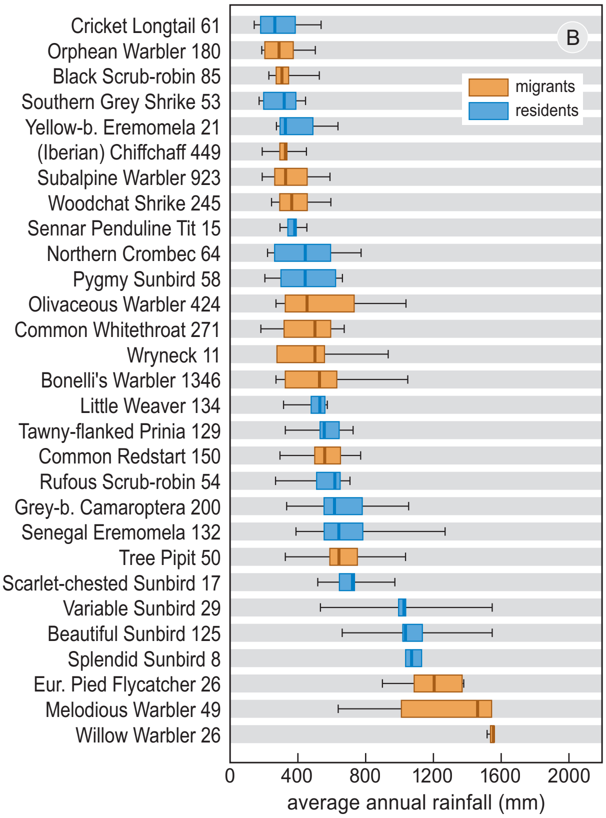


Figure 5. Distribution of (A) 56 tree species and (B) 28 bird species in West Africa as a function of annual rainfall. Box plots indicate the median with 25th and 75th percentiles (box) and 10th and 90th percentiles (whiskers). The 13 thorny tree species are marked (●). Only birds observed between early December and mid-March were selected in order to exclude migratory species wintering further south and staging in the Sahel during migration. Total number of birds is given behind their name. More details in [v].

RESULTS

Distribution

Due to the large latitudinal differences in the yearly rainfall (Figure 1), the West African landscape gradually changes from north to south, within a distance of 600–700 km, from Sahara desert to humid woodland (Figure 2), with a concomitant change in species composition of the woody vegetation (Figure 5A). It is not rainfall *per se* but rather the ground water table, determined by rainfall and local conditions linked to relief, which determines the distribution of the trees. For example, riparian tree species, such as *Acacia kirkii*, *A. nilotica* and *A. seyal*, occur in the semi-arid Sahelian zone where the large riverine floodplains are located.

The bird species, migrants as well as residents, show a species-specific distribution along the rainfall gradient (Figure 5B). The actual differences in distribution among bird species is even larger than shown. For example, Cricket Longtail *Spiloptila clamans* and Orphean Warbler also occur in still drier areas north of our most northerly plots, while the majority of Tree Pipit *Anthus trivialis*, European Pied Flycatcher *Ficedula hypoleuca*, Melodious Warbler *Hippolais polyglotta* and Willow Warbler winter further south than our plots. Consequently, had the entire range of their wintering areas been covered, northern species on average would have wintered in somewhat drier habitats and southern species in slightly wetter areas than suggested by Figure 5B.

The limited distribution of bird species within West Africa (Figure 5B) shows that many tree species listed in Figure 5A will be out of bounds for the majority of bird species. However, as most bird species are found in the latitudinal zone with an annual rainfall of 300 to 700 mm (Figure 5A), the potential overlap in usage of tree species within this narrow distributional range by the various bird species is extensive.

Tree choice by birds: ten expectations tested

The majority of insectivorous woodland birds in West Africa were recorded in very few tree species. In 119 of the 183 tree species identified in the study plots (65%) insectivorous birds were absent, increasing to 69% (126/183) when only migratory birds are considered. The 56 most common and widespread tree species used in this study showed a large variation in bird density, varying between 0 and 122 birds per ha canopy (Figure 6). Migrants preferred thorny over non-thorny tree species, with highest densities of migrants found in thorny tree species except *Salvadora persica*, a woody non-thorny species which is only attractive when carrying berries. On average, migrants reached higher densities in woody species from the dry north (Figure 6).

To investigate the expectations mentioned above, the data in the Appendix and Figure 6 were used to calculate the average bird density for the various categories of tree species (Table 1).

1. Rainfall. As expected (Figure 5B), all 13 bird species, except Grey-backed Camaroptera *Camaroptera brachyura*, were found to be (much) more common in trees from the northern Sahel (rainfall < 590 mm) than in trees from the more humid zone (rainfall >700 mm; Table 1).
2. Floodplains. Tree species growing on floodplains were indeed highly attractive to birds (Table 1), especially to (Iberian) Chiffchaff and Olivaceous Warbler, provided that the floodplain was flooded or humid (just after the flood had receded; Figure 7). In a small sample of *Mimosa pigra* thorn-bushes (1947 m^2), we recorded a high bird density of 192 birds per ha canopy in humid plots, again mostly (Iberian) Chiffchaff (90/ha) and Olivaceous Warbler (56/ha), but also Bluethroat *Luscinia svecica* (34/ha). In *M. pigra* on dry ground elsewhere, these bird species were absent. In *Prosopis juliflora* we recorded 131 (Iberian) Chiffchaffs per ha canopy in trees standing on humid ground (2065 m^2 canopy surveyed) but only 6 per ha canopy in the same tree species standing on dry ground (28,532 m^2). In *Acacia kirkii*, the floodplain specialist *Acacia* species, (Iberian) Chiffchaffs even increased from 107 birds/ha at a water column of 1–3 m deep to 138 birds/ha as the floods receded, because pools and puddles remained and insects were presumably more abundant than during the actual flooding (canopy surface surveyed: 10,194 m^2 for flooded and 5538 m^2 for re-emerged trees).
3. Tree height. Contrary to expectation, total bird density in shrubs and small tree species was similar to that in tall trees, but the species composition differed as expected, with Tawny-flanked Prinia *Prinia subflava*, Grey-backed Camaroptera and Common Whitethroat *Sylvia communis* more common in shrubs and leaf warblers in tall trees (Figure 4, Table 1).
4. Fruit. Among favoured tree species, *Salvadora persica* is an outlier, being a non-thorny shrub with the highest bird density recorded among all trees in the Sahel. In fact, *Salvadora* was the only tree species with small edible berries recorded among the 56 selected species. The presence of berries in *Salvadora* acted as a lodestone to some insectivorous birds, notably *Sylvia* species and Little Weaver

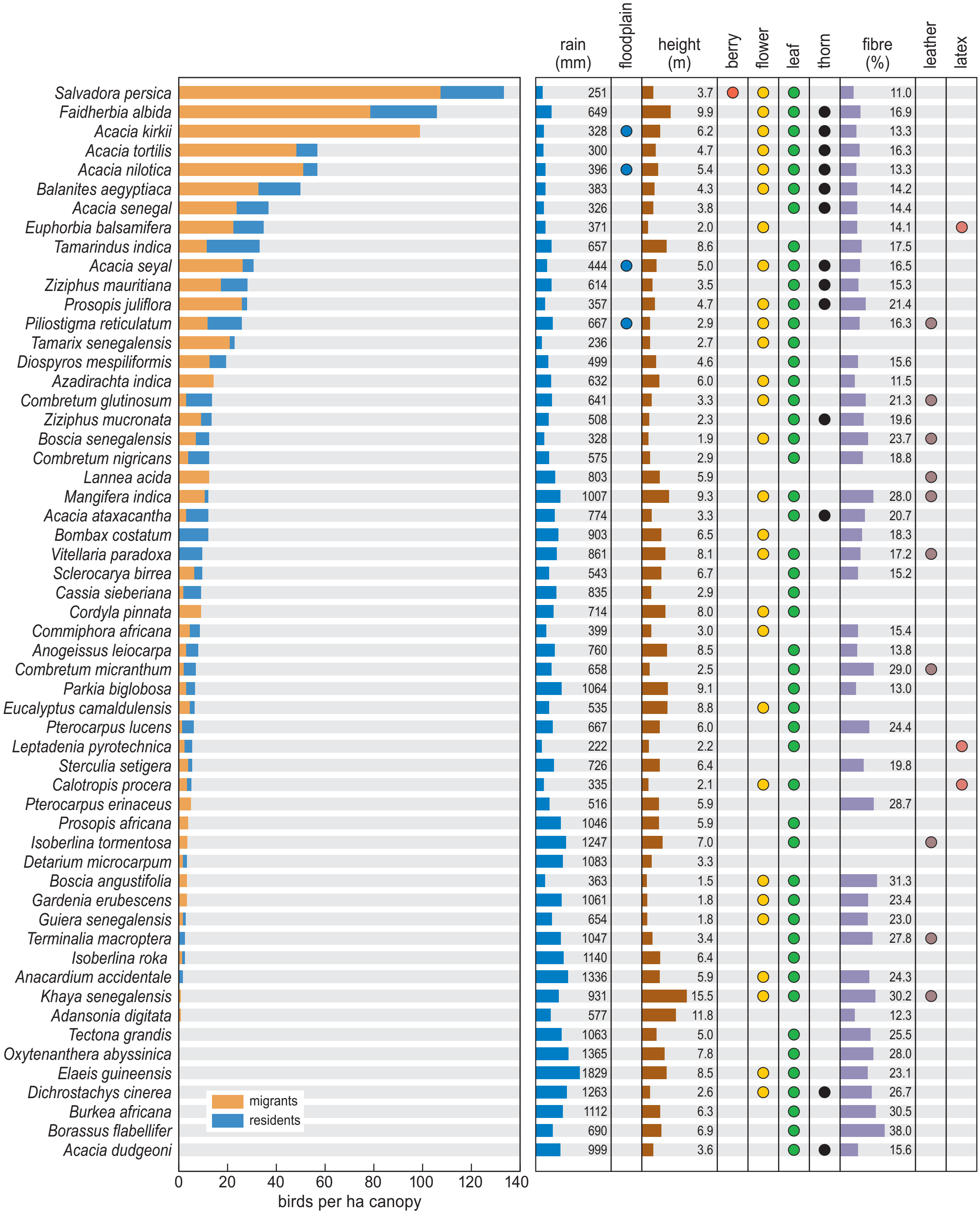


Figure 6. Densities (*n* per ha canopy) of migrants and residents in 56 tree species. Separately indicated: average annual rainfall (mm), occurrence on floodplains, average tree height (m), trees having edible berries, flowers and leaves in the dry season, presence of thorns/spines, crude fibre content of foliage (%), and having leathery leaves or leaves with latex.

but not *Phylloscopus* species (which do not take berries; Stoate & Moreby 1995). When *Salvadora* shrubs lacked berries, very few birds were recorded, as expected (Zwarts & Bijlsma 2015: their Figure 17).

5. Flowers. All bird species, except Grey-backed Camaroptera, had higher densities in tree species flowering in the dry season than tree species without flowers, but the difference is significant only in migrants (Table 1). A higher density of birds in flowering trees is only to be expected when flowers attract insects and birds actually feed on flower-visiting insects. This is true in acacias where flowering trees attracted more birds than trees without flowers, but no such effect was found in *Vitellaria paradoxa* (Zwarts & Bijlsma 2015), probably because in this species nectar is available for only a very short period of time (Nguemo *et al.* 2014).
6. Leaves. Trees without leaves were indeed rarely visited by birds, the only exception being Woodchat Shrike *Lanius senator*, a species that uses trees as a perch. The presence and abundance of foliage had a large impact on bird density, as evident from a within-tree comparison (Zwarts & Bijlsma 2015: their Figures 16 and 17). On average, however, bird density in tree species with leaves was only twice as high as in bare tree species (Table 1), because many tree species with leaves were devoid of birds (presumably for other reasons than presence/absence of foliage).
7. Thorns. Except for Beautiful Sunbird *Nectarinia pulchella*, a nectar-specialist, all bird species reached (much) higher densities in thorny than in non-thorny tree species, consistent with expectations (Table 1).
8. Crude fibre content. All bird species were more abundant in trees having foliage with a low crude fibre content. This was significant in 7 of the 8 migrants (Table 1). The average density of migrants and residents combined was 7 times higher in low fibre trees than in high fibre trees.
9. Coriaceous leaves. As expected, most bird species reached higher densities in trees with non-coriaceous leaves, but interestingly this finding only held for Palearctic species whereas 4 out of 5 African residents were (slightly) more abundant in trees with leathery leaves. However, none of the differences were significant (Table 1). Taking all coriaceous trees carrying leaves in the dry season together, the average bird density was higher than in non-coriaceous trees, but again non-significantly.
10. Latex. All bird species reached higher densities in tree species without latex, as expected (Table 1). Altogether, only five species were found to visit trees with latex, all of them of Palearctic origin. None of the differences were significant, however, as was the case with the average density of all birds in trees with or without latex.

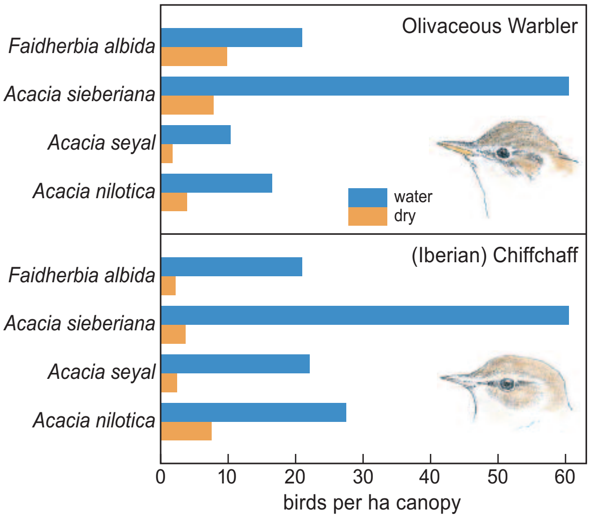


Figure 7. Density of Olivaceous Warbler (top) and (Iberian) Chiffchaff (bottom) in four tree species when flooded or on dry ground. More details in [vi].

The differences in average density within categories were overwhelmingly in favour of the predictions, i.e. 110 out of 130 comparisons (85%, Table 1). This was true for each separate category, but especially significant for rainfall, floodplain, berries, thorns and crude fibre. Of course, many categories are interrelated. For example, tree species with thorns or berries are mainly restricted to the dry north (Figure 5A) and rainfall is correlated with crude fibre ($r = 0.41$) and tree height ($r = 0.34$). Without additional data, the relative importance of the separate variables as proximate drivers of bird densities in different tree species is difficult to assess. Statistical analyses suggest that the presence of berries and thorns, as well as rainfall, were dominant factors in explaining bird densities per tree species, while other variables were of lesser importance [vii].

The difference in bird density between *Salvadora persica* (when carrying berries) and the other tree species was large, suggesting that availability of harvestable fruit may be one of the main forces in determining bird density in West African trees. Excluding *Salvadora*, birds reached much higher

Table 1. Average densities of migratory and resident bird species (n per 10 ha canopy, species with >100 records) and summed for migrants and residents, in relation to tree species occurring in dry (<590 mm rain) or humid (>700 mm) zones (both categories 40% of the tree species), outside or on floodplains, in the 40% smallest (<4 m) or 40% largest (>5.7 m) tree species, with or without berries in the dry season, with or without flowers in the dry season, leafless or having foliage in the dry season, with or without thorns, with low (<17.5%) or high (>18.3%) crude fibre content, with or without coriaceous leaves and with or without latex. The comparison between thorns, fibre, coriaceous and latex was made for trees without leaves in the dry season (hence the smaller number of tree species compared to Figure 6). Data analysed with one-way analyses of variance; significance level indicated with colours. Averages calculated over data given in Appendix (i.e. the average densities of the 56 tree species).

Condition	Rain		Floodplain		Tree height		Berries		Flowers		Leaves		Thorns		Fibre		Coriaceous		Latex	
Contrast	lo	hi	no	yes	lo	hi	no	yes	no	yes	no	yes	no	yes	lo	hi	no	yes	no	yes
n	23	23	52	4	23	22	55	1	28	28	7	49	36	13	20	20	40	9	47	2
Woodchat Shrike	15	4	9	9	8	6	9	18	6	12	23	7	4	13	12	3	8	2	7	2
Tawny-flanked Prinia	5	1	3	15	6	1	4	0	3	5	1	4	2	12	9	1	4	5	5	0
Grey-b. Camaroptera	6	7	9	9	14	6	9	40	10	8	6	10	8	13	12	9	9	11	10	0
Olivaceous Warbler	20	8	12	68	7	24	15	71	7	25	13	16	10	36	33	6	18	11	17	0
(Iberian) Chiffchaff	52	1	10	184	12	29	21	88	3	42	6	25	7	72	47	8	29	3	25	11
Bonelli's Warbler	32	1	18	68	6	27	22	0	9	35	0	25	6	78	55	3	30	1	26	0
Senegal Eremomela	5	4	5	16	5	6	6	0	6	6	3	6	5	9	11	3	5	10	6	0
Orphean Warbler	12	0	5	4	7	2	4	71	4	7	0	6	3	16	15	0	7	0	6	2
Subalpine Warbler	72	0	29	85	41	15	21	670	6	60	4	37	25	69	80	4	44	4	38	9
Common Whitethroat	21	1	10	17	18	3	9	88	5	16	17	10	8	15	17	3	10	9	10	3
Common Redstart	8	3	6	20	10	4	6	35	6	8	2	8	5	14	14	5	8	5	8	0
Beautiful Sunbird	4	1	4	9	7	5	5	0	4	6	0	5	5	6	11	2	5	10	6	0
Little Weaver	11	0	6	2	10	3	2	201	1	11	0	7	6	10	17	0	8	0	7	0
Migrants: sum	237	23	103	471	111	115	113	1076	48	211	65	139	74	320	281	34	160	44	144	30
Residents: sum	60	25	50	62	63	43	47	259	41	61	47	52	41	80	96	22	51	54	53	24
All species: sum	297	48	154	533	173	158	160	1335	89	273	111	191	115	400	376	56	211	98	196	53

■ *P* <0.001 ▨ *P* <0.01 □ *P* <0.05

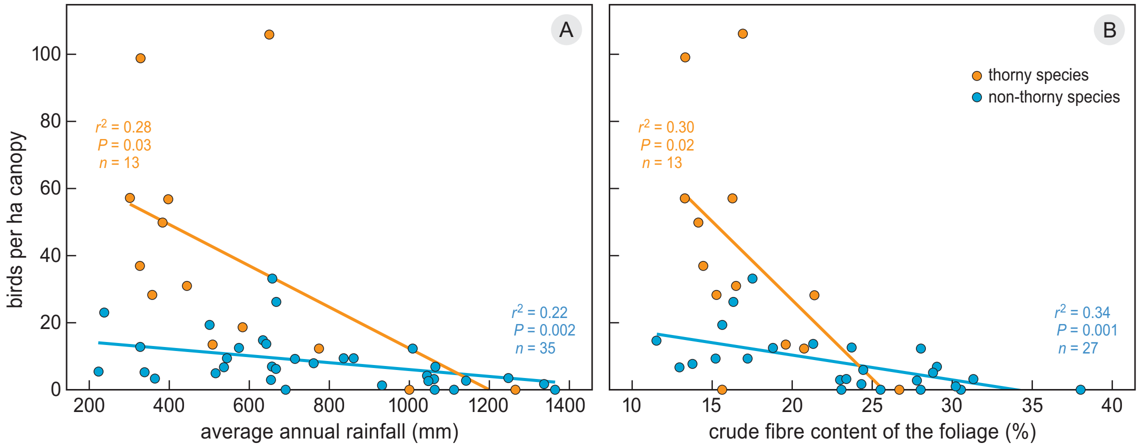


Figure 8. Average bird density per ha canopy for thorny and non-thorny woody species (without *Salvadora persica* and trees without leaves in the dry season) as a function of (A) average rainfall and (B) crude fibre content of the foliage.

average densities in thorny than in non-thorny trees. Interestingly, birds were absent in the few thorny tree species further south (rainfall > 800, figure 8A); these trends were similar for migrants and residents. Bird densities were negatively correlated with crude fibre content of the foliage (Table 1); this effect remained intact when classifying trees as thorny and non-thorny species (without *Salvadora*; Figure 8B)[viii].

Bird densities measured in the 125 tree species that were omitted from the analyses due to small sample sizes (Figure 3) show the same pattern, with highest bird densities observed in a thorny species occurring on floodplains (*Mimosa pigra*), in a fruit-bearing species (*Zanthoxylum zanthoxyloides*; Zwarts & Bijlsma 2015) and in four acacia species. In contrast, nearly all tree species with no bird records were from the humid south.

Distribution and tree preference

How to explain the higher densities of birds in thorny (and to a lesser extent non-thorny) tree species from the dry north as compared to densities in tree species in the more humid region further south (Figure 8A)? Do birds select dry savanna and therefore occur in higher densities in tree species found there? Or is it the other way round: do they live in the dry savanna because they are bound to certain tree species? To answer this question, we calculated bird density per tree species separately for zones where the annual rainfall amounted to 101–200, 201–300 mm, etc. Only four tree species had a wide enough latitudinal distribution (Figure 9) in combination with a large sample size of trees and birds (Figure 5A) to tackle this question. The distributional range is particularly large in *Faidherbia albida*, a tree species recorded from a village in Mauritania (17°N; 179 mm rain) up to coastal rice fields in Guinea-Bissau (11°N; 1659 mm).

Within tree species, wintering migratory birds showed clear shifts in species composition and density, with (Iberian) Chiffchaff, Orphean Warbler and Woodchat Shrike reaching higher densities per ha canopy in trees from the drier regions (100–400 mm rain), Subalpine Warbler *Sylvia cantillans* and Bonelli's Warbler *Phylloscopus bonelli* extending further south into the more humid regions (100–700 mm and 100–1200 mm, respectively) and Melodious Warbler and Willow Warbler only found in regions with >1200 mm of rainfall. Throughout, residents were less common than migrants and scarcer in the drier north than in the more humid south. The shift in bird species composition within each tree species closely resembled the zoning as shown in Figure 5B, based on the occurrence in woody vegetation for tree species combined. Evidently, part of the observed tree selection is determined by rainfall-related, latitudinal differences of their wintering area.

In the driest regions, i.e. Sahara and Sahel, total bird density per ha canopy was consistently high (Figure 9). The scattered trees in the Sahara did not harbour fewer birds than trees of the same species in the Sahel. In contrast, bird density decreased somewhat in the more southerly parts of the tree's distributional range. This difference was especially large in birds inhabiting *A. seyal*, which cannot be credited to regional variations in flooding (Figure 7) since all trees used in this comparison were standing on dry ground.

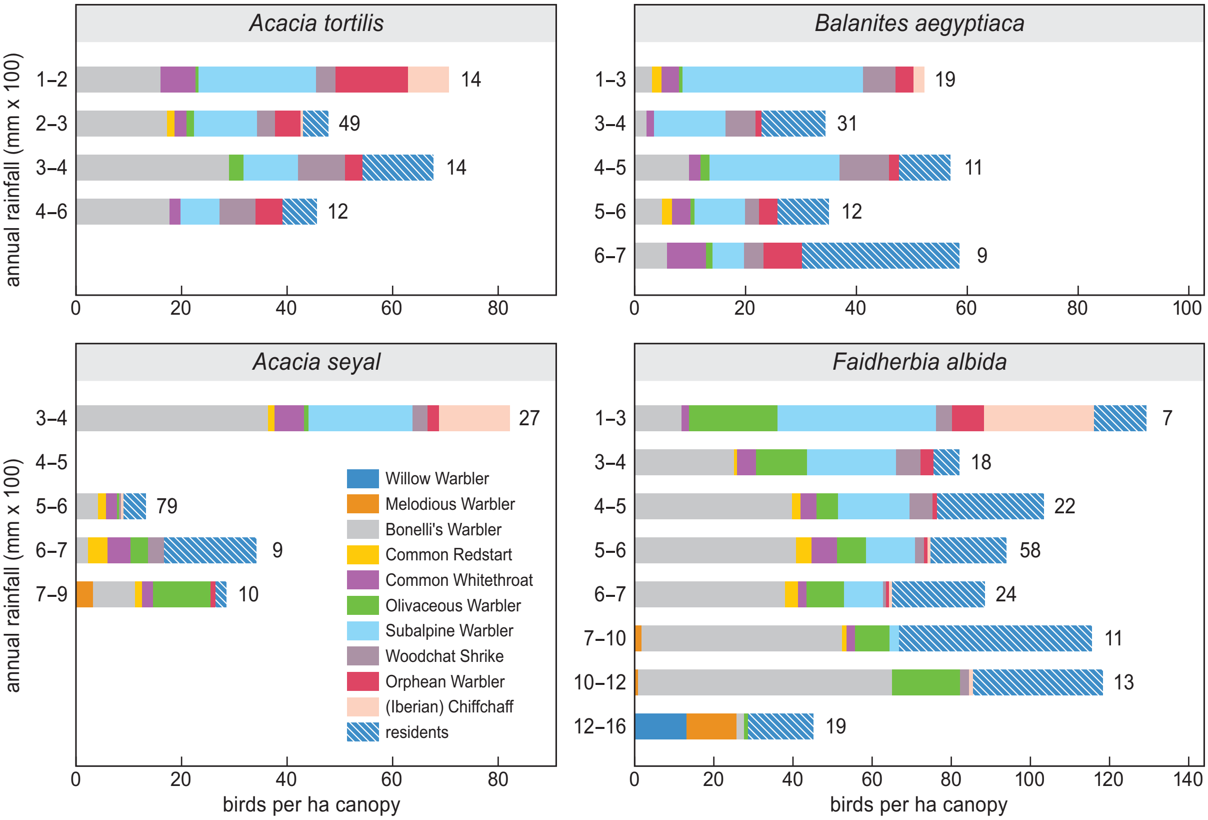


Figure 9. The average bird densities of 10 migrants and of residents in four tree species as a function of average rainfall. Categories with the lowest and highest rainfall were lumped due to small sample sizes. Total canopy surface area of the investigated trees (×1000 m^2) is shown behind the bars. Statistical details in endnote$^{\text{ix}}$.

Food supply and tree preference

Although our observations on food and feeding are haphazard, we do have some evidence that the large variation in bird density for individual trees may be explained by variations in food supply (Zwarts & Bijlsma 2015). Figure 16 in Zwarts & Bijlsma (2015), for instance, showed that *Faidherbia* trees with a lot of flying moths attracted larger numbers of birds. We have no data to show that the observed large variation in bird density between tree species (Figure 6) is paralleled by a similar variation in food supply. Even so, birds eating large prey were almost exclusively recorded in acacias and *Balanites*. The percentage of birds eating large prey differed per tree species and was positively related to the average bird density (Figure 10). This suggests that large, profitable prey are typically found in acacias and *Balanites*, and this is likely to be the explanation for why these tree species attract so many birds.

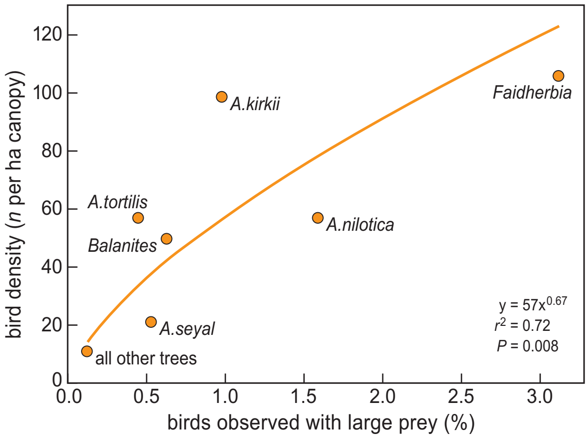


Figure 10. Bird density per tree species (data from Figure 6) as a function of the percent of observed birds eating a large prey (caterpillars of 1–5 cm and moths of c. 2 cm length, based on 83 prey-handling birds of 15 species out of 4938 birds detected during standard counts in plots from October 2012 onwards; before this date prey capture was not always noted systematically.

DISCUSSION

Thorny trees make the difference

Within sub-Saharan Africa we encountered a large diversity of tree species (183 in our extensive sample between 10ºN and 17ºN). Given this wide choice, it is remarkable that insectivorous birds were mostly concentrated in few, mostly thorny, species (Figure 6). Migratory birds completely ignored 69% of the species of trees and shrubs that were available. This suggests that food supply must differ widely among tree species. Although some of the migratory birds eat berries (Stoate *et al.* 2001, Wilson & Cresswell 2006) or drink nectar (Hogg *et al.* 1984, Salewski *et al.* 2009) during part of the wintering period, the major food resource throughout their stay in sub-Saharan Africa most likely consists of arthropods. However, species-specific diets are largely unknown (but see Stoate & Moreby 1995), and variations in bird densities are therefore difficult to interpret in terms of within- and between-tree variations in arthropod biomass and diversity (Tybirk 1993, Stoate 1997, 1998, Stoate *et al.* 2001, Vickery *et al.* 1999). Acacias have been shown to contain large numbers of arthropods, as found in Israel (Hackett *et al.* 2013), Senegal (Morel 1968, Tybirk 1993), Tanzania (Krüger & McGavin 1998) and Namibia (Theron 2010). In *Faidherbia*, caterpillars may be so common that trees are even defoliated (Dunham 1991). For most other trees little is known about arthropod abundance, but the scarce data available imply that *Balanites* and acacias harbour more arthropods than other tree species (for example *Grewia bicolor*, *Zizyphus mauritiana*, *Piliostigma reticulatum* and Neem *Azadirachta indica*; Morel 1968, Stoate 1998, Vickery *et al.* 1999).

Migratory birds in the Sahel and Sudan vegetation zone prefer acacias and other thorny mimosoid legumes over non-thorny tree species, as was found elsewhere in Africa (Ulfstrand & Alerstam 1977, Greig-Smith 1978, Rabøl 1987, Dean *et al.* 2002, Jones *et al.* 2010, Rogers & Chown 2014) and in America (Greenberg *et al.* 1997, Greenberg & Bichier 2005, Beltrán & Wunderle 2013). The explanation is that acacias invest in mechanical defence with spines and thorns to reduce the grazing pressure of large herbivores (Cooper & Owen-Smith 1986), rather than in chemical defence against arthropods feeding on foliage (Cooper *et al.* 1998, Cummingham *et al.* 1999, Ward & Young 2002). The foliage of acacias has a relatively high nutritional content (crude protein, minerals, non-structural carbohydrates) and a relatively low content of digestion-inhibiting compounds (structural carbohydrates, total phenolics, condensed tannins), resulting in a higher abundance of arthropods than in non-thorny tree species (Greenberg & Bichier 2005). Our study shows that other non-mimosoid trees with spines and thorns, such as *Balanites*, also attract relatively many birds. However, not all thorny tree species are equally attractive to birds (Figure 6), as apparent from the negative relationship of bird density in 14 thorny trees with average rainfall (Figure 8A).

In tree species with a wide geographical distribution, like *Faidherbia*, the latitudinal variation in bird densities concurs with the pattern found between tree species, i.e. lower densities in regions with higher rainfall. This might suggest that thorny trees, when not subjected to intensive grazing by large mammals, may increase their chemical defences against arthropods. This needs further research and testing.

The grazing pressure of domesticated herbivores is extremely high in the dry transient zone between the Sahara and the Sudan-Guinean vegetation zone, which explains why the Sahel is dominated by thorny tree species. Further south, with annual rainfall of >800 mm, the occurrence of the tsetse fly *Glossina* spp. (causing sleeping sickness) effectively curtailed the presence and abundance of livestock, as evident from maps showing the distribution of tsetse fly (Cecchi *et al.* 2008) and livestock (Wint & Robinson 2007; www.fao.org/ag/aga/glipha), paving the way for non-thorny trees to replace the thorny species. Non-thorny trees have better defences (chemical and/or leathery leaves) against arthropods and therefore are less attractive to birds. The question of why the desiccated, dusty Sahel attracts so many migratory birds is largely resolved, at least for woodland birds, when taking the life-histories of trees (thorny and non-thorny; foliage with high or low crude fibre content) into account.

Moreau's Paradox reversed

We started this paper with ten expectations regarding bird densities in trees, and found the largest support for four explanatory variables: berries, thorns, crude fibre and rainfall. The foliage palatability hypothesis explains why thorny woody species, which can withstand heavy grazing from large herbivores, offer a relatively rich food supply for insectivorous bird species (Greenberg & Bichier 2005). The mounting grazing pressure in the Sahel has turned the woody savanna into an even more thorny landscape than it used to be (Figure 11). In contrast, the foliage of non-thorny woody species is less palatable or even poisonous to arthropods, hence the poorer abundance of arthropods in such trees, consisting mainly of ants, flower-visiting insects and bark-dwellers.

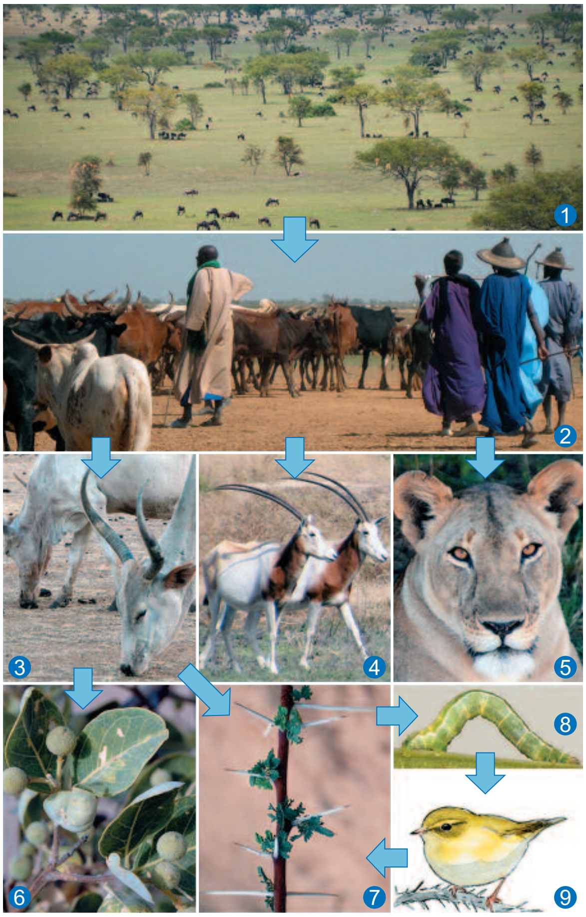


Figure 11. A historical reconstruction of grazing and its potential effect on bird distribution in the Sahel. Sahelian grassland (1), once the grazing ground of millions of wild herbivores (Spinage 1968), has seen dramatic changes in the past century. Wild herbivores have been gradually replaced by livestock (2), estimated at present at some 300 million sheep and goats and 150 million cattle, showing a long-term increase of 3.48% and 3.24% per year, respectively (source: www.faostat3.fao.org; accessed 2 November 2014). Livestock (2→3) outcompeted wild herbivores, driving the latter (close to) extinction (2→4). Grazing pressure continued to increase because large carnivores were hunted to extinction (2→5) (e.g. Brugière *et al.* 2015). Former risky areas became available as grazing ground (Ford *et al.* 2014), and grazing turned into a night and day business (as long as predators were around, cattle had to be protected in enclosures at night). Due to the mounting grazing pressure across ever larger parts of the Sahel, non-thorny trees and shrubs declined (3→6) and thorny trees and shrubs became relatively more dominant (3→7). This shift probably did not at first impact birds, because thorny trees are richer in arthropods than non-thorny woody species (7→8). The birds' predation on foliage herbivores (8→9) facilitates thorny trees by reducing the grazing pressure on foliage by arthropods (9→7) (Van Bael *et al.* 2003). In the past, with large carnivores checking numbers of Topi *Damaliscus lunatus* and other natural grazers, the Sahel may have had a more diverse woody community with fewer thorny trees. If so, the shift to a carnivore-free landscape with huge numbers of livestock may have favoured thorny trees, and consequently also the wintering conditions for Eurasian migrants. However, the ongoing increase of the grazing pressure, combined with a long-term reduction of annual rainfall in the 20th century, has reduced the woody cover in the Sahel (Gonzalez 2001, Brink & Eva 2009). Large-scale pruning of thorny trees to provide livestock with fodder further reduces the available wintering habitat of woodland birds (Zwarts & Bijlsma 2015).

This does not explain, however, why the bird density per ha canopy also declines for non-thorny woody tree species along the rainfall gradient (Figure 8A). Without empirical evidence, we cannot know for sure whether West Africa savanna trees with thorns have a higher arthropod abundance than those without; the same is true for trees with leaves of low crude fibre content. However, the systematic change in leaf traits of woody species along the rainfall gradient (e.g. Schrodt *et al.* 2015) strongly suggests that leaves of trees in the savanna are, on average, more palatable to herbivorous insects than those of trees further south. Most trees in the savanna are deciduous, while most trees in tropical forests are evergreen. Deciduous trees without leaves are not attractive to birds, but when in leaf they attract more insects than evergreen trees because trees with a shorter, more seasonal leaf-life invest less in chemical and structural defence against herbivores (Coley 1983, 1988), a trait that is conducive to higher numbers of arthropods.

The trees of the Sahel are apparently very attractive to wintering migratory birds, as also discernible from the almost complete lack of southward shifts of insectivorous Palearctic birds in the course of the winter (Cresswell *et al.* 2009, own unpubl. data). Why then do several bird species, like Common Nightingale *Luscinia megarhynchos*, Willow Warbler, Garden Warbler *Sylvia borin* and European Pied Flycatcher, still make the longer flight to winter in the mesic, arthropod-poorer habitats to the south of the Sahel where they moreover run a higher risk of exposure to avian blood parasites and their insect vectors (Waldenström *et al.* 2002)? The extra distance per se is not likely to be an energetic constraint except for species that have to interrupt their flight to refuel (like Garden Warbler; Ottosson *et al.* 2005). The advantages of wintering further south may have a bearing on avoidance of competition (but there is little evidence for this; Salewski & Jones 2006, Zwarts & Bijlsma 2015) and on the risk involved in wintering in the Sahel where conditions are less stable and sometimes downright detrimental (droughts). When rainfall is scarce, as in the Sahel, any variation in the amount of rainfall will have a comparatively larger impact than in regions with on average high(er) rainfall. Indeed, the impact of droughts on vegetation and birds is larger in the Sahel than in the Sudan vegetation zone, and in the latter larger than in the Guinean vegetation zone (Zwarts *et al.* 2009). One of the consequences of below-average rainfall in the dry savanna is a reduction of the leafing period in combination with the production of fewer leaves per tree and less (or no) flowers and fruit (Poupon 1980, de Bie *et al.* 1998). This must have a tremendous, negative impact on the food supply of leaf-gleaning, but also other arboreal, bird species, as indirectly evident from the much lower bird densities in trees with fewer leaves (Zwarts & Bijlsma 2015). Below-average rainfall has been shown to be particularly disastrous for birds wintering in the Sahel; the region then functions as an ecological trap. Even so, the risks involved in wintering in the Sahel are clearly outweighed by the better food supply in woody species compared to the mesic habitats further south (but see Figure 11 for changes to come). Moreau's Paradox should therefore have been: why do not more long-distance migrants from the Palearctic winter in the desiccated, but food-rich Sahel?

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SAMENVATTING

Veel Europese vogels overwinteren in Afrika ten zuiden van de Sahara. Daar telt vooral de Sahel, de droge vegetatiegordel direct grenzend aan de Sahara, een relatief hoge vogeldichtheid. Een ogenschijnlijk raadsel, omdat hier 's winters een uitgedroogd (en in de loop van de winter steeds droger wordend) landschap te vinden is. Waarom niet wat zuidelijker overwinteren, in een vochtiger wereld met een grotere diversiteit aan bomen? Om die vraag te beantwoorden hebben we tussen 2007 en 2015 in plots van 300 bij 50 meter alle bomen en struiken gedetermineerd, geteld en opgemeten en alle vogels per boom of struik genoteerd en op naam gebracht. De 2000 plots bestrijken een noord-zuid gradiënt van de zuidrand van de Sahara (18°N, 110 mm regenval per jaar) tot in Guinee-Bissau (11°N, 2200 mm regen) en een west-oost gradiënt van de Atlantische kust (16°W) tot in Burkina Faso (0°W). In dat gebied telden we bijna 308.000 bomen van 183 soorten. In 119 (65%) boomsoorten zagen we geen enkele insectenetende vogel (voor Europese trekvogels was dat zelfs 69%). Bij de analyse van de boomkeuze van insectenetende vogels hebben we ons beperkt tot 56 boomsoorten die min of meer wijd verspreid voorkomen of algemeen zijn.

De bulk van de insectenetende vogels werd in een beperkt aantal boomsoorten vastgesteld. Dat waren voornamelijk doorndragende soorten, met name soorten van het geslacht Acacia en *Balanites aegyptiaca*. De uitzondering op de regel werd gevonden in *Salvadora persica*, een doornloze besdrager die zeer in trek is (mits er rijpe bessen zijn) en dan verreweg de hoogste vogeldichtheid onder alle boomsoorten telt. De aantrekkingskracht van bomen met stekels en doorns zit hem waarschijnlijk in de hogere rijkdom aan insecten in vergelijking met doornloze bomen. Omdat de vraatdruk van grote grazers in de Sahel altijd hoog is geweest, eerst door natuurlijke grazers als antilopen maar tegenwoordig door vee, overwegen hier boomsoorten met stekels en doorns. Deze effectieve manier van verdedigen tegen begrazing betekent echter wel dat deze bomen minder (kunnen) investeren in de aanmaak van gifstoffen in de bladeren ter verdediging tegen plantenetende insecten. Bladeren van doorndragers zijn dan ook aantrekkelijker voor insecten dan bladeren van niet-doorndragers. Die laatste groep is dominant in de vochtiger vegetatiegordels ten zuiden van de Sahel, waar de graasdruk van grote grazers veel minder is (aanwezigheid van de door de tseetseevlieg overgebrachte slaapziekte voorkomt een hoge veedruk) en bomen zich dus niet met doorns hoeven te verweren. In plaats daarvan kan meer worden geïnvesteerd in de aanmaak van gifstoffen in de bladeren tegen insectenvraat, resulterend in minder insecten (en dus onaantrekkelijker voor insectenetende vogels). Daar komt bij dat de levensduur van bladeren in de droge Sahel zo kort is (in vergelijking met die in tropische regenwoud) dat massieve aanmaak van anti-vraatstoffen niet lonend is.

Vogeldichtheden correleerden dus voor een belangrijk deel met het voorkomen van doorndragende bomen, of beter gezegd: met de talrijkheid van insecten op de bladeren van die bomen. Maar dat was niet de enige factor. Andere factoren waren de hoeveelheid ruwe celstof in bladeren (indien weinig, dan insectenrijker en meer vogels), aanwezigheid van bladeren (het lijkt een open deur, maar inderdaad: bladloze bomen waren vrijwel vogelloos) en bloemen (bloeiende bomen trekken insecten en dus vogels aan, zelfs indien het bomen betreft waarvan de bloemen geen nectar produceren), en of de bladeren leerachtig waren of latex bevatten (in beide gevallen weinig aantrekkelijk voor insecten: dus minder vogels). Deze factoren staan uiteraard niet los van elkaar en hebben bovendien een sterke correlatie met de regencijfers: in droge gebieden staan meer doorndragende boomsoorten met een geringer aandeel ruwe celstof in het gebladerte. Deze drie variabelen leverden ook de meest significante verschillen in vogeldichtheden op indien vergeleken met hun tegendeel (droog/nat, met/zonder doorns en weinig/veel ruwe celstof in bladeren). Opmerkelijk genoeg telden doorndagers in het vochtiger zuiden lagere vogeldichtheden dan doorndragers in het droge noorden, een trend die zelfs binnen boomsoorten zichtbaar was.

Over de hele linie waren Palearctische insecteneters talrijker dan insectenetende Afrikaanse soorten; vooral in het droge noorden waren Afrikaanse insecteneters schaars. Binnen de Palearctische soorten werden duidelijke verschillen in voorkomen naar breedtegraad gevonden: Iberische Tjiftjaf *Phylloscopus iberica*, Orpheusgrasmus *Sylvia hortensis* en Roodkopklauwier *Lanius senator* bereikten hun hoogste dichtheid in de zone met 100–400 mm regenval per jaar, Baardgrasmus *S. cantillans* en Bergfluiter *P. bonelli* bij 100–700 mm, en Orpheusspotvogel *Hippolais polyglotta* en Fitis *P. trochilus* bij >1200 mm. Hoe deze soortverschillen tot stand komen, is nog een raadsel. Zeker is wel dat het geen verbazing meer hoeft te wekken waarom de droge Sahel zo aantrekkelijk is voor Europese zangvogels: daar hebben de grote grazers voor gezorgd. Hun massale aanwezigheid heeft de eigenschappen van bomen zodanig beïnvloed dat ze aantrekkelijk zijn voor insecten en daarmee voor vogels. Het raadsel waarmee Reg Moreau zich indertijd geconfronteerd zag, namelijk waarom die droge – en in de loop van de winter verder uitdrogende – Sahel zo aantrekkelijk voor vogels is, terwijl er zuidelijker groenere landschappen liggen, moet eigenlijk worden omgekeerd: waarom overwinteren er niet nóg meer Palearctische soorten in de Sahel? Zou dat te maken kunnen hebben met de smalle regenbuffer van de Sahel? Immers, als er maar iets minder regen valt dan normaal, zijn de gevolgen desastreus. In de regenrijkere landschappen ten zuiden van de Sahel zijn de gevolgen van verminderde regenval minder heftig.

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APPENDIX

Bird densities (*n* per 10 ha canopy) for the most common migratory (in bold) and resident bird species. First column gives ranking based on the densities of all species combined (see last column and Figure 6). Number of investigated trees (*n* × 100) is given in the third column. The total number of migrant and resident birds includes 17 less common migrants and 32 less common residents.

Rank	Tree or shrub	*n* × 100	**Woodchat Shrike**	Tawny-flanked Prinia	Grey-b. Camaroptera	**Olivaceous Warbler**	**(Iberian) Chiffchaff**	**Bonelli's Warbler**	Senegal Eremomela	**Comm. Whitethroat**	**Orphean Warbler**	**Subalpine Warbler**	**Common Redstart**	Beautiful Sunbird	Little Weaver	**Total of migrants**	Total of residents	Total all species
23	*Acacia ataxacantha*	47	0	3	58	0	0	0	3	0	0	3	20	0	0	92	30	122
56	*Acacia dudgeoni*	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	*Acacia kirkii*	6	0	0	0	200	561	62	0	0	3	133	11	0	0	0	990	990
5	*Acacia nilotica*	19	0	11	14	46	127	99	14	12	6	146	37	0	5	59	511	571
7	*Acacia senegal*	21	23	22	0	5	14	82	5	18	68	37	5	0	17	132	237	369
10	*Acacia seyal*	156	1	8	11	17	29	108	12	30	8	44	14	0	2	48	263	310
4	*Acacia tortilis*	138	11	0	3	12	14	188	12	22	70	122	8	0	5	89	483	572
49	*Adansonia digitata*	4	3	0	0	0	0	0	0	6	0	0	0	0	0	3	9	11
47	*Anacardium occidentale*	8	0	0	5	0	0	0	5	0	0	0	0	2	0	13	4	16
30	*Anogeissus leiocarpus*	26	0	0	11	5	0	15	22	5	0	5	0	0	0	50	29	79
16	*Azadirachta indica*	19	0	0	5	107	11	8	0	0	0	8	4	0	0	5	141	146
6	*Balanites aegyptiaca*	186	14	35	18	13	5	49	14	24	20	163	5	0	16	171	328	500
24	*Bombax costatum*	24	0	0	0	0	0	0	21	0	0	0	0	0	0	121	0	121
55	*Borassus flabellifer*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	*Boscia angustifolia*	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	33
19	*Boscia senegalensis*	248	7	5	19	2	0	0	0	37	2	14	2	0	0	57	70	127
54	*Burkea africana*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	*Calotropis procera*	81	6	0	0	0	23	0	0	0	0	6	0	0	0	18	34	52
27	*Cassia sieberiana*	51	0	14	43	7	0	0	0	0	0	0	0	0	0	72	22	94
17	*Combretum glutinosum*	3	0	0	26	2	0	2	20	7	0	5	5	34	0	106	30	136
31	*Combretum micranthum*	139	0	0	27	1	0	0	2	8	0	0	7	5	0	49	19	69
20	*Combretum nigricans*	183	0	0	0	0	0	0	0	0	0	0	41	85	0	85	41	126
29	*Commiphora africana*	9	0	0	0	0	0	0	0	0	0	0	0	0	0	42	42	85
28	*Cordyla pinnata*	2	0	0	0	0	0	55	0	18	0	0	0	0	0	0	92	92
41	*Detarium microcarpum*	25	0	0	17	0	0	0	0	17	0	0	0	0	0	17	17	33
53	*Dichrostachys cinerea*	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	*Diospyros mespiliformis*	6	0	0	0	25	25	0	0	25	0	25	0	0	0	68	126	194
52	*Elaeis guineensis*	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	*Eucalyptus camaldulensis*	106	0	0	0	22	4	13	0	2	0	0	0	0	0	21	46	67
8	*Euphorbia balsamifera*	45	0	8	24	5	42	0	0	94	0	31	16	0	0	126	225	351
2	*Faidherbia albida*	44	1	25	13	91	20	387	17	32	17	153	17	72	69	273	788	1061
43	*Gardenia erubescens*	12	0	0	0	0	0	0	0	0	0	0	32	0	0	0	32	32
44	*Guiera senegalensis*	748	0	0	10	0	0	0	0	8	0	5	0	0	0	12	17	30
46	*Isoberlina roka*	24	0	0	9	0	0	0	4	0	0	0	0	0	0	13	13	27
40	*Isoberlina tormentosa*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	34
48	*Khaya senegalensis*	1	0	0	0	0	6	6	0	0	0	0	0	0	0	0	12	12
21	*Lannea acida*	1	0	0	0	83	0	0	0	0	0	0	0	0	0	0	125	125
35	*Leptadenia pyrotechnica*	66	3	0	0	0	0	0	0	6	3	13	0	0	0	30	25	55
22	*Mangifera indica*	4	0	0	16	83	5	0	0	0	0	0	15	0	0	16	107	124
51	*Oxytenanthera abyssinica*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	*Parkia biglobosa*	4	0	0	3	0	8	6	14	3	0	3	3	0	0	37	31	68
13	*Piliostigma reticulatum*	106	0	39	11	9	19	5	39	28	0	19	19	38	0	141	120	261
39	*Prosopis africana*	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	40
12	*Prosopis juliflora*	21	0	11	6	32	151	4	0	7	0	57	4	0	0	21	262	283
38	*Pterocarpus erinaceus*	2	0	0	0	0	0	51	0	0	0	0	0	0	0	0	51	51
34	*Pterocarpus lucens*	8	0	0	21	0	0	0	14	0	0	0	14	0	0	48	14	62
1	*Salvadora persica*	3	0	0	40	71	88	0	0	88	71	670	35	0	201	259	1076	1335
26	*Sclerocarya birrea*	9	0	0	0	0	0	7	15	7	7	7	4	0	0	32	63	95
36	*Sterculia setigera*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	18	36	54
9	*Tamarindus indica*	2	0	0	54	11	11	42	0	0	11	21	11	23	0	216	117	333
14	*Tamarix senegalensis*	25	0	0	0	0	64	0	0	48	0	96	0	0	0	23	208	231
50	*Tectona grandis*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	*Terminalia macroptera*	27	0	0	0	0	0	0	14	0	0	0	0	0	0	28	0	28
25	*Vitellaria paradoxa*	31	0	1	3	0	0	0	14	0	0	0	1	11	0	93	3	96
11	*Ziziphus mauritiana*	28	5	38	48	47	16	10	0	16	10	10	57	0	22	171	114	285
18	*Ziziphus mucronata*	9	0	0	0	0	0	31	42	31	0	31	0	0	0	42	93	135

ENDNOTES

[i] We measured height and width of all trees and shrubs within the plots, but 14,294 (4.6%) individual woody plants remained unidentified, covering 59,370 m^2 (2.5%) of the canopy surface of all measured woody plants. Most unidentified woody species were shrubs (average canopy surface of 4.2 m^2), often without leaves, or trees belonging to the same genera (like *Combretum*). Woody plants were more often not identified in the humid south where species diversity is much higher than in the dry north. In the unidentified woody species, we noted 25 migrants and 11 residents, i.e. an average density of 4.2 migrants and 2.1 residents/ha canopy. This is low compared to the overall density (Figure 3), but does not deviate from the bird density reached in the woody vegetation of the humid south (Table 1).

[ii] From Le Houérou (1980) we selected 113 analyses of crude fibre content referring to dry leaves only, excluding (less reliable) analyses done on green leaves. Additional data from Babatounde *et al.* (2011) for *Elaeis guineensis*, *Euphorbia balsamifera* and *Mangifera indica*, Chabi Toko *et al.* (1991) for *Vitellaria paradoxa*, Datt *et al.* (2008) for *Azadirachta indica* and *Tectona grandis*, Mecha & Adagbola (1980) for *Anacardium occidentale*, *E. guineensis* and *Mangifera indica*, Njidda *et al.* (2014) for *Ziziphus mucronata*, Reddy & Elanchezhian (2008) for *A. occidentale* and *Ziziphus spina-christii*, Umar *et al.* (2010) for *Balanites*, *Gardenia erubescens* and *Parkia biglobosa*, and Walker (1980) for *Burkea africana* and *Dichrostachys cinerea*. The number of analyses per tree species varied between 1 and 8. The value for *A. nilotica* was substituted for *A. kirkii* (previously considered as a sub-species of *A. nilotica*). These studies were done to investigate the food quality for browsing livestock. It is not always clear whether crude fibre content is determined for the blade only, for blade + stalk or possibly even includes the twig; this probably explains part of the observed variation.

[iii] One-way analyses of variance revealed that the bird species differ significantly regarding absolute ($r^2 = 0.252$, $P < 0.001$, $n = 3106$) and relative height ($r^2 = 0.249$, $P < 0.001$, $n = 3106$).

[iv] List of English and scientific names of bird species mentioned in the paper, based on BirdLife Checklist version 7.0, except for Grey-backed instead of Green-backed Camaroptera and Southern Grey Shrike which is *L. excubitor meridionalis* in BirdLife's list.

Beautiful Sunbird *Nectarinia pulchella*
Black Scrub-robin *Cercotrichas podobe*
Bluethroat *Luscinia svecica*
Bonelli's Warbler *Phylloscopus bonelli*
Collared Flycatcher *Ficedula albicollis*
Common Chiffchaff *Phylloscopus collybita*
Common Nightingale *Luscinia megarhynchos*
Common Redstart *Phoenicurus phoenicurus*
Cricket Longtail *Spiloptila clamans*
Eastern Olivaceous Warbler *Hippolais pallida*
Eurasian Wryneck *Jynx torquilla*
European Pied Flycatcher *Ficedula hypoleuca*
Common Whitethroat *Sylvia communis*
Garden Warbler *Sylvia borin*
Grey-backed Camaroptera *Camaroptera brachyura*
Grey Woodpecker *Dendropicos goertae*
Iberian Chiffchaff *Phylloscopus ibericus*
Little Weaver *Ploceus luteolus*
Melodious Warbler *Hippolais polyglotta*
Northern Crombec *Sylvietta brachyura*
Orphean Warbler *Sylvia hortensis*
Pygmy Sunbird *Anthreptes platurus*
Rufous Scrub-robin *Erythropygia galactotes*
Scarlet-chested Sunbird *Nectarinia senegalensis*
Senegal Eremomela *Eremomela pusilla*
Sennar Penduline-tit *Anthoscopus punctifrons*
Southern Grey Shrike *Lanius meridionalis*
Splendid Sunbird *Cinnyris coccinigastrus*
Subalpine Warbler *Sylvia cantillans*
Tawny-flanked Prinia *Prinia subflava*
Tree Pipit *Anthus trivialis*
Variable Sunbird *Nectarinia venusta*
Western Olivaceous Warbler *Hippolais opaca*
Willow Warbler *Phylloscopus trochilus*
Wood Warbler *Phylloscopus sibilatrix*
Woodchat Shrike *Lanius senator*
Yellow-bellied Eremomela *Eremomela icteropygialis*

[v] The average rainfall (±SD) for tree and bird species was calculated for all data collected in the plots shown in Figure 1. Range covered by plots: 110–2200 mm. Sample size per species varied between 101 and 74,762 trees (see Appendix) and between 8 and 1346 birds (shown along the y-axis of Figure 5B). One-way analyses of variance revealed that the distribution along the rainfall gradient differed significantly for tree species ($r^2 = 0.66$; $P < 0.001$, $n = 278{,}978$ trees) and bird species ($r^2 = 0.382$, $P < 0.001$, $n = 5338$ birds).

[vi] To increase the sample size for flooded trees, data from October and November were included in this analysis. Total canopy surface investigated for trees standing in water or on dry land, respectively (m^2): *Faidherbia* (1432 and 256,518 m^2), *Acacia sieberiana* (826 and 2714), *A. seyal* (6828 and 33,447), *A. nilotica* (1825 and 8476). We did eight multinomial logistic regression analyses with canopy surface as covariate, flooding as factor and individual trees as measure to test whether the presence of one (or more) bird in a tree differed for flooded and dry trees. In each analysis, flooding had a highly significant impact on bird density (but less in *A. nilotica*): Olivaceous Warbler and (Iberian) Chiffchaff: $P < 0.001$ and $P < 0.001$ for *Faidherbia* ($n = 4869$ trees), $P = 0.003$ and $P = 0.005$ for *A. sieberiana* ($n = 131$), $P = 0.017$ and $P = 0.002$ for *A. seyal* ($n = 16{,}991$) and $P = 0.045$ and $P = 0.048$ for *A. nilotica* ($n = 2626$).

[vii] We did 13 multiple regression analyses on the data given in the appendix to investigate bird densities per tree species in relation to thorns, flowers, leaves, berries and floodplain (0 or 1) and tree height and rainfall. Fibre content was not included in these analyses because of the large number of missing values. None of the variables were significant in Grey-backed Camaroptera, Senegal Eremomela and Beautiful Sunbird. The total explained variance in the migrants varied between $r^2 = 0.36$ (Woodchat Shrike) and $r^2 = 0.92$ (Subalpine Warbler). Due to the collinearity of the variables, it is difficult to indicate how much each variable contributes to the observed variation in bird density per tree species, but three variables appear to be dominant in most analyses: berries, thorns and rain.

[viii] One may doubt whether the relationship between bird density and crude fibre content of the foliage, although significant, is causal, because of the high correlation between rainfall and crude fibre content ($r = 0.41$). We did a multiple regression analysis on the data shown in Figure 8B in which rainfall was added as second parameter: the explained variance increased from $r^2 = 0.22$ to $r^2 = 0.34$, being significant for both variables ($P = 0.023$ for rainfall and $P = 0.018$ for rain). We also found that crude fibre remained significant, independent of rainfall, by restricting the data shown in Figure 8B to tree species found in the dry north. Omitting tree species from regions with >1000 mm rain, the relationship between bird density and crude fibre content became still more negative (thorny species: $r^2 = 0.28$, $P = 0.04$, $n = 11$; non-thorny species: $r^2 = 0.40$, $P = 0.002$, $n = 19$).

[ix] We performed multinomial logistic regression analyses for the ten bird species in the four tree species, with canopy surface as covariate, rain (same categories as shown in Figure 9) and month as factors and individual trees as measure, to test whether the presence of one (or more) bird in a tree differed for the different rain zones (no analyses for Melodious Warbler and Orphean Warbler in *A. seyal*, since present in one category only). Number of trees: 16,991 for *A. seyal*, 19,748 for *A. tortilis*, 14,625 for *Balanites* and 4869 for *Faidherbia*. In all analyses, rain zone was highly significant, except for Olivaceous Warbler in *Balanites* ($P = 0.299$); $P = 0.001$ for Common Whitethroat in *Faidherbia* and Melodious Warbler in *A. tortilis*, $P = 0.017$ for Orphean Warbler in *A. tortilis* and $P < 0.001$ in the 35 other analyses.