REPRODUCTIVE SUCCESS AND SURVIVAL OF BLACK-TAILED GODWITS *LIMOSA LIMOSA* IN A DECLINING LOCAL POPULATION IN THE NETHERLANDS

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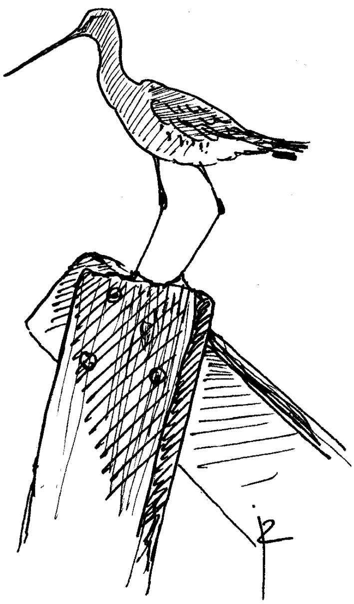

Groen N.M. & L. Hemerik 2002. Reproductive success and survival of Black-tailed Godwits *Limosa limosa* in a declining local population in The Netherlands. Ardea 90(2): 239-248.

During a monitoring study from 1984-87, a population of 70-95 breeding pairs of the Black-tailed Godwit *Limosa limosa* and their offspring were observed. Clutch size, fraction hatched, fledging probability, first year survival and the yearly resight probability for birds returning to the study area were estimated. Nest success ranged from 41.4% to 74.6%. The survival of chicks to fledging was significantly lower in cold and wet springs (20.8%) than in springs with average rainfall and temperatures (44.4%). We estimated productivity at 0.58 -1.18 fledged chicks per pair. In the course of the study the net productivity decreased. For all godwits marked as chicks, males were resighted more frequently than females and at a higher average maximum age. Annual adult survival was 81.4%, with no significant survival difference between the sexes. A population model shows that the studied population is not in balance and incurs a yearly net loss.

Key words: *Limosa limosa* - reproductive success - survival - nest success - population model - resight probability

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INTRODUCTION

In The Netherlands, meadowbirds occur predominantly in man-made habitats. They not only have to cope with natural predators and environmental characteristics, but they also have to adapt to changing farming practices (Beintema *et al.* 1985). The Black-tailed Godwit *Limosa limosa* used to flourish in the peat soil habitats in the western part of the country. Especially in reserves and plots under management restrictions, densities of breeding pairs would reach 1.5-2 pairs ha^{-1} (Groen 1993). Invertebrates profited from enrichment of the soil with manure and fertilisers and earthworms (Lumbricidae), leatherjackets (Tipulidae), snails and other species were abundant (Siepel *et al*. 1990). The combination of abundant food, at least for adult birds, and the soft peat soil, made the western part of The Netherlands a prime-breeding habitat for the Black-tailed Godwit. During 1960-80 the population in The Netherlands was estimated at 100,000-120,000 breeding pairs (Mulder 1972; Bijlsma *et al.* 2001).

In the last two decades of the twentieth century conditions have deteriorated at great pace because changing agricultural practices became harmful for Black-tailed Godwits and other breeding meadowbirds. By improving drainage systems, water tables were lowered and fertilisation shifted from late April to March. Nowadays, plots may be cultivated in March and mowed in late April, at a time when Black-tailed Godwits are still incubating (Beintema *et al.* 1985). On intensively managed farms, the number of niches for insects has diminished (Siepel *et al.*1990) because plots are ploughed, levelled, seeded with Perennial Rye-grass *Lolium perenne* and sprayed excessively with manure. As godwit chicks feed exclusively on insects, such ‘artificial pastures’ have little value for growing chicks (Schekkerman 1997). In addition, trampling by cattle and other causes of egg loss, including predation by Carrion Crows *Corvus corone*, Black-billed Magpies *Pica pica*, various species of gulls (Laridae), mammals e.g. mustelids like Stoat *Mustela erminea* and Weasel *Mustela nivalis vulgaris* and, more recently, the Red Fox *Vulpes vulpes* diminish the chance of birds reaching adulthood. All these causes, including those induced by human practices, have led to a decline in the Dutch population. Less than half of the estimated 120,000 breeding pairs present almost thirty years ago have remained (Bijlsma *et al.* 2001). To predict the fate of a local population we collected life history data on Black-tailed Godwits in a specific area. From these data we calculated the overall performance by estimating nest survival, nest success, chick survival, fledging success, productivity and return rate to the study area.

METHODS

A population of 70-95 breeding pairs of the Black-tailed Godwit was studied in Schaalsmeerpolder (52°31’N, 4°47’E) in the Wormer & Jisperveld reserve in Noord-Holland, The Netherlands in 1984-87 (Groen 1993). This polder is part of a 2200 ha wetland reserve with high water tables and restrictions in agricultural management. The soil is a soft peat, which is easily penetrated by the long bill of the Black-tailed Godwit. The Schaalsmeerpolder (ca. 70 ha) is divided into 27 plots through a system of ditches and a central canal. Another 200 ha bordering the Schaalsmeerpolder were weekly checked for colour marked birds. All plots in the Schaalsmeerpolder were subject to management agreements with local farmers (Ministry of Nature Management, Agriculture and Fisheries 1975) or were managed by a nature conservation organisation.

Natural history

Black-tailed Godwits arrived in the study area from their African wintering grounds from late February to March. Within one or two weeks after their arrival the males occupied a territory in daytime and returned to a communal roost at night. Black-tailed Godwits have a resource defence territorial system in which the male defends its territory against conspecifics (Lind 1961; Cramp & Simmons 1985) They are monogamous, have strong pair bonds and tend to be faithful to former breeding sites (Groen 1993). The onset of egg laying depends on the foraging conditions on arrival at the breeding grounds. In our study area on average 50% of pairs were incubating in the second decade of April, whereas 90% were incubating in the first decade of May (pers. obs). Incubation time in this study was 23 (22-24) days. Juveniles fledge after 27 (25-30) days (Beintema 1995). Primary moult commences late May and adults leave the breeding grounds from late July, gathering in large flocks to continue moulting (van Dijk 1980). Juveniles reside in breeding grounds until August. Adult migration passage through France and southern Europe starts from late July (Cramp & Simmons 1985; Beintema & Drost 1986) with juveniles going some weeks later to late September.

Marking adults and chicks

In 1984, 88 breeding adults (47 females, 41 males) were trapped on their nest with a drop trap (Mills & Ryder 1979) and colour marked with a unique set of 3 colour rings together with an aluminium ring of the Dutch Ringing Centre. Chicks were ringed in the nest within 2-3 h after hatching of the last chick. In the study period 752 chicks were ringed with an aluminium ring and one colour ring indicating the year cohort (Table 1). The colour ringing was a joint project by the OAG-Münster (Germany) and IBN-DLO (The

Netherlands), co-ordinated by the Wader Study Group (Beintema & Visser 1989; Beintema, *et.al*, 1995).

Nests and eggs

Nests were located and checked by weekly surveys in which all plots in the Schaalsmeerpolder were thoroughly searched (Groen 1993). On discovery of a nest, its position was plotted on a map that was calibrated using the numerous ditches on a plot. A numbered stick was placed 10 m from the nest. Numbers were noted on each side of the stick and read by telescopes or binoculars. At the office, a transparent grid with co-ordinates was laid over the nest location and then co-ordinates were assigned with an accuracy of 50 m. Standardised estimates of egg buoyancy were used to determine the stage of incubation by means of a water test (Van Paassen *et al*. 1984). This test is based on the specific angle that an egg's longitudinal axis makes in water due to the decline in specific gravity during incubation. For incomplete clutches the start of incubation and the start of egg laying was assessed.

In this study, nest success is defined as the probability that at least one egg hatched and produced a chick that departed from the nest. Nest success was calculated with the daily survival probability (p_c) using the Mayfield (1975) method. Calculation of nest survival is estimated from the formula: $p_c = A/(A+B)$ in which p_c = the probability that a nest present on one day would survive to the next, A = cumulative number of nest days during the observation period (all nests under observation), and B = total number of nests lost. The day on which a nest is lost is not counted as a nest day. Depredated, deserted or otherwise destroyed or abandoned nests were assumed to have lost midway between two checks. Nest cups that were found empty before the estimated hatching date were examined for tiny eggshell fragments. As predators and hatchlings leave big and tiny fragments of eggshells, respectively, the nest was recorded as successfully hatched if tiny fragments were found in the nest cup. Otherwise the nest was recorded as predated before hatching.

Non-fledged chicks

In spring 1984-87, weekly counts of chicks from colour marked families were made. Although individual chicks could not be recognised, the number of chicks in the brood of individually recognisable parents could be counted. Based on these counts survival of non-fledged chicks was calculated.

Resightings

Experienced research workers could distinguish male and female Black-tailed Godwits in the field. We could therefore divide the resighted birds according to gender and estimated the effect on their return tendency of both gender and weather conditions in the year of hatching. Return rates and resightings are not equivalent to true survival. Return rates are the function of at least three probabilities, including true survival, site fidelity and resighting probability. A low return rate may reflect mortality, dispersal or lack of resighting. To avoid confusion we have defined some related terms on survival used in this article. We define resightings as observations of birds marked individually (adults) or as year cohort (chicks) in the study area. Return rates are based on resightings from year to year. If birds returned with a year cohort ring and established a territory and start breeding in the study area, we attempted to trap the bird on the nest. After the bird was trapped, we replaced the year cohort ring with a unique combination of colour rings. At least 15 birds that were ringed as chicks with a year cohort ring were retrapped as breeding birds. These 15 birds could be individually recognised in later years. Not all birds ringed as chicks in the 1984-87 period and returned to the study area could be trapped in later years to be marked with a unique combination of colour rings. In the survival analyses they were treated as individuals because we could identify them either by their colour-ring(s), sex, marked or unmarked partner or their territory co-ordinates assuming complete site faithfulness.

To exclude errors in the readings of colour rings, we concluded that a marked bird had returned if we had either the ring number or at least three readings of that particular bird in one breeding season. For the survival analysis we collected data on 48 females, 85 males. Twenty birds of which sex could not be determined were excluded from the analysis. The resighting rate of colour marked adults can be interpreted as the minimum survival rate.

Resighting rates of non-breeding Godwits are based on counts in early spring and the beginning of June when birds gather in groups on favourable feeding sites or communal roosts. Beintema (1995) found an effect of rainfall in the spring of hatching on survival in later years. Therefore, we expect that the weather in its year of hatching might affect the bird's survival and thus return tendency to the study area in later years.

Population dynamics

Life history characteristics as estimated in our study can be used to calculate net fertility (Boyd 1962). Net fertility (f_n) is defined as $f_n = c.u.v.s_1/2s$, c being average number of eggs laid by a female in a year, u the nest success, v the fraction of eggs hatched of which the young are reared to full size, s_1 the survival rate in the first year after fledging, and s the adult survival rate. Life expectancy is calculated with the formula: $1/(1-s)$, where s is annual survival (Case 2000).

Statistics

In 1984-87 observation efforts were equal throughout the season, so chicks ringed in this period were used for analysing return tendencies in later years (Table 1). We used the data on resighted adult birds, of which the sex could be determined either by plumage, bill length, aerial and ground display, or copulation. Data on resighted adults that were colour ringed as chicks (year cohorts) were analysed with the proportional hazards model (Cox 1972; Kalbfleisch & Prentice 1980; Kleinbaum 1995). This model was developed for survival analysis. It estimates the effect of covariates on the probability per unit time of a certain event happening. It is a non-parametric model and therefore it is not assumed that the probability per time unit is constant or has another *a priori* specified baseline hazard (basic probability per time unit). We defined the event of interest to be the latest observation of a particular individual in the study area. So, if a marked Black-tailed Godwit from any of the 1984-87 cohorts was seen in later years, we used the latest observation of that particular bird in the analysis, i.e. the observation in which the adult bird was most advanced in age. We used equation (1) to calculate the return rate ($h(t;z)$). In the model it is assumed that the rate depends on the bird's age (t) and on two fixed covariates, its sex and weather conditions in the spring of hatching.

$$h(t;z) = h_0(t) \exp(\beta_1 z_1 + \beta_2 z_2) \quad (1)$$

Here, $h_0(t)$ is the baseline return rate at latest resighting; β_1 the effect of the first covariate (sex) z_1 and β_2 the effect of the second covariate (weather conditions in the spring of hatching) z_2. Only if β_1 deviates significantly from zero an effect of sex can be demonstrated. For the analysis, the age of returning adult birds was calculated in months from the day of hatching. The effect of the covariates on the probability per time unit of birds returning to the study area was estimated by means of likelihood maximisation. The return rate can be interpreted as the minimum survival rate.

RESULTS

Breeding density

The breeding density of the Black-tailed Godwit during the study period was relatively stable and averaged 100 (90-107) breeding pairs on the 70 ha central study plot. Due to different management schemes there was a striking difference in breeding density between birds on grazed plots (0.11-0.89 breeding pairs ha^{-1}) and those on plots that were used for haymaking later in the season (1.5-5.2 breeding pairs ha^{-1}).

Clutch size and nest success

Female Black-tailed Godwits usually lay clutches of four eggs. The mean (± SD) annual size of complete clutches ranged from 3.8 ± 0.58 (n = 95 clutches) in 1984; 3.85 ± 0.39 (n = 81) in

Table 1. Numbers of chicks ringed and fledged in 1984-1987 and the numbers of returned chicks that were observed in the study area in 1985-1999.

year	Ringed	fledged	1985	1986	1987	1988	1989	1990	1991	1992
1984	167	35	1	6	8	6	4	3	3	1
1985	228	114	-	10	25	26	13	16	14	11
1986	202	77	-	-	9	11	6	7	7	8
1987	155	32	-	-	-	3	2	2	4	2

continued	1993	1994	1995	1996	1997	1998	1999
1984	1	1	1	1	1		
1985	4	3	4	1	1		
1986	0	2	0	1	1		
1987	1	1	1	1	1	1	1

Table 2. Nest success, fraction predated, fraction abandoned nests (e.g. after trampling or mowing), daily nest survival probabilities (p_c) and hatching probabilities, p_h (=[p_c]^{25}; of nests (derived from : Groen & Buker 1991).

year	nests	nest succes	predated nests	abandoned nests	nest survival (p_c)	hatching prob. (p_h)
1984	108	61 (56.0%)	25 (23.1%)	22 (20.3%)	0.986	70.6%
1985	92	66 (71.0%)	19 (20.6%)	7 (7.6%)	0.988	74.6%
1986	115	63 (54.7%)	39 (33.9%)	13 (11.3%)	0.981	62.1%
1987	105	46 (43.8%)	53 (50.4%)	6 (5.7%)	0.965	41.4%

Table 3. Chick survival, fledging success and productivity of the Black-tailed Godwit from 1984 to 1987. In brackets 95% confidence limits.

Year	*S* (daily survival)	*F* (fledging success)	Fledged chicks/pair
1984	0.944	0.263	0.58-0.81
1985	0.975	0.423	0.97-1.18
1986	0.965	0.331	0.65-0.85
1987	0.943	0.303	0.62-0.79
1984-87	0.959 (0.948-0.970)	0.33 (0.225-0.435)	0.807 (0.52-1.09)

1985; 3.86 ± 0.41 (n = 94) in 1986 to 3.79 ± 0.52 eggs clutch^{-1} (n = 81) in 1987. The mean (± SD) clutch size over 1984-87 was 3.83 ± 0.47 eggs clutch^{-1} (n = 350). During the study period 17 replacement clutches were recorded with a mean clutch size of 3.94 ± 0.24 eggs clutch^{-1}. Nest success was calculated as: 0.71 in 1984; 0.75 in 1985; 0.62 in 1986 and 0.41 in 1987 (Table 2). The difference in nest success was significant between years (χ^2_3 = 10.6, P < 0.05). The sharp decline in nest success in 1987 was according to our observations the result of increased egg predation by Black-headed Gull *Larus ridibundus*, Stoat and Weasel.

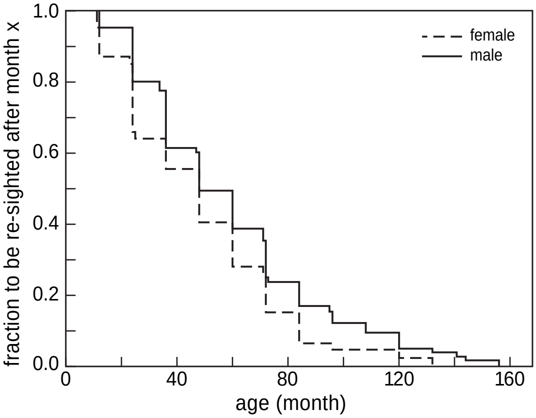

Fig. 1. Survivorship curve (percentage of birds to be resighted later on) for Black-tailed Godwits ringed as chicks in the years 1984 -1987 which returned to the study area.

Hatchling weights

Mean (± SE) hatchling masses of Black-tailed Godwits were almost constant and seemed only slightly affected by weather conditions: 1984 28.4 ± 0.178 g (n = 166); 1985 28.9 ± 0.139 g (n = 227); 1986 28.4 ± 0.171 g, (n = 248); and 1987 28.6 ± 0.179 g (n =164). The mean hatchling mass in 1985 was significant different from 1984 and 1986 (for both comparisons Students t-test, t = 2.34, P < 0.02).

Survival of chicks till fledging

To calculate survival rate (S) for chicks until fledglings we used the formula $F = S^L$ (Beintema 1995), with F = fledging success, S = daily survival of chicks until fledging, L = the period from hatching till fledging (27 d). Fledging success in 1984-87 was 0.33 (95% confidence interval: 0.23-0.44) and consequently a daily chick survival rate of 0.96 (95% confidence interval: 0.95-0.97, Table 3). Chick survival depends on weather conditions in May. In years with cold and wet conditions, 20.8% of chicks survived (1984 and 1987). In warm springs with normal precipitation, 44.4% survived (1985 and 1986; χ^2 = 46.99, P <0.001, Table 1). In the cold and wet spring of 1984 the low nest success was due to intense rainfall resulting in unhatched eggs and chicks dying during hatching.

Productivity

The productivity of the Black-tailed Godwit fluctuated in the study period. Nest success (p_h) sharply decreased from 0.75 in 1985 to 0.41 in 1987 (Table 2). On average 21.3% (range 7.0-29.6%) of the hatched clutches yielded no fledged chicks. The (fledged) chick production ranged from 0.66 chicks per pair in 1984 to 1.10 chicks per pair in 1985 (Table 3).

Adult survival

The annual survival from 1984 to 1985 of 41 males and 47 females was 0.83 (males 0.76, females 0.89), from 1985 to 1986 0.78 (males 0.71, females 0.83), and from 1986 to 1987 0.84 (males 0.86, females 0.83). The average (± SD) annual survival over this period was 0.81 ± 0.07. There was no significant difference in annual adult survival between males and females (χ^2_3 = 2.908, n.s.). Annual adult survival probability s is 0.81, and life expectancy in this study is 1/0.19 = 5.3 years.

Resightings of year-cohorts

Analysis of the latest resightings with the proportional hazards model revealed no significant effect of the weather in the year of hatching on the resighting rate in later years. The resighting rate per month was 0.017 for males and 0.020 for females, a difference tending to significance (Wald's test, df 2, 0.05 < P < 0.06). Thus, at the latest observation, the mean life expectation for males are 5 years (1/0.017 months) and 4 years (1/0.021 months) for females. This implies that the average life expectancy of returning females was approximately one year shorter. The calculated effect of sex on the return rate was 0.3, which means that females had a resighting rate that was 1.35 (= $e^{0.3}$) times higher than that for males. The resightings give a minimum estimate of yearly survival of birds from fledging to their latest resighting. So in contrast to adult survival this estimate includes the juvenile stage.

Population dynamics

The parameters for the calculation of f_n over the period 1984-87 are: c = 3.83; u = 0.62; v = 0.33; s = 0.814. The figure s_1 is difficult to estimate because the majority of juvenile Black-tailed Godwits stays in the African wintering grounds in their second calendar year. We therefore approached s_1 by dividing the number of resighted birds from a particular year cohort by number fledged in that particular cohort. Resighting rates of birds ringed as chicks for 1984 8/35 = 0.22; 1985 26/114 = 0.23; 1986 11/77 = 0.14; and 1987 4/32= 0.13, and thus s_1 (1984-87) is 49/258 = 0.19. The majority of survivors return to the breeding grounds in their third calendar year (Cramp & Simmons 1985, this study). We can therefore only calculate a s_1 for godwits returning in their second and third calendar year. Net fertility for the population is f_n = 3.83 x 0.62 x 0.33 x 0.19 / (2 x 0.81) = 0.09.

Gross fertility (= $c.v.u$) for the population is: f_g = 3.83 x 0.33 x 0.62 = 0.78 chick female^{-1}. According to Boyd (1962) the population can be considered to be in balance if $f_n = (1\text{-}s)/s^3$. The net fertility (f_n) is 0.09 and $(1\text{-}s)/s^3$ is $(1\text{-}0.814)/0.814^3 = 0.345$. Thus, net fertility is 25 % of yearly losses. The denominator s^3 was chosen because the majority of Black-tailed Godwits starts breeding in their third calendar year. Although some birds ringed as chicks returned to the study area in their second calendar year (Table 1), none of them started breeding. All birds ringed as chicks that we trapped on the nest in later years were in their 3rd calendar year or older. If we assume that godwits start breeding in their second year, then $(1\text{-}s)/s^2$=0.29 and net fertility is 31 % of yearly losses. In both cases the population is decreasing in size.

DISCUSSION

With 128-152 breeding pairs km^{-2}, breeding density of Black-tailed Godwits in this study is high. Densities in the province of Friesland average 32.2 pairs km^{-2} (SD 24.8), with 2-22 pairs km^{-2} on sandy soils and 15-83 pairs km^{-2} on humid clay soils (Beintema *et al.* 1995). Nest success in cultivated habitats depends for a considerable part on the intensity of farming in the breeding season (Beintema & Müskens 1987).

The decline in daily survival probability (p_c) of nests in 1984–87 (0.986- 0.965) is striking (Table 2). The decline in nest success from 73% in 1984 to 46% in 1987 was to our observation the combined result of an increased disturbance of breeding birds and, as a consequence, increased predation on eggs. The unattended nests were an easy prey for Black-headed Gulls and Carrion Crows *Corvus corone* (Groen & Buker 1991). Black-tailed Godwit chicks are vulnerable to rain and cold weather in the first 10-12 d after hatching (Evans & Pienkowski 1984; Beintema & Visser 1989). Daily survival rates were lowest in the wet and cold springs of 1984 and 1987 and highest in 1985. Beintema (1995) estimates a daily survival rate of 0.97 from national ringing recoveries (1976-90), and a fledging success of 0.44. We calculated daily chick survival at 0.96 and fledging success at 0.33 (Table 3), all within the limits of Beintema's (1995) results. In the wet years 1984 (0.26) and 1987 (0.30) fledging success is below the lower limits of his study.

Over four years, net production of fledged chicks was 0.81 chicks per pair. Recent studies by Schekkerman *et al.* (1998) at five sites with various management schemes yield an average of 0.43 fledged chicks per breeding pair (range 0.16-0.60). Beintema (1995), based on recoveries of ringed Black-tailed Godwit chicks in 1976-1990, came to a fledging success of 0.44.

Like many other shorebirds, the Black-tailed Godwit can be characterised as a low fecundity species (Piersma & Baker 2000), with a high adult survival (Boyd 1962; Evans 1994; Marks & Redmond 1996; this study). Total annual survival among five wintering shorebird species in Britain was 82% (range 84.5 – 76.0), with lowest survival during migration and on the wintering grounds (Evans 1994). In this study annual adult resighting rates of colour marked individuals are 81.4%, and hence survival rates corrected for site-faithfulness will be somewhat higher.

Black-tailed Godwits in The Netherlands are only *c.* five months on the breeding grounds, and the mortality here is less than 1%. This implies that adult mortality must occur during migration at staging sites or on the wintering grounds (cf. Evans 1994; Piersma & Baker 2000). Natal philopatry and the source-defence mating system of the Black-tailed Godwit (Groen 1993) are possible explanations for the lower resighting rates of males in the study area. Though we had expected to see a difference in return tendencies of chicks due to rainfall during their incubation and prefledging period, we have no evidence of return rates being thus affected. The low net fertility (0.09) is due to low resighting rates of birds returning for the first time to the study area. As we have no estimate for the dispersal of such birds we used the number of resightings in one year for each cohort to estimate s_1. Since Black-tailed Godwits stay on the African wintering grounds in their second year (Cramp & Simmons1985) the survival rate after fledging (s_1) we calculated is actually the survival at first breeding (s_3). We emphasise that the calculated s_1 (0.19) is the absolute minimum figure. Sensitivity analysis with a stage structured population model on a breeding population of Semipalmated Sandpipers *Calidris pusilla* (Hitchcock & Gratto-Trevor 1997) showed that adult survival and the number of immigrants are most influential on population growth rate. Therefore, it is obvious that adult survival matters more to population size than annual variation in breeding success. Despite high survival rates of adult Black-tailed Godwits, recruitment was below annual losses. In polders with regular farming practices recruitment will be even lower (Kruk *et al.* 1997; Schekkerman & Müskens 2000). Low recruitment, in the last decades of the twentieth century means a disproportional number of relatively old birds in the population. This may have contributed to the sharp decline of the population in the last 10-15 years in The Netherlands as shown by national census data (Bijlsma *et al.* 2001). The population in this study site dropped from an average of 105 breeding pairs in 1984-87 to 51 breeding pairs in 2001 (Van der Geld *pers. comm.*). This decline of 54 breeding pairs is less than predicted by the population model with s = 81.4 % and a net fertility of 0.09. Even if we assume that the calculated net fertility is too low it is likely that there must have been an influx of birds from outside the study area that masked the decline (cf. Hitchcock & Gratto-Trevor 1997). For other bird species like the Red Knot *Calidris canutus islandica* both survival and recruitment are related to fluctuations in wintering numbers in Britain (Boyd & Piersma 2001). In the studied population of Black-tailed Godwits particularly low rates of recruitment explains the population decline.

ACKNOWLEDGEMENTS

We would like to thank Joop Buker and Joke Winkelman for unpublished data from the Schaalsmeer study on Black-tailed Godwits. Natuurmonumenten is thanked for permission to do research on their reserve with particular thanks to Jan van der Geld (manager) and assistants. We are grateful to Hans Schekkerman, Gerrit Gort, Kees Roselaar, Theunis Piersma and two anonymous referees for their contributions in improving the manuscript. Elizabeth van Ast-Gray and Tineke Wilmink are thanked for improving the English text.

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SAMENVATTING

In een studie aan een gemerkte populatie van de Grutto *Limosa limosa* werden in de periode 1984-87 jaarlijks 70 tot 95 broedparen met hun kuikens gevolgd. Gemeten werden de legselgrootte, het uitkomstpercentage, het percentage vliegvlugge jongen, de overleving van kuikens in het eerste jaar en het percentage van de als kuiken geringde Grutto's dat werd teruggezien in het studiegebied. Het uitkomstpercentage van nesten volgens de Mayfield (1975) methode varieerde van 41.4% tot 74.6%. De overleving van kuikens tot het vliegvlugge stadium (20.8%) was in natte, koude voorjaren significant lager (44.4%) dan in voorjaren met gemiddelde temperaturen en neerslaghoeveelheid. Het broedsucces (productiviteit) van paren lag tussen 0.58 en 1.18 kuiken per paar. In de loop van de studie daalde het broedsucces aanzienlijk. De kans dat Grutto's die als kuiken zijn geringd, in het studiegebied worden

teruggezien, is voor vrouwtjes 0.021 per maand en voor mannetjes 0.017 per maand. Dit betekent voor vrouwtjes een gemiddelde leeftijd bij de laatste waarneming van circa 4 jaar (49 maanden) en voor mannetjes circa 5 jaar (59 maanden). Onder de Grutto's die als kuiken in het studiegebied waren geringd en er terugkeerden, bevonden zich meer mannetjes dan vrouwtjes. Dit komt overeen met de eerder gevonden grotere dispersie van vrouwtjes. De jaarlijkse overleving van broedvogels in het studiegebied was 81.4% per jaar. Uit de hier gepresenteerde gegevens blijkt dat de jaarlijkse sterfte van de populatie niet wordt gecompenseerd door de aanwas van jongen. De populatie in het studiegebied daalde van gemiddeld 105 broedparen in 1984-1987 naar 51 broedparen in 2001.

Received 16 July 2001, Accepted 6 January 2002
Corresponding editor: Theunis Piersma