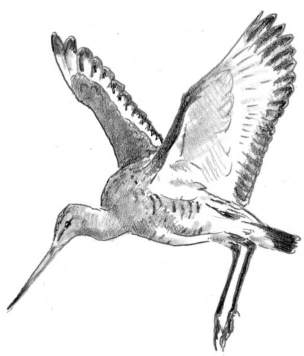
The effect of different mammalian predator management regimes on the reproductive success of Black-tailed Godwits *Limosa limosa limosa*

A.H. Jelle Loonstra[1,*], Nadja Hofmann[2], Bettina Hönisch[2], Johannes Melter[2], Marcel Holy[3], Christiaan Both[4] & Heinrich Belting[5]



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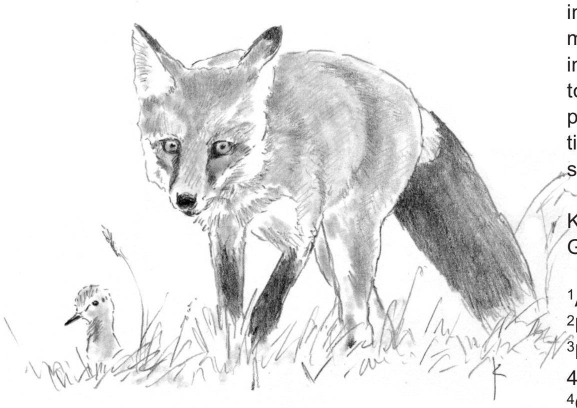
Grassland breeding waders are in strong decline in most agricultural habitats across Western Europe. Studies evidencing the negative effects of agricultural practices on wader populations are numerous, but even in most specially managed areas the decline cannot be reversed. Earlier studies have shown that predation of nests and chicks occurs frequent, and that current predator densities can add to the decline and/or prevent recovery. In this study we experimentally study the effect of different intensities of predator control of Red Fox *Vulpus vulpes*, Beech Marten *Martes foina*, Badger *Meles meles*, Pine Marten *Martes martes*, Polecat *Mustela putorius*, Stoat *Mustela erminea*, Raccoon *Procyon lotor* and Raccoon Dog *Nyctereutes procyonoides* on nest predation and chick survival of the Black-tailed Godwit *Limosa l. limosa* at lake Dümmer, Lower Saxony, Germany. The area was subdivided in two subareas (Ochsenmoor and Osterfeiner Moor), between 2009–2017 343 nests were monitored. Normal predator control was implemented in both subareas in 2009 and 2010; during these years nest survival was low. From 2011 until 2017 intensified year-round predator control was implemented in Ochsenmoor and from 2016 also in Osterfeiner Moor. From 2011 until 2015 nest survival was relatively higher in the subarea with intensified predator control (Ochsenmoor). In 2016 and 2017 predators were intensively controlled in both subareas and nest survival was similarly high in both. From 2009 until 2017 chick survival was measured using radiotelemetry on 243 chicks. Generally, we found that in the subarea with intensified predator control, chick survival was higher. Combining the estimates of nest and chick survival, we estimate that godwit pairs raised between 0.97–1.12 fledglings per season under an intensive predator control regime and only 0.09–0.18 fledglings when predators were hunted at a normal level. As godwit pairs need to produce around 0.6 fledglings per year to sustain their population, the intensified predator control in this study-area has contributed to the recent increase in the breeding population. Our results thus show that the impact of mammalian predators on the breeding productivity of godwits can be reduced by intensified predator control. The intensified control of the targeted ground predators in this subarea could have resulted in increasing densities of unhunted predators, which subsequently could reduce nest or chick survival. Within the timespan of this experimental study, we did not observe a decrease in nest/chick survival that could hint at this meso-predator release.



Key words: chick survival, nest survival, predator management, Black-tailed Godwit

[1]Altenburg and Wymenga Ecological Consultancy, Feanwâlden, The Netherlands;
[2]Bio-Consult, DulingsBreite 6-10, 49191 Belm, Germany;
[3]Natur- und Umweltschutzvereinigung Dümmer e.V., Am Ochsenmoor 52, 49448 Hüde, Germany;
[4]Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands;
[5]Staatliche Vogelschutzwarte - Naturschutzstation Dümmer, Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz Am Ochsenmoor 52, 49448 Hüde, Germany;
*corresponding author (j.loonstra@altwym.nl)

In the past decades, the loss and degradation of breeding habitat across Western Europe has resulted in strong population declines and breeding range contractions of many ground-nesting bird species (Birdlife International 2017, Newton 2004, Thorup 2006, PEBCBMS 2020). In particular for grassland breeding waders, intensification of agricultural practices like the improved drainage of grasslands and increased use of fertilizers caused a number of major changes (e.g. increase in mowing frequency, productivity of grass and advancement of phenology) in their breeding habitat that resulted in a sharp decline in productivity (Vickery *et al.* 2001, Devereux *et al.* 2004, Newton 2004, 2017, Donald *et al.* 2006, Butler *et al.* 2010, Kentie *et al.* 2018, Loonstra *et al.* 2019). As a result, the population size of for example Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa l. limosa* have diminished and their breeding distribution is now restricted to reserves and fields that are managed with agri-environmental schemes (Kentie *et al.* 2016, PEBCBMS 2020, Plard *et al.* 2020).

Despite all the conservation efforts that have been implemented to increase the productivity of grassland breeding waders through habitat improvements in their current breeding range, empirical evidence shows that most populations are still declining at an alarming rate (Kentie *et al.* 2018, Plard *et al.* 2020, Verhoeven *et al.* 2021). Increasing evidence suggests that high levels of predation on grassland breeding wader nests and chicks are currently limiting population recovery (MacDonald & Bolton 2008, Roodbergen *et al.* 2012, Mason *et al.* 2018, Verhoeven *et al.* 2021). As the effect of anti-predator behaviour in diminished and fragmented populations of semi-colonially breeding waders is becoming less strong, the decline is further accelerated (Elliot 1985, Seymour *et al.* 2003). In addition, evidence suggests that the same changes in land-use management that negatively impacted the breeding habitat of grassland breeding waders, caused a positive effect on the population growth of predators and caused an increase in overlap of habitat usage which resulted in elevated predation levels (Evans 2004). Furthermore, it is becoming evident that a number of factors, including a decrease in hunting pressure, rabies vaccination, large scale drainage of wetlands and the increased colonization of urban areas by e.g. Red Foxes *Vulpes vulpes*, Badgers *Meles meles* and Beech Martens *Martes foina*, has resulted in higher population numbers of most predators (Sainsbury *et al.* 2019). The effect of predation on the reproductive rate of waders should thus be seen in the context of a strongly modified landscape. However, as conservation measures have failed to reverse the population decline of grassland breeding waders in Western Europe, the question arises whether short-term measures, such as the removal of predators or the creation of artificial barriers for ground predators, e.g. electric fences and semi-natural barriers like ditches, should be taken to prevent local populations from extinction.

The control of predators or the creation of artificial barriers for predators that are made to improve the breeding success of grassland breeding waders is often costly, socially controversial and potentially leading to changes in predator-predator interactions that could lead to an increase in predation rates by predator species that are not controlled (Bolton *et al.* 2007, Ellis-Felege *et al.* 2012, Malpas *et al.* 2013, Oppel *et al.* 2014, Roos *et al.* 2018). Documenting the effects of a certain anti-predator measure over a long time period are thus essential to be able to make better informed economic, ecological and ethical assessments. So far, only a few experimental studies exist that studied the role of lethal predator control on the nest and chick survival of ground breeding waders (Bolton *et al.* 2007, Fletcher *et al.* 2010, Bodey *et al.* 2011, Niemczynowicz *et al.* 2017). These studies find that predator control often has a positive effect on the nest survival of ground breeding waders in Western Europe (three out of five studies), however a direct effect on the trajectory of the population size is not always present or measured (one out of two studies; Jackson 2001, Bolton *et al.* 2007, Fletcher *et al.* 2010, Bodey *et al.* 2011, Niemczynowicz *et al.* 2017). While the lack of positive population response could be the result of indi-

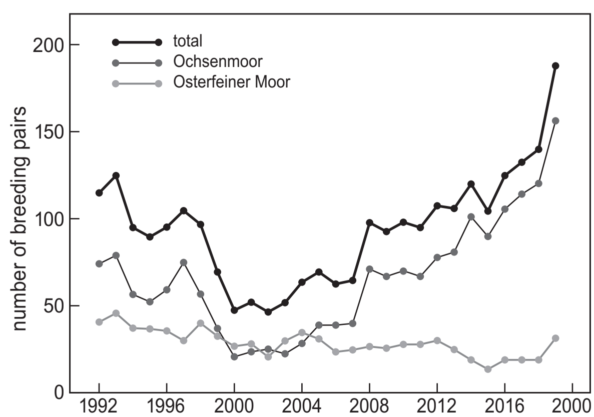


Figure 1. Number of breeding pairs of Black-tailed Godwits in the Dümmer area over the past three decades, based on atlas counts (data source: Datenbank Naturschutzstation und Naturschutzring Dümmer; see Belting *et al.* 2019). Note that in Ochsenmoor intensified predator control started in 2011, whereas in Osterfeiner Moor it started in 2016.

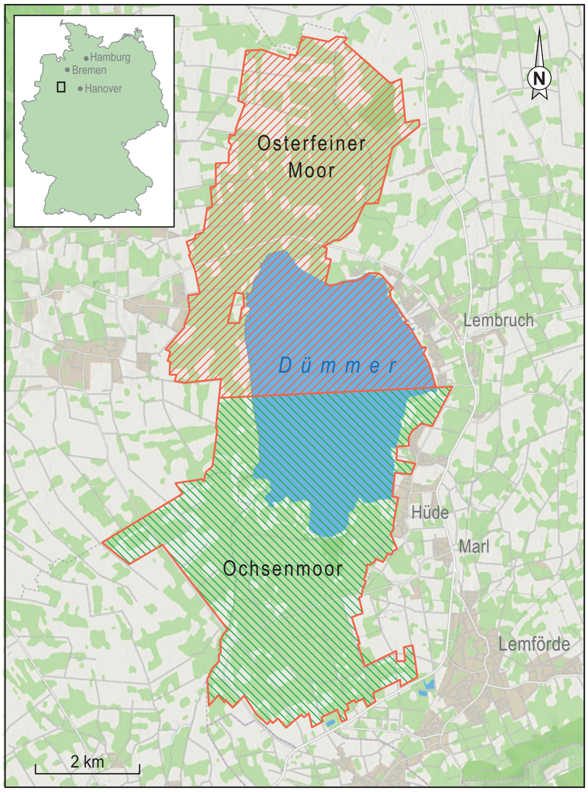


Figure 2. Map showing the study area in north-western Germany. The outlined green area is the subarea called Ochsenmoor and the outline red subarea is called Osterfeiner Moor. The inset displays the location of the study area within Germany.

viduals that emigrate to other areas, it is also possible that other population parameters, such as chick survival, are more important but have often not been measured. Thus, to be able to make a better ecological assessment of the influence of predator control on the productivity of grassland breeding waders, all relevant population parameters that influence the productivity of a population should be studied in the context of predator control.

The goal of this study was to evaluate the impact of intensified legal control of mammalian predators (Red Fox, Beech Marten, Badger, Pine Marten *Martes martes*, Polecat *Mustela putorius*, Stoat *Mustela erminea*, Raccoon *Procyon lotor* and Raccoon Dog *Nyctereutes procyonoides*) on the productivity (e.g. nest and chick survival) of breeding Black-tailed Godwits (hereafter godwits) within a meadow bird reserve in Germany (Dümmer, Lower Saxony). There was a severe decline of breeding godwits in this area until the end of the 1990s; but with the accomplishment of conservation measures including the rewetting of the area, the population of breeding godwits in the area increased until 2010 (Figure 1). Thereafter, empirical evidence suggests that nest and chick survival had decreased due to an increase in predation (Belting *et al.* 2019). To decrease predation and study the effect of predator control in this area, a predator control experiment was started in 2011 and continued until 2017. Because the area is divided by a large lake, we set up an experiment in which intensified predator control was implemented in both subareas but started in different years. First, we established nest and chick survival rates in both subareas in the absence of intensified predator control (2009–2010). Thereafter, intensified predator control was started in one subarea in 2011 (Ochsenmoor) while intensified predator control in the second subarea (Osterfeiner Moor) was implemented only from 2016 onwards. To evaluate the effect of predator control on the breeding productivity of godwits in this subarea, we monitored the effect on both nest and chick survival from 2009–2017 by intensively monitoring nests and following chicks with radio transmitters to accurately determine any changes in breeding productivity. In addition, this allowed us to quantify the relative effect of intensified predator control on nest and chick survival separately and estimate productivity with intensified predator management.

METHODS

Study area

The Dümmer area is a 'special protected area' (SPA) that consists of a large lake, marshes and grasslands in the south-west of Lower Saxony, Germany (52°30'N, 8°19'E). By rewetting formerly highly productive grasslands, this area of c. 2500 ha has turned into a well-managed nature reserve for ground breeding meadow birds (Figure 1, 2; Belting *et al.* 2019, Belting 2021). The reserve comprises two subareas that are separated by the lake Dümmer. The study area south of the Dümmer, which is named 'Ochsenmoor', covers approximately 1250 ha wet meadows (Figure 2). The other part of the Dümmer reserve is situated north of the lake Dümmer and is around 800 ha (Osterfeiner Moor). All fields are managed by the 'Niedersächsischer Landes betrieb für Wasserwirtschaft, Küsten- und Naturschutz' (Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency) for the benefit of breeding grassland breeding birds. To prevent the mechanical destruction of nests and chicks, mowing is only allowed after chicks have fledged. Furthermore, grazing by sheep and cattle is allowed on parcels without nests or when all nests have hatched and/or when the vegetation is becoming unsuitable for foraging chicks. High water tables with shallow floodings are maintained throughout the breeding season; as a result some parts are flooded until July.

Experimental study design

The predator management experiment covered the period 2009–2017 and consisted of two treatments: intensified predator control and regular predator control. During the years 2009 and 2010 there was year-round regular mammalian predator control in both subareas (occasional day and night shooting of mammalian predators by local hunters). From 2011 until 2017 intensified year-round predator control was implemented in Ochsenmoor and from 2016 onwards intensified year-round predator control was also implemented in Osterfeiner Moor (Table 1). With the implementation of this intensified predator control, not only the hunting effort increased, but also a large number of active traps were set in this subarea. All native and introduced mammalian predators underlying the Lower Saxony hunting legislation (Red Fox, Beech Marten, Badger, Pine Marten, Polecat, Stoat, Raccoon and Raccoon Dog) were controlled using legally sanctioned techniques. Besides day and night shooting, baited live traps made out of concrete pipes and additional cage traps were used to catch all mammalian predators. After catching individuals were shot. All concrete pipe and cage traps were equipped with trap monitors that immediately reported closed traps to the responsible hunters. For efficient Stoat trapping the hunting legislation allows special live traps that cannot be equipped with trap monitors, thus Stoat trapping was less intensive than trapping for all other mammals. In addition, a frequent control of known Red Fox dens and other potential settling sites of mammalian predators took place to remove cubs and adults. Legally protected predators, Weasels *Mustela nivalis* and European Hedgehogs *Erinaceus europaeus*, that occurred in the study area were not killed nor disturbed and released from the traps. There was no hunting of avian raptor or corvid species.

Table 1. Study design and sample size of monitored nests and chicks: area-year combinations with normal predator control (normal) and area-years with intensified predator control (bold).

	Osterfeiner Moor		Ochsenmoor	
	Nests (*n*)	Chicks (*n*)	Nests (*n*)	Chicks (*n*)
2009	–	–	44	20
2010	23	19	36	6
2011	15	4	**19**	**30**
2012	11	14	**20**	**16**
2013	11	–	**22**	**21**
2014	9	–	**19**	**34**
2015	18	17	**16**	–
2016	**15**	**33**	**21**	–
2017	**18**	**29**	**22**	–

Nest and chick monitoring

To evaluate the effect of predator management intensity on the nest and chick survival of breeding godwits, we monitored godwits in the Ochsenmoor and Osterfeiner Moor from 2009 until 2017. Starting from the end of March until the beginning of June in every season, we began to locate nests by observing godwits that showed nesting behaviour. Upon finding a nest, we took GPS locations of each nest, counted the number of eggs and used the egg flotation method to age eggs (Liebezeit *et al.* 2007) and marked each nest with a small stick placed on average 3 m from the nest.

We then observed each nest from a distance (every 5–10 days): if a nest was not occupied or was close to hatching, we re-visited it to determine the fate of each individual nest.

To quantify the survival of individual godwit chicks we outfitted two to four freshly hatched chicks from a nest with a 0.8-g radio-transmitter (Biotrack, Dorset, UK). These transmitters had a lifespan of at least 30 days. After removing a small piece of down, the transmitters were glued on the back of a chick using skin glue (Skin Bond, Smith & Nephew, UK, Permatyp company, US or Copydex, Pritt, UK). The total weight did not exceed 3% of the weight of an individual chick. After release, we relocated the chicks every 1–3 days using a Yagi-antenna (VR-500; Yeasu Germany GmbH) and a directional HB9CV antenna. Because of the growing feathers and risk of transmitter loss, we recaptured chicks between 8–12 days to re-glue the transmitter and to outfit each chick with a unique combination of colour rings. Relocations ended when a chick fledged, when a transmitter was found after the chick died, when a transmitter was found in the field or when we lost contact after six days. To find missing transmitters we extended our search beyond the core research area and visited known burrows of Red Foxes and nests of birds of prey to relocate potentially predated chicks. Throughout the years we maintained the same searching intensity.

Following a set of rules, we determined whether a chick was predated, had died (from starvation or other causes), fledged or lost the transmitter. If the transmitter was found in a burrow or nest of a predator or at a known plucking site, or if we found tooth marks on the transmitter or body, we assumed that a chick had been predated. If a chick was found dead without any sign of predation, we assumed that the chick had died due to other causes. If the transmitter signal stopped before the fledging date and we lost contact with all other chicks of the same family, we assumed the chick had died as well, otherwise we assumed a transmitter loss. Since the first chick in our study area was able to fly at an age of 24 days, we assumed all chicks to have fledged when they were 24 days old.

Nest survival analysis

We estimated daily nest survival (Mayfield 1961, Dinsmore *et al.* 2002) in the program MARK, using the RMark package (Laake 2013) in R (v. 4.0.3; R Core Team 2020). The nest survival model in this package enabled us to calculate estimates of the daily nest survival rate and incorporate predictor variables using a logit-link function. To calculate the nest survival of the most parsimonious model, we used the daily survival rate of this model to the power of the length of the incubation period (28 days). Besides predator management, other factors could cause variation in daily nest survival. Therefore, we included an effect of subarea (Ochsenmoor or Osterfeiner Moor), year, date and a quadratic effect of date. Competing models were all combinations of these factors, including all possible two-way interactions, models that considered only one of these factors, and a null model that assumed a constant effect. Models were ranked and selected according to their Akaike Information Criterion scores adjusted for small sample size (AIC_C; Burnham & Anderson 2002). The lowest model differing by < 2 AICc units from the second lowest and without uninformative parameters were considered the most parsimonious model. If no model was exclusive, we used model averaging to identify the most important predictor variable (Arnold 2010).

Chick survival analysis

Every year we lost contact with a number of chicks before the assumed fledging date. Because this could have been caused by malfunctioning transmitters, we are unaware of the status of all tagged chicks at every sampling occasion and our data is therefore not suitable for a known-fate analysis. We therefore used nest survival models in the package RMark to estimate the daily survival rate of the chicks. The shortest period for which we followed a brood that fledged was 24 days, we therefore considered all broods to have fledged at an age of 24 days. Although there is considerable individual and brood variation in how long young godwits remain with their parents, we used this age to take into account the possibility that fledged chicks may leave the study area. We then used RMark to evaluate models in which daily survival rate varied between predator management (normal predator control vs. intensified predator control), subarea (Ochsenmoor or Osterfeiner Moor), chick age, year, date and a quadratic effect of date. Competing models were all combinations of these factors, including all possible two-way interactions, models that considered only one of these factors, and a null model that assumed a constant effect. The most parsimonious model was selected following the method described for the nest survival analysis.

Population productivity

To estimate the productivity of the breeding godwits in the Dümmer area we built a simple population matrix that incorporates the estimated nest and chick survival until day 24 of this study (Loonstra *et al.* 2019). Thereby we presumed an average clutch size of 3.7 eggs and assumed that every godwit produces a replacement clutch after the failure of a first clutch (Kentie *et al.* 2015, Verhoeven *et al.* 2020). We then calculated the average productivity expressed as the number of fledglings per pair.

RESULTS

Nest survival

In total we monitored 343 godwit nests across all years. The most common cause of nest failure across our study was predation (normal predator control: 67.7%, intensified predator control: 32.4%). Only 1.7% of the nests in years with intensified predator control were abandoned and 6.0% in years with normal predator control.

The most parsimonious nest-survival model included an effect of year, subarea and predator management (Table 2). This model indicated that the daily nest survival rate varied between years, varied between Ochsenmoor and Osterfeiner Moor and was higher when predators were controlled more intensively (Figure 3). Across the two years with normal predator control in Ochsenmoor, nests had an average hatching probability of 0.05 (95% CI: 0.01–0.12) while nests in years without intensified predator control in Osterfeiner Moor had a 0.12 (0.03–0.30) probability of hatching (Figure 3). When intensified predator control started, hatching success increased on average to 0.44 (0.21–0.64) over all years in Ochsenmoor and 0.62 (0.36–0.81) in Osterfeiner Moor (Figure 3). For all the five years with simultaneous intensified predator control in Ochsenmoor and normal control in Osterfeiner Moor, nest survival rates were higher in Ochsenmoor, and this difference disappeared (or was even reversed in 2016) after predators were equally controlled in both subareas.

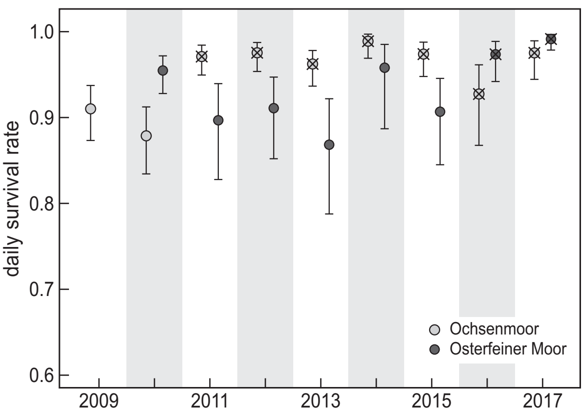


Figure 3. Daily nest survival rates estimated by the most parsimonious model for godwit nest survival during the study period, per subarea (see Table 2; year+Pman+area). White open dots are estimates for Ochsenmoor, black filled dots are the estimates for Osterfeiner Moor. Crossed dots indicate year-area combinations with intensified predator control.

Table 2. Model results examining effects of date (linear and quadratic), year, area and predator management (normal or intensified) on daily survival rates of Black-tailed Godwit nests. Models are listed in order from lowest to highest AICc values. We only show the models where the summed model weight is 0.95.

	Model	*K*	ΔAICc	Model weight	ΔDev
1	Year + Area + Pman	11	0.00[1]	0.19	15.71
2	Year : Area	18	0.05	0.18	1.58
3	Year + Area + Pman + Date	12	0.31	0.16	14.00
4	Year : Area + Date	19	0.54	0.14	0.05
5	Year : Area + Pman	19	2.08	0.07	1.58
6	Year + Area + Pman + Date^2	13	2.24	0.06	13.91
7	Year : Area + Date^2	20	2.53	0.05	0.10
8	Year : Area + Pman + Date	20	2.58	0.05	0.05
9	Year + Area : Pman	13	4.04	0.02	15.71
10	Year + Area : Pman + Date	14	4.34	0.02	13.98
11	Year : Area + Pman + Date^2	21	4.57	0.02	0.00[2]

Area: Ochsenmoor vs. Osterfeiner moor, Pman: predator management, normal predator control vs. intensified predator control, ':' indicates an interaction between effects, *K*: number of parameters, ΔDev: the Deviance relative to that of the model with the lowest Deviance, ΔAICc: AICc relative to best supported model (with the lowest AICc). [1]AICc = 640.89, [2]Deviance = 603.07.

Chick survival

Across all years we monitored the fate of 127 freshly hatched chicks (from 54 broods) in Ochsenmoor and 116 chicks (from 39 broods) in Osterfeiner Moor. The most parsimonious model explaining chick survival during the first 24 days included an effect of chick age and intensity of predator control (Table 3, Figure 4). Daily survival rates of all chicks showed a decrease over age and were significantly lower in years with normal predator control compared to the intensified control (Table 3). The most parsimonious model estimated that chicks hatched in years/subareas with intensified predator control had a 0.31 (95% CI: 0.17–0.45) probability of fledging, while chicks hatched in years/subareas with normal predator control had a 0.11 (0.04–0.22) probability of reaching the age of fledging (Figure 4).

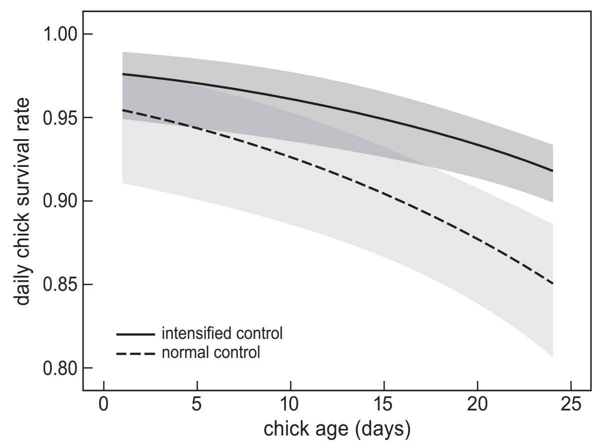


Figure 4. Daily survival rate of Black-tailed Godwit chicks as measured with radio-transmitters in years with intensified predator control and years with normal predator control in relation to chick age, as estimated from the most parsimonious model (see Table 3; Pman + Age). Shaded area show 95% confidence intervals.

Population productivity

Mean productivity (the number of expected fledglings per pair) in years with normal predator control was 0.09 (95% CI: 0.004–0.180) in the Ochsenmoor and 0.18 (95% CI = 0.007–0.380) in Osterfeiner Moor. In years with intensified predator control the number of fledglings per pair increased to 0.97 (0.23–1.42) in Ochsenmoor and 1.09 (0.35–1.60) in Osterfeiner Moor. The increase in productivity was mainly driven by the

Table 2. Model results examining effects of date (linear and quadratic), year, area, predator management (normal or intensified), its interactions and chick age effects on daily survival rates of Black-tailed Godwit chicks. Models are listed in order from lowest to highest AICc values. We only show the models where the summed model weight is 0.95.

	Model	*K*	ΔAICc	Model weight	ΔDev
1	Area + Pman + Chick Age : Date	4	0.00[1]	0.12	10.12
2	Pman + Chick Age	3	0.76	0.08	12.89
3	Area + Pman + Chick Age	4	1.13	0.07	11.25
4	Area + Pman : Chick Age + Date	5	1.22	0.06	9.33
5	Area + Pman : Chick Age	4	1.42	0.06	11.54
6	Area + Pman + Chick Age : Date^2	5	1.90	0.05	10.00
7	Area + Pman + Chick Age + Date	5	2.07	0.04	10.18
8	Pman : Chick Age + Date	4	2.27	0.04	12.39
9	Pman + Chick Age : Date	3	2.31	0.04	14.45
10	Pman + Chick Age : Date^2	4	2.34	0.04	12.46
11	Pman + Chick Age + Date	4	2.52	0.03	12.64
12	Area + Pman : Chick Age + Date^2	6	3.10	0.02	9.19
13	Area : Chick Age + Date	4	3.36	0.02	13.48
14	Area+ Pman + Chick Age + Date^2	6	3.69	0.02	9.77
15	Pman : Chick Age	3	3.90	0.02	16.03
16	Pman + Date	3	3.93	0.02	16.06
17	Date	2	4.07	0.02	18.21
18	Area + Date	3	4.12	0.02	16.25
19	Pman + Chick Age + Date^2	5	4.14	0.01	12.25
20	Pman : Chick Age + Date^2	5	4.15	0.01	12.25
21	Area : Date	3	4.19	0.01	16.32
22	Pman : Date	3	4.24	0.01	16.37
23	Area : Pman + Chick Age	6	4.29	0.01	10.38
24	Area + Pman + Date	4	4.51	0.01	14.63
25	Area + Chick Age : Date^2	4	4.58	0.01	14.70
26	Area + Chick Age + Date	4	4.75	0.01	14.87
27	Area + Pman : Date	4	4.86	0.01	14.98
28	Area : Chick Age + Date^2	5	5.06	0.01	13.17
29	Chick Age : Date^2	3	5.20	0.01	17.33
30	Chick Age + Date	3	5.36	0.01	17.49
31	Area + Chick Age : Date	3	5.57	0.01	17.70
32	Area : Pman + Chick Age + Date	7	5.62	0.01	9.69
33	Pman + Date^2	4	5.76	0.01	15.89
34	Date^2	3	5.85	0.01	17.98
35	Area + Date^2	4	5.93	0.01	16.05
36	Area : Date^2	4	6.06	0.01	16.18
37	Year : Area + Chick Age + Date^2	16	6.76	0.00	0.00

Area: Ochsenmoor vs. Osterfeiner Moor, Pman: predator management, normal predator control vs. intensified predator control, ':' indicates an interaction between effects, *K*: number of parameters, ΔDev: the Deviance relative to that of the model with the lowest Deviance, ΔAICc: AICc relative to best supported model (with the lowest AICc). [1]AICc = 662.48, [2]Deviance = 644.33.

strong effect of intensified predator control on nest-survival in both subareas (8.8 times higher in Osterfeiner Moor and 5.2 times higher in Ochsenmoor in years with intensified predator control; Figure 4). In addition, chick survival was three times higher in years with intensified predator control (Figure 4).

DISCUSSION

Our study shows that an intensification of year-round control of mammalian predators is linked with a significant increase in nest and chick survival of Black-tailed Godwits breeding in the Dümmer area. To maintain a stable breeding population of godwits, it has been estimated that each pair has to raise around 0.60 fledglings per year (Schekkerman & Müskens 2000). Without intensified year-round predator control of the target predators (but with normal predator control), godwits produced between 0.09–0.18 fledglings per pair which is much lower than the required number to maintain a stable population. Hence, in both subareas intensified predator control led to population productivity numbers that ultimately would lead to a growing population of breeding birds. Our findings thus support, but also contradict the conclusions from previous studies on the effect of predator removal, which found clear effects of predator removal on nest-survival but not always on productivity, which also includes chick survival (Jackson 2001, Bolton *et al.* 2007, Fletcher *et al.* 2010, Bodey *et al.* 2011, Niemczynowicz *et al.* 2017). A possible reason for this apparent discrepancy might be that of the two studies that monitored the effect of predator management on population growth, both only counted the number of breeding individuals. However, it can be argued that the correlative link between the number of breeding individuals and predator management is likely to take a longer time than most studies and is also affected by other ecological processes, such as emigration of individuals to other areas.

To examine the effects of predator management, confirmation that effective trapping has occurred is clearly essential (Bolton *et al.* 2010). Unfortunately, we only have anecdotic evidence from unstandardized monitoring efforts and hunting bags that at least confirm the high number of yearly removals of predators in years with intensified predator control (M. Holy unpubl. data.). The yearly removal of predators thus seems to suggest that the yearly immigration of predators results in hunters maintaining a high hunting effort. This is an important message since most grassland breeding waders breed in restricted areas like the Dümmersee area where predators can immigrate into the area. When predator control is applied it is thus of importance to maintain these measures for a long period and with a high intensity. In several of the years with intensified predator control, hunters removed multiple predator litters during the breeding season, while trail cams and night observations suggested that all target predators were removed at the start of the breeding season (M. Holy unpubl. data). In addition to the yearly removal of predators, managers thus also have to take notice of predators that immigrate into the area during the breeding season.

While the hunting intensification for almost all mammal species increased, we have to consider the meso-predator release hypothesis which postulates that a decrease in density of selected predators may cause an increase in the density in other predators, which may subsequently still keep predation rates high (Elmhagen & Rushton 2007, Ritchie & Johnson 2009). Potentially, increased densities of predators like Weasel, European Hedgehog or raptor species such as Common Buzzard Buteo buteo could have resulted in similarly low rates of nest and chick survival of ground breeding meadow birds when the other predators were culled. Unfortunately, we have not monitored the densities of these other predators and cannot test the effect of predator control over the course of this experiment on their population trends. However, nest survival varied between years with intensified predator control and additional field observations do suggest that part of the nest predation was caused by predators other than the target predators. We therefore cannot completely rule out that the intensified removal of most ground predators influenced the population trend of other nest or chick predators. Although the length and set-up of our study was too short to test effects of meso-predator release on smaller predators, it is clear that within the time frame of the current study the densities of these other predators did not increase to such an extent that nest survival of godwits was negatively affected. In fact, at the end of our experiment productivity was still above the required values for population stability.

Interestingly, we found that predator control had the largest relative effect on nest survival, which could be for a number of reasons. A first explanation is that the controlled mammals are more effective in predating nests than chicks, and as a result the removal of these predators will have a higher impact on nest survival (Schekkerman *et al.* 2008, Mason *et al.* 2018). Furthermore, in contrast to nest survival, chick survival is likely to be influenced by more factors than predation management alone. For instance, it is very well plausible that the condition of chicks or local weather circumstances can cause chicks to die directly or to take more risks in their search for food (Beintema & Visser 1989, Loonstra *et al.* 2018, 2019). Nonetheless, this interaction once again illustrates that all ecological conditions for the survival and fledging of godwit nest and chicks should be optimized when legal predator removal is implemented (Kentie *et al.* 2015).

This study uncovered some of the ecological effects on the population of godwits breeding in the Dümmer area after the implementation of intensive predator control. While nest and chick survival were far below sustainable levels before the intensification of predator control, this population turned into a source after this was implemented (Schekkerman & Müskens 2000, Kentie *et al.* 2015, Loonstra *et al.* 2019). However, different studies have found varying effects of predator control; therefore, we argue that our results might differ depending on the ecological context (Newton 1993, 2017). For instance, the base-line population levels of different predators can differ between areas and the effects of predator control are also likely to differ between areas due to the possibility of predator immigration (Bolton *et al.* 2007). Furthermore, the availability of alternative prey during and outside of the breeding season might differ between areas and will affect the population dynamics of the different predators (Laidlaw *et al.* 2019). We therefore argue to carefully implement and monitor the effect of predator control, since confounding effects might further accelerate the decline of a population.

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SAMENVATTING

In de meeste West-Europese landbouwgebieden staan weidevogels onder grote druk. Een belangrijke oorzaak hiervan zijn de negatieve effecten van de huidige landbouwmethoden op de overleving van nesten en uitgekomen kuikens. Maar zelfs in gebieden die speciaal voor weidevogels worden ingericht gaan de soorten vaak achteruit. Uit eerder onderzoek is gebleken dat predatie van eieren en kuikens door de huidige hoge predatordichtheid aan die achteruitgang bijdraagt en herstel van de populatie voorkomt. Wij hebben in 2009–2017 in twee deelgebieden in de Duitse deelstaat Nedersaksen de overleving van 343 nesten en van 243 kuikens (door middel van radiotelemetrie) van de Grutto *Limosa limosa* experimenteel onderzocht door in sommige jaren in één of beide deelgebieden bestrijding van acht grondpredatoren te intensiveren, en het voorplantingssucces van de Grutto in die gebieden en jaren te meten en te vergelijken met dat in jaren en gebieden waar de bestrijding van grondpredatoren niet was geïntensiveerd. In 2009 en 2010 werd in beide deelgebieden op de acht grondpredatoren slechts op beperkte schaal gejaagd. In beide jaren was de nestoverleving laag. In 2011–2015 was de nestoverleving in het deelgebied waar de bestrijding was geïntensiveerd, hoger dan in het deelgebied waar dit niet het geval was. In 2016 en 2017 werd de jacht op de grondpredatoren in beide deelgebieden geïntensiveerd. In beide gebieden was de nestoverleving hoog. In het algemeen was de kuikenoverleving hoger wanneer de jacht op de grondpredatoren was geïntensiveerd. Combinatie van nest- en kuikenoverleving leerde dat jaarlijks 0,97–1,12 jongen per paar werden grootgebracht wanneer de grondpredatoren intensief werden bestreden en 0,09–0,18 jong per paar wanneer dat niet had plaatsgevonden. Intensieve bestrijding van bepaalde predatoren zou een toename van andere predatoren tot gevolg kunnen hebben (met als gevolg een verhoging van nest- en kuikenverlies). Wij hebben daarvoor geen aanwijzingen gevonden, maar misschien was de onderzoekperiode daarvoor te kort.

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