The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland

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Summary

1. Like many farmland birds, the largest European population of the black-tailed godwit *Limosa limosa*, in The Netherlands, has been declining for decades despite conservation measures including agri-environment schemes (AES). In a new experimental AES aiming to reverse this decline, collectives of farmers implemented spatially coordinated site-level habitat management ('mosaic management') including delayed and staggered mowing of fields, refuge strips and active nest protection.

2. We evaluated the effectiveness of mosaic management by measuring godwit breeding success in six experimental sites and paired controls. Productivity was higher in mosaics than in controls due to fewer agricultural nest losses. Chick fledging success was poor in both treatments. Productivity compensated for adult mortality in only one AES site.

3. Although creating chick habitat was a major management goal, the availability of tall grass during the fledging period did not differ between treatments, mainly because rainfall delayed mowing in all sites and study years. However, chick survival increased with the availability of tall grass among sites. Higher chick survival will thus enhance the positive effect of mosaic management in drier years, but sensitivity to weather represents a weakness of the AES design.

4. Available estimates of productivity in Dutch godwits suggest a strong reduction over the past 20 years and implicate chick survival as the main driver of their decline. Earlier mowing of grassland is the main causal mechanism, but changes in vegetation structure and composition, and increased predation may also have contributed.

5. *Synthesis and applications.* Demographic rates like breeding success are useful parameters for evaluating effects of management. Mosaic management increases the productivity of black-tailed godwits, but does not ensure long-term population viability for this flagship species of wet grassland bird communities. More stringent management prescriptions need to improve both the area and the quality (vegetation structure) of grassland mown late. Management efforts should be concentrated in areas with favourable pre-conditions in order to improve overall effectiveness.

Key-words: agri-environment scheme, grassland birds, chick survival, breeding productivity, conservation, mowing date

Introduction

Throughout Europe, biodiversity is declining in agricultural landscapes (Donald, Green & Heath 2001; Benton *et al.* 2002; Flade *et al.* 2006) including lowland wet grasslands which form the habitat of a formerly rich and diverse breeding bird community (Beintema, Dunn & Stroud 1997; Wilson, Ausden & Milsom 2004). Negative effects of agricultural intensification on the birds' reproductive output are generally considered to be the main cause of these declines (Vickery *et al.* 2001; Newton 2004).

The Netherlands encompasses a large expanse of wet grassland devoted to intensive dairy farming and holds internationally important populations of grassland shorebirds.

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This includes 47% of the European population of black-tailed godwit *Limosa limosa* Linnaeus, a species listed as globally near-threatened (IUCN 2007). The Dutch population declined from > 125 000 breeding pairs around 1960 to *c.* 62 000 in 2004, of which 60–75% breed in agricultural grasslands (SOVON 2002; Teunissen & Soldaat 2006). Reduced breeding productivity has been implicated as the main cause of this decline (Kruk, Noordervliet & ter Keurs 1997; Schekkerman & Müskens 2000).

Conservation measures for 'meadowbirds' in The Netherlands have included (i) reserves where biodiversity takes priority over agricultural production (currently *c.* 18 000 ha), (ii) Agri-Environment Schemes (AES) reimbursing farmers for less intensive field use (27 000 ha) and for protecting shorebird clutches during farming operations (123 000 ha), and (iii) similar nest protection by volunteers and unpaid farmers (*c.* 200 000 ha; Musters *et al.* 2001; van Paassen 2006). In 2005, AES received 87% of the €31 million national budget for meadow bird conservation.

Management prescriptions of existing AES focus on postponement of cutting and grazing of individual fields, usually until 1–15 June. This reduces destruction of eggs and chicks (Beintema & Müskens 1987; Kruk, Noordervliet & ter Keurs 1997) and increases the availability of chick foraging habitat (Schekkerman & Beintema 2007). As godwit broods migrate towards unmown fields, this may also enhance the productivity of pairs breeding in the surrounding area. However, most existing studies have failed to show positive effects of AES on shorebird breeding densities (Kleijn *et al.* 2001; Kleijn & van Zuijlen 2004; Verhulst, Kleijn & Berendse 2007). Because the effects on breeding productivity were not investigated in these studies, the possibility remains that AES lead to more fledged chicks but these settle outside the managed sites. However, it is clear that existing AES have not halted the countrywide decline of black-tailed godwit and other grassland birds (Teunissen & Soldaat 2006).

Acknowledging the importance of farmland for godwits and the need for spatially coherent management (Whittingham 2007), Dutch conservation organizations designed a new AES to optimize breeding conditions for black-tailed godwits within the constraints of modern dairy farming. In this scheme, collectives of farmers coordinate field use at the site level to provide sufficient foraging habitat for chicks and create spatial heterogeneity providing resources for all age classes of godwits (and other meadowbird species) within reachable distance throughout the breeding season (Benton, Vickery & Wilson 2003). 'Mosaic management' was put into practice for 3 years in six experimental sites to investigate its feasibility and conservation performance.

This study evaluated the effect of mosaic management on breeding output of black-tailed godwits. We focused on productivity for three reasons. First, it is the demographic variable that the AES aims to increase. Secondly, breeding output may respond to management immediately, while observing an increase in density within a few years is less likely in a long-lived species like black-tailed godwit. Thirdly, productivity provides a direct measure of the contribution of management to the wider population while density effects may be confounded by dispersal in addition to local breeding success.

We tested two criteria of AES effectiveness: (i) productivity should be increased in areas subject to the management prescriptions, and (ii) productivity should at least balance adult mortality in AES sites so that the population is sustainable. Productivity should be approximately 0·6 fledged young per breeding pair (Schekkerman & Müskens 2000). Based on our study and previous productivity estimates, we discuss the outlook for conservation of black-tailed godwits in modern farmland.

Methods

EXPERIMENTAL AGRI-ENVIRONMENT SCHEME

Mosaic management was established at six lowland wet grassland sites in The Netherlands during 2003–2005. Sites were selected on the basis of willingness to cooperate among farmers and the presence of reasonable numbers of breeding godwits. At each site, 6–10 farmers participated in an area of 215–334 (mean 281 ± SD 53) ha. Within most sites, some land was owned by non-participants (9 ± 9%). One site included part of a meadowbird reserve (4%) and two bordered on reserves. Table 1 lists the practical components of the AES, their rationale, and area contracted. Mosaics were designed to offer ≥ 1 ha of preferred grassland (sward height ≥ 15–20 cm, Schekkerman & Beintema 2007) per godwit brood throughout the chick-rearing period, based on previously observed maximum brood densities (Schekkerman, Teunissen & Müskens 1998). Field use was spatially coordinated to allow all broods to reach suitable grasslands within a few 100 m distance.

STUDY DESIGN

Each of the six experimental AES sites was paired with a control site (223 ± SD 118 ha). Selection criteria for control sites were proximity to the AES site (0–5 km, mean 2·2 ± 2·4 km), similarity in landscape, field size and shape, and water level, and the presence of > 20 godwit pairs. Some control sites included a few fields under other AES contracts. Nest protection was employed on nearly all fields in five AES sites and on about 50% in the sixth; it was nearly complete in three, partial in two, and absent in one of the control sites. Average godwit territory densities were 27·5 ± SE 4·5 km^{-2} in experimental sites and 19·0 ± 3·7 km^{-2} in controls.

Breeding productivity was measured in 1 year in each AES-control pair, and two site pairs were studied per year. One site pair was studied both in 2004 and 2005; results were averaged where appropriate. In one control site, we failed to estimate productivity as volunteers stopped marking clutches in response to the presence of a red fox *Vulpes vulpes* Frisch. As this was probably unrelated to management, excluding this site will not have biased the results.

Measuring breeding productivity (B, fledged young per breeding pair) is difficult in nidifugous birds like godwits, as broods move around and often remain hidden in vegetation. We combined data on hatching success of the majority of nests in the study area with chick survival in a sample of radio-tagged broods to estimate productivity as: $B = U \times [1 + (V \times (1 - U)] \times L \times K$, where U = probability that a clutch survives to hatching, V = probability that a failed clutch is replaced (0·5, based on Schekkerman & Müskens 2000),

Table 1. Components of the mosaic management AES with rationale and average proportion of area contracted in the six experimental sites

Management component	Rationale	%
First cut postponed until 1 or 8 June	Chick-feeding habitat and shelter	11
First cut postponed until 15 or 22 June	Chick-feeding habitat and shelter	7
Grazing followed by rest until 15 June	Chick-feeding habitat in late spring	4
Sequentially mowing out strips to feed to cattle in stable	Diverse sward height within field, suitable for foraging adults and chicks	4
Leaving uncut strips at early-cut fields	Escape havens during mowing; feeding habitat and shelter during brood movements	2
First cut in May staggered in three tranches separated by ≥ 1 week	Allow broods to find unmown grass nearby when field of residence is cut	58
Grazing	No specific conservation rationale	13
Flooding grassland, 15 February to 15 April or 15 May	Early-season resting and feeding habitat for adults	1
'Nest protection'; marking and mowing around clutches or placing nest protectors over nests	Avoid agricultural egg losses due to mowing or trampling	86
Reduced driving speed during mowing	More chicks able to escape machines	86

L = number of eggs hatched per successful clutch, and K = probability that a chick survives to fledging.

FIELD METHODS

Volunteers, farmers and researchers located the majority of godwit nests in the study sites (usually > 80%, judged from territory counts), and marked them with sticks at 1–3 m distance. Hatching dates were predicted by floating eggs in water. Nest survival was monitored through repeated visits at intervals from several days to 2 weeks. Some volunteers recorded only whether nests were successful (≥ 1 eggs hatched; eggshell fragments present), but in 63% of 364 successful nests, the number of remaining eggs was recorded, and hence, by subtraction from clutch size, the number of chicks hatched was obtained.

Chick survival was estimated by radio-tagging one parent or the chicks themselves in 5–20 (11·5 ± 5·2) broods per site. Adult godwits were trapped on the nest during late incubation or on newly hatched young, individually colour-ringed and fitted with small radio transmitters as described in Warnock & Warnock (1993). Transmitters (BD-2, Holohil, Canada/Microtes, The Netherlands) weighed 3 g (0·9–1·3% of body mass) and signals ranged from 0·5 to 1 km on the ground and up to 2 km in flight. Chicks were tagged at hatching (71% of N = 226, usually two chicks per brood of four) or at a later age, using smaller transmitters (LB-2, Holohil/Microtes, 1·0 g, 0·5–3·5% of body mass) with a range of 50–300 m depending on the chicks' position and behaviour.

When godwits are approached by observers, diagnostic alarm calls and behaviour show reliably whether living chicks are present, but it was often impossible to count chicks in the tall grass. However, around the fledging age (*c.* 25 days), chicks more often leave cover and they are guarded by a parent until 30–33 days old, allowing the number of fledged young to be established. For the single successful tagged parent of which we did not know how many chicks fledged (one out of 14), we used a mean for known broods (1·5, Schekkerman & Müskens 2000).

Tagging parents does not yield insight into the causes of chick deaths, which is important for interpreting variation in breeding success. Therefore, in 2004 and 2005, we tagged the chicks themselves, so that dead chicks could be recovered. In 2004, only chicks were tagged. Although most chicks whose radio signal disappeared before the fledging age were recovered dead, 22% were not, leaving doubt about their fate (dead, tag failure, or moved beyond the search range). In 2005, both a parent and two chicks were tagged in the focal broods. This greatly facilitated determining their fate, as adults could be located from greater distances and their behaviour observed after their chicks' signal was lost. This confirmed that all 49 'missing' chicks had died; their parents stopped alarming before the fledging age, except in one case where a tag-less sibling survived. In addition, from the number of tagged and tag-less chicks fledged within each brood, we confirmed that chick survival was not reduced by tagging (Schekkerman, Teunissen & Oosterveld in press).

Broods were relocated every 1–4 days. The presence of living chicks was deduced from their parents' behaviour or from fluctuations in the strength of chick radio signals, indicating movement. Chicks were recaptured every 4–7 days to check transmitter attachment and weigh the birds. Missing signals were searched throughout the study area as well as in woodland potentially containing predators' haunts up to *c.* 5 km away. We also used a metal detector to search under known nests of grey heron *Ardea cinerea* Linnaeus and raptors up to 10 km from the study site. Causes of death were deduced from the state and location of chick remains.

The agricultural use of all fields in the study areas was recorded at least weekly. The availability of suitable chick habitat was calculated from these data as: %(chick grass) = %(uncut grassland) + 0·7 × %(regrowth) + 0·5 × %(refuge strips + strip mowing). All these swards were ≥ 15–20 cm high; 'regrowth' refers to fields cut or grazed earlier in the spring. Weighting factors reflect the proportion of fields covered by tall grass and its suitability as chick habitat (Schekkerman, Teunissen & Müskens 1998). Uncut grassland made up the majority of 'chick grass' (64 ± 39%).

STATISTICAL ANALYSES

Hatching success was calculated from daily clutch survival probabilities (Aebischer 1999), assuming a total exposure of 25 days. For broods with a tagged parent, chick survival was calculated as the number of chicks fledged (day 25) divided by the number of eggs hatched. Survival of tagged chicks without a tagged parent (2004) was estimated with the Kaplan–Meier estimator (Kaplan & Meier 1958), as several chicks were tagged when ≥ 1 day old and others lost their tag. Maximum and minimum estimates were made by treating chicks that remained 'missing' as either dead or censored from the day their radio signal was lost. In 2005, we ascertained that all 'missing' chicks died before fledging, but as broods without a tagged parent may be more easily missed during searches and predation seemed more severe in 2005; this result may not be directly applicable to 2004. However, as most missing chicks probably died, minimum

estimates were given five times greater weight than maximum estimates. Standard errors for productivity were obtained by bootstrapping, resampling from the probability distributions for the number of chicks hatched per successful clutch (normal distribution), clutch survival (beta distribution), and chick survival (beta distribution).

The effect of AES management was evaluated by pairwise tests, comparing the availability of brood habitat, clutch survival, chick survival and productivity between experimental and nearby control sites with analysis of variance, using 'site pair' as a blocking factor. To take into account differences between sites in the precision of productivity estimates, these were weighted by the reciprocal of their coefficient of variation.

The relationships between breeding parameters and the availability of chick habitat were tested by linear regression of the site estimates on the average proportional area of unmown grassland or 'chick grass' during the main chick period. The latter was defined for each site as running from the date when 25% of all local clutches had hatched to 25 days after the date when 75% had hatched. Median hatching dates differed between sites by up to 4 weeks.

We calculated an index of chick condition at each capture (2004 and 2005 only) by dividing body mass by the mass predicted at the chick's age from the growth curve reported by Beintema & Visser (1989b). No indices were calculated for chicks < 3 days old as the curve underestimates mass at these ages. Condition was compared between AES and control sites in a linear mixed model including chick and site pair as random variables, and chick age and management as fixed variables. In a second model with chick and site as random variables, we tested for associations between condition and the area of late-mown grassland.

Results

AGRICULTURAL FIELD USE

The area of uncut grass and 'chick grass' declined with date in both experimental and control sites (Fig. 1). The availability of these field types during the main fledging period did not differ between AES sites and controls (uncut 29 ± SE 4% vs. 25 ± 5%, $F_{1,5} = 1.01$, $P = 0.36$; 'chick grass' 37 ± 4% vs. 33 ± 4%, $F_{1,5} = 0.74$, $P = 0.43$), and neither did the date on which it fell below 50% (19 vs. 18 May, $F_{1,5} = 0.11$, $P = 0.75$). The lack of a treatment effect on habitat availability was not caused by farmers ignoring AES prescriptions. Mosaic management was somewhat 'diluted' by fields owned by non-participants and by one AES site including 18% arable
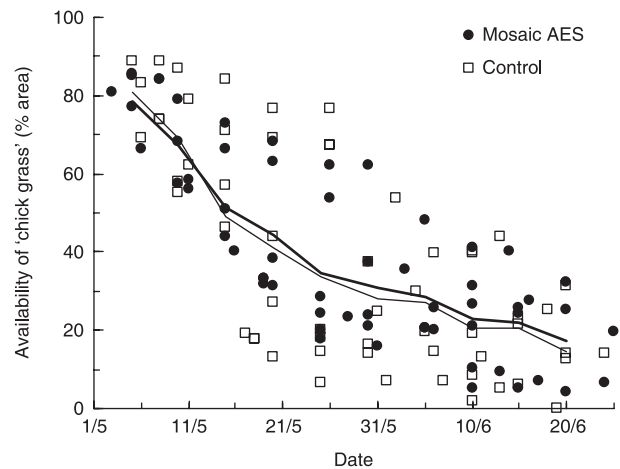

Fig. 1. Availability (% of area) of 'chick grass' (see Methods) in the experimental AES sites (closed dots, bold line) and in control sites (open squares, thin line). Symbols denote actual values, lines treatment averages.

land, versus 5% in the control. Secondly, field use in two control sites was relatively low-intensity, although still within the range of modern farmland. Most important, in all three study years, rainfall forced farmers to postpone mowing to mid- or late May in both experimental and control sites.

GODWIT REPRODUCTION

Clutch survival (≥ 1 egg hatched) ranged between 14% and 87% and was higher in experimental sites than in controls (Table 2). The difference was caused primarily by larger agricultural losses (to mowing and trampling) in control sites. Predation probability did not differ between treatments. The variation in clutch survival among sites was unrelated to the proportion of grassland not yet cut or grazed in the chick period (linear regression, $F_{1,10} = 0.05$, $P = 0.82$), possibly due to more intensive nest protection by volunteers and farmers in the AES sites.

The mean number of chicks hatched per successful nest varied from 2·8 to 3·9, but did not differ between AES sites and controls (Table 2). The mean number of chicks hatched

Table 2. Reproductive parameters of godwits in AES sites and controls. Differences were tested by analysis of variance on site values weighted by (1 cv $^{-1}$), but unweighted means are presented here

Productivity component	Mosaic AES		Controls		Difference		
	Mean	SE[1]	Mean	SE[1]	F[2]	d.f.[3]	P[4]
Clutch survival (U)	0·50	0·03	0·33	0·03	32·7	1,5	0·002
Clutch failure, agricultural causes	0·06	0·03	0·29	0·11	6·45	1,5	0·052
Clutch failure, predation	0·32	0·08	0·37	0·11	0·58	1,5	0·48
Chicks hatched/successful clutch (L)	3·39	0·10	3·22	0·10	1·6	1,5	0·26
Chicks hatched/breeding pair	2·09	0·15	1·37	0·15	13·4	1,5	0·015
Chick survival to fledging (K)	0·11	0·02	0·11	0·02	0·07	1,4	0·81
Chicks fledged/breeding pair (B)	0·28	0·05	0·16	0·05	6·82	1,4	0·059

[1]standard error; [2]*F*-statistic, ANOVA; [3]degrees of freedom; [4]two-tailed probability.

Fig. 2. Survival (±SE) of black-tailed godwit chicks to fledging in relation to the availability of uncut grassland and 'chick grass' during the main chick period (black: experimental sites, grey: controls; we failed to estimate productivity in one control). Lines fitted by logistic regression. (a) uncut grassland (logit $S = 0{\cdot}05 \times -3{\cdot}93$, $F_{1,9} = 4{\cdot}58$, $P = 0{\cdot}061$); (b) 'chick grass' (logit $S = 0{\cdot}07 \times -5{\cdot}05$, $F_{1,9} = 6{\cdot}91$, $P = 0{\cdot}027$).
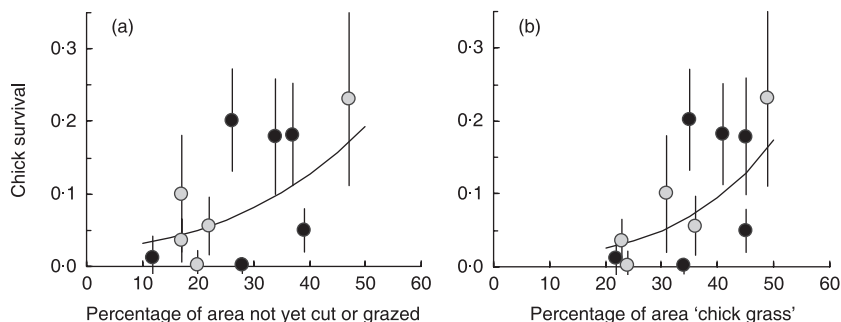
Fig. 3. Productivity (young fledged /breeding pair ± SE) of black-tailed godwits in 11 study sites (black, experimental; grey, controls) in relation to the availability of uncut grassland ($F_{1,9} = 1{\cdot}48$, $P = 0{\cdot}26$) and 'chick grass' ($F_{1,9} = 2{\cdot}02$, $P = 0{\cdot}19$) during the main chick period. The grey bar indicates productivity required for a stable population. In one site pair we estimated productivity in 2 years but grassland use was not quantified in the first year; the first year estimates (not shown) were $0{\cdot}20 \pm 0{\cdot}16$ for the mosaic and $0{\cdot}06 \pm 0{\cdot}05$ for the control site.
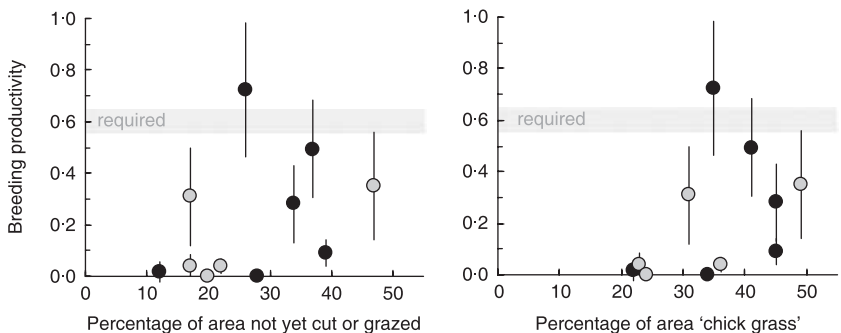
per breeding pair, integrating clutch survival, probability of replacing a lost clutch and the number of chicks hatched, was higher in AES sites than in controls (Table 2). The survival of chicks to fledging averaged 11% (range 0–23%) and did not differ between AES and control sites (Table 2). However, chick survival was positively correlated with the availability of uncut fields and 'chick-grass' during the main fledging period (Fig. 2).

The number of young fledged per breeding pair was almost twice as high under mosaic management as in the control sites (0·28 vs. 0·16; Table 2). In contrast to chick survival, breeding productivity was not significantly correlated with the availability of tall grassland in the fledging period (Fig. 3), mainly because hatching success varied independently. Breeding output exceeded 0·6 young per pair, required to balance mortality, in only one out of seven estimates in AES sites. It was < 0·4 young per pair in all control sites (Fig. 3).

Of 205 chicks of which the radio signal was lost before fledging, 22% were never recovered, 11% were found dead by unknown causes, 52% were eaten by predators, 7% were killed during grass harvesting, and 8% died in other ways. The proportions did not differ among treatments (χ^2 test, $\chi^2_4 = 6{\cdot}50$, $P = 0{\cdot}16$). Given that most 'missing' chicks must have died (indicated by their tagged parents' behaviour) and may have been transported out of the search range by predators, 'predation' accounted for more than half and up to 80% of chick losses. However, we could not usually distinguish whether chicks had been taken alive or found dead by a predator. Birds (seven species) were identified as chick predators more often than mammals (four species); common buzzard *Buteo buteo* Linnaeus (≥ 9%) and stoat *Mustela erminea* Linnaeus (≥ 8%) were identified most frequently.

The average condition index of chicks in 2004 and 2005 was 0·85 (SE = 0·01, $N = 175$ measurements on 110 chicks); hence, growth rates were lower than reported by Beintema & Visser (1989b). Effects of age and management treatment were not significant (Wald tests: age $W_1 = 2{\cdot}50$, $P = 0{\cdot}11$; management 3·43, $P = 0{\cdot}06$), and chick condition was unrelated to the availability of uncut fields during the fledging period ($W_1 = 0{\cdot}00$, $P = 0{\cdot}94$).

Discussion

Our study adds significantly to the scant data on black-tailed godwit productivity in The Netherlands. The available estimates were obtained with different methods and in different sites with varying management and therefore do not constitute a true monitoring series, but taken together, they indicate that breeding success has declined in the past 20 years (Fig. 4). Although predation has led to very low hatching success in several sites in recent years, clutch survival seems to have declined less generally than chick survival. Due to clutch replacement, it also has a smaller effect on breeding output. There is little indication that adult survival has declined structurally (Fig. 4), suggesting that reduced chick survival has been the main driver of the population decline.

EFFECTIVENESS OF MOSAIC MANAGEMENT

Godwit breeding productivity was 75% higher in AES sites than in the paired controls. This difference was barely significant in a two-tailed test but from a knowledge of farming practice and godwit biology, a higher breeding output was expected in AES sites and use of a one-sided test can therefore be
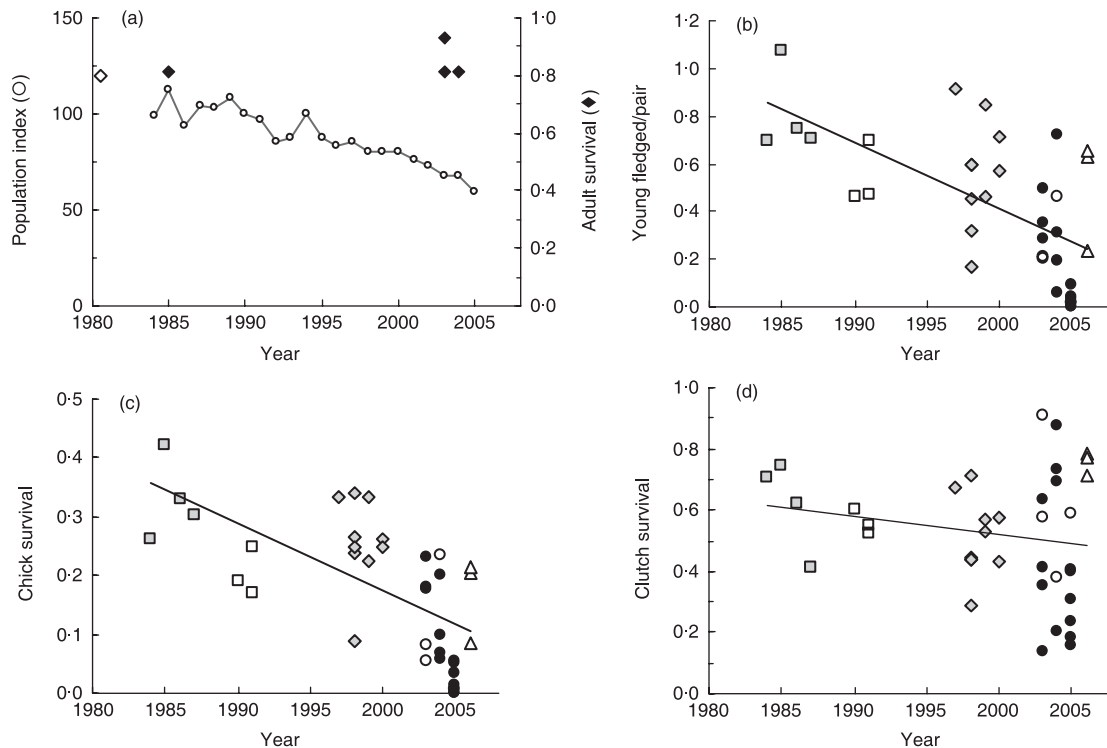
Fig. 4. Changes in population parameters of black-tailed godwits in The Netherlands. (a) Population indices derived from the SOVON/CBS meadow bird monitoring scheme (dots connected by line), and available estimates of adult survival ($\diamond$ ring-recoveries, (Beintema & Drost 1986); $\blacklozenge$ mark-resighting, (Groen & Hemerik 2002; Roodbergen, Klok & Schekkerman in press). (b–d) total breeding productivity (b), and chick (c) and clutch survival (d) for the studies in (b). Symbols denote different studies: $\blacksquare$ (Groen & Hemerik 2002), colour-marked adults; $\square$ (Kruk, Noordervliet & ter Keurs 1997), colour-marked adults; $\blacklozenge$ (Schekkerman & Müskens 2000), radio-tagged adults; $\bullet$ this study; $\bigcirc$ (Teunissen, Schekkerman & Willems 2005), radio-tagged chicks $\triangle$ Teunissen unpublished, radio-tagged adults. The linear trend over time is negative for population index ($F_{1,20} = 113 \cdot 7$, $P < 0 \cdot 001$), total breeding success ($F_{1,35} = 23 \cdot 7$, $P < 0 \cdot 001$) and chick survival ($F_{1,35} = 29 \cdot 0$, $P < 0 \cdot 001$), but not for survival of clutches ($F_{1,35} = 1 \cdot 43$, $P = 0 \cdot 24$) and adults ($F_{1,4} = 1 \cdot 69$, $P = 0 \cdot 26$).

defended. A weakness in this study was that sites were not selected randomly but used criteria including a positive attitude of farmers towards conservation. This may have led to bias towards a positive 'meadowbird history'. As a consequence, higher godwit densities may have accumulated in AES sites through local production or immigration. However, reproductive success is sensitive to actual conditions during the breeding period, and much less likely than breeding density to reflect historical instead of current management. We therefore consider our results indicative of a positive effect of mosaic management on godwit productivity.

The higher breeding success in AES sites arose almost entirely through a higher survival of clutches, due to lower agricultural nest losses. The greater intensity of nest protection in the AES sites than in controls probably contributed to this. Nest protection is carried out on *c.* 30% of the agricultural grassland area in The Netherlands (van Paassen 2006), but its nearly complete coverage in the AES sites was part of the management prescriptions. Previous studies from The Netherlands have shown that differences in meadowbird breeding density between fields managed under AES and controls can be accounted for by differences in groundwater levels rather than any effect of management itself (Kleijn & van Zuijlen 2004; Verhulst, Kleijn & Berendse 2007). However, the higher

nest survival found here is unlikely to be related to environmental factors that happen to correlate with fields selected for AES management.

Although mosaic management explicitly aims to increase chick survival, this did not differ between AES sites and controls. A primary objective – making available more 'chick grass' than in conventionally farmed sites – was not achieved. Rainfall forced farmers to postpone mowing in both AES and control sites, and led to a very similar timing of the first cut. It also led to a less spatially diverse grassland use than intended, as cutting was no longer staggered with weekly intervals but proceeded rapidly on fields scheduled for mowing in May when weather improved. Nevertheless, chick survival was positively correlated with the availability of tall grass among sites, irrespective of their treatment status, indicating that mowing later is beneficial to chicks. It suggests that in years with drier May weather, resulting in earlier mowing on conventional farms, better chick survival will add to the higher productivity in AES sites. However, our results do show that AES management overlaps with between-year variation in conventional farmland use, and will therefore not deliver value for money in all years, unless prescriptions ensure that mowing is still spread in time and space after an initial postponement.

Average productivity of black-tailed godwits in AES sites (0·28 fledged young pair^{-1}) was clearly below the *c.* 0·6 required for reproduction to balance mortality. This criterion is based on estimates of 60% first-year post-fledging survival, 85% adult annual survival, and first breeding at 2 years (Beintema & Drost 1986; Groen & Hemerik 2002). Its magnitude depends particularly on adult survival, which should be as high as 92% for the observed productivity to be sufficient. Annual survival of colour-marked adult godwits in two of our study sites in 2003–2005 was 81% (95% CI, 73–87%; Roodbergen, Klok & Schekkerman in press). It is therefore improbable that mean adult survival in AES sites reached 92% and we conclude that the observed breeding productivity was insufficient to sustain the population.

Our productivity estimates assume that black-tailed godwits re-lay only once after clutch loss (which is generally the case), and that replacements yield as many fledglings as first clutches. While we did not find a decrease in chick survival with date (own unpublished data), clutch survival may decline later in the season (Beintema & Müskens 1987). As more clutches were lost in the control sites, productivity would be reduced further here and the differences between treatments would be more pronounced, but it would not affect our conclusion that productivity in AES sites was insufficient. Hence, godwit populations under mosaic management still depend on immigration for their long-term persistence. As our results show that even fewer young fledge in conventional farmland, the necessary recruits should come from meadowbird reserves, but there are too few data to evaluate whether breeding success is sufficient there.

MECHANISMS REDUCING CHICK SURVIVAL IN FARMLAND

Several factors probably contribute to the observed decline in chick survival. The correlation between fledging success and availability of uncut grassland points to the importance of the mowing regime. Earlier and faster mowing means that an increasing proportion of chicks will encounter machinery and will be faced with large expanses of homogeneous short swards offering little food and cover.

Deaths by cutting and harvesting made up at least 7% of chick losses in our study, but may have been underestimated. Some chicks may have been scavenged from recently cut fields, and some transmitters may have been destroyed by machinery or buried in silage stacks. Some broods escape mowing (Kruk, Noordervliet & ter Keurs 1997) by moving to nearby uncut fields but these are equally dangerous when fields are cut in rapid succession. Cutting grassland later and spread in time and space will thus reduce mortality.

A detailed analysis of chick mortality in the current study sites and three other sites found that predation was twice as high when broods stayed in recently cut or grazed fields compared to uncut fields (Schekkerman, Teunissen & Oosterveld in press). Short swards evidently render chicks vulnerable to (avian) predators. Hence, a scarcity of uncut grassland that forces broods to use cut fields will increase predation losses.

Invertebrates are less abundant in cut than in uncut grassland, leading to a reduction in foraging success of chicks to a degree large enough to compromise their growth (Schekkerman & Beintema 2007). Although chicks grew more slowly in our study than those observed by Beintema & Visser (1989b) in 1976–1985, we did not find a correlation between chick condition and the availability of tall grass, and only 2% of the recovered chicks evidently starved to death (uninjured, condition index *c.* 0·5). However, chicks with a deteriorating condition may be quickly eliminated by predators (Swennen 1989; Schekkerman, Teunissen & Oosterveld in press).

Earlier mowing dates may not explain the observed decline in chick survival completely. In agreement with our study, Schekkerman & Müskens (2000) found that chick survival increased with the area of grassland mown late in nine farmland sites in 1997–2000, yet average survival was notably higher than in the current study (mean 26%, Fig. 4) despite a smaller proportion of fields being mown late (11 ± 2% cut after 31 May vs. 21 ± 6% in the current study). This suggests that additional factors are involved.

Between 1990 and 2005, an average 8% of all grasslands in the north and west Netherlands were reseeded annually (Statistics Netherlands), leading to a strong increase in productive grass monocultures at the expense of herb-rich fields. This is likely to have reduced arthropod abundance and diversity (Vickery *et al.* 2001; Atkinson *et al.* 2006; Schekkerman & Beintema 2007), and impaired the chicks' ability to move and capture prey in the resulting dense vegetation (Butler & Gillings 2004; Wilson, Whittingham & Bradbury 2005). The quality of grassland as chick foraging habitat may thus have declined independent of cutting dates.

Poor condition and survival may also result from unfavourable weather (Beintema & Visser 1989a; Schekkerman & Visser 2001). Linear trends over 1976–2005 (data from the Royal Netherlands Meteorological Institute) suggest a slight increase in mean daily maximum temperature (from 16·1 to 17·3 °C), no change in wind speed and an increase in rainfall duration (from 4 to 6% of time), but these changes were not significant due to interannual variability (linear regression, $P = 0.15–0.34$). As warmer weather and increasing rainfall will have opposite effects on chicks, it is unclear how climate variation has affected conditions for growth.

Our finding that 50–80% of non-surviving chicks were taken by predators, frequently common buzzard, suggests that predation pressure may have increased. Since the late 1970s, buzzards have (re)colonized the entire Dutch 'meadowbird landscape' (SOVON 2002), and other raptors have followed. Simultaneously, intensive farming practices have rendered godwit chicks vulnerable to predators by reducing the availability of cover and the density of nesting birds that can cooperate to evict predators (Green, Hirons & Kirby 1990). The observed frequency of 'predation' could overestimate its importance if it included much scavenging or concerned mainly chicks with reduced survival prospects due to other factors. The telemetry data suggest that scavenging was not very common, but we did observe that chicks in poor condition were more prone to disappear. However, the high predation

losses are only partly explained by such interaction effects (Schekkerman, Teunissen & Oosterveld in press).

MANAGEMENT RECOMMENDATIONS

Godwit chick survival has been reduced in recent decades by progressively earlier mowing dates, which has increased mowing mortality, reduced food availability, and increased the vulnerability of chicks to predators. At the same time, the quality of uncut grasslands as foraging habitat has deteriorated and important predators have increased. These changes mean that more stringent conservation measures are necessary now than a few decades ago to raise breeding productivity to a level that can sustain the population. Breeding output was higher under mosaic management than in control sites, but chick survival needs to be more than doubled to achieve long-term sustainability. Many other grassland birds face similar problems (Donald, Green & Heath 2001, Teunissen & Soldaat 2006).

Their low productivity indicates that prospects are bleak for maintaining black-tailed godwit populations in farmland if no effective conservation measures are put in place. Our results indicate that both the proportion of grassland mown late and its quality as chick habitat must be improved substantially. AES prescriptions do not include specifications on fertilizer input or floral composition of fields contracted for late mowing. Including such entry criteria would promote an open vegetation structure with abundant insects. However, these criteria would decrease the flexibility in field use that currently makes the AES attractive to farmers. On balance, fewer sites with more specific prescriptions will yield greater conservation benefit to black-tailed godwit than widespread efforts that are not effective in the long-term. Concentrating conservation efforts in godwit strongholds will be more feasible and will facilitate optimization – by choice of location or by management – of environmental conditions including landscape structure, water levels, disturbance and predation pressure.

Acknowledgements

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