The Ongoing Decline of the Breeding Population of Black-Tailed Godwits Limosa l. limosa in The Netherlands is Not Explained by Changes in Adult Survival

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The ongoing decline of the breeding population of Black-tailed Godwits *Limosa l. limosa* in The Netherlands is not explained by changes in adult survival

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The Black-tailed Godwit *Limosa limosa* is a characteristic breeding wader of wet grasslands in The Netherlands which has suffered a strong population decline since the 1960s. Low breeding success has been implicated as the main driver of this decline and here we examine whether changes in adult survival could also have played a role. Adult godwits were colour-ringed and resighted from 2002 through 2005 at four study sites in The Netherlands. Apparent adult survival was estimated in program MARK using Burnham's model for both live resightings and dead recoveries. In addition, nest site fidelity was estimated at two of the sites by recording the distance between nest locations in successive years. Apparent adult survival was 0.93 (SE 0.03) in one study area and 0.81 (SE 0.04) in the other three sites. Overall apparent adult survival was 0.83 (SE 0.03). These values are similar to estimates from the 1970s and 1980s. Nest site fidelity was higher in the site with highest survival (median distance between nests in successive years: 49 m vs. 252 m in the other site), suggesting that the difference in apparent survival may result from differences in emigration rates. Thus, our results suggest that current adult survival is not different from rates 30 years ago, and therefore do not point to reduced adult survival as the driver behind the current population decline of Black-tailed Godwits.

Key words: adult survival, nest site fidelity, demography, population decline, Black-tailed Godwit

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INTRODUCTION

The Black-tailed Godwit Limosa limosa limosa is a characteristic breeding bird in Dutch meadows, but, as in the rest of Europe, numbers have been declining rapidly (BirdLife International 2004, Teunissen *et al.* 2005a) since the 1960s (Bijlsma *et al.* 2001). Intensification of agriculture and habitat loss due to land use change are considered major causes of the decline in meadow birds (Beintema *et al.* 1995, Wilson *et al.* 2004), while more recently predation of eggs and chicks may also have played a role (Teunissen *et al.* 2005b). Around 40% of the European population of the Black-tailed Godwit breeds in The Netherlands (BirdLife International 2004), which therefore play an important role in its conservation. Agri-environment schemes, compensating farmers for restrictions posed on agricultural activities that are harmful to breeding meadow birds, have been instituted, and a widespread nest protection campaign has been employed to halt further population declines in meadow birds on agricultural lands. Despite these measures, most species continue to decline (Teunissen & Soldaat 2006).

Data on demographic parameters in recent time are now necessary for better insight into processes underlying population decline and to increase effectiveness of conservation measures. Population decline may be caused by a reduction in reproduction, survival or both (Begon *et al.* 2005). For the Black-tailed Godwit, Kruk *et al.* (1997), Schekkerman & Müskens (2000) and Schekkerman *et al.* (2008) showed that reproduction in Dutch agricultural grasslands is often low and insufficient to compensate for adult mortality. Similarly, Ratcliffe *et al.* (2005) demonstrated that flood-dependent variation in productivity is likely to explain differences in population trends at the Ouse and Nene washes in England. However, these studies have used adult survival rates based on data from the 1970s and 1980s and from the subspecies *L. l. islandica* and the validity of these predictions therefore depend on whether or not these rates have indeed changed over time or differ between subspecies. Habitat and climatic changes in wintering areas (western Africa) or at stop-over sites, such as the conversion of wetlands to rice fields (Windmeijer & Andriesse, unpubl. data) and the decrease in rainfall (Hulme 1992, Dai *et al.* 2004), may have affected adult survival. In many European breeding birds wintering in Western Africa, adult survival is correlated with Sahel rainfall (Witstanley *et al.* 1974, Den Held 1981, Cavé 1983, Kanyamibwa *et al.* 1990, Peach *et al.* 1991, Kanyamibwa *et al.* 1993, Szep 1995, Foppen *et al.* 1999).

In The Netherlands several survival studies have been conducted. Beintema & Drost (1986) analyzed national ring recovery data from the period 1974–1980. They could only give a rough estimate for adult survival due to the low number of recoveries of godwits ringed as adult. Van Noordwijk & Thomson (2008) have recently analyzed national ring recovery data for the period 1960–2000, but they encountered problems in estimating survival rates towards the end of that period, because the number of individuals ringed in these years was lower and the reporting rate had declined from 9% in 1960 to 1% in 2000. Groen & Hemerik (2002) estimated return rates of colour-ringed Black-tailed Godwits in Polder Schaalsmeer in 1984–1987. Between 1987 and the present study there have been no additional colour-ring studies. Reliable estimates of adult survival rates in recent time are therefore still lacking, and we cannot yet exclude reduced adult survival as a factor contributing to the population decline.

Adult mortality often cannot be distinguished from permanent emigration, especially when survival analyses are based on data from local colour-ringing studies. Therefore information on nest site fidelity is valuable to complement local studies on survival, as low nest site fidelity is likely to be associated with an increased probability of temporary or permanent movements from the study area, resulting in lower resighting probability and/or apparent survival rate.

In this paper, we report estimates of survival in four colour-ringed Black-tailed Godwit populations in The Netherlands in recent time (2002–2005) and compare these with available literature data. In two of our study sites nest site fidelity is also estimated.

METHODS

Study areas

Research was carried out at four sites in The Netherlands (Fig. 1): Blokland (52°13'N, 4°49'E, province of Utrecht, c. 180 ha), Zeevang (52°31'N, 4°58'E, Noord-Holland, c. 130 ha), Schipluiden (51°59'N, 4°18'E, Zuid-Holland, c. 215 ha) and Delfstrahuizen (52°53'N, 5°50'E, Friesland, c. 310 ha). Current breeding densities of Black-tailed Godwits and recent population trends in these four study sites are detailed in Table 1.

N / sq. km
- 0 – 0.1
- 0.1 – 5
- 5 – 10
- 10 – 20
- 20 – 30
- >=30

Figure 1. The distribution of the Black-tailed Godwit in The Netherlands (Teunissen *et al.* 2005a) and the location of six study sites. 1=Blokland, 2=Zeevang, 3=Schipluiden, 4=Delfstrahuizen, 5=Workumerwaard (Both *et al.* 2006), 6=Schaalsmeer (Groen & Hemerik 2002). N/sq. km = breeding pairs per km^2
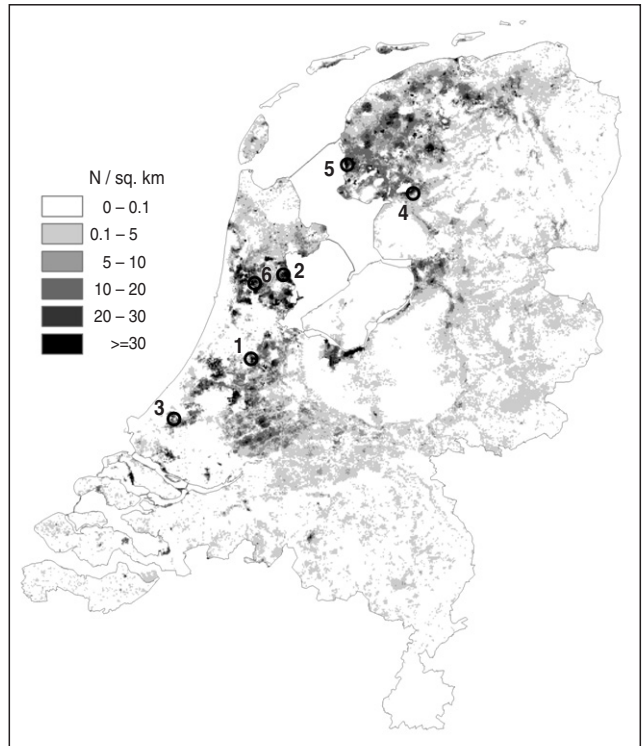
Table 1. Breeding densities, trends and adult survival estimates of Black-tailed Godwits at six sites in The Netherlands. Site numbers refer to the numbers in Fig. 1. Study periods are given between brackets.

Site	Current breeding density (pairs km^{-2})[1]	Trend[2]	Adult survival
1. Blokland	9–15[a]	+ (1975–1983), – (1991–2005)[abc]	0.81 (2002–2005, SD 0.04, n = 45)[l]
2. Zeevang	27–47[a]	± (1983–2006)[ad]	0.93 (2002–2005, SD 0.03, n = 54)[l]
3. Schipluiden	34[e]	+ (1973–1990), ± (1990–2005)[gh]	0.81 (2003–2005, SD 0.04, n = 17)[l]
4. Delfstrahuizen	27[e]	± (2000–2004)[f]	0.81 (2003–2005, SD 0.04, n = 16)[l]
5. Workumerwaard	32–59[i]	+ (1981–1989), ± (1989–2006)[ij]	0.95 (2004–2005, n = 65)i
6. Schaalsmeer	51[k]	– (1984–2001)[k]	0.81 (1984–1987, SD 0.07, n = 88)[k]

[1] the breeding density in Workumerwaard is given in nests km^{-2}
[2] + increasing, ± stable, – decreasing

Sources: [a]Roodbergen, unpubl. data, [b]Kuijk & van Dijk unpubl. data, [c]van den Bijtel, unpubl. data, [d]Provinciale Waterstaat van Noord-Holland, unpubl. data 1985, [e]Schekkerman et al. 2008, [f]Schekkerman, unpubl. data, [g]Klemann 2002, [h]van Paassen, unpubl. data, [i]Both *et al.* 2006, [j]Brandsma, Hoekstra & Nauta, unpubl. data, [k]Groen & Hemerik 2002, [l]this paper.

The sites are a mixture of intensively and extensively used grasslands, either mown for silage or grazed by dairy cattle and sheep. In Blokland and Zeevang roughly one third of the area is under management agreements, some aiming to protect meadow birds and some to increase plant diversity. The agreements directed at protection of meadow birds usually restrict farming activities, e.g. by protecting nests during farming activities, delaying mowing dates and leaving patches unmown to facilitate cover during the fledging phase. Both sites hold high densities of breeding meadow waders, mainly Black-tailed Godwits, Lapwings *Vanellus vanellus*, Redshanks *Tringa totanus* and Oystercatchers *Haematopus ostralegus*.

Polder Blokland was reclaimed from a peat bog in the Middle Ages by diking the peat land and lowering the ground water table (Bijlmakers & de Swart 1995). To improve the soil structure and fertility, municipal waste from the cities of Amsterdam and Utrecht has been deposited here since the 16th century until 1950. Because of this deposition, the top layer of the soil has been contaminated with heavy metals and organic pollutants (Klok *et al.* 2006).

Polder Zeevang is situated near the IJsselmeer, formerly a brackish bay open to the Wadden Sea prior to closure in 1932. After the peat marshlands were drained and cultivated around 1000–1100, the dehydrated peat sank beneath sea water level and was flooded frequently by the sea, despite the many dikes and dams built in the 13th century (Heidinga 1977). The polder could only be accessed by boat and was used extensively for haymaking and livestock grazing, until large-scale redistribution of land in the 1950s, construction of roads, and further lowering of the groundwater table facilitated agricultural intensification. The area is still relatively moist in spring due to high groundwater levels.

The data from Schipluiden and Delfstrahuizen derive from an evaluation of management agreements, aiming at the conservation of Black-tailed Godwits within an economically sustainable farming practice (see Schekkerman *et al.* 2008, where detailed site descriptions can be found). At Schipluiden c. 17% of the area is under management agreements, at Delfstrahuizen this percentage is higher, 36% (H.S., unpubl. data). All areas were situated on peat, or on clay on peat soils.

Capture and ringing

Adult Black-tailed Godwits were captured on the nest using a kidney-shaped walk-in trap or a small clap net and marked with colour-rings in 2002, 2003 and 2004. Eggs were replaced by artificial eggs during capture attempts to avoid damage. Trapping was conducted at the end of incubation, when godwits are eager to incubate and the probability of abandonment of the nest is minimal (Bub 1976). At five nests, both partners were trapped and ringed, at all other nests only one incubating parent was caught. Captured godwits were measured and weighed and provided with an individual combination of darvic colour-rings and a metal ring with an individual number to facilitate individual recognition without recapture. Sex was determined from biometry and plumage characters; this may have involved a few sexing errors (Schroeder *et al.* 2008). Adult godwits were colour-ringed in Blokland (45 birds; 2002–2004), Zeevang (54 birds; 2002–2004), Schipluiden (17 birds; 2003) and Delfstrahuizen (16 birds; 2003).

Apparent adult survival

Apparent adult survival was estimated from annual return rates of marked adults. Between 2003 and 2005, the study sites and their immediate surroundings, as well as some nearby collective roosting sites (maximum distance 12 km), were searched throughout spring (from end of February to July), starting with the arrival of the first godwits, using binoculars and a telescope with magnification 20–60x. Readings were made at close range and under good conditions.

Information on live resightings and dead recoveries was collected in an encounter histories file, with sex and study site as grouping factors. Data were analyzed with the model for joint live and dead encounters of Burnham (1993) in program MARK (White & Burnham 1999). This model gives

estimates for true survival (*S*), site fidelity (*F*), resighting probability of live animals (*p*) and reporting rate of dead animals (*r*), which are computed via numerical maximum likelihood techniques. Live resightings and dead recoveries were restricted to the study sites, consequently the site fidelity parameter *F* could not be estimated and was fixed to 1. Parameter *S* therefore did not represent true survival but 'local' or 'apparent' survival, which is potentially confounded with permanent emigration from the study sites.

The subset of models with different parameter constraints to be tested was based on *a priori* expectations. The reporting rate was expected to differ between Zeevang and the other sites, as in Zeevang nests were found by scanning the ground and nest search effort was high, while grassland swards were short. Furthermore, in Delfstrahuizen and in one year (2005 in Blokland and Zeevang) resighting rate was expected to be lower, due to a lower frequency of visits.

Our initial model included site and time effects (site x year) for resighting rate and survival and only site effects for reporting rate, as we did not have enough data to also include year. Next, models were simplified by testing all possible combinations (16) of parameter constraints based on the above *a priori* expectations:

– Two different parameter sets for reporting rate *r*: *r* constant (*r*(.)), and a separate *r* for Zeevang vs. all other sites (*r*(Z)).

– Five different parameter sets for resighting rate *p*: *p* constant (*p*(.)), a separate *p* for Delfstrahuizen only (*p*(D)), a separate *p* for Zeevang and Blokland in 2005 and Delfstrahuizen combined (*p*(Z05B05D)) and a separate *p* for both Zeevang and Blokland in 2005 and for Delfstrahuizen (*p*(Z05B05,D)).

– Six different parameter sets for apparent survival *S*: *S* constant (*S*(.)) and a separate *S* for each study area (*S*(a)). Because one of our best models estimated site-specific survival (see Results), we simplified this model by including a separate *S* for each study site, by singling out each study site from the rest, which resulted in four new models (S(Z), S(B), S(D), S(S)).

We used Akaike's Information Criterion, corrected for small sample size (AICc), for model selection (Burnham & Anderson 2002). Models within 2 AICc units of the model with lowest AICc value (ΔAICc < 2) were considered to be substantially supported by the data.

The most general model (the one including all terms considered relevant, Model 14 in Table 2) was tested for overdispersion by calculating both the bootstrap Goodness of Fit ĉ and the median ĉ (White & Burnham 1999). The data were not overdispersed (bootstrap GOF ĉ = 0.912, estimated median ĉ = 0.983). The variance inflation factor ĉ was estimated with a free parameter for *F*, since GOF testing cannot be performed with fixed parameters. It gave exactly the same results for all estimated parameters (*F* = 1.0, SE < 0.01) and model deviance as the most general model with *F* fixed at 1.

Nest site fidelity

To identify the nests belonging to colour-ringed godwits, nests were observed with a telescope after disturbance, until one of the partners returned to incubate. Nest ownership was also established when a colour-ringed partner left the nest or during capture attempts. The location of the nest was determined with a GPS. From these data the distance between nests of the same individual in successive years was calculated, which was used as a measure of nest site fidelity. Throughout this paper, nest site fidelity refers to the degree of fidelity to the nest site of the previous year, expressed in distances in meters. Thus, the larger the distance between nest sites in successive years, the lower the nest site fidelity. A one-sided Mann-Whitney U test was performed to compare nest site fidelity in Blokland and Zeevang and in males and females, as we expected the nest site fidelity to be higher in the site with highest apparent survival (Zeevang, see Results) and in males (Groen 1993).

The study site in Blokland is somewhat larger and has a different shape than the site in Zeevang (180 vs. 130 ha), which might cause a bias in nest site fidelity estimates as in larger areas larger distances can be observed (van Noordwijk 1995). To

Table 2. Survival models for the Black-tailed Godwit and their characteristics. AICc is the Akaike's Information Criterion corrected for small sample size. S = survival probability, p = resighting probability, r = reporting rate of dead birds. Fidelity rate (F) is fixed to 1 in all models. Parameter estimates of models 1, 3 and 10 are given in Table 3.

No.	Model[1]	AICc	DAICc	Number of parameters	Deviance
10	S(Z)p(Z05B05D)r(Z)	313.85	0.00	6	30.40
1	S(.)p(D)r(.)	317.54	3.69	4	38.23
2	S(.)p(D)r(Z)	317.73	3.88	5	36.35
3	S(a)p(Z05B05D)r(Z)	317.81	3.96	8	30.17
4	S(.)p(Z05B05D)r(Z)	317.95	4.10	5	36.58
5	S(.)p(Z05B05D)r(.)	318.14	4.29	4	38.83
6	S(.)p(.)r(.)	318.71	4.86	3	41.45
11	S(S)p(Z05B05D)r(Z)	318.75	4.90	6	35.31
7	S(.)p(.)r(z)	318.77	4.92	4	39.46
12	S(B)p(Z05B05D)r(Z)	318.93	5.08	6	35.48
8	S(.)p(Z05B05,D)r(Z)	319.23	5.38	6	35.78
9	S(.)p(Z05B05,D)r(.)	319.23	5.38	5	37.86
13	S(D)p(Z05B05D)r(Z)	319.50	5.65	6	36.05
14	S(axt)p(axt)r(a)	343.24	29.39	28	10.61

[1]The information between brackets shows for which group a separate parameter is calculated. Groups are separated by commas. a = site, Z = Zeevang, B = Blokland, D = Delfstrahuizen, S = Schipluiden, t = time, 03 = 2003, 04 = 2004, 05 = 2005, '.' = constant. For example: S(a) p(Z05B05,D) r(Z) has a separate parameter for survival in each of the four sites, one for resighting probability in Blokland and Zeevang in 2005, one for resighting probability in Delfstrahuizen, one for resighting probability in Zeevang and Blokland in 2003 and 2004 and in Schipluiden, one for reporting rate in Zeevang, and one for reporting rate in the other three sites, and F = 1.

correct for such a bias, we randomly and without replacement assigned returning breeders of year x to the nests observed in the same site in year x+1. This procedure was repeated 1000 times for each year and site combination, to obtain distributions of random distances. Observed distances by year and site were compared to these distributions, and if the probability of a random value being smaller than the observed value was less than 0.05 (one-sided $\alpha = 0.05$, Dingemanse *et al.* 2003) we concluded that godwits tended to nest significantly closer to their previous nest site than expected. Finally, we calculated the differences between observed values in Blokland and those in Zeevang and between random values in both sites. The mean difference in observed distances in the two sites was said to be significant if random differences were either smaller or larger in no more than 2.5% of cases (two-sided $\alpha = 0.05$).

We estimated the number of individuals that were likely to nest outside the study sites, and may thus not have been resighted, by drawing a circle around each nest with a radius of the site-specific median distance and estimating the area of these circles inside and outside the study site. Statistical analyses were carried out in Genstat version 9 (Payne *et al.* 2006).

RESULTS

Apparent adult survival

In total, data on 393 bird years were collected. During the study, seven godwits were found dead, usually showing signs of predation; one godwit in each area, except in Zeevang, where four dead godwits were found (see Appendix 1).

Our initial best model (Model 1) estimated

Table 3. Parameter estimates, standard errors and 95% confidence intervals of the models 1, 3 and 10 of Table 2. Parameters are all annual rates and probabilities. See Table 2 for an explanation of models and parameters.

| Model: | 1 | | | 3 | | | 10 | | |
| | S(.)p(D)r(.) | | | S(a)p(Z05B05D)r(Z) | | | S(Z)p(Z05B05D)r(Z) | | |
Parameter	Estimate	SE	95%CI	Estimate	SE	95%CI	Estimate	SE	95%CI
S(.)	0.83	0.03	0.78–0.88	-	-	-	-	-	-
S(Z)	-	-	-	0.93	0.03	0.84–0.97	0.93	0.03	0.84–0.97
S(B)	-	-	-	0.82	0.05	0.72–0.89	-	-	-
S(D)	-	-	-	0.81	0.08	0.60–0.92	-	-	-
S(S)	-	-	-	0.78	0.08	0.60–0.90	-	-	-
S(BDS)	-	-	-	-	-	-	0.81	0.04	0.73–0.87
p(D)	0.84	0.10	0.54–0.96	-	-	-	-	-	-
p(ZBS)	0.97	0.02	0.90–0.99	-	-	-	-	-	-
p(Z03Z04B03B04S)	-	-	-	0.98	0.02	0.91–0.99	0.98	0.02	0.91–0.99
p(Z05B05D)	-	-	-	0.88	0.05	0.76–0.94	0.88	0.05	0.76–0.94
r(.)	0.13	0.05	0.06–0.24	-	-	-	-	-	-
r(Z)	-	-	-	0.40	0.20	0.11–0.78	0.40	0.20	0.11–0.77
r(BDS)	-	-	-	0.08	0.05	0.03–0.23	0.08	0.05	0.03–0.23

constant survival and reporting rates, and a separate resighting rate for Delfstrahuizen vs. the other three sites (Table 2). Corresponding estimates were 0.83 ± 0.03 for the overall apparent adult survival rate, 0.84 ± 0.10 for resighting rate at Delfstrahuizen, 0.97 ± 0.02 for resighting rate at the other sites and 0.13 ± 0.05 for reporting rate (Table 3). Eight other models (Models 2–9) fitted the data equally well (DAICc<2, as compared to Model 1). One of these models (Model 3) included site-specific survival. Estimated survival rates derived from this model suggested that survival was higher in Zeevang compared to the other three study sites (0.93 ± 0.03 in Zeevang vs. 0.82 ± 0.05 in Blokland, 0.81 ± 0.08 in Delfstrahuizen and 0.78 ± 0.08 in Schipluiden, Table 3). We then simplified the model further (following procedures outlined in the Methods) and found a new best model (Model 10, Table 2) that confirmed this notion. This model fitted the data best, with an AICc value more than 2 units smaller than all other models (DAICc ≥ 3.69, Table 2).

According to this model, apparent survival was 0.93 ± 0.03 in Zeevang and 0.81 ± 0.04 in the other sites (Table 3). Resighting probability was high in Schipluiden and in 2003 and 2004 in Zeevang and Blokland (0.98 ± 0.02) and somewhat lower in 2005 in Zeevang and Blokland and in Delfstrahuizen in all years (0.88 ± 0.05). Reporting rate was higher in Zeevang (0.40 ± 0.20) than in the other study sites (0.08 ± 0.05).

Nest site fidelity

The distance between nests in successive years ranged from 4 to 855 m (median 49 m) in Zeevang, and from 4 to 812 m (median 252 m) in Blokland. Nearly 60% of all nests were located within 100 m of the nest site of the previous year: 64% in Zeevang and 47% in Blokland. Nest site fidelity was higher in Zeevang than in Blokland ($n_Z = 25$, $n_B = 15$, $U = 126.5$, $P = 0.045$). When accounting for dependency in the observations by (randomly) excluding values originating from the same individuals in subsequent years, the difference was still significant ($n_Z = 22$, $n_B = 12$, $U = 85.5$, $P = 0.048$). After excluding pairs that remained together in both years, females tended to nest further away than males, but this difference

was not significant ($n_m = 10$, $n_f = 25$, $U = 88.0$, $P = 0.093$).

Mean observed distances between nests in consecutive years were significantly smaller than mean random distances in both sites and all years ($P < 0.01$), except in Blokland in 2002 ($P = 0.077$). Mean distances observed in Zeevang were 240.3 m smaller than those observed in Blokland, while mean random distances were 56.3 m larger in Zeevang than in Blokland, but this difference was not significant ($P = 0.121$).

In Blokland c. 10–15% of individuals may have bred outside the study area in the next year and were thus more likely to have been missed, while in Zeevang this value was around 0–5%.

DISCUSSION

Apparent adult survival appeared to be higher in Zeevang than in the other sites. Assuming these estimates reflect true survival and would remain constant over age and years, a godwit in Zeevang would have an adult life expectancy ($-1/(\ln S)$, Lawless 1982) of nearly 14 years, while in the other three sites life expectancy would only approach 5 years.

In this local study the fidelity parameter F cannot be estimated, and therefore it is hard to say whether true survival, site fidelity or both are higher in Zeevang compared to the other sites. Nest site fidelity based on nests identified within the study areas tended to be higher in Zeevang than in Blokland, although the sample size was too small to draw firm conclusions. This result suggests that lower apparent survival in Blokland may be partly caused by birds moving out of the area, as illustrated by the simple analysis showing that in Blokland c. 10–15% of breeding godwits is likely to have bred outside the study area in the next year compared to 0–5% in Zeevang.

The apparent survival of 0.93 in Zeevang is in the range of the preliminary estimate of survival in the Workumerwaard in the northwest of The Netherlands (Fig. 1), where a return rate of 0.95 was found in 2004–2005 (Both *et al.* 2006). After

correcting for the resighting probability, the corresponding survival rate may be even higher in Workumerwaard. In Workumerwaard nest site fidelity is probably high, as there is no suitable breeding habitat in the area surrounding the study site (Both *et al.* 2006) which might explain the high estimate for apparent survival in this population. The high apparent survival in Zeevang is also comparable to the survival of 0.87–0.94 in the *islandica* subspecies reported by Gill *et al.* (2001). *L. l. islandica* breeds almost exclusively on Iceland and winters on the coast of Western Europe (Gunnarsson *et al.* 2005a). The survival estimates for *L. l. islandica* are independent of nest site fidelity, as most resightings originate from wintering sites all over Western Europe and from spring staging sites in Iceland (Gill *et al.* 2001). Possibly, the differences in apparent survival between Blokland, Delfstrahuizen and Schipluiden on the one hand and Zeevang, Workumerwaard and Iceland on the other are primarily caused by differences in site fidelity. If so, apparent survival estimates in the first three sites are more strongly confounded with emigration rates and therefore less reliable, and possibly underestimated. More data on nest site fidelity and resightings outside the study areas are needed to see whether this is the case. Such knowledge is of high importance for effective species conservation, as in general in long-lived species a small increase in adult survival can have a disproportionately large effect on population viability as compared to a similar increase in reproduction (Stahl & Oli 2006).

Nest site fidelity is considered to be positively related to habitat quality (Groen 1993, Ganter & Cooke 1998, Badyaev & Faust 1996). Groen (1993) found that Black-tailed Godwits breeding at higher quality habitat and with successful nests are more faithful to their breeding sites. Also, breeding pair densities can be higher at better quality sites, leaving fewer vacancies and forcing individuals to remain on their former territory. Indeed, Zeevang seems a good quality site, as breeding pair densities are high in this area and, in contrast to most breeding areas in The Netherlands, the population in this study area did not

decline over the last decades (Table 1). However, reproductive output in Zeevang was similar to the reproductive output in the other three areas (Roodbergen unpubl. data, Schekkerman *et al.* in press 2008) and no significant positive relation between nest success and associated nest site fidelity could be found in the present study.

Differences in apparent survival between sites might also originate from differences in true survival, for instance due to different wintering and stopover sites, as is the case in the Icelandic godwit. In *islandica*, godwits breeding on high quality habitat also overwinter on high quality sites, and *vice versa* (Gunnarsson *et al.* 2005a,b), which is also reflected in survival (Gill *et al.* 2001). To shed more light on differences in true survival rates between Dutch breeding populations, data on wintering and stopover locations of these birds are needed.

The polluted soil at Blokland may also have negatively influenced adult survival at this site, but as apparent adult survival in Blokland was similar to that in Delfstrahuizen and Schipluiden, which are not polluted, we cannot relate the lower survival at Blokland to this factor.

The apparent adult survival in the four areas under study in the period 2002–2005 is comparable to the return rate of 0.81 in 1984–1987 estimated by Groen & Hemerik (2002, Table 1), and the rough survival estimate of 0.8 in 1974–1980 reported by Beintema & Drost (1986). These historical survival data and the data presented in this paper were probably all collected in relatively good quality habitat and do not necessarily reflect the situation in less profitable breeding areas. Yet, estimated apparent survival rates in Zeevang and Workumerwaard, which are probably more reliable than those in the other study sites, are high and resemble those found in subspecies L. l. islandica, whose numbers have increased substantially in recent decades (BirdLife International 2004). It is also worth noting that there is no obvious relation between the recent adult survival estimates (all within the range 0.81–0.95) and the population trends at the five sites concerned (Table 1).

Our overall survival estimate of 0.83 is even higher than the 0.77 reported by van Noordwijk & Thomson (2008), though this may also be caused by differences in methods (mostly live resightings vs. dead recoveries). Van Noordwijk & Thomson (2008) did not find strong indications for changes in either adult or juvenile survival in the period 1960 to 2000, except for a reduction in adult survival in the late 1990s. Because this occurred near the end of their study period, van Noordwijk & Thomson (2008) could not distinguish whether this was a structural decline or a short-term catastrophic event. Our data, revealing adult local survival rates in the early 21st century that are as high as values observed in 1970s and 1980s, suggest that the latter is more likely to have been the case. Therefore we conclude that our results do not support the hypothesis that the current population decline in The Netherlands is caused by a decrease in adult survival. Instead, there is evidence that the survival of godwit clutches and particularly chicks has decreased over the past decades (Schekkerman *et al.* 2008). Little is known on juvenile survival. Studies on other grassland shorebirds also do not reveal negative trends in adult survival (Lapwing, Bak & Ettrup 1982, Peach *et al.* 1994; Redshank, Thompson & Hale 1993, Insley *et al.* 1997, Ottvall 2005; Oystercatcher, Neve & van Noordwijk 1997, Atkinson *et al.* 2005), while reproduction has declined in most species (Hulscher & Verhulst 2003, Besbeas *et al.* 2002, pers. comm. H. Hötker).

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SAMENVATTING

De Grutto *Limosa limosa* is in Nederland een karakteristieke weidevogel van natte graslanden, waarvan de aantallen sinds de jaren zestig van de twintigste eeuw sterk in aantal zijn afgenomen. Een lage reproductie wordt gezien als de belangrijkste oorzaak voor de afname. In dit artikel bekijken wij of een verandering in de overleving van volwassen Grutto's hierbij ook een rol kan hebben gespeeld. Daartoe zijn in de periode 2002–2005 in vier onderzoeksgebieden volwassen Grutto's voorzien van kleurringen en is in de daaropvolgende jaren hun terugkeer naar het broedgebied bepaald. De schijnbare overleving (kans dat een vogel overleeft tot het volgende jaar en terugkeert naar het broedgebied) werd geschat met behulp van het programma MARK, waarbij gebruik werd gemaakt van het model van Burnham voor waarnemingen aan zowel levende als dode Grutto's. Tegelijkertijd is de broedplaatstrouw bepaald in twee van deze gebieden door de afstand te

bepalen tussen nesten van een zelfde individu in opeenvolgende jaren. In één gebied was de schijnbare overleving 0,93 (standaardfout 0,03), in de drie andere gebieden 0,81 (standaardfout 0,04). De overleving in de vier gebieden samen was 0,83 (standaardfout 0,03). Deze waarden zijn vergelijkbaar met waarden uit de jaren 1970 en 1980. De broedplaatstrouw was hoger in het gebied met de hoogste schijnbare overleving (geometrisch gemiddelde afstand tussen nesten in opeenvolgende jaren 49 m tegen 252 m in het gebied met de laagste schijnbare overleving). Dit wijst erop dat het verschil in schijnbare overleving kan zijn veroorzaakt door verschillen in de mate van emigratie. Onze resultaten wijzen erop dat de overleving van volwassen Grutto's in de laatste 30 jaar niet is afgenomen en dat er dus geen reden is om aan te nemen dat de huidige populatieafname wordt veroorzaakt door een afgenomen overleving van de volwassen vogels.

Appendix 1. Summary of the live and dead encounters input file used for the survival analysis in MARK. Occ. = occasion of release, j = year in which godwits released at occasion i are resighted or reported respectively. For live recapture data, the number of releases (R(i)) are shown on the left side, and the number of live recaptures for each occasion is shown for each set of releases. For dead recovery data, the number of releases for the last live release (R(i)) is shown on the left side, and the number of dead recoveries for each occasion and release is shown.

Study site		Live encounters						Dead recoveries					
	Occ.	R(i)	j = 2	3	4	Total		Occ.	R(i)	j = 1	2	3	4	Total
Zeevang	1	19	15	1	0	16		1	3	2	0	0	0	2
	2	31		29	0	29		2	2		1	0	0	1
	3	49			41	41		3	8			0	0	0
								4	41				1	1
Blokland	1	23	20	0	0	20		1	3	0	0	0	0	0
	2	30		21	1	22		2	8		1	0	0	1
	3	33			25	25		3	8			0	0	0
								4	26				0	0
Delfstrahuizen	1	0	0	0	0	0		1	0	0	0	0	0	0
	2	16		9	2	11		2	5		1	0	0	1
	3	9			8	8		3	1			0	0	0
								4	10				0	0
Schipluiden	1	0	0	0	0	0		1	0	0	0	0	0	0
	2	17		13	0	13		2	4		1	0	0	1
	3	13			10	10		3	3			0	0	0
								4	10				0	0