

Survival of Spoonbills on Wadden Sea islands

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The Spoonbill populations in Europe are fragmented and threatened. The dynamics of the species is poorly known but ringing and observation programmes are under way. Here we estimated the local survival of two colour-ringed populations of Spoonbills in the Netherlands. Adult survival and sighting rates, estimated with the Cormack-Jolly-Seber model, were high and constant over a 10-year period (1986–1996) and no differences could be detected between the two populations. Juvenile survival, estimated from the observed return rate, did not vary over a 5-year period (cohorts 1986–1990). However, at least in one of the two populations, the proportion of birds returning by two years of age increased over a 9-year period (cohorts 1986–1994). Thus there is only weak support for the idea that the recent increase in population size was driven by an increase in local survival. Our work on survival provide a first step towards a larger appreciation of the population dynamics and life-history of the Spoonbill.

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The Spoonbill *Platalea leucorodia* is a threatened species in Europe (Tucker and Heath 1994). The populations of this very conspicuous bird are scattered, with colonies sometimes separated by hundreds of kilometres. In Western Europe large populations are only found in Spain and the Netherlands; smaller populations occur elsewhere, mostly in France, Italy and Portugal. The spatial dynamics of the Spoonbill over its range remains largely unknown, but research is now under way in several regions, by means of large-scale long-term ringing and sighting programmes (e.g. de le Court and Aguilera 1997, van Dijk and Overdijk 1996). Thus we may hope to gain access to the key demographic parameters to understand the spatial dynamics, viz. breeding success, dispersal, survival; here we are concerned with the latter. Isolated populations are also potentially useful for the study of between-population variation in life-history. For example, populations in the Netherlands migrate 2000 km farther than populations in southern Spain, almost doubling the total distance from breeding to wintering grounds. This dif-

ference may correlate with changes in life-history, perhaps causing an increase in mortality.

The colonies in the Netherlands represent about half of the total population of Spoonbills in Western Europe. Before 1900, there were at least 1000 breeding pairs but numbers declined, with as few as 150 breeding pairs in 1968. The banning of pesticides, protection of breeding grounds and other conservation measures have allowed the species to make a steady recovery, so that by 1995 there were about 800 breeding pairs, producing some 1150 juveniles (van Dijk and Overdijk 1996). The aim of the current protection plan (van Ommering and Walter 1994) is to secure the sustainability of the population in the Netherlands. In this respect, it is important to have good estimates of demographic parameters. Here we use data from the colonies on Vlieland and Terschelling, two neighbouring islands in the Wadden Sea, where the population size has recently increased (Fig. 1). Our aim is to provide reliable estimates of local survival, and to assess whether the recent increase in population size can be linked to

an increase in juvenile or adult survival rate. Furthermore, we want to evaluate the usefulness of the present ringing programme for the monitoring of survival.

The Spoonbill

The Spoonbill is a migratory bird, wintering mainly in Mauritania and Senegal. It is a colonial nester, breeding in close proximity to shallow waters, where it feeds on small aquatic prey (sticklebacks in fresh waters, shrimps in coastal areas). There is a single clutch, of 3–4 eggs. The species is socially monogamous. Sexual dimorphism is slight (leg and bill size). The age at maturity is not well known: there are a few observations of birds breeding at age 2 but most birds start breeding at age 4. Non-breeding birds either stay on the wintering grounds or come back to the breeding grounds during summer. Maximum observed longevity (in the Dutch Ringing Scheme data) is 28 years.

The major current breeding colonies in the Netherlands are on Wadden Sea islands (Texel, Terschelling, Vlieland, and Schiermonnikoog), in Flevoland (2 colonies), Zuid Holland (1 colony) and Noord Holland (1 colony). Older colonies (e.g. Naardermeer) have disappeared or are declining; feeding and breeding grounds have recently shifted from inland to coastal areas. The Dutch colonies are the most northerly in the world; other breeding grounds are in France (Loire Atlantique), Spain (Andalusia), Portugal, Italy, Greece, and Central and Eastern Europe. Spoonbills are faithful to their natal colony, except when the breeding ground is disturbed (pers. obs.). Dispersal between different colonies (>100 km) has been recorded but is infrequent (2.4% of colour-ringed birds; de le Court and Aguilera 1997).

Material and methods

All birds were ringed before fledging (15–30 days after hatching), in 4–5 sessions at 3-week intervals. The ringers estimate that they ring at least 95% of all fledglings produced in any one year. Ringing started on Terschelling in 1982 and on Vlieland in 1983. Since then, most birds have been ringed every year with two colour rings and a numbered aluminium ring, but individual colour rings were not used in 1985 and there was no ringing in 1995. A few birds have lost one colour ring, hindering individual recognition in the field; the known (i.e. minimum) number of birds per year is between 1 and 12.

Individuals were identified in the field from the colour rings with a telescope. The effort was intensive from 1983 onwards and the time spent sighting birds was similar every year (ca 320 hours/year). In the

following analyses, only sightings of live birds in the field were used. The sex of most birds was unknown or unreliable, and so the analyses combine the two sexes.

Adult survival analyses were made using the Cormack-Jolly-Seber (CJS) model following the statistical framework reviewed by Lebreton et al. (1992). We used the program SURGE 4.2 (Pradel and Lebreton 1993). In summary, sighting histories are modelled as the outcome of the probabilities of surviving and of being sighted when alive. In the models, both survival and sighting rates can differ between years and/or different classes of individuals (e.g. natal colony). Survival and sighting rates and their variances are estimated using maximum likelihood methods. Different models can be compared using likelihood ratio tests, enabling the factors affecting survival and/or sighting rate to be identified. The selection of the most parsimonious model can also be made using the Akaike Information Criterion (see Lebreton et al. 1992). The goodness-of-fit to the CJS model was tested by the method developed by Burnham et al. (1987; program RELEASE).

Results

Number of birds ringed and sighted

The numbers of birds ringed and sighted each year are given in Table 1. Birds ringed in 1996 are not used in any of the following analysis.

Sightings in the Netherlands were made from March to September. Many individuals were observed several times in a single year (mean number of sightings per individual per year = 4.3, range 1–39). These multiple sightings are, however, not useful for survival analysis: only one data point per year is used here. Of the birds seen within the Netherlands, the majority were sighted at least once per year within 50 km (i.e. foraging range) of their natal colony. This proportion increased with age (72% for age 1, 84% for age 2, 92% for age 3 or

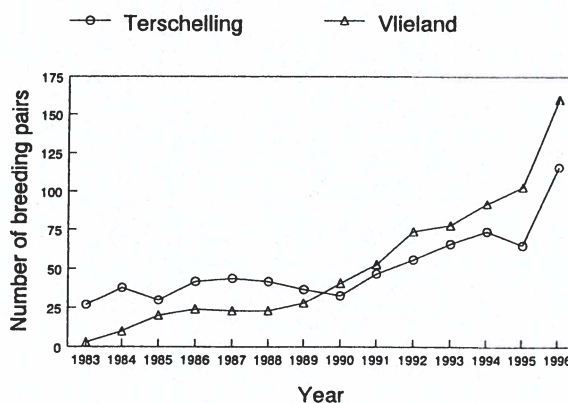


Fig. 1. The size of the Spoonbill populations on Terschelling and Vlieland in 1983–1996.

Table 1. Annual numbers of Spoonbills ringed (on the left) and sighted at age one year old or older (on the right).

	Terschelling	Vlieland	Total ringed	Terschelling	Vlieland	Total sighted
1982	45	0	45	0	0	0
1983	43	2	45	1	0	1
1984	47	20	67	0	0	0
1985	28	26	54	6	1	7
1986	62	47	109	7	1	8
1987	50	38	88	14	3	17
1988	61	56	117	13	9	22
1989	76	57	133	20	8	28
1990	69	77	146	28	16	44
1991	70	94	164	36	22	58
1992	113	148	261	41	26	67
1993	106	144	250	60	46	106
1994	142	145	287	83	74	157
1995	0	0	0	107	91	198
1996	104	115	219	121	128	249
Total	1016	969	1985	537	425	962

more). Concomitantly, the proportion of birds sighted in any year only outside the Netherlands decreased with age: 75% for age 1, 35% for age 2, 14% for age 3 and 8% for age 4 or more, the majority (85%) being sighted in Spain, France and Portugal, i.e. along the European part of the migration flyway, throughout the year, with peaks in March–April and September–October (migration periods). Sightings outside the Netherlands represented 17% of the data suitable for survival analysis but, not being the product of any consistent effort, their distribution was highly heterogeneous in time and space. They have therefore not been used in the present analyses.

Age at return to the breeding grounds

There was much variation in the age at which birds were first observed on the breeding grounds after their first migration to Africa. We used the cohorts of birds born in 1986–1990 (before 1986, the sample sizes are too small; after 1990 data are biased because some birds do not return until they are at least 6 years old) to test whether the age at return varied over time or between the two islands. This data set contains 593 individuals (318 born on Terschelling, 275 born on Vlieland), of which 181 have subsequently returned to the breeding grounds (i.e., the Netherlands). The mean age at which birds were first sighted back in the Netherlands did not vary over the cohorts nor did it differ between the two islands (ANOVA, island: $F_{1,171} = 1.87$, $p = 0.17$; cohort: $F_{4,171} = 0.11$, $p = 0.98$; island \times cohort interaction: $F_{4,171} = 0.67$, $p = 0.61$). The modal age of return to natal areas in the Netherlands was three years (Table 2).

Adult survival

In this analysis, local adult survival is the probability of surviving from one breeding season to the next. To estimate adult survival, we used all sightings of birds known to have returned to the Netherlands, and sighted between 1986 and 1996. The data set contains 418 individuals sighted in 954 bird-years.

The goodness-of-fit to the Cormack-Jolly-Seber model was tested (Burnham et al. 1987) and rejected ($\chi^2 = 68.5$, $df = 29$, $p = 0.0001$): birds sighted for the first time were less likely to be sighted again than birds already sighted before. Because this problem may be an effect of age (immature birds being likely to have lower survival and/or sighting rate), we repeated the test by limiting the data to sightings of birds aged more than 4 years. In this second analysis, the goodness-of-fit to the CJS model was globally accepted ($\chi^2 = 20.0$, $df = 17$, $p = 0.27$), although one of the four components (3.SR) was still significant ($p = 0.04$), but the effect was much smaller and the problem was clearly limited to only one

Table 2. Age of Spoonbills at return to the breeding grounds (cohorts 1986–1990; $n = 181$).

Age	Percent
1	4.4
2	8.3
3	30.9
4	18.8
5	19.3
6	13.3
7	3.9
8	1.1

year (1994). Inspection of the data suggested that ring loss and the presence of transient birds may have caused this problem; but other causes could not be rejected. Because this residual deviation from the CJS model was limited to only one year, and because we could not identify its cause unambiguously, we have not modelled it in the survival analysis with SURGE.

We started the survival analysis with a full Cormack-Jolly-Seber model, i.e. with both survival and sighting rate being time-dependent, and with different parameters for each island (40 parameters, six of which could not be estimated either because of the structure of the model or scarcity of data). Several reduced models were tested, with survival and/or sighting rate constant over time and with or without grouping the two populations. The lowest Akaike Information Criterion was obtained for the simplest model, with survival and sighting rate constant over time, and no differences between the colonies (two parameters). The full model could be reduced to this optimal model without any significant loss of information (Likelihood ratio test, $\chi^2 = 38.2$, $df = 32$, $p = 0.21$). Thus there was no statistical effect of time (year) on survival or sighting, and no statistical difference between the two islands. In this optimal model, the estimated survival rate was 0.83 (s.e. = 0.04). The estimated sighting rate (the probability of observing an adult bird, at least once per year, if alive) was 0.82 (s.e. = 0.04).

Because the goodness-of-fit analysis suggested an age effect, we also compared models where survival and/or sighting probability were either constant over time or age-dependent (nine age classes, the last one covering age 10 and above). Data from the two islands were pooled, as we found no effect of location in our previous analysis. The effect of age on survival was not significant (Likelihood ratio test, $\chi^2 = 13.6$, $df = 8$, $p = 0.09$). Thus the model in which survival is constant over time but sighting rate varies with age was accepted, and had the lowest AIC. Further reduction of the model was not possible, as the effect of age on sighting rate was significant (Likelihood ratio test, $\chi^2 = 19.2$, $df = 8$, $p = 0.01$). Inspection of the parameters showed that sighting rate was lower for the first two age classes than for older birds (age 2: sighting rate = 0.50, s.e. = 0.10; age 3, sighting rate = 0.72, s.e. = 0.08, age 4 and above, sighting rate 0.80–0.90, s.e. 0.03–0.06). Birds younger than 4 years old are probably non-breeders and are therefore more difficult to observe. Birds 4 years or more should constitute a more homogeneous set. Therefore we repeated the analyses by limiting the data to sightings of birds aged 4 or more. This restricted data set contained 304 individuals in 686 bird-years. The effect of age was no longer significant, neither for survival nor for sighting (Likelihood ratio test, $\chi^2 = 14.6$, $df = 10$, $p = 0.15$) and the model in which both survival and sighting are independent of time was therefore accepted. From this model, we obtained our best estimates of survival rate (0.83, s.e. = 0.02) and sighting rate (0.85, s.e. = 0.02).

Juvenile survival

We used the proportion of juveniles observed returning to the breeding grounds as a measure of local juvenile survival. This proportion confounds the actual local survival rate and the sighting probability. Annual rates of the latter are extremely difficult to estimate here because, for young birds, we cannot separate sighting probability from returning probability. However, we have already shown that the sighting rate of adults was high and did not vary over time and that the mean age at return to the colony did not change over time (birds born 1986–1990; see previous section). We can therefore assume that temporal changes (if any) in the proportion observed returning should not be caused by changes in sighting probability and/or changes in the age at return.

By using the proportion of birds observed returning, the true (local) survival will be underestimated because sighting rate is not taken into account. However, the bias can be estimated and turns out to be very small. The probability of escaping sighting depends on the number of years spent in the colony (at age > 0) before disappearing from the population. The probability of spending only one year in the colony and escaping sighting is $(1 - s)(1 - r)$, where s is the survival rate and r is the resighting rate; both rates were considered constant over time, as indicated by our analysis of adult survival. Under our estimates, this probability was 0.026. The probability of spending two years in the colony and escaping sighting was $s(1 - s)(1 - r)^2 = 0.003$. For longer periods, the probability becomes negligible. Thus we will use a correction factor of 1.029 (see below).

In a first analysis, we used the cohorts of birds born between 1986 and 1990 and sighted between 1987 and 1996. For these five cohorts, there was no difference in the probability of returning between the two islands nor was there any systematic temporal change among the cohorts (Logistic regression; island, $\chi^2 = 1.9$, $df = 1$, $p = 0.16$; cohort, $\chi^2 = 0.2$, $df = 1$, $p = 0.66$; island \times cohort interaction not significant). In the absence of any detectable variation in space or time, we can combine the observations over the 5 years and the two islands. Overall, 181 out of 593 juveniles returned to the breeding grounds. Because some birds are not observed returning until they are at least 6 years old, the observations may still be incomplete for the later cohorts. From the proportions in Table 2, we expect 99% of the birds born in 1989 to have returned within the observation period but only 95% of the birds born in 1990. Therefore we expect 2.3 juvenile individuals to have returned without ever being observed. Incorporating this slight correction, we obtain a return rate of 0.31 (± 0.04 , 95% confidence interval by normal approximation). To obtain our estimate of juvenile local survival, we correct this estimate for sighting rate (see above)

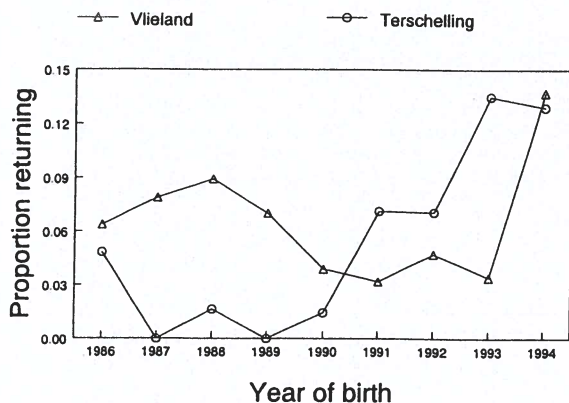


Fig. 2. The proportion of Spoonbills born in 1986–1994 returning by two years of age.

and obtain 0.32 as our best estimate of juvenile survival.

The above analysis is based on five cohorts only because the later cohorts are too recent for an adequate proportion of the birds to have returned. To test for a possible trend during a longer period of time, we performed a second analysis by including all the birds born between 1986 and 1994, but calculating return rate by the age of two years (106/1575 birds). In this data set (see Fig. 2), the proportion that returned by the age of two increased significantly over the years on Terschelling (Logistic regression, $\chi^2 = 25.9$, $df = 1$, $p < 0.0001$), but not on Vlieland ($\chi^2 = 1.0$, $df = 1$, $p = 0.31$). However, the most recent value for Vlieland is the highest for that island, suggesting a similar trend.

Discussion

We have obtained a reliable estimate of adult local survival for Spoonbills on the Wadden Sea islands. The quality of this estimate comes from using the new statistical methods for analysing survival from resighting data. Reliable survival estimates from other Spoonbill populations have not yet been published, but a survival analysis of the Spanish population is well under way (Claudine de le Court, pers. comm.), so that the demography and life-history of these two populations can be contrasted. Compared with similar European species, our estimate falls between the adult survival rate of Greater Flamingos *Phoenicopterus ruber* in Camargue (0.93, but 0.76 in a year with a severe cold spell; Cézilly et al. 1996) and that of the declining White Stork *Ciconia ciconia* population in Alsace (0.65; Kanyamibwa et al. 1990).

Juvenile survival is always hard to estimate, especially in species such as the Spoonbill where young

return to the colony at various ages (see Pradel et al. 1997 and references therein for a new approach to this problem). We could not detect any temporal changes in juvenile survival for the birds of the 1986–1990 cohorts. However, over a longer period, there was an increase in the return rate of Spoonbills by the age of two and the data suggest that this change has taken place in the more recent years. This increase could be caused either by an increase in juvenile survival and/or a decrease in the age of return to the colony. Only future observations can settle this matter, but both possibilities suggest an increase in the quality of the juveniles produced. An alternative explanation might be that immature Spoonbills tend to return to the Netherlands at a higher rate because local conditions have deteriorated in the African or other European regions where immatures would otherwise spend the summer period and/or conditions have improved in the Netherlands.

In principle the recent increase in population size (Fig. 1) may have been a consequence of a change in survival rate. We could not detect any increase in adult survival and we have obtained only weak evidence for an increase in juvenile survival. Note also that birds returning to the breeding grounds (here, the Netherlands) are not necessarily breeding, so that an increase in juvenile survival does not necessarily imply an increase in recruitment. Thus there is little evidence of a present change in survival that could cause the increase in population size. However, the recovery of the Spoonbill populations in the Netherlands predates the period covered in this study. Therefore we cannot exclude that there was an increase in survival early during the recovery period and that survival then stabilised at a higher value causing the population increase. However, it is likely that other factors have played a major role in the recent population increase. Such factors, not considered here, are brood size at fledging and age at first breeding (which could vary independently of age at return to the breeding grounds). Changes in these factors are probably the results of protection and management measures, which aimed at increasing the quality of the breeding grounds by limiting human disturbance and increasing the quality and/or availability of foraging areas. On the other hand, migration to and from the winter quarters, and wintering in Africa, probably remain the major sources of mortality. Indeed, the majority (66%) of the 256 recoveries of dead Spoonbills in the Dutch Ringing Scheme are from countries outside the Netherlands, and this proportion is an underestimate because the reporting rate in Africa is likely to be much lower than on the breeding grounds. Therefore survival may have remained relatively unaffected by conservation measures on the breeding grounds.

The sighting probability was high and constant over time, which is testimony to the quality of the observa-

tion programme. The ringing and sighting programme run on Terschelling and Vlieland over the last 10 years has proved adequate for monitoring Spoonbill survival and the continuation of such programmes should be encouraged. For future monitoring of survival (juvenile and adult), we recommend to keep the effort concentrated on a small number of intensively studied colonies. If, for lack of resources, only part of the nestlings can be ringed, then great care should be taken to avoid any bias in ringing by using a stringent random sampling scheme.

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