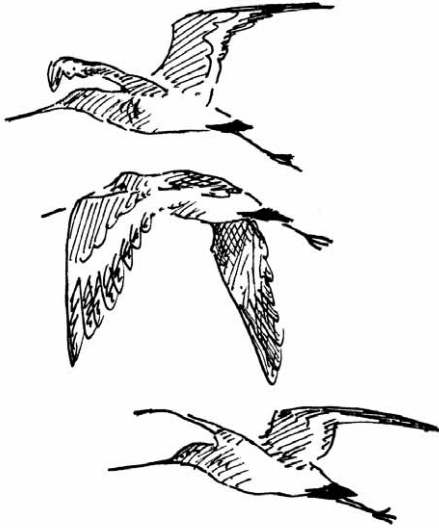# Survival rates of Black-tailed Godwits *Limosa limosa* breeding in The Netherlands estimated from ring recoveries

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The Netherlands holds internationally important numbers of Black-tailed Godwits *Limosa limosa*, and reports of a substantial population decline have prompted concern. One way of narrowing the list of possible causes of this decline is to identify the demographic processes responsible. For this reason, we conducted a survival analysis for the period 1960 to 2000 based on dead recoveries of godwits. Although declining sample sizes and falling reporting rates reduced the precision of estimates in later years, we concluded that adult survival had dropped significantly in the late 1990s from 0.77 to 0.40. Data were too sparse to estimate juvenile survival in this period. Apart from this sharp drop, we found no evidence of long-term trends in either first-year or adult survival. We found no evidence for effects on survival estimates of shifts in the spatial distribution of recoveries or in the reported causes of death. These large-scale analyses of birds recovered dead complement more intensive mark-resighting studies at individual sites. Given the falling reporting rates of dead birds and consequent loss of precision of survival estimates, intensive mark-resighting programmes have an increasingly important role to play in the study of survival rates.

Key words: *Limosa limosa*, waders, population decline, mortality, life history, hunting

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INTRODUCTION

A large part of the world population of the Black-tailed Godwit *Limosa limosa limosa* breeds in The Netherlands. Reports of a substantial decline in national numbers of breeding pairs are therefore reasons for concern (SOVON 2002, Teunissen & Soldaat 2006). The Black-tailed Godwit mainly breeds in agricultural grasslands and is therefore sensitive to changes in agricultural practices (Beintema *et al.* 1991, Kruk *et al.* 1996, Kruk *et al.* 1997, Kleijn & van Zuijlen 2004, Klok *et al.* 2006, Schekkerman & Beintema 2007).

Substantial numbers of Black-tailed Godwit chicks and adults have been ringed annually for the last forty years. Together with reasonable numbers of dead birds being reported, these data allow us to calculate annual survival rates of young and

old birds and to detect any changes in these parameters over time. In this study we aim to supplement the results from shorter intensive studies (Kruk *et al.* 1997, Groen & Hemerik 2002, Roodbergen *et al.* unpubl.) with an updated analysis of the broader data. The previous analysis of these data by Beintema & Drost (1986) covered the first part of the decline of the Dutch godwit population. For information about the species and its breeding ecology, we refer to the above mentioned studies. There are a number of important differences between survival analysis based on recoveries of dead birds, such as performed here, and analyses based on recaptures or resightings of live birds. Intensive studies are bound to be limited in space, and thus emigration of individuals cannot be distinguished from mortality. Most reports of dead birds come from abroad and the cause of death is related to hunting. It is therefore likely, but not certain, that the chance of being shot and reported is independent of the breeding locality in The Netherlands. Thus, the survival estimates derived in this study are an average for the ringed population. On the other hand, reports of dead birds are dependent on the willingness of hunters to report rings of shot birds, which may change over time, while shifts in hunting practices would also have a big impact on reporting rate. To counter these potential biases, we explored any heterogeneity in the spatial distribution of the reporting sites.

In a stable population, reproduction and survival are in balance. The consequences of changes in survival for the population size depend strongly on the life history. In order to give an indication of the consequences of the survival rates reported in this study, a simple population matrix model is used to calculate the required number of chicks to be produced per pair per year for a stable population.

First, we analyse the spatio-temporal structure of all ringing and recovery data of the Black-tailed Godwit deployed with rings of the Dutch ringing scheme (Netherlands, Arnhem; NLA). Subsequently, we apply standard survival estimation, with particular attention for the question whether we have sufficient data to document variation in survival rates. Finally, we discuss the implications of

the results for collecting data for an adequate monitoring.

METHODS

Data came from the ringing scheme of the Dutch Centre for Avian Migration and Demography. All recovery, recapture and ringing data of Black-tailed Godwits with Arnhem rings were provided in the standard EURING format (van Noordwijk *et al.* 2003). Ringing data have been computerised back to 1959. For some of the analyses, all data were used, but for the main analysis of survival rates data from 1960 to 2000 inclusive were used. Moreover, only recovery reports of birds reported as dead, but unknown how long precisely ($n = 164$) or freshly dead ($n = 757$) were used. Ring reports without reference to the bird or of birds of completely unknown status ($n = 132$) or long dead ($n = 69$) were excluded. The latter category contained several records where the reporting date exceeded the recorded maximum age by many years and many of the reports were considered suspect. For the same reason, reports where a different species ($n = 59$) was reported were excluded.

Data selections and counts were made in a spreadsheet and survival analyses were performed with the computer programme MARK version 3.01 (White & Burnham 1999). Years were defined as 12-month periods from the date of ringing. This means that survival estimates refer to the period from one breeding season to the next, because all birds were ringed in the breeding season or shortly thereafter. The base model consisted of 41 periods; annual survival S_a and reporting rates R_a were set equal for all age classes, except for the first year of birds ringed as unfledged chicks, for which a separate survival rate S_j and a separate reporting rate R_j were tested. There were not sufficient data to estimate a separate survival rate for the second year as well. It was not possible to get independent estimates for all parameters. For each of the parameters and for various combinations of parameters, linear or quadratic regressions on year were fitted. Nomenclature follows standard practice (Lebreton

et al. 1992). Three types of estimates were used: constant over time, denoted by '.', as a linear regression on time, denoted by 'T', and variable over time, denoted by 't'. Thus, the first-year (=juvenile) survival estimates were for the period of exactly one year after ringing of the chicks. This implies that any changes in reproductive rates up to the moment chicks were ringed were not included in the analysis. In principle, one could analyse the brood size at ringing, but the quality of these data was too heterogeneous for any firm conclusions. Thus, there were 164 parameters in the base model. We used standard models for analyses (logit link functions and variance estimation based on the Hessian). Although estimates of overdispersion differed slightly between models, the same correction factor (c-hat = 2.3) was used throughout. The major power of modern software lies in the fitting of different models to the data and subsequent tests which model fits the data best. The general logic is to choose the simplest model, unless a more complicated model fits the data better (Anderson & Burnham 1999). Model selection was based on the adjusted Akaike Information Criterion and on likelihood ratio tests between the best fitting models (Anderson & Burnham 1999).

One of the major assumptions underlying survival models is that all individuals have the same chance of dying and of being found and reported when they are dead. It was therefore important to scrutinise the data for potential violations of this assumption. In particular, we analysed the geographic distribution of where birds were ringed by province in The Netherlands.

Population model
In the Discussion, the consequences of adult and juvenile survival rates on the population structure are explored based on a simple Leslie-matrix model written in a spreadsheet programme. At each time step, numbers of individuals in each age class were rounded to integers after adding a uniformly distributed random variable between –0.5 and 0.5 to avoid biases with low numbers (without this procedure 2 individuals with survival of, for example, 0.76 remain two individuals for ever). The

reproductive rate leading to a population growth rate of 1.0 (=stable population size) was calculated for the survival rates observed and for different reproductive scenarios.

RESULTS

Data heterogeneity
The total number of Black-tailed Godwits ringed in The Netherlands grew to a level of about 1000 per year in the 1960s and declined strongly in the early 1990s (Fig. 1). The numbers of birds reported dead followed the annual fluctuations in numbers ringed, while declining at the same time. Thus, over the study period the proportion recovered dropped from 4% to 1% (Table 1). Only for the last few years this might have been due to the fact that a substantial number of individuals was still alive.
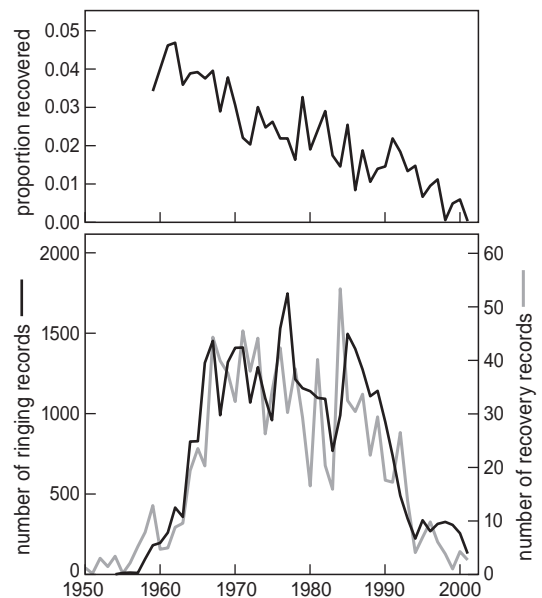

Figure 1. Total numbers of Black-tailed Godwits ringed in The Netherlands per year (left axis) and numbers recovered per year. The proportion of birds ringed that have been reported dead, classified by year of ringing, is indicated at the top. For separate reporting rates of juveniles and adults see Fig. 7.
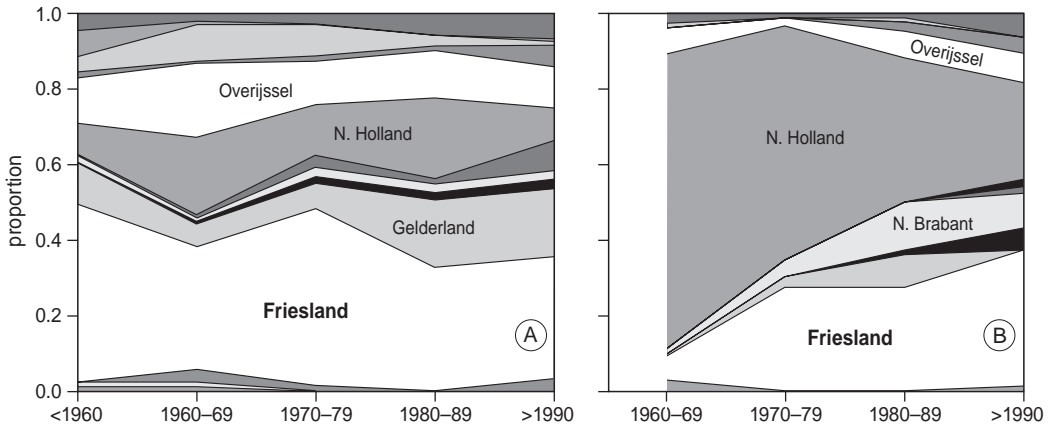
Figure 2. Proportions of chicks (A) and adults (B) ringed per province or island in the Waddensea, given per 10-year period. Total numbers ringed per period are 316, 7586, 12074, 9603 and 4181 for chicks, and 374, 906,1965 and 602 for adults.

Table 1. Numbers of Black-tailed Godwits ringed and reported per five years of ringing. Proportions reported between brackets.

	ringed as chicks				ringed as adults		
	ringed	reported			ringed	reported	
		in first year		later			
1960–1964	2048	19	(0.0093)	49	(0.0239)	27	5	(0.1852)
1965–1969	5538	77	(0.0139)	96	(0.0173)	347	15	(0.0432)
1970–1974	5997	51	(0.0085)	88	(0.0147)	354	19	(0.0537)
1975–1979	6077	56	(0.0092)	65	(0.0107)	552	14	(0.0254)
1980–1984	4087	34	(0.0083)	48	(0.0117)	1019	27	(0.0265)
1985–1989	5517	44	(0.0080)	34	(0.0062)	946	18	(0.0190)
1990–1994	2468	29	(0.0125)	9	(0.0036)	319	2	(0.0063)
1995–2000	1583	5	(0.0032)	3	(0.0019)	248	4	(0.0161)

Whereas the distribution of nestlings ringed per decade was remarkably constant, the adults ringed in the first decades came largely from one single province (Fig. 2). This could have been a problem in reporting rate heterogeneity if reports came from within The Netherlands. However, the majority of reports on dead adults came from abroad which makes a major bias less likely. The geographic distribution of the reports is given in two ways: by country (Fig. 3) and by distance between the site of ringing and the site of recovery (Fig. 4). In both cases, the distribution is relatively constant over time, with an increase in reports from Senegal and Guinea Bissau (at 4500 km) in the last two decades and an almost complete disappearance of reports from Italy, Morocco and southern Spain (2000 km) in the 1990s. In the 1990s the proportion of reports from The Netherlands has increased. This mainly concerns a relative increase in proportion of birds found dead as
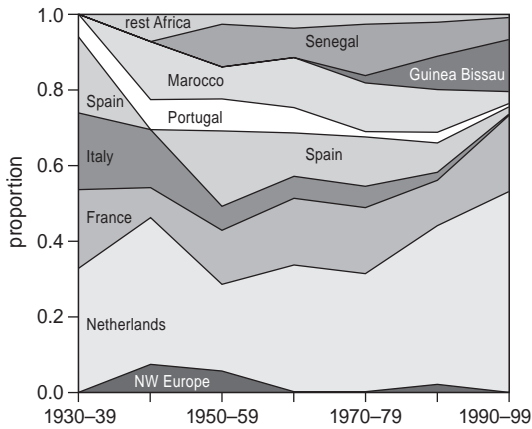
Figure 3. Proportions of recoveries by country and by 10-year period. The number of records per period are 17, 13, 35, 221, 366, 329 and 159.
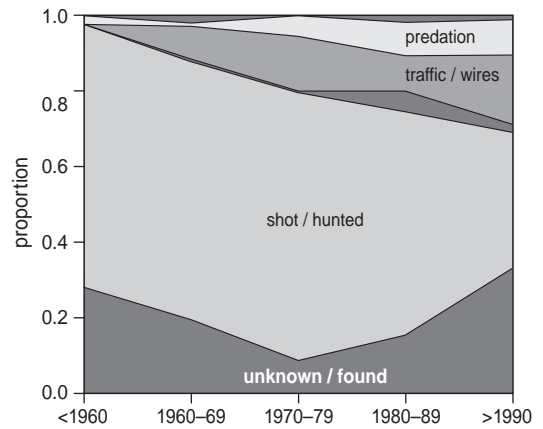

Figure 5. Reported causes of death by 10-year period. Numbers of records are 53, 175, 313, 259 and 121.
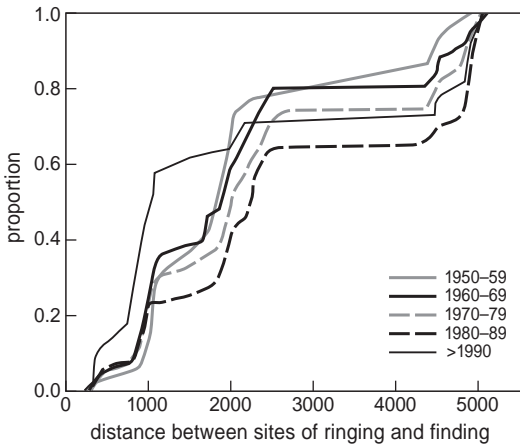

Figure 4. Location of recoveries at >250 km from site of ringing by distance between site of ringing and recovery. Proportions recovered at distances of 4500–5000 km increase over time (mainly in Guinea Bissau and Senegal, see Fig. 3), whereas proportions decrease at 2000 km (southern Spain and Morocco) after 1990.

The reported causes of death should be treated with some caution, but in broad categories they seem reasonably constant over time, although the category shot/hunted has declined over the last two decades (Fig. 5). Localities differed considerably in the reported cause of death (Fig. 6). Nearly all foreign recoveries reported shot or hunted as cause of death and nearly all other causes of death were reported from The Netherlands. Within the Dutch data, there are no clear changes in proportion of reports referring to traffic, wires or predation as presumed cause of death.

Survival analysis

Table 2 reports the best ten survival models, on the basis of the AIC. Model 1) with constant juvenile survival and constant adult survival and reporting rates as linear regressions on time is the preferred model. However, the AICs of the subsequent three models differ by less than 2 from the preferred model, which means no 'significant' differences exist (Anderson & Burnham 1999). We discuss therefore the common features of all models that fit the data more or less equivalently.

Several features are noteworthy. All models with a separate reporting rate for first- year birds fit much better than models with a reporting rate

chicks, due to a decrease in reports of old birds. The proportion of recoveries at 2000 km has declined strongly (Fig 4). In contrast, the recoveries at around 1000 km (southern France and northern Spain) and around 4500 km were similar in proportion.
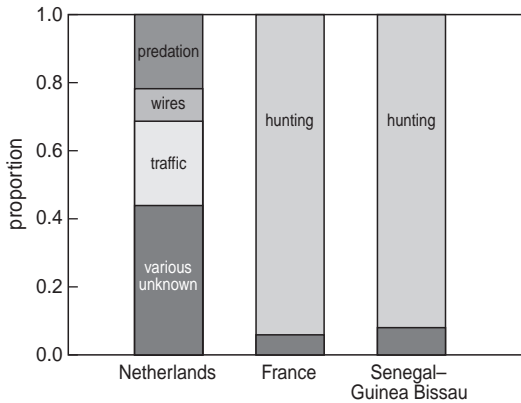
Figure 6. The interaction between location and four main reported causes of death, illustrated by the data from The Netherlands ($n = 288$), France ($n = 172$) and Senegal and Guinea Bissau ($n = 151$).

combined for juveniles and adults (not given). Second, models where adult survival, juvenile survival and juvenile reporting rate are either constant or a linear function of time are very similar. Neither on the basis of AIC (Table 2), nor on the basis of likelihood tests (Online appendix 1) can these models be distinguished. In contrast, assuming a constant reporting rate for adults caused a worse model in all combinations (Table 2). In fact,

the estimates for models where the survival estimates were regressions on time, showed a slight increase in both adult and juvenile survival, while the estimates for the reporting rates were similar (Table 3). Producing separate estimates for adult and/or juvenile survival for each year did not improve the fit of the model (Table 2) and there were no obvious trends in the estimates (Fig. 7, Online appendix 2), even though there was considerable annual variation in the estimates.

The striking feature of separate reporting rates for first-year birds was that the reporting rate for juveniles was almost constant, whereas the reporting rate for adults showed a strong decline from almost 9% around 1960 to 1% in 2000. There is, of course, a substantial risk that such a strong drop in reporting rate goes together with heterogeneity in the data. However, the geographic distribution of the recoveries was constant and did not show major changes, except for the disappearance of reports from Southern Spain and Morocco in the last decade (Fig. 3).

Survival in recent years
Although the best fitting models resulted in either constant adult survival or adult survival that increased slightly over time, the separate estimates for individual years resulted in a number of very

Table 2. Summary statistics of the ten most important models for survival estimation. C-hat was estimated at 2.30. NP = number of parameters.

| Model		QAICc	Delta QAICc	QAICc weight	NP	QDeviance
1)	$S_{j\cdot}\ S_{a\cdot}\ R_{jT}\ R_{aT}$	4698.89	0.00	0.362	6	335.40
2)	$S_{j\cdot}\ S_{a\cdot}\ R_{j\cdot}\ R_{aT}$	4699.31	0.41	0.294	5	337.82
3)	$S_{j\cdot}\ S_{aT}\ R_{jT}\ R_{aT}$	4700.60	1.71	0.154	7	335.11
4)	$S_{jT}\ S_{a\cdot}\ R_{jT}\ R_{aT}$	4700.89	2.00	0.133	7	335.40
5)	$S_{jT}\ S_{aT}\ R_{jT}\ R_{aT}$	4702.60	3.71	0.057	8	335.11
6)	$S_{j\cdot}\ S_{a\cdot}\ R_{jT}\ R_{a\cdot}$	4735.46	36.57	0.000	5	373.97
7)	$S_{j\cdot}\ S_{a\cdot}\ R_{j\cdot}\ R_{a\cdot}$	4736.06	37.16	0.000	4	376.57
8)	$S_{jt}\ S_{a\cdot}\ R_{jT}\ R_{aT}$	4749.45	50.56	0.000	46	305.85
9)	$S_{j\cdot}\ S_{at}\ R_{jT}\ R_{aT}$	4750.01	51.12	0.000	46	306.41
10)	$S_{jt}\ S_{at}\ R_{jT}\ R_{aT}$	4801.67	102.78	0.000	86	277.79

Parameter subscripts: j = juvenile, a = adult, . = constant, T = Trend, linear regression on year, t = separate estimates for each year.

Table 3. Estimates for survival and reporting rates with standard errors and confidence interval (CI) based on models 1 and 5 in Table 2. For estimates from linear regressions, the estimates for the first and the last year are given. C-hat in the models is 2.3.

Parameter	Estimate	SE	95% CI
Model 1			
S_a	0.772	0.005	0.761–0.782
S_j	0.361	0.010	0.341–0.381
$R_{a\ 1960}$	0.088	0.007	0.075–0.103
$R_{a\ 2000}$	0.012	0.003	0.007–0.021
$R_{j\ 1960}$	0.019	0.002	0.016–0.023
$R_{j\ 2000}$	0.011	0.005	0.004–0.026
Model 5			
$S_{a\ 1960}$	0.751	0.015	0.720–0.779
$S_{a\ 2000}$	0.799	0.057	0.665–0.889
$S_{j\ 1960}$	0.358	0.008	0.343–0.373
$S_{j\ 2000}$	0.366	0.065	0.249–0.500
$R_{a\ 1960}$	0.086	0.008	0.072–0.104
$R_{a\ 2000}$	0.012	0.007	0.004–0.040
$R_{j\ 1960}$	0.019	0.002	0.015–0.023
$R_{j\ 2000}$	0.011	0.006	0.004–0.029

Table 4. Estimates for adult survival rates in models for all eight, the last two or just the last five-year period. In all models presented, juvenile survival is constant and both juvenile and adult reporting rates are linear regressions on year.

Parameter	Estimate	SE	95% CI
Model S_j . $S_{a\ 8p}$			
S_a (60–64)	0.777	0.025	0.724–0.822
S_a (65–69)	0.783	0.020	0.741–0.819
S_a (70–74)	0.743	0.016	0.711–0.772
S_a (75–79)	0.789	0.010	0.768–0.809
S_a (80–84)	0.796	0.014	0.768–0.822
S_a (85–89)	0.776	0.011	0.753–0.797
S_a (90–94)	0.746	0.020	0.705–0.783
S_a (95–00)	0.402	0.012	0.379–0.425
Model S_j . $S_{a\ 3p(30,5,6)}$			
S_a (60–89)	0.777	0.012	0.753–0.799
S_a (90–94)	0.745	0.026	0.691–0.793
S_a (95–00)	0.401	0.011	0.379–0.422
Model S_j . $S_{a\ 2p(35,6)}$			
S_a (60–94)	0.774	0.0111	0.752–0.795
S_{ac} (95–00)	0.405	0.1604	0.156–0.715
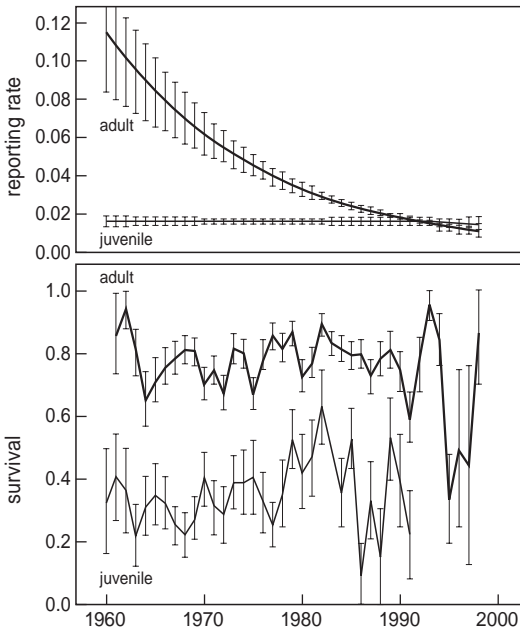
low estimates in the last years of the study period. To investigate whether there were real indications for a low adult survival, years were grouped into five-year periods to achieve larger sample sizes per period. In the first seven periods, adult survival estimates varied between 0.74 and 0.80 with standard errors between 0.01 and 0.025 (Table 4). In contrast, the estimate for the last period (1995–2000) was much lower at 0.40 ± 0.012. Nevertheless, the fit of this model with eight periods to the data was not significantly better than a model with a constant survival.

Figure 7. Annual estimates (± 1 SE) of survival of juveniles and adults. Estimates with SEs >0.25 or <0.01 have been omitted. In the top panel, the fitted estimates of the reporting rates (± 1 SE) are given separately for juveniles and adults. Estimates based on model 10, Table 2.

DISCUSSION

The main result reported here is that adult survival has probably been exceptionally low in several years between 1995 and 2000. There is no evidence for major changes in adult or juvenile survival rate of Black-tailed Godwits between 1960 and 1995. Likewise, there is no evidence for changes in the survival rate in the first year following ringing of chicks between 1960 and 2000. A model with a constant adult survival rate of 0.77 and a juvenile survival of 0.36 gives the best fit to the data, although the difference with models where adult and/or juvenile survival show a slight increase over time is not significant. The low adult survival in the last 5-year period does not appear in models with linear or quadratic trends over time. The low adult survival in recent years only becomes apparent when this period is specifically investigated. There are two reasons for this apparent contradiction. First, there is the general problem that towards the end of the study, some of the birds are still alive and thus information about their survival is still 'in the air'. Second, the numbers ringed are much lower in the last ten years and together with the strong reduction in reporting rate, the small numbers will lead to a low weight of the data from this last period in the overall regression models. The estimate for adult survival in the last 5-year period is based on only 21 records. The decline in reporting rates is a general phenomenon that has also been noted elsewhere (Baillie 2001).

Even though it appeared not possible to demonstrate annual fluctuations in survival rates, the best estimates show a number of features that can be checked against independent evidence. Groen & Hemerik (2002) performed a detailed study on one specific population for four years. They report adult return rates for three years, which are very close to our survival estimates for the same years (Table 5). Their return rates would approach true survival if resighting probability and breeding site fidelity were 100% in their study, which is not an unlikely assumption. Estimates for juvenile survival are more difficult to compare due to the generally high natal dispersal in waders. Indeed, it is noticeable that the return rates estimated by Groen & Hemerik are lower than our estimates of juvenile survival (Table 5).

Our survival estimates are based on when birds were reported dead and thus on the age distribution. This makes these estimates relatively insensitive to dispersal and these estimates are therefore good average values for the population ringed. The distribution of birds ringed over The Netherlands was quite reasonable at the scale of provinces and has been constant over time, at least for chicks ringed. We may thus ask the question which reproductive rate is necessary to maintain a stable population size given the survival rates obtained. The answer to this question depends on the reproductive strategy and specifically on the age at first reproduction. Let us assume that no birds breed when one year old and that all birds breed when three years of age (Table 6). One would then need between 1.6 and 2.2 chicks per pair per year to have a stable population size depending on the proportion of two- year old birds

Table 5. Comparison of annual estimates in this study with those of Groen & Hemerik (2002). The age class definitions do not match precisely.

	Adult return rate, Groen & Hemerik	Adult survival, this study	Juvenile return rate, Groen & Hemerik	Juvenile survival, this study
1984–1985	0.83	0.82	0.22	0.36
1985–1986	0.78	0.79	0.23	0.53
1986–1987	0.84	0.80	0.14	0.09
1987–1988			0.13	0.33

Table 6. Calculation of number of chicks (at ringing age) to be produced per breeding pair for a stable population. These calculations are based on estimated average juvenile and adult survival rates (Table 2, model 1). Modelled for varying percentages of one- and two-year old birds reproducing. One-year old birds are in their second calendar year.

Percentage of birds reproducing per age class			Number of chicks required
1 year	2 years	≥ 3 years	
0	0	100	2.12
0	50	100	1.85
0	80	100	1.72
0	100	100	1.64
20	80	100	1.62
20	100	100	1.55

that breed and for an adult survival of 0.77 and a juvenile survival of 0.36. The unit 'chicks per pair' is here measured at the age of ringing, which varies from day of hatching to two weeks after hatching. In practice this means that given an average clutch size of slightly less than 4 eggs (Groen & Hemerik 2002), the loss of clutches and broods of up to one week should not exceed 50%. When clutches are lost very early in the season these may be replaced and this would increase the tolerance for early clutch loss.

In this very simple model calculation, a reduction of the adult survival to 0.4 for five consecutive years, would lead to a reduction of the breeding population by 92%. Since the actual observed reduction is much smaller (data from SOVON-CBS), the estimates of an adult survival of 0.4 are probably too low. In theory, it is possible that the low adult survival was partially compensated by a higher proportion of young birds breeding, a higher number of chicks at ringing age per pair and/or a higher juvenile survival. The first of these mechanisms would lead to a smaller reduction in breeding pairs than the actual reduction in population size. In order to assess the third of these potential compensatory processes, we have to look at our estimation process in more detail.

The primary quantity that is estimated in our models is always a product of survival rates and a reporting rate. Thus the number of individuals ringed as nestling in year 0 and recovered during year 5 is equal to $N_{j0}*S_{j0}*S_{a1}*S_{a2}*S_{a3}*S_{a4}*(1-S_{a5})*R_{a5}$. When $S_{a1}=S_{a2}=S_{a3}=S_{a4}=S_{a5}$ this reduces to $N_{j0}*S_{j0}*(S_a)^4*(1-S_a)*R_{a5}$. Thus, the estimation of adult and juvenile survival are strongly interdependent and one indication that the estimate of 0.4 for adult survival may be too low is that when fitting separate juvenile survival rates for the same periods we obtain relatively high estimates for juvenile survival. Realising how the calculated survival rates are derived also makes it clear that we cannot discriminate between a reduced survival for several years or one single catastrophic year.

In the years following the end of this study, mark-resighting studies of colour-ringed Black-tailed Godwit populations were started in five sites in The Netherlands. Estimates of apparent adult survival from the period 2002–2005 varied between 0.81 and 0.95 (Roodbergen *et al.* unpubl.). Although these results were derived from few localities that may or may not be representative for The Netherlands as a whole, they indicate that adult survival has not been low throughout the country in the years after our study ended. They may suggest that the observed reduction of adult survival may have been a temporary event, but a continuation of ringing studies will allow us to draw more firm conclusions.

The strong decrease in reporting rate of adult birds seriously hinders the estimation of survival rates. Given that most reports from abroad resulted from hunting, it is not clear to what extent the decline in reports was due to lower hunting pressure or due to a lower reporting rate of the hunted birds. The observation that recoveries from southern Spain and Morocco became practically absent in the last decade, while recoveries from northern Spain and southern France are still present, makes it more likely that the cause lies in the behaviour of the birds than in human reporting behaviour. It is a fact, however, that reports of birds dying from non-hunting causes abroad are practically non-existent. This implies

that recapturing and resighting birds that have been previously ringed will become ever more important in collecting data on survival. At present, the methods used for analysis of live recapture data assume a closed population study within which observation probabilities can be estimated as rates applicable to all individuals. Spatial heterogeneity could in principle be taken into account either by using multistate models (Lebreton *et al.* 1999) or by using separate observation probabilities per area. However, in multistate models, the number of parameters rapidly becomes too high to be practicable. Only with external independent information or assuming time independence of area specific observation probabilities can these be estimated with any precision. Methods for dealing with such heterogeneity have to be developed further. In the meantime, ringing schemes should continue to promote the collection of resighting and retrap data, since these become more important with the declining reporting rates of dead birds.

Conclusions

Given the conservation issues involved, it is important to formulate precisely what can and what cannot be concluded from these analyses. Any change in reproductive output during the study period is outside the scope of this study. There is no evidence for any changes in survival for the first year after ringing of chicks throughout the study period, but the absence of evidence is no evidence for an absence. Direct estimates of chick survival made by observing individually marked broods suggested that survival of chick between hatching and fledging has declined considerably over the past two decades (Schekkerman *et al.* in press). Our analyses suggest that major changes in population trajectory during the 1970s must have been due to changes in breeding success. There are indications, that the adult survival rates have been exceptionally low during the second half of the 1990s. These results apply to the population ringed, which is reasonably distributed over The Netherlands. It is an open question whether the low adult survival has been due to a unique event

or due to a systematic change in conditions. A lower adult survival should have dramatic consequences for the age distribution of breeding adults and obtaining data on such age distributions would be the most direct way to investigate a continued occurrence of low adult survival.

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SAMENVATTING

De berichten over de achteruitgang van de Grutto *Limosa limosa* in Nederland zijn zorgwekkend, omdat een belangrijk deel van de wereldpopulatie in ons land broedt. Een van de stappen in het ophelderen van de oorzaken van deze achteruitgang is om de daarbij betrokken demografische processen nader te bestuderen. Er zijn enkele studies over overleving gebaseerd op terugvangsten en aflezingen uit beperkte studiegebieden en beperkte periodes. De enige studie over de overleving gebaseerd op alle Nederlandse ringgegevens over een langere periode is echter al weer enige decennia oud. De hier gepresenteerde analyses zijn gebaseerd op alle in Nederland geringde Grutto's uit de periode 1960 tot 2000 die dood zijn teruggemeld. Alhoewel de nauwkeurigheid van de overlevingsgetallen tegen het einde van de studieperiode kleiner wordt door kleinere aantallen geringde individuen en door een afname van de meldingskans (van 9% in 1960 tot 1% in 2000), lijkt er in de laatste jaren van de onderzochte periode een dramatische afname te zijn geweest van de jaarlijkse overleving van volwassen Grutto's van 77% tot ongeveer 40%. Uit een analyse van de geografische spreiding van de herkomst van de terugmeldingen blijkt een toename van meldingen uit het overwinteringsgebied en een sterke afname van terugmeldingen uit Marokko en Zuid-Spanje.

Appendix 1. Likelihood ratio test results of the models 1–5 and of survival parameters. *Limosa limosa* NLA dead recoveries 1960–2000 (Tests based on c-hat = 2.3)

Reduced Model	General Model	Chi-sq.	*df*	*P*
$S_{j.}\, S_{a.}\, R_{j.}\, R_{aT}$	$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	2.42	1	0.120
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{j.}\, S_{aT}\, R_{jT}\, R_{aT}$	0.29	1	0.590
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jT}\, S_{a.}\, R_{jT}\, R_{aT}$	0.00	1	0.986
$S_{j.}\, S_{a.}\, R_{jT}\, R_{a.}$	$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	38.57	1	<0.001
$S_{j.}\, S_{a.}\, R_{j.}\, R_{a.}$	$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	41.16	2	<0.001
$S_{j.}\, S_{a.}\, R_{j.}\, R_{aT}$	$S_{j.}\, S_{aT}\, R_{jT}\, R_{aT}$	2.71	2	0.259
$S_{j.}\, S_{a.}\, R_{j.}\, R_{aT}$	$S_{jT}\, S_{a.}\, R_{jT}\, R_{aT}$	2.42	2	0.299
$S_{j.}\, S_{a.}\, R_{j.}\, R_{aT}$	$S_{j.}\, S_{a.}\, R_{jT}\, R_{a.}$	–36.16	0	-
$S_{j.}\, S_{a.}\, R_{j.}\, R_{a.}$	$S_{j.}\, S_{a.}\, R_{j.}\, R_{aT}$	38.75	1	<0.001
$S_{j.}\, S_{aT}\, R_{jT}$ Ra li	$S_{jT}\, S_{a.}\, R_{jT}\, R_{aT}$	–0.29	0	-
$S_{j.}\, S_{a.}\, R_{jT}\, R_{a.}$	$S_{j.}\, S_{aT}\, R_{jT}\, R_{aT}$	38.86	2	<0.001
$S_{j.}\, S_{a.}\, R_{j.}\, R_{a.}$	$S_{j.}\, S_{aT}\, R_{jT}\, R_{aT}$	41.46	3	<0.001
$S_{j.}\, S_{a.}\, R_{jT}\, R_{a.}$	$S_{jT}\, S_{a.}\, R_{jT}\, R_{aT}$	38.57	2	<0.001
$S_{j.}\, S_{a.}\, R_{j.}\, R_{a.}$	$S_{jT}\, S_{a.}\, R_{jT}\, R_{aT}$	41.17	3	<0.001
$S_{j.}\, S_{a.}\, R_{j.}\, R_{a.}$	$S_{j.}\, S_{a.}\, R_{jT}\, R_{a.}$	2.59	1	0.107

Models 1, 8–10

Reduced Model	General Model	Chi-sq.	*df*	*P*
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jT}\, S_{aT}\, R_{jT}\, R_{aT}$	0.29	2	0.865
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{a.}\, R_{jT}\, R_{aT}$	29.56	40	0.887
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{j.}\, S_{at}\, R_{jT}\, R_{aT}$	28.99	40	0.901
$S_{j.}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{at}\, R_{jT}\, R_{aT}$	57.62	80	0.969
$S_{jT}\, S_{aT}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{a.}\, R_{jT}\, R_{aT}$	29.27	38	0.844
$S_{jT}\, S_{aT}\, R_{jT}\, R_{aT}$	$S_{j.}\, S_{at}\, R_{jT}\, R_{aT}$	28.70	38	0.862
$S_{jT}\, S_{aT}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{at}\, R_{jT}\, R_{aT}$	57.33	78	0.959
$S_{jt}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{j.}\, S_{at}\, R_{jT}\, R_{aT}$	–0.56	0	-
$S_{jt}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{at}\, R_{jT}\, R_{aT}$	28.06	40	0.922
$S_{jt}\, S_{a.}\, R_{jT}\, R_{aT}$	$S_{jt}\, S_{at}\, R_{jT}\, R_{aT}$	28.63	40	0.910

Appendix 2. Estimates from model 10 (Table 2). Reporting rates linear regression on time, survival estimates per year. In Italics, estimates excluded from further consideration, because SE <0.001 or SE >0.25.

	Sa	s.e.	low lim	up lim	Sj	s.e.	low lim	up lim	Ra	s.e. Ra	Rj	s.e. Rj
1960	*1.000*	*0.000*	*0.999*	*1.000*	0.301	0.171	0.081	0.680	0.126	0.010	0.016	0.001
1961	0.870	0.201	0.169	0.995	0.381	0.152	0.148	0.685	0.118	0.009	0.016	0.001
1962	0.943	0.088	0.404	0.997	0.330	0.122	0.143	0.592	0.111	0.007	0.016	0.001
1963	0.806	0.107	0.520	0.941	0.205	0.115	0.060	0.508	0.104	0.006	0.016	0.001
1964	0.663	0.113	0.421	0.842	0.297	0.085	0.160	0.484	0.097	0.004	0.016	0.001
1965	0.726	0.097	0.506	0.873	0.331	0.094	0.177	0.533	0.091	0.002	0.016	0.001
1966	0.768	0.078	0.584	0.886	0.310	0.079	0.178	0.481	0.085	0.000	0.016	0.000
1967	0.795	0.066	0.636	0.896	0.242	0.066	0.136	0.392	0.080	0.000	0.016	0.000
1968	0.820	0.058	0.679	0.907	0.216	0.084	0.094	0.422	0.074	0.000	0.015	0.000
1969	0.813	0.061	0.666	0.905	0.269	0.080	0.142	0.451	0.070	0.000	0.015	0.000
1970	0.710	0.064	0.571	0.818	0.389	0.096	0.225	0.584	0.065	0.000	0.015	0.000
1971	0.756	0.059	0.623	0.853	0.302	0.106	0.139	0.537	0.061	0.000	0.015	0.000
1972	0.684	0.066	0.542	0.798	0.284	0.119	0.112	0.557	0.057	0.000	0.015	0.000
1973	0.825	0.060	0.677	0.913	0.390	0.113	0.202	0.618	0.053	0.000	0.015	0.000
1974	0.805	0.058	0.666	0.895	0.390	0.131	0.179	0.652	0.049	0.000	0.015	0.000
1975	0.681	0.055	0.565	0.779	0.410	0.151	0.170	0.703	0.046	0.000	0.015	0.000
1976	0.803	0.065	0.646	0.901	0.332	0.130	0.135	0.611	0.043	0.000	0.015	0.000
1977	0.861	0.055	0.716	0.938	0.260	0.104	0.109	0.504	0.040	0.000	0.015	0.000
1978	0.827	0.057	0.686	0.913	0.365	0.144	0.146	0.659	0.037	0.000	0.015	0.000
1979	0.870	0.054	0.723	0.945	*0.536*	*0.131*	*0.292*	*0.764*	0.035	0.000	0.015	0.000
1980	0.737	0.067	0.588	0.847	0.440	0.161	0.179	0.739	0.032	0.000	0.015	0.000
1981	0.777	0.061	0.636	0.875	0.484	0.169	0.200	0.779	0.030	0.000	0.015	0.000
1982	0.897	0.049	0.755	0.961	0.646	0.162	0.314	0.879	0.028	0.000	0.015	0.000
1983	0.836	0.054	0.701	0.918	*1.000*	*0.000*	*1.000*	*1.000*	0.026	0.000	0.015	0.000
1984	0.820	0.057	0.680	0.907	0.371	0.151	0.142	0.678	0.024	0.000	0.015	0.000
1985	0.797	0.063	0.648	0.893	0.545	0.136	0.290	0.778	0.023	0.000	0.015	0.000
1986	0.805	0.061	0.658	0.898	0.109	0.107	0.014	0.514	0.021	0.000	0.015	0.000
1987	0.731	0.080	0.549	0.858	0.353	0.166	0.116	0.693	0.020	0.000	0.015	0.000
1988	0.788	0.075	0.607	0.899	0.187	0.193	0.019	0.735	0.018	0.000	0.015	0.000
1989	0.813	0.080	0.608	0.924	0.552	0.164	0.251	0.819	0.017	0.000	0.015	0.000
1990	0.746	0.088	0.541	0.880	0.420	0.193	0.133	0.774	0.016	0.000	0.015	0.000
1991	0.598	0.094	0.409	0.761	0.240	0.159	0.054	0.637	0.015	0.000	0.015	0.000
1992	0.766	0.112	0.489	0.918	*1.000*	*0.000*	*1.000*	*1.000*	0.014	0.000	0.015	0.000
1993	0.953	0.071	0.477	0.998	*0.000*	*0.000*	*0.000*	*0.000*	0.013	0.000	0.015	0.000
1994	0.840	0.117	0.489	0.967	*0.000*	*0.000*	*0.000*	*0.000*	0.012	0.000	0.015	0.000
1995	0.315	0.164	0.093	0.671	*0.346*	*0.299*	*0.038*	*0.876*	0.011	0.000	0.015	0.000
1996	*0.433*	*0.268*	*0.082*	*0.867*	*1.000*	*0.000*	*1.000*	*1.000*	0.010	0.000	0.015	0.000
1997	*0.286*	*0.298*	*0.022*	*0.875*	*1.000*	*0.000*	*1.000*	*1.000*	0.010	0.000	0.015	0.000
1998	0.769	0.247	0.179	0.981	*0.417*	*0.425*	*0.023*	*0.957*	0.009	0.000	0.015	0.000
1999	*0.358*	*0.300*	*0.042*	*0.878*	*1.000*	*0.000*	*1.000*	*1.000*	0.008	0.000	0.015	0.000
2000	*0.000*	*0.000*	*0.000*	*0.001*	*0.693*	*0.447*	*0.035*	*0.993*	0.008	0.000	0.015	0.000