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Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture

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Abstract Grassland-breeding shorebirds show widespread declines due to a reduction in breeding productivity following agricultural intensification. However, there is also concern that increasing predation causes further declines or precludes population recovery. Predation may itself be enhanced by agriculture through changes in habitat or food availability, but little is known about the mortality of nidifugous shorebird chicks. We studied mortality by radio-tagging 662 chicks of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* in 15 farmland sites in the Netherlands. Tagging and handling had no effect on the condition and survival of godwit chicks, but body condition was reduced by 6–11% in lapwing chicks wearing a tag for longer than 3 days. Fledging success was 0–24% in both species. Mortality was highest in young chicks but remained considerable until after fledging. Losses were traced mostly to predators (70–85%; 15 species, predominantly birds), but at least 5–10% were due to mowing, and 10–20% were due to other causes, including entrapment in ditches and starvation. Chicks staying in fields that were cut before the next radio check were found much more often as mowing victims and somewhat more often as prey remains than chicks in fields not cut, indicating that predation includes a limited amount of scavenging. The predation hazard for godwit chicks was higher in recently cut or grazed fields than in the tall, uncut grasslands they preferred, while that for lapwing chicks was lowest in grazed fields. In godwit chicks, poor body condition increased mortality risk, not only from starvation but also from other causes. Predation on godwit chicks was thus enhanced by intensive farming through a decline in the availability of cover, augmented by a reduced body condition, possibly due to food availability problems. Changes in farming practice may therefore help reduce predation pressure, though the observed interactions explained only part of the high predation rate in godwits and none in lapwings. Predator abundance has increased in Dutch wet grassland regions, and chick predation has become a factor that should be considered in planning the type and location of conservation measures.

Keywords Agricultural intensification · Chick survival · Condition · Predation · Shorebirds

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Introduction

The study of processes affecting reproduction and mortality is important to gain an understanding of the population

dynamics of animals and to identify appropriate conservation strategies for declining species (Green 2002). Most shorebirds (Charadrii) breeding in wet grasslands have shown severe population declines throughout western Europe (Thorup 2006), and a reduction in breeding output has been identified as the main driver of several of these declines (Green 1988; Peach et al. 1994; Besbeas et al. 2002; Ottvall 2005; Schekkerman et al. 2008). There is broad agreement that this reduced breeding productivity is caused primarily by agricultural intensification, leading to an increase in direct clutch and chick mortality and to food availability problems (Beintema et al. 1997; Vickery et al. 2001; Wilson et al. 2004; Schekkerman and Beintema 2007). However, concerns have also been raised that predation causes population declines or precludes recovery in response to conservation measures (Grant et al. 1999; Langgemach and Bellebaum 2005; Bolton et al. 2007). A complicating factor in the ensuing discussions about conservation strategies is the possibility that predation eliminates mainly prey with already reduced survival prospects (Swennen 1989) or interacts with agricultural land use (Evans 2004). For example, changes in farming practice may alter the amount of protective cover or, via effects on food availability, the chicks' risk-taking behaviour and escape response.

Chicks of most shorebird species are precocial and feed themselves. The resulting high energy requirements make them sensitive to foraging conditions (Schekkerman and Visser 2001), while the associated activity and movements may also render them vulnerable to predators and fatal accidents. Because shorebirds often re-nest after clutch failure but usually not after losing chicks (Cramp 1983), chick survival is a key component of breeding productivity in this group, but the importance of different loss factors is much less well known for chicks than for eggs.

With the development of small radio transmitters that can be attached to chicks, a practical method has become available to investigate fledging success and the causes of chick death in precocial birds. Radio-tagging has been used to study chick mortality in ducks (Korschgen et al. 1996; Pietz et al. 2003), gamebirds (Riley et al. 1998; Larson et al. 2001), bustards (Combreau et al. 2002) and shorebirds (Miller and Knopf 1993; Grant et al. 1999; Pearce-Higgins and Yalden 2003; Ratcliffe et al. 2005; Bolton et al. 2007). A potential drawback of radio-tagging is that the transmitters may affect the chicks' behaviour or physiology and reduce their survival prospects. Thus, it is important to check whether such negative effects influence the outcome of telemetry studies (Kenward et al. 1993; Whittingham et al. 1999; Grant 2002; Krapu et al. 2006).

In the study reported here, we quantified the importance of different mortality factors, including the roles of predation and agricultural management, for chicks of the two most abundant grassland shorebirds in The Netherlands, Northern Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa*. We describe causes of death, identity of predators and associations between mortality and chick age, body condition and agricultural field use. We also investigated whether tagging and handling chicks affected their growth and survival.

Methods

Study species and areas

Both of the species studied breed primarily in agricultural grasslands in the Netherlands, but their chicks differ in ecology. While Black-tailed Godwit chicks prefer tall, structured swards and feed on invertebrates living in the vegetation, their Northern Lapwing counterparts frequent short grass, muddy ground and ditch edges, and take invertebrates mainly from the soil surface (Beintema et al. 1991). Both species have declined in the Netherlands, godwits much more strongly than lapwings (SOVON 2002; Teunissen and Soldaat 2006).

The data were compiled from two studies conducted in 2003–2005, one into the effects of predation on meadow bird populations (Teunissen et al. 2005, 2006), and the other on the effectiveness of a new agri-environment scheme (AES) for improving breeding success of godwits (Schekkerman et al. 2005, 2008). Chicks were studied in 15 sites (lapwing, seven sites; godwit, 11 sites) scattered through the Netherlands (Table 1). Godwits were studied in grasslands used for dairy farming; lapwings in both grasslands and sites with mixed arable and dairy farming. One grassland site was managed entirely and one was partly managed as a nature reserve. In four of the godwit study sites, an experimental AES aimed at improving breeding conditions for Black-tailed Godwits was implemented, with measures that included postponing grass mowing and leaving refuge strips when cutting (Schekkerman et al. 2008). Although some sites in the predation study were selected on the basis of above-average rates of clutch predation, this does not imply that chick predation was also above average, as predation rates on eggs and chicks were not strongly correlated ($r_s = 0.37$ in godwits, 0.44 in lapwings; Teunissen et al. 2005).

Radio-tagging and tracking chicks

A total of 297 lapwing and 365 Black-tailed Godwit chicks were radio-tagged during the study period, 15–53 (godwit) or 22–58 (lapwing) per site and year. Chicks were tagged within a day after hatching (godwit 86%, lapwing 32%) or

Table 1 Study sites with general characteristics, study year(s) and species

Site number	Site[a]	Province	Habitat (soil)	Management	Year	Species
1	Arkemheen	Gelderland	Grassland (clay/peat)	Dairy farming + reserve	2003–2004	L,G
2	IJsseldelta	Overijssel	Grassland (clay)	Dairy farming, maize	2003	L,G
3	Soest	Utrecht	Grassland (clay/peat)	Dairy farming + maize	2003	L
4	Leende	Noord-Brabant	Mixed farmland (sand)	Arable + dairy farming	2004	L
5	Ruinen	Drenthe	Mixed farmland (sand)	Maize + dairy farming	2004	L
6	Texel	Noord-Holland	Mixed farmland (sand)	Arable + dairy farming	2004	L
7	Tijnje	Friesland	Grassland (peat)	Meadow bird reserve	2005	L,G
8	Gerkesklooster	Friesland	Grassland (clay)	Dairy farming with AES	2004	G
9	Grijpskerk	Groningen	Grassland (clay)	Dairy farming	2004	G
10	Oldeboorn A	Friesland	Grassland (peat)	Dairy farming with AES	2005	G
11	Oldeboorn B	Friesland	Grassland (peat)	Dairy farming	2005	G
12	Amstelveen	Noord-Holland	Grassland (clay/peat)	Dairy farming with AES	2004–2005	G
13	Mijdrecht	Utrecht	Grassland (clay/peat)	Dairy farming	2004–2005	G
14	Noordeloos	Zuid-Holland	Grassland (peat)	Dairy farming with AES	2005	G
15	Ottoland	Zuid-Holland	Grassland (peat)	Dairy farming	2005	G

L, Lapwing; G, godwit; AES, Agri-environment scheme aimed at improving godwit breeding success

[a] Sites ranged in size from 117 to 493 ha [mean 268 ± 110 (SD) ha]

at older ages. We used small 153-MHz VHF transmitters (type LB-2; Holohil, Canada, assembled by Microtes, the Netherlands) weighing 1.0 g and measuring 5 × 10 × 3 mm equipped with a 12-cm whip antenna (battery life ≥40 days). Signal range was usually 100–300 m, more under some conditions (≥1 km when up in a raptor nest), and less in others (down to <50 m when in a ditch or burrow). Transmitters were glued to a 1.5 × 1.5-cm piece of cloth with superglue, and this was attached to the down on the chick's back, just outside the centre of the synsacrum, with latex-based glue retaining some flexibility (Uhu-Creativ, Uhu, Germany). Chicks were recaptured every 4–7 days to check and restore tag attachment, which deteriorated over time due to breakage of down and growth of underlying feathers. Two chicks were tagged in broods of four, one or two in broods of three. All chicks were ringed, and bill length and body mass were recorded at each capture. Age at first capture of chicks not ringed at hatching was estimated from bill length (Beintema and Visser 1989). We calculated an index of condition at each capture by dividing the observed body mass by the mass predicted at the chick's age from published growth curves (Beintema and Visser 1989).

Tagged broods were relocated every 1–5 days (median 2 days) using hand-held receivers and antennas. The presence of living chicks was deduced from their parents' alarm behaviour and fluctuations in the strength of their radio signals, indicating movement. Steady signals were followed up to check whether chicks were alive. Missing chicks were searched for throughout the study area and in bushes and woodlots potentially containing predators'

haunts up to several kilometres away. Before the batteries expired, most study areas were traversed completely on foot to search for weak signals from transmitters in ditches and burrows. We also searched for rings and transmitters with a metal detector under nesting trees in Grey Heron *Ardea cinerea* colonies and some known raptor nests up to a distance of 10 km.

In 2005, in sites 10–15 only (Table 1), one of the parents of the tagged godwit chicks was also fitted with a transmitter (Holohil type BD-2). This greatly facilitated assessing the chicks' fate, as the transmitter signals were stronger, and adults could still be located and their behaviour observed after their chicks' signals were lost. Adult behaviour reliably shows whether chicks are alive until about 1 week after fledging (Schekkerman and Müskens 2000).

The cause of death of recovered chicks was deduced from the state and location of the remains (Teunissen et al. 2008). Locations in particular were often informative (e.g. in ditch, among recently cut grass, under raptor nest or plucking tree, in stoat burrow), but the state of the carcass and/or the transmitter (condition, bite or plucking marks) also conveyed information. Nevertheless, several cases were left as 'unknown', 'eaten by bird', 'not eaten', etc. Field notes and photographs were re-examined after the study to standardise between-observer interpretation and utilise experience gained. Transmitters found detached without traces of violence were considered to have fallen off a live chick if tag attachment had last been checked >5 days earlier; otherwise they were categorised as 'chick dead or transmitter lost'.

The locations of radio-tagged broods were recorded on maps. The agricultural status of all fields in the study areas was mapped at least once but usually several times a week (less often in sites 6, 8 and 9). Categories were based on crop type (grass/arable), sward height and whether fields had been cut or grazed (Table 3).

Survival analysis

Survival curves were derived according to Kaplan and Meier (1958), including the staggered entry of chicks ringed at different ages and right-censoring. Observations on tagged chicks could end in several ways: (1) the chick survived until it lost the transmitter or observations were stopped after fledging or at the end of the season (censored, i.e. removed from the sample at this time); (2) the dead chick or its ring were recovered; (3) its transmitter was found and categorised as 'chick dead or transmitter lost'; (4) its signal was lost before the fledging age, but neither chick nor transmitter were recovered (i.e. dead, tag failure or moved beyond the search range). Minimum and maximum estimates of survival were calculated by treating chicks from categories (3) and (4) as dead and censored, respectively, from the day their signal was lost.

The effects of environmental covariates on the mortality of unfledged chicks were explored with proportional hazard models (Cox 1972), using procedure RPHFIT in GENSTAT (Payne 2005). Models were run for the overall probability of a chick disappearing and for separate competing risks: missing (no remains recovered), predation (total and by bird or mammal separately), agricultural, and other losses. The models assume an unspecified baseline hazard function (similar to the reciprocal of the Kaplan–Meier survival curve) that is modified proportionally by covariates which may vary in time but are assumed to be constant during the intervals between consecutive localisations of the chick. Covariates examined were site/year (always included to correct for differences in general conditions, including landscape and predator abundance), chick age (always included), type of field in which the chick was observed at the start of the interval, agricultural activity on this field during the interval and chick body condition. Information was not available on all covariates for each interval. For categorical covariates, a category 'unknown' was included to ensure that all intervals contributed to the baseline hazard and models could be fitted. Because this 'unknown' category affects the degrees of freedom for the overall test of significance of the covariate, effects were evaluated from the 95% confidence intervals of the ratios between the mortality risk for each level of the covariate and the baseline hazard [hazard ratios (HR); interval including 1 or not].

Our analysis of the associations between mortality and field characteristics was complicated by the fact that broods often moved between fields during the interval between radio checks. Godwit chicks changed fields in 59% of 860 intervals; lapwings were more sedentary and moved in 26% of 988 intervals. By selecting intervals lasting ≤ 2 days for godwits and ≤ 3 days for lapwings, we minimised the probability that chicks changed field while still retaining most of the data in the analysis [godwits: 55 vs. 74% moved in intervals of 0–2 and >2 days ($n = 716$ and 144), respectively; $\chi_1^2 = 17.6$; $P < 0.001$; lapwings: 25 vs. 42% moved in intervals of 0–3 and >3 days ($n = 896$ and 92), respectively; $\chi_1^2 = 17.6$; $P < 0.001$). Body condition indices were used for intervals both following and preceding the measurement.

Evaluating effects of radio-tagging

Negative effects of radio-tagging on chicks may arise through entanglement in vegetation (not observed) or by chicks becoming more easily detectable to predators, either because of the transmitters themselves or as a result of handling (scent or behavioural changes). Transmitters may also affect chick growth and condition by hampering feeding or increasing energy expenditure, with possible consequences for risk-taking behaviour and escape response. We checked for such effects in three ways.

We examined the effect of tagging and handling on growth rate using the fact that not all chicks were tagged at the same age. If negative effects occur, the condition index of chicks wearing a transmitter for some time should be less than that of same-age chicks caught for the first time. This was tested in a linear mixed model including site/year and chick identity as random variables (accounting for repeated measures on the same chicks), and chick age and 'days tagged' (tag worn 0, 1–3, or >3 days) as fixed variables. Observations on chicks <3 days old were excluded, as the growth curve underestimates the mass of newborn chicks, and effects are less likely to show up so early.

Short-term effects of handling on survival were examined by comparing, in a proportional hazard model, mortality over intervals between radio localisations in which chicks were handled (measured and weighed) at the start with that over intervals in which their initial live status was deduced from a distance by the radio signal. Finally, in sites 10–15 in 2005, the survival of tagged godwit chicks ($n = 127$) could be directly compared with that of their tagless siblings ($n = 100$). In these broods, half of the chicks and one of their parents were radio-tagged, and both the number of chicks hatched and the number fledged (tagged and total) were known from visual observations made around the fledging age.

Results

Effects of radio-tagging on chicks

In godwit broods with a radio-tagged parent, five of the six chicks surviving to fledging were tagged; for the sixth chick, status was uncertain (possibly failed tag). Counting this latter case half in both categories, survival was marginally higher in tagged chicks (GLM with binomial distribution and logit link, $F = 4.27$, $P = 0.04$). Although the number fledged is small, this does not indicate a lower survival for tagged chicks.

The mortality of godwit chicks over intervals between successive observations was not higher when they were handled and measured at the start of the interval than when they were located from a distance only (hazard ratio HR $= 1.05$, $F_1 = 0.11$, $P = 0.74$, $n = 685$ handled, 676 non-handled). The same result was obtained in lapwings (hazard ratio 1.08, $F_1 = 0.20$, $P = 0.66$, $n = 642$ handled, 734 non-handled).

The condition index of godwit chicks was 0.89 on average (SD $= 0.15$, $n = 391$) and declined with age (Wald test, $W_1 = 7.82$, $P = 0.005$; Fig. 1a), indicating a lower growth rate than that observed 25 years ago by Beintema and Visser (1989). Tagging and handling did not depress the growth rate in godwit chicks: inclusion of the variable 'days tagged' (0, 1–3, or >3 days) did not significantly improve the model fit ($W_2 = 1.16$, $P = 0.56$; interaction age × 'days tagged' $W_2 = 4.62$, $P = 0.10$). In lapwings, condition indices were higher on average (1.06 ± 0.19, $n = 658$) and did not decline with age ($W_1 = 1.95$, $P = 0.16$; Fig. 1b), but 'days tagged' had a significant effect that increased with age ($W_2 = 35.7$, $P < 0.001$; interaction age × 'days tagged' $W_2 = 7.97$, $P = 0.019$). Lapwings that had worn a tag for >3 days were 6% lighter than tagless chicks when 5 days old; this difference increased to 11% at 30 days of age ($P < 0.001$).

Chicks tagged for 1–3 days did not differ from tagless chicks in terms of condition ($P = 0.37$).

Overall survival and age

The fate of 23% of all radio-tagged chicks remained uncertain as no remains were found, and in a further 3% we were unsure whether the chicks had lost their transmitter or died (Table 2). Observations on godwit broods with a tagged parent in 2005 (sites 10–15) showed that all 49 chicks that remained 'missing' had actually died; the parents stopped alarming before the chicks were 25 days old, except in one case where a tagless sibling fledged. Hence, true survival was very likely closer to the minimum than to the maximum estimates.

Survival to fledging was low in both species (Fig. 2). The minimum estimate varied between sites/years from 0 to 24% in godwits (mean 7%, SD = 7%, $n = 14$ sites) and from 0 to 23% in lapwings (mean 14%, SD = 8%, $n = 8$). In both species, survival was especially low in 2005 (mean 3 and 4%, respectively). Mortality was highest in the first days after hatching, then it more or less stabilised before a further decrease around the fledging age (Fig. 2). Appreciable mortality still occurred after fledging, especially in lapwing chicks. The initial phase of high mortality lasted longer and encompassed a larger proportion of the total losses in lapwings than in godwits.

Causes of death

Of all chicks lost before fledging (dead or 'missing'), the cause of death remained unknown in 38%, 47% were found to have been eaten by predators, 5% were victims of agricultural activities and 9% succumbed to other causes (Table 2). As part of the 'missing' chicks were probably removed by predators (see Discussion), predation (including scavenging) was the primary cause of mortality.

Fig. 1 Condition index of chicks in relation to age, at first capture (without radio tag) and at later captures (with tag)
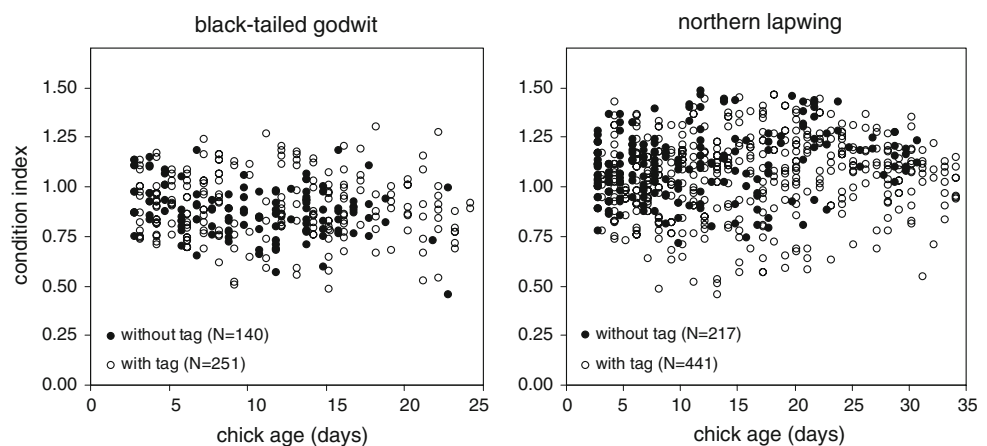
Table 2 Summary of fates and causes of death of radio-tagged chicks, pooled over study sites and years

Fate	Total		Godwit		Lapwing		Difference[a]	
	Number	Percentage	Number	Percentage	Number	Percentage	χ_1^2	P value
Number of chicks tagged	662		365		297			
Survived observation period	119	18	49	13	70	24		
Loose transmitter: lost or dead	23	3	6	2	17	6		
Missing, no remains found	150	23	83	23	67	23		
Dead, transmitter or chick found	370	56	227	62	143	48		
Causes of death (% of lost chicks)	543		316		227			
'Missing' + 'transmitter lost or dead'	173	32	89	28	84	37	3.24	0.072
Dead, cause unknown	35	6	28	9	7	3	6.84	0.009
Eaten by bird	155	29	83	26	72	32	1.38	0.24
Eaten by mammal	65	12	50	16	15	7	9.37	0.002
Eaten, predator unknown	35	6	16	5	19	8	2.24	0.13
Agricultural activity and trampling	26	5	22	7	4	2	7.46	0.006
Drowned/stuck in ditch/trench	29	5	15	5	14	6	0.50	0.48
Starvation/illness	13	2	9	3	4	2	0.65	0.42
Other causes	11	2	4	1	7	3	2.16	0.14

[a] Difference gives χ^2-test of differences in prevalence between godwits and lapwings

Fig. 2 Survival curves (*upper panels*) and daily survival rates (*lower panels*, with smoothing splines, $df = 4$) of Black-tailed Godwit and Northern Lapwing chicks, pooled over sites and years. Maximum and minimum estimates are based on different assumptions about the fate of 'missing' chicks; minimum values are more likely to be true (see Methods). *Grey areas* indicate ages at which chicks had fledged. Godwit sample size varied from 298 chicks at hatching to 39 at fledging and 9 on day 40 (3,526 chick-days in total); lapwing sample size varied from 66 at hatching to 131 on day 4, 51 at fledging and 18 on day 45 (3,349 chick-days in total)
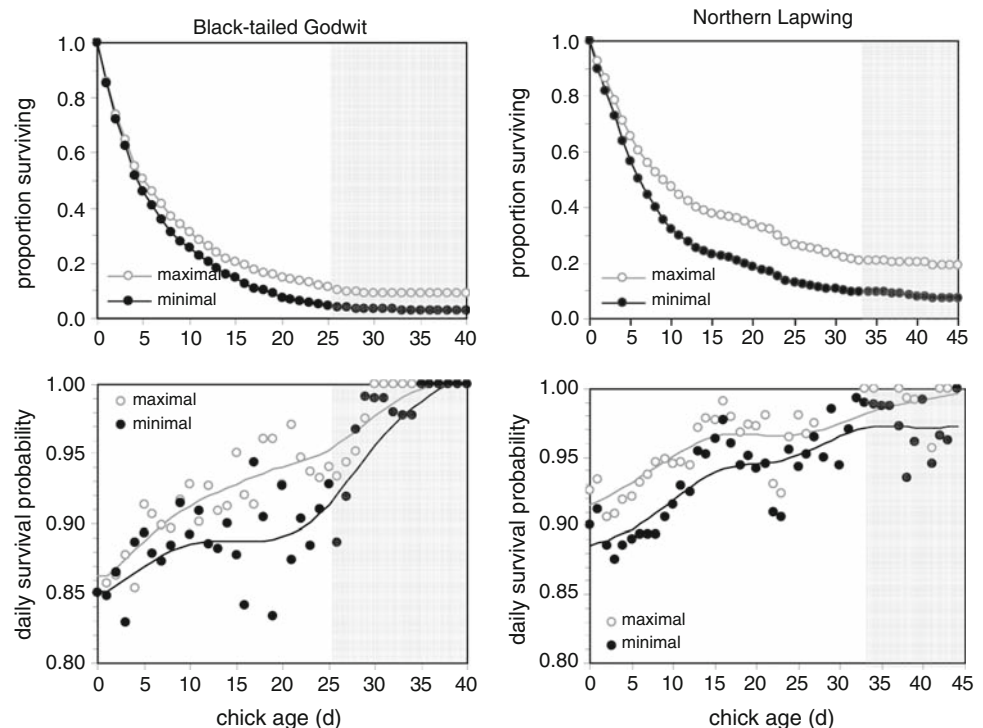
Predation hazard declined with chick age by 7% per day (proportional hazard model, godwits $F_1 = 10.9$, $P < 0.001$; lapwings $F_1 = 16.6$, $P < 0.001$). Birds were more often identified as chick predators than mammals, particularly with respect to lapwings (Table 2). The four species most frequently identified were Grey Heron *Ardea cinerea* (18% of 255 chicks found predated), stoat/weasel

Mustela erminea/nivalis (15%), Common Buzzard *Buteo buteo* (12%) and the Carrion Crow *Corvus corone* (6%); 11 other species made up ≤2% each (White Stork *Ciconia ciconia*, Goshawk *Accipiter gentilis*, Sparrowhawk *Accipiter nisus*, Marsh Harrier *Circus aeruginosus*, Common Kestrel *Falco tinnunculus*, Jackdaw *Corvus monedula*, Lesser Black-Backed Gull *Larus graelsii*, Common Gull

L. canus, Rat *Rattus* sp., Domestic Cat *Felis catus* and Red Fox *Vulpes vulpes*). Lapwing chicks were taken more often by herons than godwit chicks (11 vs. 26%, $\chi_1^2 = 7.90$, $P = 0.005$), while godwit chicks were taken more by stoats (8 vs. 20%, $\chi_1^2 = 5.49$, $P = 0.02$) and buzzards (6 vs. 17%, $\chi_1^2 = 6.30$, $P = 0.01$); both species were taken equally by crows (6 vs. 7%, $\chi_1^2 = 0.11$, $P = 0.74$). Godwit chicks preferred tall vegetations (94% of 1036 localisations in fields with uncut or regrowing sward >15–20 cm high vs. 37% of 1186 localisations of lapwing chicks in this habitat) where they were proportionally more often taken by mammals (mostly stoats) than in short swards (43 vs. 20% of predations by mammals, $\chi_1^2 = 4.62$, $P = 0.032$; Table 3).

All agricultural losses concerned chicks killed during mowing and harvesting of grass, except for one newborn lapwing trampled by cattle. More godwit than lapwing chicks fell victim to mowing (Table 2) due to the godwits' preference to forage in tall grassland ready to be mown. In godwit chicks, the risk of mortality by mowing tended to decline with age (−10%/day, $F_1 = 3.60$, $P = 0.058$), although chicks up to 23 days old were killed by machines. Too few lapwings were killed by mowing to find an age effect.

About 5% of lost chicks died in wet (both species) or dry (lapwing only) ditches. Although chicks swim well, ditches can form a trap when the sides are too steep to climb. The risk of entrapment in ditches declined with age in lapwings (−17%/day, $F_1 = 14.1$, $P < 0.001$) but not significantly in godwits (−10%/day, $F_1 = 2.17$, $P = 0.14$). Other causes of death included starvation or illness (2%), acute exposure to cold or rain (1%) and aggression by conspecifics (one case).

Mortality and field use

Compared to the most-used field type (uncut grassland), the risk that godwit chicks were taken by a predator was twice as high as that in recently cut or grazed fields with a short sward (Table 3). This effect was caused by avian predators and translated into a 1.4-fold higher overall mortality. The risk of predation by mammals was especially high in previously cut fields with a regrowing sward, but as mammal predation was less frequent, this did not translate into a higher overall mortality. The only significant effect of field type on the mortality of lapwing chicks was a lower risk of predation (by birds) in grazed fields. The predation hazard for godwits was also low here, but not significantly different from that in uncut grassland (Table 3).

Godwit chicks located in fields with a tall (uncut or regrowing) sward were 13 times more likely to be found as a mowing victim when the field was cut during the subsequent interval than when it was not, but the associated 50% increase in overall mortality was not significant (Table 3). No lapwing chicks were killed by mowing in intervals ≤3 days. Because avian predators and scavengers are often attracted to mowing activity, it was of interest to know whether other risks increased when the field was cut. Hazard ratios for predation (particularly by birds) were greater than 1, but the effect was not significant (godwit $P = 0.15$, lapwing $P = 0.10$). It was significant in godwits when only 1-day intervals were considered (HR = 22, $P = 0.07$). The probability that chicks went 'missing' was not associated with cutting of the field (Table 3).

Mortality and condition

A low body condition index greatly increased the risk of dying by 'starvation or illness' in both species (Table 4), which is expected as the diagnosis was based on a lack of injuries combined with a poor condition. The mean condition index of chicks considered to have died from starvation was 0.48 (SD = 0.06, range 0.41–0.56, $n = 10$). Condition affected the overall risk of mortality in godwits but not in lapwings, and there was also a near-significant tendency for godwit chicks in poor condition to be lost to causes other than starvation or illness. This was not so much due to predation (except by mammals) as to a higher probability to end up 'missing' (Table 4). In lapwings, no condition effects were observed on risks other than starvation.

Discussion

Radio-tagging as a method to study chick mortality

Our study did not reveal any negative effects of radio-tagging and handling on the condition and survival of Black-tailed Godwit chicks. Northern Lapwing that had worn a tag longer than 3 days were 6–11% lighter than same-age chicks captured for the first time. This result suggests that tags induced negative effects on growth by reducing the chicks' insulation, increasing energy costs of locomotion or impairing foraging success. Lapwing chicks are smaller than their godwit counterparts and, therefore, the transmitter adds proportionally more to their body mass (5.7 vs. 3.5% at hatching, decreasing to 0.5% at fledging), which may help explain why we did not observe a condition effect in godwits. We found no association between condition and the overall survival of lapwing chicks (Table 4), but condition indices ≤0.6, associated with a strongly increased risk to be found starved, were only observed in tagged lapwings (Fig. 1). Since no adult lapwings were radio-tagged, we were unable to directly compare the survival of tagged chicks with that of tagless

Table 3 Proportional hazard analysis for different causes of death in relation to the field type where chicks stayed at the start of observation intervals and (for chicks in uncut or regrowing grassland) to whether the field was cut during the interval

Field type	n	Lost (dead/missing)		Predation total		Predation by birds		Predation by mammals		'Missing' (not recovered)		Mowing and trampling	
		HR	95% CI	HR	95% CI	HR	95% CI	HR	95% CI	HR	95% CI	HR	95% CI
Black-tailed Godwit													
Uncut grass[a]	638	1.0		1.0		1.0		1.0		1.0		1.0	
Regrowing grass[b]	70	1.1	0.6–2.2	1.9	0.6–5.7	0.5	0.0–4.2	**5.2***	**1.2–23.8**	0.7	0.2–2.5	0.4	0.0–4.3
Refuge strips[c]	36	2.0[†]	1.0–4.1	1.9	0.7–5.4	1.0	0.3–3.4	0.0	0–>100	1.4	0.3–6.5	9.7[†]	0.7–122
Grazed grass[d]	105	0.7	0.4–1.3	0.6	0.2–1.8	0.8	0.2–2.8	0.6	0.1–4.5	1.1	0.5–2.2	0.0	0–>100
Short grass[e]	135	1.4[†]	0.9–2.2	2.0*	1.1–3.7	3.2**	1.5–6.7	1.0	0.3–3.4	1.1	0.6–2.4	0.0	0–>100
In uncut and regrowing grass													
Field not cut in interval	601	1.0		1.0		1.0		1.0		1.0		1.0	
Field cut in interval	46	1.5	0.8–2.8	1.8	0.6–5.6	2.8	0.7–11.0	1.3	0.1–13.8	0.8	0.2–2.6	**13.4****	**3.2–56**
Northern Lapwing													
Uncut grass[a]	175	1.0		1.0		1.0		1.0		1.0		No fit	
Regrowing grass[b]	303	0.9	0.4–1.6	0.7	0.3–1.6	1.0	0.3–3.0	0.1[†]	0.0–1.3	1.6	0.5–5.1	–	–
Grazed grass[d]	349	**0.5***	**0.3–0.9**	**0.2****	**0.1–0.6**	**0.2***	**0.1–0.7**	0.5	0.1–3.1	1.4	0.5–4.3	–	–
Short grass[e]	87	1.1	0.5–2.4	0.8	0.3–2.8	2.1	0.5–9.7	0.0	0–>100	2.7	0.8–9.0	–	–
Arable[f]	104	0.9	0.4–2.3	0.3	0.1–1.3	0.7	0.1–4.5	0.1	0.0–2.9	3.0	0.7–12.6	–	–
In uncut and regrowing grass													
Field not cut in interval	450	1.0		1.0		1.0		1.0		1.0		–	–
Field cut in interval	28	1.1	0.3–3.8	1.6	0.3–8.3	4.6[†]	0.8–27.8	0.1	0–>100	1.4	0.2–12.9	–	–

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$

Hazard ratios (HR) are given relative to the site- and age-specific mortality risk in uncut grasslands (baseline hazard), with 95% confidence limits (CI). Ratios significantly different from 1 are given in bold. n is the total number of intervals (≤2 days in godwits, ≤3 days in lapwings) for each type

a Grassland not yet cut or grazed in the present year; vegetation usually ≥15–20 cm high

b Grassland previously cut or grazed; vegetation regrown to ≥15–20 cm

c Recently (≤3 weeks ago) cut grassland with strips of tall vegetation; usually 2- to 10-m-wide strip left uncut

d Currently grazed grassland; vegetation height dependent on time grazed

e Recently cut or grazed grassland where regrowing vegetation has not yet reached 15–20 cm

f Diverse arable crops, including maize fields within grassland areas

Table 4 Hazard ratios for different causes of death, for a reduction in the body condition index of chicks from 1 (baseline hazard) to 0.6 (a very poor condition; Fig. 1)

Hazard type	Black-tailed Godwit (n = 554)			Northern Lapwing (n = 825)		
	HR	95% CI	P value	HR	95% CI	P value
All mortality (dead and missing)	3.0	1.6–5.6	<0.01	1.1	0.7–1.6	0.67
All except starvation/illness	1.9	1.0–3.8	0.06	1.0	0.7–1.5	0.99
Predation (total)	1.0	0.4–2.7	0.99	0.9	0.5–1.7	0.86
Predation (bird)	0.8	0.2–3.5	0.82	0.7	0.3–1.5	0.40
Predation (mammal)	2.7	0.4–16.0	0.29	1.4	0.2–8.1	0.70
'Missing'	2.1	0.7–6.2	0.17	0.8	0.5–1.5	0.56
Other (including starvation)	219.6	12.5–3872	<0.01	20.5	3.6–116	<0.01

Hazard ratios (HR) are given with 95% confidence limits (CI) and P values indicating whether they differ significantly from 1. Models for agricultural losses did not converge

siblings, as in the godwits, but a study in the UK did observe that poor condition induced by repeated handling reduced the survival of lapwing chicks (F. Sharpe et al., unpublished). Other studies have generally not found adverse effects of back- or leg-mounted tags in chicks of shorebirds and gamebirds (Kenward et al. 1993; Whittingham et al. 1999; Grant 2002). Nevertheless, there may be effects of telemetry studies that cannot be detected by within-brood comparisons. For example, the effects of repeated disturbance during the tracking of broods will affect both tagged and tagless chicks equally.

Notwithstanding these potential problems, radio-tagging provides the only feasible method to study causes of death of chicks. In our study, 6–9% of observed deaths could not be attributed to a cause, and 23% of all chicks disappeared without a trace. The contribution of different mortality factors may well differ between 'missing' chicks and those found dead. Indeed, it is even uncertain whether 'missing' chicks died or survived with a failed tag or after moving out of the search area. The resulting minimum and maximum estimates of chick survival lay so far apart (Fig. 2) that estimating reproductive success from tagging chicks would be problematic without additional information. In the Black-tailed Godwit and in Eurasian Curlew *Numenius arquata* studied by Grant (2002), the additional tagging of one parent greatly enhanced the interpretation of the chicks' fate and the precision of survival estimates. None of the 'missing' chicks of tagged godwits survived to fledging. As tagged parents are easier to relocate than tagged chicks and as mortality seemed especially high in 2005, this result may not hold for all missing chicks, but it is very likely that most signal losses reflected chick deaths. Transmitters may have been destroyed by mowing and harvesting machinery or buried in silage stacks (signals are lost when buried >1.5 m deep, unpublished observations), but as the probability that a chick ended up 'missing' was not higher if the field in which it stayed was cut during the

observation interval, this is unlikely to have occurred frequently. Some signals may have been lost when chicks drowned, but as most ditches in our study areas were shallow, this was probably not a major cause of signal loss either. It is highly probable that most 'missing' transmitters were destroyed by predators or carried out of the search range to distant sites or deep burrows.

In bird species where parents stay with the brood until fledging, we recommend tagging both chicks and parents to study details of chick mortality, including causes of death. If the primary aim is to quantify breeding success or brood movements, we prefer tagging parents only as it makes tracking less time-consuming and minimises negative effects on chicks.

Identifying predators

No less than 15 species were identified as chick predators in this study, with Common Buzzard, Grey Heron and stoat/weasel recorded the most frequently. The large fraction of unidentified causes of death calls for caution in interpreting the importance of different species, as some may leave more readily identifiable remains than others. Red foxes might be particularly likely to bury or destroy transmitters, but in two of our study sites where foxes were known to be absent neither the fraction lost to unknown causes (30 vs. 39%, $\chi^2_1 = 0.92$, $P = 0.34$) nor the share of mammals in known predations (41 vs. 26%, $\chi^2_1 = 2.61$, $P = 0.11$) were lower than in the eight sites where foxes were present. This makes it unlikely that foxes were responsible for the majority of unexplained losses. Stoats and weasels also bury chicks underground (often in European Mole *Talpa europaea* tunnels), but in several cases where we located such caches, we could pick up the signals from distances up to 50–100 m. Nevertheless, buried tags are less easily located than tags under raptor nests or plucking trees, and we may have missed those buried deep.

However, such bias would have to be strong to fully explain the large share of avian predators in chick predation. This contrasts with predation on shorebird eggs, where mammals, particularly Red Foxes, usually take a larger share (Langgemach and Bellebaum 2005; Bolton et al. 2007; Teunissen et al. 2006).

The greater contribution of stoats and smaller share of herons in the predation of godwit than lapwing chicks (Table 3) is probably associated with vegetation preferences. Stoats do not usually hunt and are less likely to approach chicks unnoticed in the short (cut and grazed) swards preferred by lapwing chicks, but herons often forage in short (cut) grassland swards (unpublished observation).

Disentangling the roles of predation and agriculture

Chick survival rates observed in this study are low compared to previously published estimates, both for Black-tailed Godwits (7 vs. 9–46%; Beintema 1995; Ratcliffe et al. 2005; Schekkerman et al. 2008) and Northern Lapwings (14 vs. 7–50%; Galbraith 1988; Baines 1990; Beintema 1995). Predation was the most frequent direct cause of death; we estimate that 70–85% of all lost chicks were taken by predators, 5–10% were mowing victims and 10–20% died of other causes. However, mowing losses may have been underrecorded, as in 2004 the first grass cut was already underway in some sites before we tagged most chicks. Also, in the four godwit AES sites, grassland use included measures aimed at avoiding chick losses. Mowing losses tended to be lower in AES sites than in controls, but the difference was not significant (5 vs. 11%, Schekkerman et al. 2008). Finally, mowing victims may have been removed by scavengers, and as we could rarely deduce this from the remains, these would have been recorded as predated. Avian predators regularly foraged among the cut grass on recently mown fields. If many dead or injured chicks were taken here, not only a chick's probability to be found as a mowing victim but also its probability to be found 'predated' should be higher if its field of residence was cut during the interval between observations than if it was not. Although predation hazard ratios tended to be greater than 1 if the field was cut, the effect was significant only for 1-day intervals in godwits. Scavenging probably occurs mainly on the first day after mowing, and its effect may be diluted by 'true' predation over longer observation intervals. Although some chicks may thus have been removed from cut fields by predators, their number was probably smaller than that of identified mowing victims, otherwise a clearer effect on predation hazard would be expected.

Predation may be enhanced by farming practice through changes in the vulnerability of prey to predators. Godwit chicks were two- to threefold more likely to be killed by a (avian) predator if they stayed in recently cut or grazed fields than in uncut grasslands, which form their preferred habitat (Table 3). The small chicks are less visible here, while the detection of predators is taken care of by the larger parents. Hence, godwit broods that are forced to forage in or frequently travel through cut fields due to a scarcity of uncut grassland are more likely to suffer predation losses. By multiplying the observed average daily survival rate with the field-type-specific hazard ratio divided by the average of the hazard ratios for all field types weighted according to their frequency of use (Table 3), 2.7% of chicks instead of the observed 7.2% are predicted to fledge if broods had to stay in short-sward grasslands throughout. Survival would increase to 8.7% if broods stayed in uncut fields continuously. Field use can thus induce a more than threefold change in predation rate, but this interaction effect does not explain why godwit chicks survived poorly in all field types in our study. Nevertheless, overall survival of Black-tailed Godwit chicks increases with the availability of tall (not cut or grazed or sufficiently regrown) grassland swards during their prefledging period (Schekkerman and Müskens 2000; Schekkerman et al. 2008).

Predation on lapwing chicks was not reduced on uncut fields. Their earlier hatch dates, (causing fields to have shorter swards when visited by lapwings than by godwits) and the fact that within uncut fields lapwing chicks will feed in patches with less vegetation may contribute to this. Lapwings prefer short swards, including grazed fields where they ran a significantly lower predation risk that was also observed (but was not significant) in godwits. It is possible that some predator species, including herons and stoats, avoid foraging in fields with livestock.

The importance of predation may be overestimated if it selectively affects individuals with already reduced survival prospects (e.g. Swennen 1989). Might predation represent the final elimination of shorebird chicks that lag behind in growth because of suboptimal feeding conditions? Godwit growth in our study was retarded in comparison to measurements from the 1980s (Beintema and Visser 1989), and this may reflect a deteriorated food supply due to agricultural intensification (Schekkerman and Beintema 2007). In both godwit and Lapwing chicks, the likelihood to be found starved increased with declining body condition, but other hazards increased only in godwit chicks, where the probability to end up 'missing' was elevated rather than that of predation. This is unexpected given our interpretation that most 'missing' chicks were depredated. Modifying daily survival rates by the estimated hazard ratio predicts that average chick survival would increase to just 11% in godwits at a mean body condition of 1 instead of the observed 0.89. In lapwing chicks, the

condition had no significant effect on deaths other than by starvation and did not affect overall mortality rate. This suggests that predators did not strongly select chicks in poor condition, but it cannot be excluded that chicks experiencing food shortage extend their foraging activity or take more risks and are eliminated even before their condition is visibly affected. A poor condition did increase predation on lapwing chicks in a similar study in the UK (F. Sharpe et al., unpublished).

Conservation implications

Our results indicate that predation on godwit chicks is increased up to threefold by intensive agricultural grassland use through a reduced availability of fields with protective cover, and possibly also by a reduction of food availability, leading to poor body condition or risky foraging behaviour. Cutting fewer grasslands early will therefore reduce predation losses in addition to direct losses due to mowing and starvation. However, these interactions between predation and agriculture explained only part of the high predation rate observed in godwit chicks and none in lapwing chicks. Some frequent chick predators have increased notably in numbers in the wet grassland regions of the Netherlands. Common Buzzards were absent here until the 1980s, but they now occur nearly everywhere (SOVON 2002). Goshawk, sparrowhawk, White stork, Carrion crow, gulls and Red Fox have also increased. These increases partly represent a return to natural population levels after historical reduction by human persecution and pollution, but it is greatly enhanced by man-made changes opening up formerly unsuitable landscapes to several of these species. Though Grey Heron has been common throughout and stoat and weasel have declined, overall predator abundance has probably increased. Simultaneously, changes in farming practice have made grassland birds more vulnerable to predation through the interactions described here and by reducing—via breeding density—the ability of meadowbirds to cooperatively evict potential predators (Green et al. 1990). Over the past 20 years, prefledging survival of Black-tailed Godwit chicks has declined significantly in the Netherlands (Schekkerman et al. 2008). Little historical data are available on the mortality of lapwing chicks, which are less sensitive to changes in grassland cutting regimes. Between 1990 and 2000, lapwings declined less rapidly in the Netherlands than Black-tailed Godwits (−0.5 vs. −1.9% per year), but since 2000 the population has shown an annual 3.4% decline that approaches that of godwits (−5.6%; Teunissen 2007). It is possible that the recent acceleration in the declines of both species shows the additive effect of increased predation on top of that of ongoing agricultural intensification.

An increasing predation pressure makes conservation measures to counteract negative effects of modern farming even more urgent than before. 'Shallow' measures that worked 30 years ago may no longer suffice to raise meadowbird breeding productivity to a level that can sustain the population. Control of predation is a complex matter scientifically, ethically and practically, and requires careful consideration of all available options (Bolton et al. 2007). There is much to gain by considering effects on predation risk in the development of practical conservation measures and in concentrating these in areas with optimal external preconditions, including a landscape structure that does not sustain high predator densities or in areas where such conditions can be created.

Zusammenfassung

Kükensterblichkeit von Uferschnepfe Limosa limosa und Kiebitz Vanellus vanellus im Feuchtgrünland: Einfluss von Prädation und Landwirtschaft

Watvögel, die im Grünland brüten, nehmen aufgrund eines Rückgangs im Reproduktionserfolg nach Intensivierung der Landwirtschaft weiträumig ab. Außerdem besteht Grund zur Annahme, dass ein Anstieg in der Prädation zu einer weiteren Abnahme führt, oder eine Bestandserholung unmöglich macht. Prädation selbst wiederum könnte von der Landwirtschaft durch Veränderungen in Lebensraum oder Nahrungsverfügbarkeit verstärkt werden, aber über die Mortalität nestflüchtender Watvogelküken ist nur wenig bekannt. Wir untersuchten die Mortalität von Uferschnepfen- und Kiebitzküken, indem wir 662 Küken an 15 landwirtschaftlich genutzten Standorten in Holland telemetrierten. Bearbeitung und Besenderung hatten keinen Einfluss auf die Kondition und die Überlebensrate der Uferschnepfenküken, aber die Körperkondition der Kiebitzküken, die einen Sender länger als drei Tage trugen, war um 6–11% verringert. Bei beiden Arten betrug die Ausfliegerate 0–24%. Bei jungen Küken war die Mortalität am höchsten, blieb aber bis nach dem Ausfliegen erheblich. 70–85% aller Verluste gingen auf das Konto von Beutegreifern (15 Arten, überwiegend Vögel), mindestens 5–10% waren auf eine Mahd zurückzuführen und 10–20% hatten andere Ursachen, wie Einschluss in Gräben und Verhungern. Küken auf Flächen, die vor der nächsten telemetrischen Erfassung gemäht worden waren, wurden viel häufiger als Mahdopfer wieder gefunden und etwas häufiger in der Form von Beuteresten, als Küken auf ungemähten Flächen. Demnach finden sich unter den Prädationsereignissen in geringem Maße auch Fälle, in denen bereits tote Küken gefressen wurden. Für Uferschnepfenküken war die Prädationsgefahr auf kurz

zuvor gemähten oder beweideten Flächen höher, als im bevorzugten hohen, ungeschnittenen Grasland. Für Kiebitzküken war das Prädationsrisiko auf beweideten Flächen am geringsten. Eine schlechte körperliche Verfassung erhöhte bei den Uferschnepfen die Sterblichkeit nicht nur durch Verhungern, sondern auch durch andere Ursachen. Demnach erhöhte eine intensivierte Landwirtschaft die Prädation der Uferschnepfenküken aufgrund einer Abnahme an verfügbarer Deckung, verstärkt durch eine verschlechterte Körperkondition, möglicherweise aufgrund von Problemen in der Nahrungsverfügbarkeit. Änderungen in der Bewirtschaftungspraktik könnten folglich dazu beitragen, den Prädationsdruck zu verringern, wenngleich die festgestellten Zusammenhänge die hohe Prädationsrate bei den Uferschnepfen nur zum Teil und bei den Kiebitzen überhaupt nicht erklären. In Holland hat die Häufigkeit von Beutegreifern in Gebieten mit Feuchtgrünland zugenommen, und die Kükenprädation ist zu einem wichtigen Faktor geworden, der bei der Planung von Schutzmaßnahmen bezüglich Art und Ort berücksichtigt werden sollte.

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