



Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits *Limosa limosa*

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Effective conservation of endangered species requires a solid understanding of the demographic causes of population change. Bird populations breeding on agricultural grasslands have declined because their preferred habitat of herb-rich meadows has been replaced by grassland monocultures. The timing of agricultural activities in these monocultural grasslands is critical, as they often coincide with the nesting phase of breeding birds. Here, we aim to identify the effect of habitat management and targeted nest protection on nest survival of Black-tailed Godwits *Limosa limosa* in the Netherlands, a population that has shown a 70% reduction in breeding population size since the 1970s. To protect nests in monocultures from destruction, farmers are paid to either delay mowing or leave a patch of unmown grass around the nest, a patch which in practice varied in size. In herb-rich meadows, which are typically managed for bird conservation purposes, mowing occurs after hatching. Nest survival declined as the season advanced, more steeply on monocultures than on meadows. Targeted nest protection was only partially successful, as nest predation was considerably higher on mown grassland monocultures with small unmown patches around the nest than in mown monocultures with large unmown patches and in unmown fields. Increased predator densities over the years have been suggested as an important cause of the trend towards lower nest survival, but here we show that nest survival was higher on herb-rich meadows than on monocultures, and similar to the 1980s. It thus seems that increased predator densities are an increased threat during the egg stage only if habitat quality is low. High-quality habitat in the form of herb-rich meadows therefore provides a degree of protection against predators.

Keywords: agricultural intensification, facilitation, grassland management, mowing, nest survival, predation, shorebird.

Avian nest survival is an important demographic parameter that is influenced by a combination of species-specific life history traits and concurrent environmental conditions (Martin 1995, Grant & Shaffer 2012). In bird populations breeding on grasslands with intensive agricultural use, nest survival has declined (Kruk *et al.* 1997, Newton 2004, Roodbergen *et al.* 2012). Grassland birds tend to suffer high nest losses due to nest

destruction by agricultural activities (Kruk *et al.* 1997, Teunissen *et al.* 2008, Gruebler *et al.* 2012) and trampling by livestock (Beintema & Müskens 1987), and to higher predation rates (Evans 2004, Whittingham & Evans 2004) than birds breeding on land where agricultural use is less intensive. The higher predation rate may be caused by an increase in predator densities (Evans 2004, Roodbergen *et al.* 2012), but nests may also have become more vulnerable to predation because habitat quality has declined (Evans 2004).

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Table 1. Overview of grassland habitats, their management regimes, area managers and percentage of this habitat in our research area (7697 ha grassland), and across the Netherlands (932 000 ha grassland). Source: Netherlands Enterprise Agency (RVO) and Teunissen & van Paasen (2013).

Grassland habitat	Management regime	Manager	Research area (%)	The Netherlands (%) ^a
Herb-rich	No chemical pesticides, no liquid manure, no disturbance between 1 April and 15 June, no reseeding of fast-growing grass	Nature organizations	12	3
Herb-rich	No chemical pesticides, no liquid manure, no disturbance between 1 April and 15 June, no reseeding of fast-growing grass	Individual farmers	7	9
Herb-rich	Per clutch payment	Individual farmers	1	
Herb-rich	No management		2	
Monoculture	No chemical pesticides, no liquid manure, no disturbance between 1 April and 15 June, no reseeding of fast-growing grass	Nature organizations	1	
Monoculture	No disturbance between 1 April and 22 June	Individual farmers	4	2
Monoculture	Per clutch payment	Individual farmers	20	17
Monoculture	No management	Individual farmers	52	69

^aGrassland habitat is presumed, as there is no countrywide information on herb-richness, and we assumed grasslands without subsidized management for herb-richness to be monocultures.

Open ground-nesting waders are especially vulnerable to predation (MacDonald & Bolton 2008), to the extent that sandpipers show seasonal 'olfactory crypsis' to avoid detection during incubation (Reneerkens *et al.* 2005). Predation pressure may vary between habitats because of habitat-specific predator densities (e.g. Martin 1993) or because of variable nest concealment (Davis 2005). Furthermore, nest survival rates may vary temporally across the breeding season (Grant & Shaffer 2012). Predator pressure varies during the season as predators need to feed their young, incubating birds change their behaviour during the season, or growing vegetation alters nest cover.

The Netherlands hosts 85% of the breeding population of the East-Atlantic flyway population of Black-tailed Godwits *Limosa limosa limosa* (Thorup 2006). Despite a high level of public awareness and a suite of conservation measures (Kleijn *et al.* 2001, Verhulst *et al.* 2007), this grassland breeding wader species has shown a steady decline in the Netherlands, with a total loss of c. 70% since 1970 (van Dijk *et al.* 2010). This rapid population decline has led the IUCN to qualify Black-tailed Godwits as 'Near-Threatened' on the Global Red List of threatened species (Bird-Life International 2012). The two main explanations for this decline are habitat deterioration as a consequence of agricultural intensification, and increased predation rates on nests and chicks (Gill *et al.* 2007). Here, we assess whether these two processes have affected nest survival, and discuss

whether targeted conservation measures have been successful.

Black-tailed Godwits prefer to breed in grasslands that are herb-rich and have high water tables (meadows) (Groen *et al.* 2012, Kentie *et al.* 2014). Up to 50 years ago, wet herb-rich meadows were widespread in the Netherlands, but most agricultural grasslands have been transformed into grassland and maize monocultures intensively managed for maximum dairy production (Groen *et al.* 2012, Bos *et al.* 2013) (Table 1). Grassland monocultures are regularly reseeded with highly productive ryegrasses *Lolium* sp., and they are deeper drained and more heavily fertilized to facilitate earlier and more frequent mowing for the production of cattle feed (Kleijn *et al.* 2010, Musters *et al.* 2010, Schroeder *et al.* 2012). At present, mowing on these monocultures starts during the nesting phase of Godwits, compared with a century ago, when it was unlikely that any meadow was mown during the entire Godwit breeding season (Thijsse 1903). Thus, Godwit nests on monocultures, and nests of species of the associated bird community such as Northern Lapwings *Vanellus vanellus*, Redshanks *Tringa totanus* and Eurasian Oystercatcher *Haematopus ostralegus*, face the risk of being destroyed by machinery.

Targeted nest protection has been implemented to reduce losses due to mowing (agri-environmental schemes). Farmers receive payments for leaving nests undestroyed when the grass is mown, or for putting a metal frame over the nest to protect it

from trampling when the field is grazed, so that the intensive use of the agricultural land can continue (Verhulst *et al.* 2007). We observed large variation in the size of such unmown patches, which range from 1 to 150 m². Another protection measure that is less often implemented is delayed mowing of the whole field, for which farmers also receive compensation for lost income.

In addition to the risk caused by early mowing, Godwit nests may now be exposed to higher predation rates than in the past, as predator control has decreased (Gill *et al.* 2007), and Red Foxes *Vulpes vulpes* have colonized the lowlands of the Netherlands since 1990 (Mulder 1992). Indeed, in areas where predation is high, Red Foxes and Stoats *Mustela erminea* are important predators of wader nests (Teunissen *et al.* 2008). Moreover, agricultural intensification may have increased the accessibility of grasslands for predators (Evans 2004, Teunissen *et al.* 2008), reduced crypsis of the nests due to homogeneous swards amplified by early mowing, or changed the availability of alternative prey for predators. For instance, in an experiment in which the main nest predators (Feral Cat *Felis catus*) were removed from an agricultural area, nest success of St Helena Plovers *Charadrius sanctaehelenae* only showed a marginal increase, as increasing number of rats *Rattus* spp. became the important nest predator, whereas in natural areas, where rat numbers remained stable, the increase of nest success was much higher (Opper *et al.* 2014). Whether an interaction between higher predator numbers and agricultural intensification has influenced nest survival differently in the two habitats has not yet been explored for Godwits.

In this study, we were primarily interested in comparing daily nest survival rates of Godwits in their traditional breeding habitat, herb-rich meadows, and in the grassland monocultures that have largely replaced this traditional habitat. We first assessed whether there was a seasonal trend in daily nest survival rates, then evaluated the effectiveness of nest protection by comparing the success of nests in small or large patches of unmown grass with the success of nests in unmown fields. Finally, to put the estimated survival rates of nests on meadows and monocultures in a historical context, we compared current nest survival rates with those on meadows in 1980–83 (Beintema & Müskens 1987). This also enabled us to evaluate the possibility that increased densities of predators

such as the Red Fox are indeed responsible for reducing nest survival.

METHODS

Study area

From 2007 to 2012 we monitored 2030 nesting attempts of a partially colour-ringed population of Godwits in a 8480-ha area in southwest Friesland, the Netherlands (centre of study area: 52°57'N, 5°27'E). The study area consisted of wet, herb-rich meadows (20%), intensively managed grassland monocultures (69%) and arable fields (11%) (Groen *et al.* 2012). Meadows were mostly managed for bird or plant conservation (Table 1), meaning that the water table was relatively high (on average 25 cm below the surface), no herbicides or pesticides were used, fertilizer levels were lower and mowing was postponed until after 15 June, by which time most bird eggs would normally have hatched. Grassland monocultures consisted of fields with reseeded fast-growing rye grasses where water tables were kept at least 60 cm below the surface (Groen *et al.* 2012). Monocultures were mown during the nesting phase of the Godwits. Arable fields were mostly used for growing maize. We excluded the fates of 18 Godwit nests on arable fields.

Nest monitoring

Each year the study area was searched for Godwit nests during the entire breeding period from the start of April to mid-June by local volunteers and our own field team consisting of field assistants, students and volunteers (15 members per year). Nests were found by observing pairs of Godwits for nest-indicating behaviour and/or by walking the fields to flush incubating individuals. Nests found on monocultures were marked with sticks placed on average 5 m from the nest, a traditional way of indicating to farmers where a nest could be spared while mowing. On herb-rich meadows only about 10% of the nests were marked, as mowing there takes place after hatching. We took GPS locations of all nests and used the egg flotation method (Liebezeit *et al.* 2007) to age nests (estimated number of days since laying of first egg) and to predict laying date and hatching date (25 days after laying date, Beintema *et al.* (1995)).

Because visiting nests may potentially influence predation rates of ground-nesting birds in positive (Verboven *et al.* 2001) or negative ways (Ibáñez-Álamo *et al.* 2012), we revisited nests only on average 4 days before the predicted hatching date. If the eggs showed no sign of hatching (i.e. breaks or holes), we returned 2 days later, otherwise we returned the following day. We did not visit nests in the early morning (when we could have left a dew trail) or the 2 h preceding sunset (to prevent leaving a scent trail for nocturnal ground predators). We avoided trampling the vegetation around the nest and never put research materials on the ground next to the nest.

We considered a nest hatched if we found at least one chick in the nest, or if we found broken eggs without blood or yolk and membranes clearly visible, or tiny egg fragments in the bottom of the nest. A nest was considered unsuccessful when we found abandoned eggs, egg remains without membranes, or with yolk or blood (other than blood vessels in the membranes), an empty nest without any remains of eggs, or if we were unable to relocate a nest after a field was mown and the nest cup thus removed. Although a few nests were clearly repeat breeding attempts of birds that had lost their earlier nest, we were unable to correct for repeat nesting attempts because in most cases a pair's full nesting history was unknown. Godwits are precocial, and chicks leave the nest within about 24 h of hatching (Schekkerman & Boele 2009). From 2008 onwards, we recorded whether fields with visited nests were mown and, if so, whether the farmer left a small (< 5 m in diameter) or a large (> 5 m in diameter) area of unmown grass around a nest.

Data analysis

Not all nests were found immediately after the eggs were laid; some nests could have been predated before their discovery, which means that the proportion of successful nests would be an overestimate. Median nest age when found was 8 days (range: 0–25 days), with no difference between nests on meadows or monocultures (Kruskal–Wallis test: $\chi^2 = 0.11$, $df = 1$, $P > 0.5$). To account for this overestimation, we estimated daily nest survival rates (Mayfield 1961), which could vary for nest age, throughout the season, per year and per management type. Daily nest survival was modelled with the package RMark version 2.0.8 in

R 2.14.0 (R Development Core Team 2011), which uses the R interface to run nest survival models in the program MARK (White & Burnham 1999). When a nest is lost between two visits, MARK calculates the probability of survival for each day in between the visits with a likelihood function (Dinsmore *et al.* 2002). Because we usually returned to the nest at the end of the incubation period, eggs in unsuccessful nests that were found early in their incubation period would have a large interval in which they could have failed. We used simulated data to check whether long time-intervals between nest checks could have influenced outcomes, assuming that eggs were laid and found at random within the season, which yields nests with different observation periods. We found no evidence for biased outcomes due to our revisiting schedule (Supporting Information Appendix S1, R code given in Supporting Information Appendix S2).

In cases where nests were last visited after the eggs hatched, or in cases of unsuccessful nests that should have hatched eggs, we used predicted hatch date as the last check date. Nests with unknown fates were removed from the analysis ($n = 141$), as were nests with infertile and addled eggs that were incubated long beyond the predicted hatching date ($n = 24$). In MARK it is possible to include individual covariates with a logit link function. We tested for nest age effects, linear seasonal trends, quadratic seasonal trends, year effects and grassland management effects (meadows vs. monocultures). Nest age can have a large effect, as nests in locations most at risk will be predated at an earlier age (Klett & Johnson 1982, Grant *et al.* 2005), parent birds may defend their nest more vigorously later in the season (Smith & Wilson 2010), and predators have a higher likelihood of finding the nest as incubation age increases. Nests may also become more detectable with time as increased use may increase the scent and marks in the vegetation. We included linear or quadratic seasonal trends, to assess whether survival had a linear or bimodal pattern during the season. To avoid over-fitting of the data, we did not consider more complex seasonal trend models. Sample sizes are given in Table 2.

To limit the number of models and to prevent over-fitting, we used a hierarchical approach with a set of *a priori* models. We first examined the effects of nest age and grassland management on daily nest survival, and we assumed that effects of

Table 2. Number of nests used in the analyses across years. The totals of meadows and monocultures were used for modelling seasonal daily nest survival models. Discrepancies in sample sizes occurred because for some nests it was not noted whether the grass was mown.

Year	Meadows <i>n</i>	Monocultures <i>n</i>	Mowing (monocultures)			Historical dataset	
			Unmown	Large area	Small area	Year	<i>n</i>
2007	207	84				1980	315
2008	189	125	68	12	33	1981	348
2009	253	94	56	20	10	1982	346
2010	242	104	80	10	9	1983	442
2011	161	51	40	8	3		
2012	225	112	96	8	3		

nest age were independent of year. We continued to use these effects (if the model was supported, i.e. $\Delta AIC_c < 2$) in subsequent models when testing for year effects and linear seasonal trends and quadratic seasonal trends. Because years and seasonal trends may differ between meadows and monocultures, we also fitted interactions.

For the historical comparison, we reanalysed data on nest survival of 1451 nests monitored between 1980 and 1983 in the Dutch provinces North Holland ($n = 940$), South Holland ($n = 153$) and Friesland ($n = 358$) (Table 2), all of which data were from herb-rich meadows (A.J. Beintema pers. comm.). These nests had been marked with sticks placed inconspicuously in a nearby ditch, and were visited once or twice a week (Beintema & Müskens 1987). As we wanted a general comparison between nests from between 1980–1983 and 2007–2012, we excluded year and time in the season effects. Nest age was not measured in the historical dataset and was thus excluded as well. We assumed that nests in both datasets were found at similar ages, and that the relation of age to daily survival rate did not differ either. We combined both datasets and we compared nest survival of the categories *Meadows 1980–83*, *Meadows 2007–2012* and *Monocultures 2007–2012*, and compared this with the model where *Meadows 1980–83* and *Meadows 2007–2012* were combined, and to the model with the intercept only: three models in total.

Model selection of nest survival models was done with the second-order AIC (Akaike information criterion) for small samples (AIC_c) (Burnham & Anderson 2002). Because the candidate model set contained interactions, it was not possible to use model averaging in the interpretation of parameter estimates (Grueber *et al.* 2011). No

goodness-of-fit test for nest survival models is currently available (Dinsmore *et al.* 2002).

To evaluate the effectiveness of nest protection, we assessed whether the survival of nests on monocultures was affected by the size of the patch left unmown around the nest. If nests were rapidly predated after mowing, the effective sample size (number of days under observation) would become too small to separate daily survival rate into before and after mowing, and therefore this particular analysis could not be done in MARK. Instead, we considered mowing as an experimental treatment and analysed the differences of apparent nest success rates (successful nests divided by total nests). We compared four categories: nests on mown monocultures where a large patch of unmown grass was left around the nest, where a small patch of unmown grass was left around the nest, nests on monocultures which were unmown during the observation period, and nests on meadows (which were also unmown). For this analysis, we excluded nests around which all the grass was removed. Of this last group, two were destroyed during mowing, from three nests the eggs were taken out by the farmer or local volunteers during mowing and returned afterwards, of which one nest hatched successfully, and the remaining seven nests were either predated before mowing or destroyed. Sample sizes are shown in Table 2.

We used a generalized linear mixed model with a binomial error distribution and year as a random effect (package 'lme4' in Program R), and used likelihood-ratio tests (LRTs) for backward stepwise model selection. To account for the fact that nests found early during incubation would have a lower chance to survive until hatching than nests found later in the cycle, nest age at discovery was used as a covariate. We tested whether laying date, which

Table 3. Model results of the first selection step modelling daily nest survival of Black-tailed Godwit nests in 2007–2012, where we included grassland management (meadows or monocultures) and nest age effects.

Model	<i>k</i>	AIC _c	ΔAIC _c	<i>w_i</i>	Deviance
man + age	3	3520.49	0.00	1.00	3514.49
man	2	3537.96	17.47	0.00	3533.96
age	2	3551.78	31.29	0.00	3547.78
Intercept	1	3570.47	49.99	0.00	3568.47

age, nest age; *k*, number of parameters; man, grassland management; *w_i*, AIC_c weights.

was centralized by subtracting the yearly mean, and its interaction with the mowing category affected nest success. As the effect of laying date may differ between years, we verified that the model including laying date, as random slope, did not show a better fit than the model without this random slope (LRT: $\chi^2 = 5.80$, *df* = 2, *P* > 0.05). To assess whether mowing influenced birds to abandon their nests, we tested with a Pearson's chi-squared test whether unsuccessful nests in monocultures in unmown fields, and mown fields with a large or small patch around the nest, differed in the proportion of nests predated or abandoned. However, it was not possible to distinguish between a predated nest and a nest from which the eggs were taken away after it was abandoned. We referred to the outcomes of this analysis as 'nest success', and to the outcomes of the MARK analysis as 'nest survival'.

RESULTS

We used data from 1847 Godwit nests for the analyses, of which 69% occurred on herb-rich meadows. Of all nests, 676 (36%) did not hatch: 74% were predated, 20% were abandoned and in 6% of the cases the field was mown without us being able to relocate the nest. This would mean that either the nest was destroyed during mowing, or that it was predated before mowing.

Nest age, management effects and seasonal effects on nest survival

In the first model selection step, daily nest survival rate was best explained by both nest age and grassland management (Table 3). Nests with freshly laid eggs had a lower daily survival rate than nests later in the incubation stage, and nests in meadows

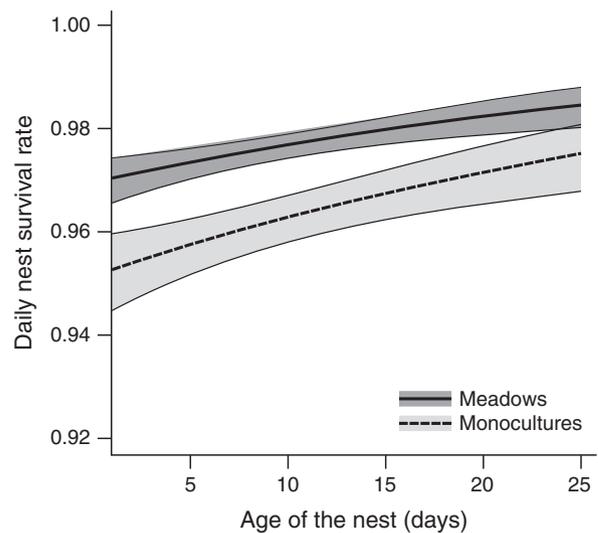


Figure 1. The effect of nest age on daily survival rates of Black-tailed Godwit nests in herb-rich meadows and grassland monocultures. Estimates are derived from the top model in Table 3.

had a higher daily survival rate than nests in monocultures (Fig. 1). In the subsequent model selection step, daily nest survival rate was best described with an annual effect and with a decline during the season that in most years was more pronounced for nests in monocultures, as indicated by the interaction of management * year (Table 4, Fig. 2). Table 5 shows the parameter estimates of the best model.

Comparison with 1980–83

Daily nest survival rates of nests in meadows in 1980–83 and nests in meadows in 2007–2012 were similar, and were higher than daily nest survival of nests on monocultures in 2007–2012 (Fig. 3). Merging the meadow nests from both periods into one category only changed the AIC_c by –0.25 relative to the original model (AIC_c 8083.10 vs. 8083.35 with one extra degree of freedom), emphasizing that the best support was for similar nest survival rates on meadows in both periods, and monocultures having lower survival (Burnham & Anderson 2002, Arnold 2010). There was little support for the intercept model (AIC_c = 8106.28).

Effect of mowing

Between 2008 and 2012, respectively 40, 35, 19, 22 and 10% of the 456 nests on monocultures

Table 4. Model results of examining effects of season (linear and quadratic), year, grassland management type (meadows or monocultures), its interactions and nest age effects on daily survival rates of Black-tailed Godwit nest from 2007 to 2012. We only show the models where the summed w_i is 0.95.

Model	k	AICc	Δ AICc	w_i	Deviance
man + age + year + S + man*year + man*S	15	3433.17	0.00	0.50	3403.15
man + age + year + S + man*year + man*S + year*S	20	3435.36	2.19	0.17	3395.32
man + age + year + SS + man*year + man*SS	17	3435.93	2.76	0.13	3401.91
man + age + year + S + man*year	14	3436.60	3.44	0.09	3408.59
man + age + year + S + man*year + year*S	19	3437.64	4.47	0.05	3399.60
man + age + year + SS + year*man	15	3438.28	5.11	0.04	3408.26

age, nest age; k , number of parameters; man, grassland management; S, seasonal effect; SS, quadratic seasonal effect ($S + S^2$); w_i , AICc weights. *Interaction.

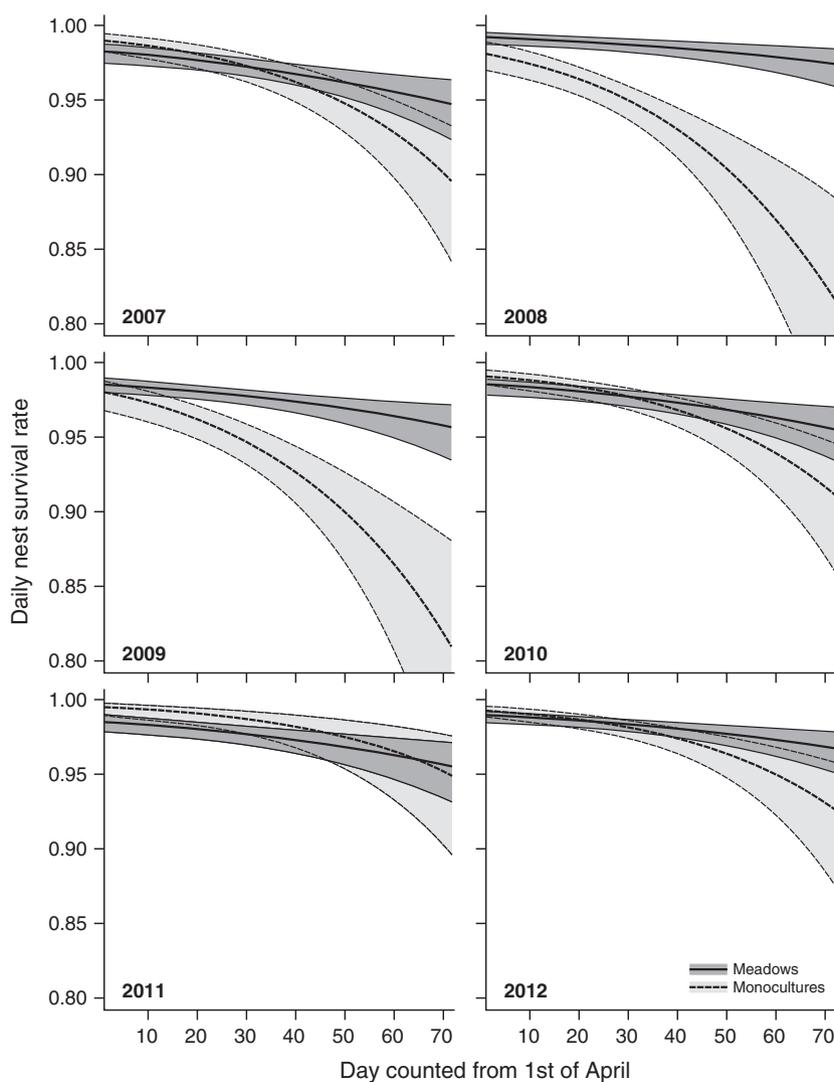


Figure 2. Estimated daily survival rate of Black-tailed Godwit nests for each year (2007–2012) separately in relation to season (day since 1 April) for nests on meadows and monocultures. Model selection results are presented in Table 4, and parameter estimates are presented in Table 5. The grey shadings are the 95% CI.

Table 5. Parameter estimates of the best model ($< 2 \Delta AIC_c$) on daily nest survival rate of nests in 2007–2012 (model selection results are in Table 4). Note that daily nest survival rate is estimated in logits.

	Model 1		
	Estimate	se	95% CI
Intercept	4.121	0.307	3.519–4.723
Management ^a	–0.573	0.361	–1.28 to 0.135
Nest age	0.043	0.008	0.027–0.058
Year ^b			
2008	–0.654	0.213	–1.071 to –0.237
2009	–0.698	0.219	–1.127 to –0.269
2010	0.197	0.229	–0.252 to 0.646
2011	0.782	0.361	0.074–1.489
2012	0.396	0.244	–0.081 to 0.874
Season	–0.034	0.006	–0.047 to –0.022
Management*year			
2008	1.426	0.288	0.861–1.99
2009	0.924	0.268	0.398–1.45
2010	0.007	0.278	–0.539 to 0.552
2011	–0.590	0.404	–1.381 to 0.201
2012	0.137	0.296	–0.444 to 0.718
Management*season	0.018	0.008	0.003–0.033

^aReference management is grassland monocultures. ^bReference year is 2007.

were on fields that were mown during the period of observation (Table 2). Nests on unmown meadows had a higher apparent success rate (% success-

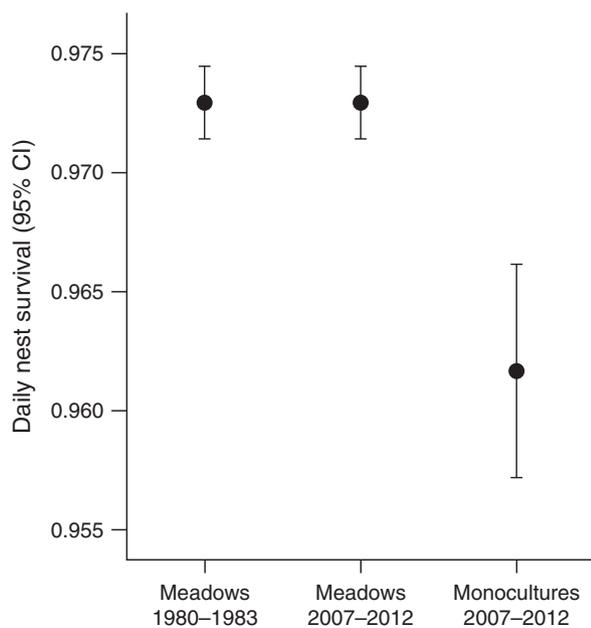


Figure 3. Daily nest survival of Black-tailed Godwit nests on meadows in 1980–83 and on meadows and monocultures in 2007–2012.

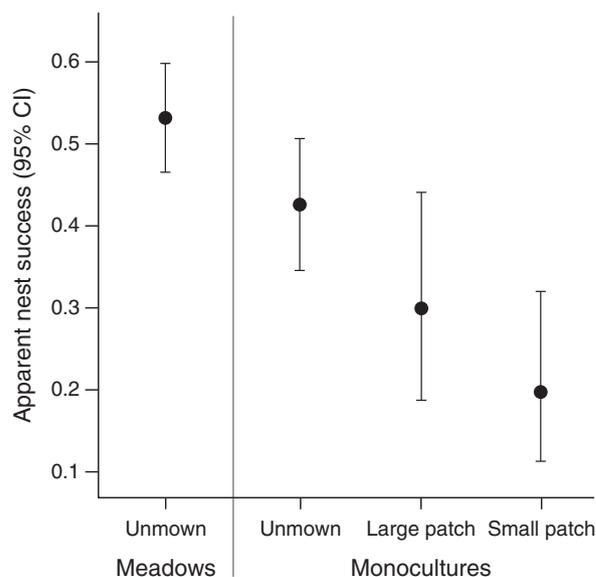


Figure 4. Apparent nest success of nests on meadows and monocultures which were unmown, mown with a large patch (> 5 m in diameter) or mown with a small patch (< 5 m in diameter) of unmown grass left grass around the nest. Statistics are summarized in Table 6.

ful \pm 95% confidence intervals (CIs): 56, 49–62, percentage on the basis of a nest on day 1) than nests in unmown monocultures (45, 37–53, Fig. 4). Nests in mown monocultures with a large patch left around the nest did not significantly differ in apparent success (32, 20–46) from nests in monocultures in fields that were left unmown dur-

Table 6. Results of the generalized linear mixed model for the effect of mowing on apparent nest success of Godwits, with the categories unmown monoculture (intercept), mown monoculture leaving a large (> 5 m in diameter) or small area (< 5 m in diameter) of unmown grass around the nest, and unmown meadow. Note that the estimates are given as logits.

Parameter	Estimate	se	z-value	P
Intercept ^a	–0.310	0.167	–1.850	0.064
Mown monoculture – large area unmown	–0.542	0.305	–1.779	0.075
Mown monoculture – small area unmown	–1.093	0.325	–3.366	< 0.001
Unmown meadow	0.436	0.140	3.115	0.002
Laying date ^b	–0.028	0.006	–4.433	< 0.001
Nest age	0.100	0.011	8.868	< 0.001
Random effects				
Year		0.035		(Variance)

^aUnmown monoculture; ^bstandardized by year.

ing their observation period. However, the success of nests in fields with a small patch of grass left around the nest did differ significantly from the success of nests in unmown monocultures (21, 12–34). The age of the nest at discovery had a positive relationship and laying date a negative relationship with nest survival (Table 6). The interaction laying date \times mowing category was not significant and was removed from the model (LRT: $\chi^2 = 3.54$, $df = 3$, $P > 0.3$). The proportion of predated (51%) or abandoned (49%) nests did not differ between unsuccessful nests in unmown fields, and in mown fields where a large or where a small patch was left around the nest ($\chi^2 = 0.42$, $df = 2$, $P > 0.5$).

DISCUSSION

In southwest Friesland, one of the core breeding areas of the threatened continental Black-tailed Godwit, average nest survival in intensive agricultural monocultures was lower, and declined more strongly over the season, than in herb-rich meadows, agricultural grasslands managed in more traditional ways. This is linked to the fact that the mowing of grass monocultures started during the nesting phase of the Godwits, so that most monocultures were mown before the end of the incubation period. Indeed, the seasonal decline was strongest in years when mowing was earlier and consequently more nests occurred on monocultures that were mown (i.e. in 2008 and 2009).

When not protected, mowing usually leads to nest destruction (Bollinger *et al.* 1990, Schekkerman *et al.* 2009, Gruebler *et al.* 2012). In our study, even though their locations were marked with sticks to alert the mowing farmer, a small number of nests were nevertheless destroyed. However, even when nests are spared by leaving a small (< 5 m in diameter) patch of grass around the nest, mowing still lowered nest survival. We found that abandonment did not differ between these nests and those in unmown monocultures, which suggests that nests in unmown patches of grass were easier to detect for predators and/or attracted predators at a higher rate. Nests in larger patches of unmown grass (> 5 m around the nest) had higher survival that was similar to nests in unmown monocultures. Herb-rich meadows were usually mown after 15 June, a time when 98% of the eggs in nests under our observation would have hatched. This later mowing probably

explained why nest survival on these meadows declined less strongly with date. The still existing small negative seasonal trend in daily nest survival rate might be explained by late breeding birds being of lower individual quality (Verhulst *et al.* 1995) or by higher predator activity (Sperry *et al.* 2012) or abundance later in the season. These explanations are not mutually exclusive, and with the current data we cannot distinguish between the two.

Although nest survival on meadows was higher than on monocultures in general, at local scales high nest predation still occurred. For instance, one of our meadow areas (the Sudermarpolder in the south) was part of a study on predation pressure in 2004 (Teunissen *et al.* 2008) and was especially chosen because of its high predation pressure. During our study period, nests built here also had a high probability to be predated by Red Foxes (G. Hoekstra unpubl. data).

An increase in predator densities is often suggested as one of the key causes of decreasing reproductive success of meadow-breeding birds in Europe (Malpas *et al.* 2012, Roodbergen *et al.* 2012). Interestingly, our comparison of historical (1980–83) and contemporary (2007–2012) nest survival rates does not support the suggestion that nest survival shows a decrease in every habitat, as one would expect if increased predator densities were the only culprit. In fact, nest survival remained stable in the traditional habitat, on herb-rich meadows, indicating an interaction between higher predator numbers and agricultural intensification. Herb-rich meadows may provide safer nest locations. However, other factors negatively affecting nest survival in herb-rich meadows may have changed simultaneously and may have compensated for an increase in nest predation. For instance, the risk of trampling (Beintema & Müskens 1987) has decreased, as cattle are now mainly housed indoors (Bont & Everdingen 2004). Moreover, a change in the suite of predators or a change in abundances of alternative prey for the predators may also lead to changes in nest success rates, as has been shown for Greater Snow Geese *Anser caerulescens atlanticus* (Bêty *et al.* 2002). Greater knowledge on the dynamics of food webs of these managed grasslands may help explain the lack of success of targeted predator control (Bolton *et al.* 2007).

We could not include nest age in the models comparing historical with contemporary nest survival, as nest age was not measured in the

historical dataset. Yet, as is often found (Dinsmore *et al.* 2002, Smith & Wilson 2010, Grant & Shaffer 2012), for the contemporary dataset, daily nest survival rate increased with nest age. This may be because nests in a risky location would have a higher chance to be predated at an early age than nests at safer locations (Klett & Johnson 1982). Additionally, birds may defend their nests more vigorously at the end of incubation (Smith & Wilson 2010). In our comparative analysis we had to assume that these mechanisms of nest loss have not changed between the periods. We made the assumption that nests were on average at similar ages when found in the two periods, as any difference in average nest age must be rather large (± 10 days, Fig. 1) to have an effect on the conclusions.

That agricultural intensification could lead to higher nest predation rates may relate to increased nest detectability due to mowing. However, it could also be explained by higher nest detectability *per se*. In the more homogeneous vegetation on monocultures, whether mown or not, nests may be more conspicuous (Evans 2004), and the behaviour of breeding birds may also be different. Furthermore, a lower abundance of alternative prey for the main predators (Laidlaw *et al.* 2013) may also lead to higher predation rates on nests of breeding waders (Bodey *et al.* 2010). Indeed, a positive correlation has been found between nest success of Mallards *Anas platyrhynchos* and the abundance of rodents, with Striped Skunks *Mephitis mephitis* as principal shared predator (Ackerman 2002). In addition, birds breeding on monocultures may have a lower nest defence because adult body condition is lower and risk-taking higher (Evans 2004). With respect to the latter, we did not find a difference between relative body masses of birds breeding on meadows and monocultures (R. Kentie unpubl. data). Nevertheless, lower nest defence may be caused by the decreased densities of Godwits and other waders breeding on monocultures, as they are more successful at defending their nests against predators when they defend them together (Dyrce *et al.* 1981, Berg *et al.* 1992).

Nest losses in meadow birds such as Godwits thus appear conditional on habitat management, to which the timing of mowing contributes in grassland monocultures. Increases in spring temperatures have helped earlier mowing far beyond any advances in Godwit breeding dates (Kleijn *et al.* 2010, Schroeder *et al.* 2012), and this may

magnify the effects of mowing in the grassland monocultures. Currently, a large portion of the subsidies for meadow-bird conservation is spent on agri-environmental schemes to protect nests in monocultures from agricultural activities (Musters *et al.* 2001, van Paasen & Teunissen 2010). As only few nests hatch even when spared by leaving a small unmown patch, and as chicks from such nests have a lower survival probability than chicks hatched on herb-rich meadows (Kentie *et al.* 2013), to help the conservation of Godwits such money seems better spent enabling farmers to maintain wet herb-rich meadows that are mown later. As degradation of breeding habitat also plays a role in the decline of other grassland bird populations (e.g. Newton 2004, Lloyd & Martin 2005, Gruebler *et al.* 2012), such a change of management practices would help the meadow-bird community at large.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Main results of simulation analysis of different nest visiting scenarios.

Table S1. Model selection results for a simulated dataset with constant nest survival.

Table S2. Model selection results for a simulated dataset where daily nest survival decreased during the season.

Figure S1. Results of the model estimates of the simulated dataset where daily nest survival was constant, for two nest visiting scenarios.

Figure S2. Results of the model estimates of the simulated dataset where daily nest survival decreased during the season, for two nest visiting scenarios.

Appendix S2. R script to test effects of different nest revisit scenarios.