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Timing of breeding and reproductive output in two Black-tailed Godwit *Limosa limosa* populations in The Netherlands

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To get a better understanding of the current population decline of Black-tailed Godwits in The Netherlands, we determined reproductive parameters in two Dutch breeding populations over the period 2002–2005 and investigated the relationship between reproductive output and timing of breeding. Annual median laying dates ranged from 14 to 25 April, and median hatching dates from 11 to 28 May. Sites differed in laying dates but not in hatching dates. Daily survival rate of nests was positively correlated to nest age and was affected by year and by the interaction of year and site, but not by laying date. The number of eggs hatching per successful nest also did not depend on laying date. Maximum chick survival (maximum estimate of the number of chicks fledged divided by the number of chicks hatched from the nest) and the probability of raising at least one chick to fledging declined significantly with hatching date, resulting in a decline of reproductive output with laying date. Minimum chick survival correlated negatively with cumulative minimum temperature during the first week after hatching. Duration of rainfall during the chick-raising period did not affect chick survival. Our estimates of reproductive output were lower than found in previous studies, and in most years reproductive output was too low to compensate for adult and juvenile mortality. Five possible proximate causes for the seasonal decline in chick survival are discussed: parental quality, weather conditions, food availability, predation pressure and mowing of the grassland habitat.

Key words: timing of breeding, reproductive output, chick survival, *Limosa limosa*, meadow birds

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INTRODUCTION

The Black-tailed Godwit *Limosa l. limosa* is a long-distance migrant breeding in European agricultural grasslands and wintering in western Africa. Around 40% of the population breeds in The Netherlands. As in most meadow birds, breeding numbers have rapidly declined all over Western Europe during the last 40 years (BirdLife International 2004). Insufficient reproduction is generally assumed to have caused the population decline (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Ratcliffe *et al.* 2005, Schekkerman *et al.* 2005). Survival prospects seem to have played only a minor role in the decline as adult survival rates have remained stable in The Netherlands over the past decades (Roodbergen *et al.* 2008).

Timing of breeding is an important factor in the breeding ecology of birds in seasonal environments (Brinkhof *et al.* 1997, Both & Visser 2001) as the period of maximum food requirements of chicks must coincide with maximum food availability (e.g. Högstedt 1974, Newton & Marquiss 1984, Visser *et al.* 1998). Proximate factors for a proper timing are the food available to females before egg laying or weather conditions early in the season. In bird species as Great Tit *Parus major* and Pied flycatcher *Ficedula hypoleuca* climate change caused a mismatch between timing of breeding and optimal conditions for reproduction (Visser *et al.* 1998, Both & Visser 2001). In agricultural landscapes, birds face human-induced factors due to changes in land management, which may change even more rapidly than natural factors. Beintema *et al.* (1985) showed that mean hatching dates of chicks, as calculated from ringing data, had advanced by two weeks from 1911 to 1974 in six meadow bird species, amongst them the Lapwing *Vanellus vanellus* and Black-tailed Godwit. They considered this advance a result of a similar advance in mowing dates and/or in seasonal food availability for adults due to increased use of fertilizers. Both *et al.* (2005), however, argued that climate change, not agricultural intensification, caused laying dates to advance in Lapwing over the period 1901–2003. Whatever the underlying cause, a change in laying dates may lead to a mismatch between the timing of breeding and the optimal window for rearing young in meadow birds.

In this paper we investigate the relationship between the reproductive output of two Dutch breeding populations of Black-tailed Godwits and the timing of breeding. Considering the changes in management practices and in climatic conditions, it is possible that the timing of breeding is no longer matched to optimal conditions for reproduction, or even that conditions are never good enough for sufficient reproduction. We monitored two colour-ringed breeding populations over four years and assessed breeding pair densities, laying and hatching date, nest and chick survival and overall reproductive output.

METHODS

Study areas

Fieldwork was carried out at two sites in the western part of The Netherlands: Polder Blokland (52°13'N, 4°49'E, province of Utrecht, c. 180 ha) and Polder Zeevang (52°31'N, 4°58'E, province of Noord-Holland, c. 130 ha). The two sites are similar in soil characteristics and agricultural management. Both polders originate from peaty marshlands and therefore mainly consist of peat soils, and are a mixture of intensively and extensively used grasslands, either mown for silage or grazed by dairy cattle and sheep. In both sites roughly one third of the area is under management agreements, some aiming to protect meadow birds (i.e. birds breeding in agricultural grasslands) and some to increase plant diversity. The agreements directed at meadow birds usually restrict farming activities, by e.g. delaying mowing dates and leaving patches unmown for the chicks to hide in, and protect nests during these activities. Both sites hold high numbers of breeding meadow birds, mainly Black-tailed Godwits, Lapwings, Redshanks *Tringa totanus* and Oystercatchers *Haematopus ostralegus*. A more detailed description of the study sites can be found in Roodbergen *et al.* (2008).

Data collection

During the study period, we measured breeding pair densities (2003–2005), laying and hatching date, nest success, proportion of eggs hatched per successful nest (2002–2005) and chick survival (2002–2004). The frequency of field visits was 5–6 days per week during the peak of the breeding season (4 days per week in 2005). In Zeevang more volunteers searched for nests and the grass started growing later in the season than in Blokland, which made it easier to find nests and to observe colour-ringed godwits.

Breeding pair densities

The number of breeding territories was estimated using standardized territory mapping (Teunissen & van Kleunen 2000). From April to June, three mapping censuses were made and a breeding territory was assigned if a pair or a male was present on the territory during at least two visits, of which at least one in the period from 10 April to 10 May. Because individual birds can easily be missed during observations, in addition to the territory mapping the number of nests was counted as a proxy for breeding pair density.

Nests and laying dates

The study areas were searched for nests by volunteers and MR. Nests found were marked with a bamboo stick at a distance of 2 m and checked at least once a week. A GPS was used to determine their coordinates. If the clutch was complete when found, i.e. containing four eggs, the laying date was estimated by floating two eggs in an incubometer (van Paassen *et al.* 1984). If the clutch was still incomplete (< 4 eggs) the laying date could be estimated more precisely, as usually one egg is laid per day (Cramp & Simmons 1983). For those statistical analyses in which laying date was included only clutches found incomplete and freshly completed (≤ 2 days old) were used, to avoid possible errors of the estimate for laying date. In Black-tailed Godwits, the incubation time is c. 23 days and all eggs hatch within one or two days (Cramp & Simmons 1983). At each successful nest the number of eggs hatched was determined by checking for remaining unhatched eggs.

Chick survival

As godwit chicks leave the nest soon after hatching and seek food and shelter in tall vegetation, they are difficult to observe. In contrast, adults tending chicks are very conspicuous and chick survival can be estimated by following broods of which at least one of the parents is individually marked. Adult godwits were captured on the nest (Roodbergen *et al.* 2008), measured, weighed and provided with an individual combination of Darvic colour rings and a metal ring with an individual number. In all cases but five, capture attempts were ceased after capture of one of the partners. The sex was determined from biometry and plumage characteristics (Schröder *et al.* 2008).

In addition to colour ringing, in 2003 and 2004 most of the godwits caught were equipped with a radio-transmitter, making it easier to locate the family during the chick-rearing period. Transmitters weighed c. 3 g and emitted a signal at a specific frequency around 153 MHz, which could be received up to a distance of a few hundred metres when in tall grass to over one kilometre when in flight. To attach the transmitter, feathers on the back were clipped and the transmitter was glued to the remaining feather parts with cyanoacrylate, the antenna protruding behind the tail (Warnock & Warnock 1993). The transmitter would thus fall off during moult before autumn migration. During the study period 99 adult godwits were ringed (Blokland: 45, Zeevang: 54). In Blokland 22 of these godwits were equipped with a transmitter and in Zeevang 23.

Individual families were checked twice a week in 2002, 2003 and 2004 with binoculars and a 20–60x telescope. At every visit the presence or absence of families and chicks was noted and at the age of 25–35 days the number of fledglings per family was counted. Chicks were assumed to have fledged successfully if they were still alive at the fledging age of 25 days (Cramp & Simmons 1983, Schekkerman & Müskens 2000). If the exact number of fledglings could not be determined, a minimum and a maximum estimate were used. The minimum estimate was set to the number of chicks that were observed to have reached the fledging age, or to zero if a family disappeared before the chicks reached the fledging age. The maximum estimate was equal to the number of chicks that hatched in a nest, or the maximum number possible if less chicks than that were known to be alive with certainty at some time before the fledging age. When a family disappeared from the study area immediately after hatching all chicks were assumed to have died. In about half of these cases the marked parents were resighted without chicks within 25 days after hatching, confirming that none of the young had fledged.

Weather data

Data on daily minimum temperature and duration of rainfall during the breeding season measured near Schiphol airport (c. 10 and 30 km from Blokland and Zeevang, respectively) were obtained from the Royal Dutch Meteorological Institute (KNMI). These weather data were summed over the first week after hatching (when chicks still depend on brooding by their parents for thermoregulation) and over the whole chick rearing period until fledging (25 days).

Reproductive output

Reproductive output (Y, number of fledglings produced per breeding pair) was calculated using the following formula (Schekkerman & Müskens 2000):

$Y = (1 + R \times (1 - N)) \times N \times E \times C$,

in which N represents nest success (the probability that a nest hatches one or more chicks), R the probability of a replacement clutch after nest failure, E the number of eggs hatching per successful nest and C chick survival until fledging. The probability of a replacement clutch (R) was assumed to be 0.5, following Schekkerman & Müskens (2000). Nest success and chick survival of replacement clutches was assumed equal to that of first clutches.

The last part of the formula, number of eggs hatched times chick survival ($E \times C$) can be replaced by the probability that a pair raises at least one chick to fledging (S) times the number of fledglings per successful pair (F). The formula for Y can then be rewritten to:

$Y = (1 + R \times (1 - N)) \times N \times S \times F$.

Data analysis and statistics

Nest success was calculated from daily survival rates DSR following Mayfield (1975) as $DSR^{np} \times 100\%$, in which the nest phase np (day of laying first egg to day of hatching) was assumed to be constant over years and sites at 26 days (Cramp & Simmons 1983). Chick survival was calculated by dividing the total number of chicks fledged by the total number of eggs hatched in each successful clutch.

To select the best models describing reproductive output, we used GLMs and the RSEARCH command in Genstat (Payne *et al.* 2006) using the AIC criterion. Explanatory variables were laying and hatching dates, and year and site effects and their interactions, if significant. We explored four response variables: 1) daily survival rate of nests DSR (binomial distribution with logit link function and binomial totals of one), 2) number of eggs hatched per successful nest (binomial distribution with logit link function and binomial totals set to four, the maximum and usual number of eggs per nest), 3) minimum and maximum number of chicks fledged (chick survival, binomial distribution with logit link function and binomial totals set to the number of chicks hatched in a nest) and 4) minimum and maximum probability of a pair being successful (at least one chick fledged, binomial distribution with logit link function and binomial totals set to one), together with the total number of chicks fledged per successful pair (Poisson distribution with logarithm link function). The variables included in the models describing the four response variables are given below.

1) DSR: Godwits usually start continuous incubation after laying the last or penultimate egg (Cramp & Simmons 1983). During the laying period, the nest is often left unattended and may therefore be more vulnerable to predation (Beintema & Müskens 1987). In addition, godwits are more eager to incubate towards the end of the nest

phase. Therefore we included effects of nest age in addition to those of date in the model describing the DSR. For nest age and date, a quadratic term was also included. To test these effects, we only included nests of which the start of laying was recorded with sufficient precision (see paragraph on nests and laying dates), as well as the date of hatching or failure, excluding nests that were visited less frequently than once a week. 2) The number of eggs hatched per successful nest: this metric is sensitive to both partial clutch losses (eggs disappearing due to e.g. predation) and hatching failure, and was tested for date effects. 3) Minimum and maximum chick survival and 4) minimum and maximum probability of a pair being successful: as it was sometimes difficult to determine how many chicks of a family fledged, but easier to determine whether or not any chicks fledged, we used the probability of a pair being successful, i.e. fledging at least one chick, together with the total number of chicks fledged per successful pair as an alternative measure of fledging success. We included hatching date and weather variables (cumulative minimum temperature and duration of rainfall during seven and 25 days after hatching) in the models describing minimum and maximum chick survival and the minimum and maximum probability of a pair being successful.

In addition, the age at which the last chick of a brood had disappeared before reaching the fledging age of 25 days, i.e. had presumably died, was calculated by taking the average of the age at which any chicks of a family were last recorded present, i.e. chick(s) seen or parents alarming, and the age at which they were first recorded absent, i.e. no chicks present and parents not alarming.

We used a level of significance of $\alpha = 0.05$.

RESULTS

Breeding pair densities

Breeding pair densities were nearly three times as high in Zeevang as in Blokland, both when territories and numbers of nests are considered. In Blokland the number of breeding pairs declined during the study period from 0.150 territories ha^{-1} in 2003 to 0.094 in 2005, with a mean of 0.129 (nest densities dropped from 0.194 nests ha^{-1} in 2002 to 0.111 in 2005, with a mean of 0.189), while in Zeevang numbers fluctuated between 0.269 territories ha^{-1} in 2005 to 0.469 in 2004, with a mean of 0.364 (nest densities were 0.592 nests ha^{-1} in 2002 and 0.715 in 2004, with a mean of 0.638).

Laying and hatching dates

Median laying dates ranged between sites and years from 14 to 25 April, median hatching dates from 11 to 28 May (Table 1). After log-transformation of the laying dates, both laying date and hatching date differed significantly between years (laying: $n = 251$, $P < 0.001$; hatching: $n = 159$, $P = 0.007$), and godwits tended to both lay and

Table 1. Median laying and hatching dates of Black-tailed Godwits in two study sites in The Netherlands in 2002–2005. Sample sizes are given between parentheses. Only nests found within 5 days from the start of laying are included for the laying date and nests visited at least once a week for the hatching date.

Year	Median laying date			Median hatching date		
	Blokland	Zeevang	Overall	Blokland	Zeevang	Overall
2002	25 April (20)	22 April (35)	22 April (55)	21 May (17)	20 May (16)	20 May (33)
2003	24 April (20)	21 April (45)	22 April (65)	28 May (17)	16 May (35)	17 May (52)
2004	14 April (25)	14 April (51)	14 April (76)	11 May (10)	11 May (27)	11 May (37)
2005	21 April (9)	15 April (46)	16 April (55)	26 May (10)	11 May (27)	13 May (27)
Overall	22 April (74)	19 April (177)	20 April (251)	22 May (54)	15 May (105)	16 May (159)

Table 2. Reproductive parameters and associated reproductive output of Black-tailed Godwit at two study sites in the years 2002–2005. Min. and max. prob. success = minimum and maximum probability of a pair being successful in raising chicks. Values given in bold were used to calculate reproductive output Y (see text).

Parameter	Blokland				Zeevang				Mean
	2002	2003	2004	2005	2002	2003	2004	2005	
Nest success N (*n* nestdays, nests)	**0.46** (463, 31)	**0.37** (439.5, 35)	**0.19** (388.5, 37)	0.45 (210, 17)	**0.22** (501, 50)	**0.71** (979, 62)	**0.28** (886, 76)	0.49 (724, 48)	**0.39** (4591, 356)
No. hatched per successful nest E (SD, *n*)	**3.412** (0.712, 17)	**3.235** (1.033, 17)	**3.500** (0.850, 10)	3.182 (0.603, 11)	**3.500** (0.857, 18)	**3.605** (0.623, 43)	**3.379** (0.820, 29)	3.532 (0.654, 47)	**3.464** (0.744,192)
% hatched per successful nest (SD)	88.0 (16.0)	82.4 (26.2)	87.5 (21.2)	84.1 (16.9)	87.5 (21.4)	90.7 (15.4)	87.1 (20.7)	90.4 (15.2)	87.2 (2.85)
Min. chick survival C_{min} (SD, *n*)	**0.266** (0.097, 16)	**0.046** (0.030, 11)	**0.185** (0.094, 9)	-	**0.031** (0.031, 8)	**0.093** (0.053, 17)	**0.127** (0.042, 19)	-	**0.133** (0.250, 80)
Max. chick survival C_{max} (SD, *n*)	**0.781** (0.102, 16)	**0.205** (0.121, 11)	**0.324** (0.135, 9)	-	**0.156** (0.124, 8)	**0.226** (0.096, 17)	**0.233** (0.086, 19)	-	**0.340** (0.044, 80)
Min. prob. success S_{min} (SD, *n*)	0.438 (0.512, 16)	0.182 (0.404, 11)	0.333 (0.5, 9)	-	0.125 (0.354, 8)	0.177 (0.393, 17)	0.368 (0.496, 19)	-	0.288 (0.456, 80)
Max. prob. success S_{max} (SD, *n*)	0.813 (0.403, 16)	0.273 (0.467, 11)	0.444 (0.527, 9)	-	0.25 (0.463, 8)	0.294 (0.470, 17)	0.368 (0.496, 19)	-	0.425 (0.498, 80)
Min. fledged per successful pair F_{min} (*n*)	2.14 (7)	1 (2)	1.67 (3)	-	1 (1)	2 (3)	1.14 (7)	-	1.61 (23)
Max. fledged per successful pair F_{max} (*n*)	3.31 (13)	3 (3)	2.5 (4)	-	2 (2)	2.6 (5)	2.14 (7)	-	2.77 (34)
Min. reproductive output Y_{min}	0.53	0.07	0.17	-	0.03	0.27	0.16	-	0.23
Max. reproductive output Y_{max}	1.56	0.32	0.30	-	0.17	0.66	0.30	-	0.59

hatch earlier in Zeevang, though the difference between sites was only significant for laying date ($P = 0.041$). Godwits started laying c. one week earlier in the last two years than in the first two. Hatching dates followed the pattern of laying dates.

Nest success

Daily survival rates (DSR) of nests varied between 0.937 and 0.987, resulting in a nest success varying between 19% and 71%, respectively (Table 2). Of the five different parameters included in the model describing DSR (year, site and their interaction, nest age and date), year (aliased with the interaction of year and site), interaction of year and site ($n = 3015$, $P = 0.006$) and a linear function of nest age proved significant ($P < 0.001$). DSR tended to increase with nest age, from 0.921 when the first egg had been laid (age: 1 day), to 0.981 just before hatching (age: 25 days).

Number of eggs hatched per successful nest

The number of eggs that hatched from successful nests did not differ between years or sites and tended to decrease with hatching date, but this effect was not significant (Table 2).

Chick survival and pair success

Chick survival and probability of a pair being successful was lowest in Zeevang in 2002 (0.03–0.16 and 0.13–0.25, respectively) and highest in Blokland in that same year (0.27–0.78 and 0.44–0.81, respectively, Table 2). Both maximum chick survival and maximum probability of a pair being successful differed between years ($n = 80$ families, $P = 0.03$ and 0.042, respectively). Maximum chick survival differed between sites, being higher in Blokland than in Zeevang ($P = 0.026$).

Both minimum and maximum probability of a pair being successful decreased with hatching date ($n = 80$ families, $P = 0.002$ and $P < 0.001$, respectively). The same goes for minimum and maximum chick survival, though the effect was not significant in the former ($P > 0.05$ and $P = 0.018$, respectively). Nests of successful pairs hatched on average about one week earlier than nests of pairs which failed to fledge young.

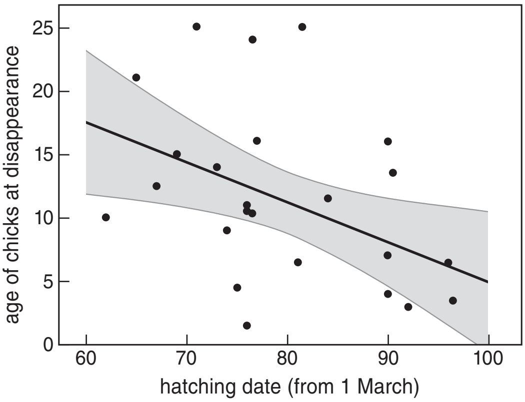

Figure 1. Estimated age at which the last chick(s) of a brood disappeared against their hatching date in days from the beginning of March ($n = 26$ broods, $P = 0.023$).

Of all weather variables, only the cumulative minimum temperature during the first week after hatching had a significant negative effect on minimum chick survival ($P = 0.022$).

Of some pairs it remained unknown whether they raised any fledglings or not. Excluding these pairs did not change the outcome of these analyses.

Minimum and maximum number of fledglings *per successful pair* did not differ between years and sites and did not depend on hatching date.

The age at disappearance of the last chick did not differ between years or sites but decreased linearly with increasing hatching date ($n = 26$, $P = 0.023$, Fig. 1).

Reproductive output and timing of breeding

Mean reproductive output in the period 2002–2004 at the two study sites was estimated at 0.23–0.59 fledglings per breeding pair (Y_{min} and Y_{max} in Table 2).

The outcomes of statistical tests on the date dependence of the probability of a pair being successful were more consistent than those on the date dependence of chick survival (see above), and estimates of pair success were probably more reliable than estimates of chick survival. Therefore we used pair success (S, calculated using the statistical model for the minimum and maximum

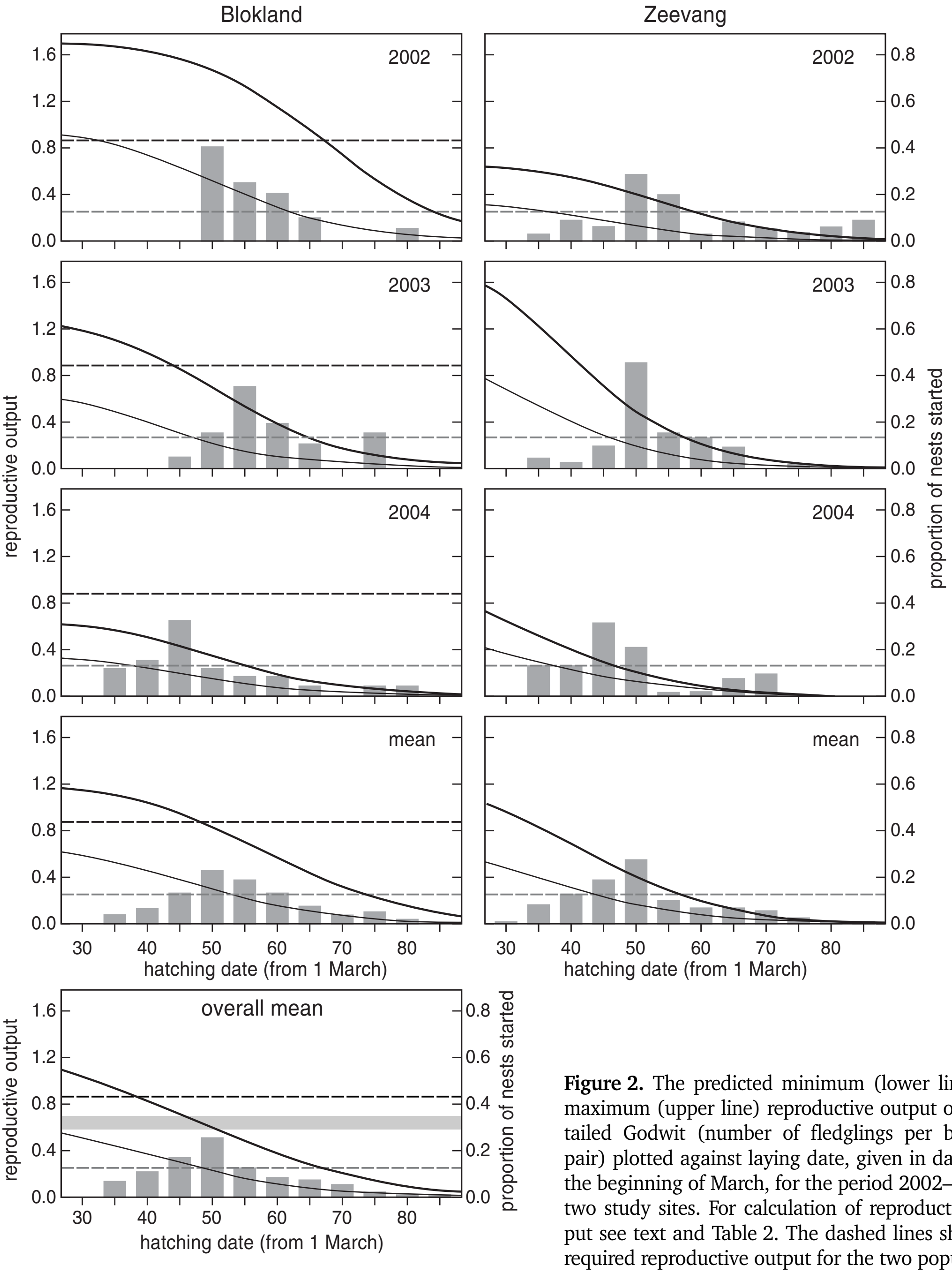

Figure 2. The predicted minimum (lower line) and maximum (upper line) reproductive output of Black-tailed Godwit (number of fledglings per breeding pair) plotted against laying date, given in days from the beginning of March, for the period 2002–2004 in two study sites. For calculation of reproductive output see text and Table 2. The dashed lines show the required reproductive output for the two populations to be stable. In the figures for Blokland the required reproductive output of Zeevang is also included, as the survival rate in Blokland may be underestimated due to a lower breeding site fidelity (see Discussion). The grey band in the lower panel indicates the required reproduction as estimated by Schekkerman & Müskens (2000, 0.6–0.7 fledglings per breeding pair). The bars represent the proportion of nests started during each five-day period.

probability of a pair being successful) multiplied by the number of fledglings per successful pair (F, Table 2) for the calculations of the date dependent reproductive output. The number of fledglings (F) per successful pair was assumed to be constant and mean minimum (1.61) and maximum (2.77) values were used. For the other variables, the year and site-specific values from Table 2 were used for the calculation of Y.

The relationships between reproductive output and laying date are shown in Fig. 2. Averaged over years and sites, the predicted number of fledglings per breeding pair decreased from c. 0.57–1.11 for clutches initiated on 28 March (first hatching date minus 26 days) to 0.22–0.59 for clutches initiated on 20 April, the median date, and 0.01–0.05 for those initiated on 26 May (last hatching date minus 26 days, final graph in Fig. 2). This means that an early nest is predicted to produce 2–2.5 times as many fledglings as a late nest, this factor being somewhat higher in Zeevang (2.5–3, median laying date 19 April) than in Blokland (1.5–2.5, median laying date 22 April, Table 1 and Fig. 2).

DISCUSSION

Nest success

The daily survival rate (DSR) of nests increased with nest age. During laying, nests are often left unattended and therefore probably run a higher risk of being detected and depredated. The DSR of nests of meadow birds has been found to be lower during laying (Beintema & Müskens 1987). In addition, at the end of the nest phase, godwits are more keen to resume incubation after disruption, which could imply a lower rate of desertion and increased incubation bouts and nest defence, decreasing predation rates. DSR does not seem to depend on the timing of laying, though the outcome may be different in areas where nests are not protected during agricultural activities and grazing and in years with severe weather in early spring. In all study years daily mean temperatures in March and April were at or above average and dropped only once below zero in 2005 at the beginning of March (based on data from 1981–2000), which may hide date effects present in other years.

Hegyi & Sasvari (1998) also did not find any effect of laying date on clutch survival in Lapwings and godwits. However, Teunissen *et al.* (2005) found a quadratic effect of date on daily survival rates of godwit and Lapwing nests, but they did not correct for effects of nest age. In their study, predation rates increased at both ends of the breeding season. As early in the season many nests are still in the laying phase, this may partly explain why early nests would have lower survival rates. However, it does not explain lower nest survival at the end of the season. If nest success declines with breeding season, reproductive output will decline even more than suggested by our results.

Chick survival and reproductive output

Except for Blokland in 2002, chick survival and reproductive output were lower than reported in most previous Dutch studies, but similar to Schekkerman *et al.* (2008a) who studied reproductive success in the same period. According to Schekkerman and Müskens (2000), each breeding pair needs to produce at least 0.6–0.7 fledglings per year to ensure a stable population, assuming an adult survival of 0.80–0.85 and first year survival after fledging of 0.6–0.7. Reproductive output reached this value only once in Blokland (in 2002) and possibly once in Zeevang (maximum, but not minimum reproductive output in 2003). Performing the same calculations with site-specific adult survival estimates of 0.93 for Zeevang and 0.81 for Blokland (Roodbergen *et al.* 2008), the reproductive output should be around 0.26 fledglings per year for the first and 0.87 for the second site. Only half of the maximum estimates (in 2002 in Blokland and in 2003 and 2004 in Zeevang) and one out of six of the minimum estimates reached these values (Zeevang 2003, Table 2). However, if apparent adult survival in Blokland is underestimated due to lower breeding site fidelity at this site (as suggested by Roodbergen *et al.* 2008) and should in reality equal adult survival at Zeevang, reproductive output should have been sufficient at this site in 2002 (both minimum and maximum estimate), and possibly in 2003 and 2004 (maximum estimate).

It is unlikely that all adult godwits attempt to breed every year, hence the mean reproductive output of the whole population will be even lower than our estimates. Schekkerman *et al.* (2008a) show that chick survival and reproductive output have declined substantially over the past 30 years.

Timing of breeding and reproductive output

Reproductive output declined rapidly during the breeding season due to declining chick survival. This decline is probably even underestimated as parameter R, the probability of a replacement clutch after nest failure, is not constant but decreases with date and/or nest age (Schekkerman & Müskens 2000, Buker & Winkelman 1987), and as the decline in chick survival was not incorporated in the estimate of productivity from replacement clutches. At the population level, the effect of timing of breeding may even be stronger, as in many bird species, early-born chicks have a higher post-fledging juvenile survival, start breeding at a younger age and/or are more successful in their first breeding attempt (Newton & Marquiss 1984, Spear & Nur 1994).

Possible causes of decrease in chick survival with hatching date

Both chick survival and probability of a pair being successful decreased with increasing hatching date. So did the age at which the last chick of a brood had disappeared, which reinforces these findings, even if this age may not be representative for all chicks of a family. A decrease in chick survival with hatching date is found in many bird species (e.g. Spear & Nur 1994, Brinkhof *et al.* 1997, Arnold *et al.* 2004, Arnold *et al.* 2006). Among meadow birds, it has been observed in Oystercatchers (Harris 1969), Lapwings (Hegyi & Sasvari 1998) and Black-tailed Godwits (Hegyi & Sasvari 1998, Schekkerman *et al.* 2005), but not in the Redshank (Ottvall 2005).

The strong decline in chick survival, and thus in reproductive output, with hatching date may have several proximate causes.

(1) Parental quality. In many bird species, good quality and/or experienced individuals start breeding earlier than conspecifics of lower quality, and have a higher reproductive output (e.g. Newton & Marquiss 1984, Perdeck & Cavé 1992, Blomqvist *et al.* 1997, Arnold *et al.* 2004). Therefore, a correlation between timing of breeding and reproductive output may reflect parental quality rather than calendar date per se. Many studies have focused on separating timing of breeding effects from the effect of parental quality with the help of experimental manipulations (Common Terns *Sterna hirundo*: Arnold *et al.* 2004, European Coots *Fulica atra* Brinkhof *et al.* 1993, 1997). In our data we did not find any correlations between different aspects of parental quality (percentage of summer plumage, weight, condition) and hatching date nor any difference in hatching dates of nests of godwits that did and did not return the next year (unpubl. data, MR).

(2) Weather conditions. Good weather conditions can be very important, especially for chicks in their first week, as they cannot maintain their own body temperature and need to be brooded regularly by their parents. In cold and wet weather, chicks cool down more quickly and need to be brooded more often. This leaves them less time to search for food, which may cause reduced growth and finally starvation (Beintema & Visser 1989, Schekkerman & Boele in Schekkerman 2008.). In addition, food in the form of vegetation-dwelling insects may be less available and/or less accessible in such periods. Groen & Hemerik (2002) found that chick survival is lower in cold and wet springs. In our three years of data on chick survival, however, we did not find any significant correlations with rainfall and a negative correlation between minimum chick survival and cumulative minimum temperature during the first week after hatching. This may be an artefact caused by the effect of hatching date, as minimum temperatures increase with increasing date, while chick survival decreases. The lack of an effect of rainfall or low temperatures on chick survival may be due to the above average spring temperatures in these years. In 1984, 1986 and 1987, three out

of four years from the study period of Groen & Hemerik (2002), mean temperatures were below average, especially early in the breeding season. However, it does not seem likely that weather effects are responsible for the decrease in chick survival with hatching date.

(3) Food availability. Arthropod densities and biomass tend to increase in April and May, peak at the end of May and beginning of June, and decrease during the second half of June, partly due to mowing (Beintema *et al.* 1991, Schekkerman & Beintema 2007, Struwe-Juhl 1995). As chicks grow, their energy requirements increase (Schekkerman & Visser 2001), and possibly only in early chicks these requirements are met during the whole chick-rearing period. Later chicks will encounter less favourable food conditions at older ages, when energy requirements are highest. Indeed Beintema *et al.* (1991) found that daily weight gain in chicks older than 3 days declined with date. Chicks with a lower condition have a lower survival probability (Schekkerman *et al.* 2005). Although this daily weight gain already started declining at the end of May and Beintema *et al.* (1991) argue that the 'reduced growth does not correspond with a decrease in insect abundance, which takes place later', a relationship between insect abundance and chick growth cannot be excluded, as the timing of peak abundance of insects varied greatly with sampling method used and was measured in only two areas, while chick survival was based on national ringing data. Moreover, while insect abundance in preferred, uncut meadows peaks in late May, the availability of such meadows is already declining strongly before that date due to mowing. Their alternative explanation was that older chicks switch to feeding on earthworms, which become less available later in the breeding season. However, this switch seems unlikely, as we have never observed chicks feeding on earthworms, not even around fledging (pers. obs. MR).

(4) Predation pressure. In many areas predation is the main cause of death in godwit chicks, involving different species of predatory birds and mammals. According to Schekkerman *et al.* (2008b), predation has increased since the 1980s. They estimate that 70–85% of all disappearing chicks died from predation. Their data show that in godwits the probability of a chick disappearing, which usually meant it died, increased linearly with date, while the probability that a chick was predated by a bird showed a quadratic relationship with date, increasing in May and decreasing in June (Teunissen *et al.* 2005). They also found that predation, especially by birds, was highest on meadows with short grass where chicks are more visible, which may explain the predation peak at the end of May, when most meadows have been mown.

(5) Mowing. Mowing may influence chick survival directly and indirectly. As godwit families prefer meadows with tall vegetation, the chicks repeatedly run the risk of being killed during mowing activities (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Schekkerman *et al.* 2005, Teunissen *et al.* 2005). Schekkerman *et al.* (2008b) estimate that at least 5–10% of all chicks fall victim to agricultural activities. Kruk *et al.* (1997) estimate that 3–36% of the chicks present in a field died during mowing. As young chicks are more vulnerable to mowing (Kruk *et al.* 1997), this activity will have a stronger impact on late hatching broods. Mowing also negatively affects food availability, as it decreases densities of vegetation dwelling arthropods (Schekkerman & Beintema 2007, see point 3 above), and increases predation rates by removing cover (see 4). Chick survival is positively correlated with the percentage of meadows with tall vegetation during the chick-rearing period (Schekkerman *et al.* 2005). In the study sites of Schekkerman *et al.* (2005) in the years 2003–2005, 20% of the grassland area had been mown or grazed by the first week of May, while by the third week of June this percentage had increased to 100%. As the area of meadows with tall vegetation decreases, godwit families become more concentrated in these meadows and mowing and predation losses are likely to increase. Our data on mowing dates in Blokland in 2003 show that mowing started on 6 May, 22 days before the median hatching date, the percentage

of area that had been mown increasing gradually until 58% on 26 June (date of last measurement). Most mowing occurred that year from 25 to 31 May, just around the median hatching date. The remaining 42% of the area, which had not been mown, was mostly grazed by cattle and/or sheep.

Parallel to chick survival, reproductive output declines in many bird species during the breeding season (Newton & Marquiss 1984, Spear & Nur 1994, Arnold *et al.* 2004, Thyen & Exo 2005, Arnold *et al.* 2006). However, increased chick mortality later in the breeding season may explain – or contribute to – population declines, if the slope of the curve describing the relationship between chick survival and hatching date has become steeper over the past decades. Beintema (1995) found a slight seasonal decrease in recovery rates of godwit chicks in the period 1976–1985, but only in wet and not in dry years. However, the advance in ringing dates in meadow bird chicks in the period 1911–1974 described by the same author (1985) may indicate that selection pressure for early breeding has indeed become stronger. Also, if chicks that hatch late now have a lower survival than in the past, less late hatching chicks will be caught and ringed, and ringing dates will advance. However, ringing dates of Dutch godwit chicks have not shown a continued advance after the 1970s (van Santen 2000). Schekkerman (2008) extended the analysis of ringing dates of chicks of the Black-tailed Godwit in The Netherlands through 2006 and showed that since 1970 there has been no further advancement in laying date, and indeed in the four most recent years of the data set there is an unmistakable delay in laying date.

Considering the strong decline in reproductive output with laying date described in this paper, the question arises why Black-tailed Godwits did not further advance their laying dates, as this might theoretically greatly improve their breeding success and, consequently, fitness. Godwits usually arrive in The Netherlands at the end of February, at least a month before they start breeding. Timing of arrival, therefore, does not seem to be a constraint. It would be interesting to know the condition of the godwits at arrival and, being income breeders (Klaassen *et al.* 2001), how fast they can acquire enough reserves for breeding at or near their breeding grounds. Besides food, another factor which may be important for breeding is grass height: as godwits prefer to breed in tall grass, grass height may be limiting early in the season. Also, laying early may be too risky due to cold weather spells, especially if the value and/or occurrence of replacement clutches has decreased.

Management

Black-tailed Godwit reproduction rates may be greatly enhanced by facilitating early breeding, taking measures to increase nest success of early breeders, and by promoting chick survival late in the breeding season. This can be achieved by avoiding intensive grazing and other agricultural activities before and during the breeding season. Moreover, chick survival can be improved by delaying mowing and securing spatial heterogeneity, so godwits find suitable breeding habitat at any time during the breeding season. Mosaic management, a newly developed agri-environment scheme, includes the latter two recommendations, but does not sufficiently improve chick survival (Schekkerman *et al.* 2008a). However, results on effectiveness of an improved version of this type of management, in which the minimum area of suitable chick habitat available at any time was increased, look promising (Teunissen *et al.* 2007).

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SAMENVATTING

Om beter te begrijpen waarom de Grutto *Limosa limosa* in Nederland in aantal achteruitgaat, hebben wij in de periode 2002–2005 het voortplantingssucces bepaald van twee Nederlandse broedpopulaties. Verder hebben wij bekeken hoe de productie van jongen samenhangt met de timing van het broeden. De jaarlijkse legdata (mediane waarden) varieerden van 12 tot 25 april, de uitkomstdata van 11 tot 28 mei en beide verschilden significant tussen jaren. De legdata verschilden ook significant tussen gebieden. De dagelijkse overlevingskans van een nest nam toe met toenemende leeftijd en was afhankelijk van jaar en de interactie tussen jaar en gebied, maar niet van de datum waarop de eieren werden gelegd. Ook het aantal eieren dat uitkwam per succesvol nest was niet afhankelijk van de legdatum. De maximale kuikenoverleving (de schatting van het maximale aantal kuikens dat vliegvlug werd, gedeeld door het aantal uitgekomen kuikens) en de kans dat van een gezin minstens één kuiken vliegvlug werd, namen significant af met de datum van het uitkomen van de eieren. Dit resulteerde in een afname van het aantal jongen dat vliegvlug werd per nest met de legdatum. De kuikenoverleving was niet afhankelijk van de cumulatieve neerslagduur tijdens de opgroeifase, terwijl de minimale kuikenoverleving negatief gecorreleerd was met de cumulatieve minimum temperatuur tijdens de eerste week na uitkomen. Het aantal geproduceerde vliegvlugge jongen was in de meeste jaren te laag om te compenseren voor de sterfte van juveniele en adulte Grutto's en was lager dan in voorgaande studies. Mogelijke proximate oorzaken voor de afname van de kuikenoverleving gedurende het seizoen worden besproken: individuele kwaliteit van de oudervogels, weerseffecten, voedselsituatie, predatie en maaibeheer.

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