

ADULT SURVIVAL RATES OF SHAG  
*PHALACROCORAX ARISTOTELIS*, COMMON  
GUILLEMOT *URIA AALGE*, RAZORBILL *ALCA*  
*TORDA*, PUFFIN *FRATERCULA ARCTICA* AND  
KITTIWAKE *RISSA TRIDACTYLA*  
ON THE ISLE OF MAY 1986-96

M.P. HARRIS<sup>1</sup>, S. WANLESS<sup>1</sup> & P. ROTHERY<sup>2</sup>

<sup>1</sup>*Institute of Terrestrial Ecology, Hill of Brathens, Banchory, Kincardineshire AB31 4BY, Scotland, U.K.;* <sup>2</sup>*Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE28 2LS, England, U.K. e-mail mph@ceh.ac.uk*

*On the Isle of May between 1986 and 1996, the average adult survival of Shags *Phalacrocorax aristotelis* was 82.1%, Common Guillemots *Uria aalge* 95.2%, Razorbills *Alca torda* 90.5%, Puffins *Fratercula arctica* 91.6% and Kittiwakes *Rissa tridactyla* 88.2%. Shags, Razorbills and Puffins all had a single year of exceptionally low survival but these years did not coincide. In contrast, Kittiwake survival declined significantly over the period and there was evidence that substantial non-breeding occurred in several years. Breeding success of Kittiwakes also declined, which gives rise to concern for its future status. Given a high enough level of resighting, return rates (the proportion of birds known to be alive one year that were seen the next year) on a year-by-year basis provide a reasonable indication of relative changes in adult survival.*

Harris M.P., S. Wanless & P. Rothery 2000. Adult survival rates of Shag *Phalacrocorax aristotelis*, Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Puffin *Fratercula arctica* and Kittiwake *Rissa tridactyla* on the Isle of May 1986-96. *Atlantic Seabirds* 2(3/4): 133-150.

## INTRODUCTION

Seabirds are a conspicuous component of marine and coastal ecosystems and Britain holds internationally important populations of several species. Typically seabirds exhibit deferred maturity, high adult survival and low reproductive rates, and consequently their populations sizes tend to be relatively stable (Lack 1966). Simple models demonstrate that with this suite of demographic parameters, declines in population size are more sensitive to reductions in adult survival than to either juvenile survival or breeding success (e.g. Croxall & Rothery 1991). The effect is more pronounced in those species with the highest adult survival rates and lowest reproductive rates (in a North Atlantic context this includes the auks and Procellariiformes) compared with those having lower

adult survival rates and higher reproductive rates (e.g. gulls and cormorants). There is additional value in monitoring seabird survival since, as Cairns (1987) pointed out, relationships between seabird population parameters and the marine environment are likely to be logistic. Adult survival is least sensitive to perturbations in the environment and as such may serve to monitor changes over ranges where other parameters, such as productivity, have 'bottomed-out' at zero. For many species, adult survival also provides an opportunity to monitor changes occurring in the wintering areas whereas productivity monitors only factors acting during the summer; from a conservation perspective, adult survival rate is clearly a key parameter to measure. Thus, an aim of the UK Joint Nature Conservation Committee's (JNCC) Seabird Monitoring Programme, established in 1986, was (and is) to obtain estimates of adult survival for a range of seabirds representing different life history and foraging strategies.

Adult survival estimates can be obtained from analysis of records of birds that have been ringed as chicks with conventional metal rings and subsequently been retrapped and/or recovered (e.g. Harris *et al.* 1994). However most colony-specific survival rates (including those described in this paper) are derived from birds that are individually colour-ringed as adults and then recorded as being present or absent in each successive season. This approach is only possible at colonies where adults are accessible for ringing and can easily be visually checked. Thus, the number of sites in the UK where survival data are collected is much lower than the number where reproductive output is monitored. Moreover, in general, obtaining adult survival rates requires a considerable commitment both within and between seasons, so survival monitoring has largely been restricted to the main JNCC sites. This paper presents a detailed analysis of adult survival rates of Shag *Phalacrocorax aristotelis*, Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Puffin *Fratercula arctica* and Kittiwake *Rissa tridactyla* at one of these sites, the Isle of May, between 1986 and 1996.

## METHODS

The Isle of May National Nature Reserve, Firth of Forth (56°11'N, 2°33'W), is one of the largest seabird colonies in east Scotland. In 1992, half-way through this study, there were 1600 pairs of Shags, 11,500 pairs of Guillemots, 1900 pairs of Razorbills, 21,000 pairs of Puffins and 6900 pairs of Kittiwakes on the island. Each summer, starting in 1986, breeding adults of all five species were caught and individually colour-ringed. Our aim was to have at least 120-150 marked individuals of each species present in the populations at the end of each summer. This target was exceeded in all species except the Razorbill. The mean annual totals of colour-ringed individuals alive in the population were 149

Shags, 390 Guillemots, 61 Razorbills, 163 Puffins and 153 Kittiwakes. The total numbers of birds included in the analyses were: Shag (246 males, 238 females, 3 unsexed), Guillemot (302, 269, 28), Razorbill (56, 44, 20), Puffin (129, 118, 127) and Kittiwake (122, 126, 111).

Many individuals were sexed by bill or head+bill measurements (Puffin, Harris 1979; Kittiwake, Coulson *et al.* 1983), size and vocalisations (Shag, Snow 1963), pairings with birds of known sex or, in a minority of cases, by direct observations of mating birds (Guillemot and Razorbill and some individuals of other species). From 1987 onwards, thorough and widespread searches for these marked individuals were carried out on the island.

Annual survival and resighting probabilities were estimated using Cormack-Jolly-Seber models running in the program SURGE 4.2 (Pradel & Lebreton 1993). The analysis cannot separate survival and permanent emigration. However, all these species exhibit high colony fidelity once individuals have recruited into the breeding population (Lloyd & Perrins 1977; Aebischer 1995; Fairweather & Coulson 1995; Harris *et al.* 1996). The approach follows Lebreton *et al.* (1992) in fitting models to allow examination of effects of year and differences between sexes. These models increased in complexity from the simple case of constant survival and resighting probability to the most general model, which allowed identification of separate patterns of annual variation in survival and resighting for males and females (Appendix I). The goodness-of-fit of each model was measured by the Akaike Information Criterion (AIC), i.e. minus twice the log likelihood plus twice the number of estimated parameters. Low values of AIC indicate parsimonious models and provide a basis for model selection. Likelihood ratio tests were used to calculate the statistical significance of differences between years and sexes in survival and resighting probabilities.

The goodness-of-fit of the Cormack-Jolly-Seber model was examined using TESTS 2 and 3 of the program RELEASE. However, for each species the resighting rate was very high so that most of the birds were resighted in the first year after release. In this case, the component 3.Sm of TEST 3 and TEST 2 are not informative, and most of the information relating to goodness-of-fit resides in TEST 3.SR (Lebreton *et al.* 1992). The corresponding values for the five species were: Shag:  $\chi^2 = 8.97$ ,  $df = 10$ ,  $P = 0.53$ ; Guillemot:  $\chi^2 = 7.27$ ,  $df = 11$ ,  $P = 0.78$ ; Razorbill:  $\chi^2 = 5.51$ ,  $df = 10$ ,  $P = 0.86$ ; Puffin:  $\chi^2 = 12.6$ ,  $df = 11$ ,  $P = 0.32$ ; Kittiwake:  $\chi^2 = 11.87$ ,  $df = 11$ ,  $P = 0.37$ . Thus, there was no evidence that subsequent resighting depended on whether the bird had been previously resighted. Furthermore, the high resighting rate suggests that the survival estimates should be robust to heterogeneity in resighting.

Tests for trends in annual survival used a random effects model (Burnham *in press*) with a linear trend on a logistic scale plus a random year

effect, i.e.  $\log [S_t/(1 - S_t)] = a + bt + \epsilon_t$ , where  $S_t$  is the actual survival for year  $t$ . The null hypothesis of no trend ( $b = 0$ ) corresponds to a random series. This is more realistic and less restrictive than the null hypothesis of constant survival, which is actually tested by comparing models using SURGE. The variance of the random year effect is obtained from the variation in the annual survival estimates after allowing for the effect of their sampling variances and covariances. The slope ( $b$ ) is estimated by generalised least squares (Burnham *in press*).

We used the samples of sexed birds to examine sex differences in survival. As in some earlier analyses (Harris & Wanless 1995, Harris *et al.* 1997), the survival of sexed individuals appeared to be consistently higher than the survival of unsexed birds, probably due to the chances of a bird being sexed increasing with the number of years that it is recorded. Consequently, in population terms we consider that the best estimates of survival are those for all individuals rather than the subset of sexed birds.

Survival between two years is referred to by the former year, i.e. 1995 refers to survival between the 1995 and 1996 breeding seasons.

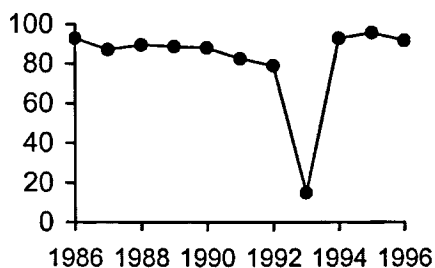
## RESULTS

**Survival** Annual survival estimates for males, females and all individuals are given in Appendix IV. Sex differences in survival were not statistically significant (Appendix III), but this says little about the possible magnitude of the effect. Estimated mean differences (males – females) over the 11 years are (95% confidence interval): Shag -0.6% (-4.2%, 3.0%), Guillemot 0.2% (-1.4%, 1.8%), Razorbill -3.0% (-7.0%, 1.0%), Puffin -0.02% (-2.4%, 2.4%) and Kittiwake -0.6% (-3.4%, 2.2%). Temporal changes in the overall estimates are shown in Figure 1. In all species, a model with annual variation in survival was among the three most parsimonious models having low AIC values (Appendix II), and differences between years were highly statistically significant (Appendix III).

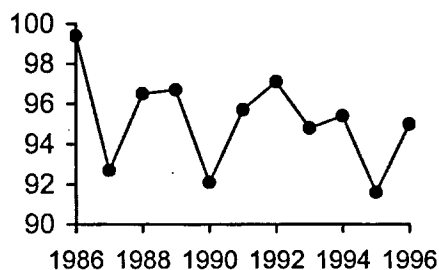
Guillemot survival appeared fairly stable, varying between 92% and 99% over the study period. Shag survival was extremely low in 1993 (15% compared with an average of 89% for the other 10 years). Puffin survival was poor in 1990 using both sexes combined (79%), although the effect was less in the separate analyses for males (88%) and females (85%). Also, over the 11 years mean survival was lower in the total group than in either sex. This might be due to a bias arising from sexing birds, i.e. those birds that survive are more likely to be sexed by observations of mating, combined with the high proportion of unsexed birds. However, the results for Kittiwake, which also included many unsexed birds, revealed very similar estimates in all three analyses. Razorbill

survival was relatively low in 1995 (73% compared with a long-term average of 91%).

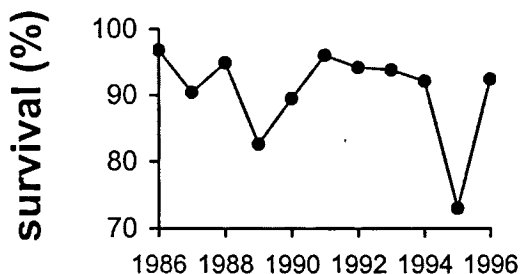
### Shag



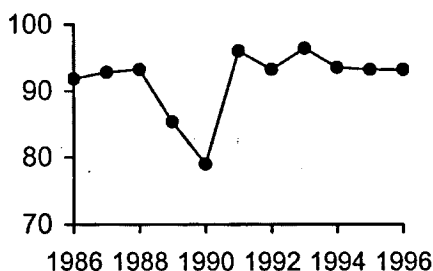
### Guillemot



### Razorbill



### Puffin



### Kittiwake

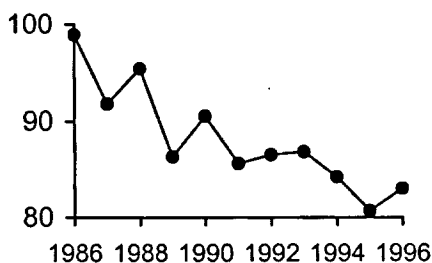


Figure 1. Annual estimates of the survival of adult Shag, Common Guillemot, Razorbill, Puffin and Kittiwake on the Isle of May 1986-96. For details see Appendix IV.

In contrast to the other species, survival in the Kittiwake declined significantly during the period from 99% in 1986 to 83% in 1996 (Burnham's test for trend with random year effect:  $b = -0.13$ ,  $SE = 0.036$ ,  $t_9 = -3.64$ ,  $P < 0.01$ ,  $SD$  [random effect] = 0.22). There was a suggestion that survival rates in the Razorbill and Guillemot were correlated ( $r = 0.58$ ,  $n = 11$ ,  $P = 0.06$ ), but no other pairwise correlations approached statistical significance.

In all species, the survival calculated for any given year was significantly correlated with the return rate the following year, i.e. number of birds seen in the second year / number of birds seen in the first year (all  $r > 0.78$ ,  $P < 0.005$ ), indicating that the return rate in any year was a good indicator of survival from the previous season. The average difference between the two estimates was 1.8% ( $SE = 0.7$ ) in the Guillemot, 4.8% ( $SE = 1.5$ ) in the Shag, 6.0% ( $SE = 0.7$ ) in the Kittiwake, 6.7% ( $SE = 1.4$ ) in the Razorbill and 8.4% ( $SE = 1.9$ ) in the Puffin.

**Resighting probability** Estimated resighting probabilities for males, females and all birds are given in Appendix V. Average values for all five species were high: Shag (92%), Guillemot (98%), Razorbill (91%), Puffin (88%) and Kittiwake (90%). For each species, time-dependent resighting rates and sex effects occurred in one or more of the three most parsimonious models selected by AIC. The year effect was highly statistically significant in all species except Guillemot, but differences between sexes were not statistically significant for any species (Appendix III).

## DISCUSSION

Comparisons of survival rates of the various seabird species monitored on the Isle of May with those obtained elsewhere in Europe, indicated broadly similar overall values (Table 1). The Isle of May data illustrate clearly that over an 11-year period species showed very different temporal patterns in survival and, in particular, highlight the lack of interspecific concordance in years of exceptionally low survival. Hence, conditions which culminated in high mortality appeared to be species specific, so from a conservation point of view, monitoring adult survival of one species cannot be used as a proxy for other species at a particular colony, even if they are closely related and/or apparently have similar life history or feeding strategies.

Table 1. Some estimates of the long-term survival (%) of adult Shag, Guillemot, Razorbill, Puffin and Kittiwake in Europe.

Place	Years	Adult survival	Source
<b>Shag</b>			
Isle of May, Scotland	1986-96	82.1	This study
Isle of May, Scotland	1967-92	87.8*	Harris <i>et al.</i> 1994
Farne Islands, England	1962-70	82.8	Potts <i>et al.</i> 1980
<b>Guillemot</b>			
Isle of May, Scotland	1986-96	95.2	This study
Isle of May, Scotland	1982-95	94.8*	Harris <i>et al.</i> 2000
Canna, Scotland	1983-95	92.4	Harris <i>et al.</i> 2000
Colonsay, Scotland	1984-95	96.7	Harris <i>et al.</i> 2000
Hornøya, Norway	1989-96	95.8	Erikstad <i>et al.</i> 1998
<b>Razorbill</b>			
Isle of May, Scotland	1986-96	90.5	This study
Skomer, Wales	1972-94	90.1	Poole <i>et al.</i> 1998
<b>Puffin</b>			
Isle of May, Scotland	1986-96	91.6	This study
Isle of May, Scotland	1973-92	93.6*	Harris <i>et al.</i> 1997
Skomer, Wales	1972-94	91.3	Poole <i>et al.</i> 1998
Røst, Norway	1990-96	92.7	Erikstad <i>et al.</i> 1998
Hornøya, Norway	1991-96	86.0	Erikstad <i>et al.</i> 1998
<b>Kittiwake</b>			
Isle of May, Scotland	1986-96	88.2	This study
North Shields, England	1954-84	80.1	Aebischer & Coulson 1990
North Shields, England	1987-92	79.0	Fairweather & Coulson 1995
Skomer, Wales	1978-94	87.2	Poole <i>et al.</i> 1998
Brittany, France	1980-85	80.8	Danchin & Monnat 1992
Hornøya, Norway	1990-95	80.3	Erikstad <i>et al.</i> 1998

\* Includes some of the data incorporated in the current study.

Comparison of our colony-based adult survival estimates with records of birds washed up on beaches shows that low survival years for Shags (1993), Razorbills (1995) and Puffins (1990) on the Isle of May all coincided with years when winter wrecks of these species were recorded in north and east Scotland (Harris *et al.* 1991; Bourne 1996; Swann & Butterfield 1996; Harris & Wanless 1996). Exceptionally high numbers of Guillemots were also washed up on beaches during February and March 1994 (Bourne 1994; Brindley 1994). However, most of the birds involved appeared to be immatures and survival rates of adults on the Isle of May between 1993 and 1994 did not indicate any substantial increase in mortality (Fig. 1). Guillemots were also involved in the

Razorbill wreck in the 1995-96 winter. In this case no detailed information on the age of birds found dead is available. However, judging from our survival estimates, the lowest recorded during the study, and also the fact that ten Guillemots ringed on the Isle of May that were old enough to breed were reported dead, some adults probably were involved. The magnitude of the reduction in survival of Guillemots (91.6% compared with the 11-year average of 95.2%) was, however, much less than for Razorbills (73.0% compared with 90.5%).

In a 34-year study of Kittiwakes at North Shields, Aebischer & Coulson (1990) found significantly higher survival in females (81.8%, 95% confidence interval: 80.1% - 83.4%), than in males (78.3%, 95% confidence interval: 76.4% - 80.0%). However, this difference of 3.5% is not significantly different from the Isle of May difference of 0.6% after allowing for errors in both estimates. No sex differences in survival were reported by Golet *et al.* (1998) for Kittiwakes in Alaska whereas in northern Norway Erikstad *et al.* (1998) found that, in general, males survived better than females.

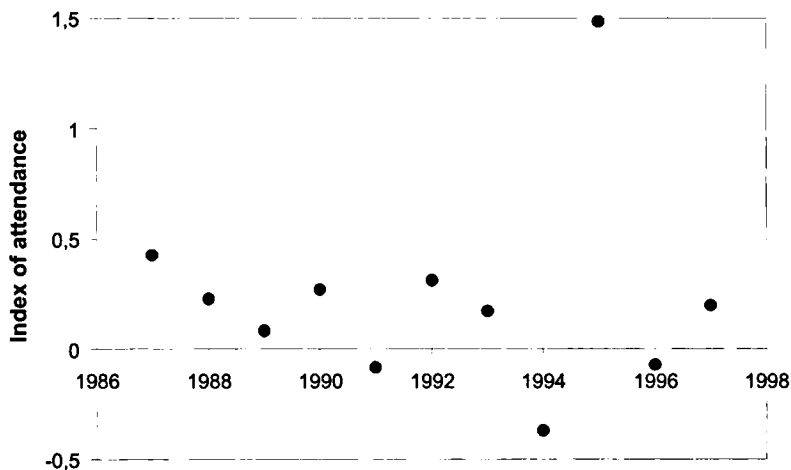


Figure 2. Annual indices of attendance of adult Kittiwakes on the Isle of May. Negative values suggest a considerable amount of non-breeding.



While results for Razorbill, Puffin, Guillemot and Shag indicate that survival rates were generally high and that poor survival years occurred only infrequently, a radically different pattern was shown by Kittiwake, survival of which declined significantly during the study. This downward trend is of particular concern because reproductive output of this species has also declined on the Isle of May over this period (Harris & Wanless 1997; personal data). The consequences of this reduction in adult survival were investigated in more detail following the approach of Ollason & Dunnet (1978). Thus an annual 'Index of Attendance' was obtained by multiplying the number of breeding pairs in one year (personal records) by the year-specific survival rate to give an expected number of pairs surviving to the next year. The difference between this value and the number of nests actually counted in June was expressed as a proportion of the counted nests to give an index which measured the attendance at the colony of first-time and experienced breeders (Figure 2). The index took positive values if the number of pairs recorded exceeded the predicted number of survivors, while negative indices indicated that observed numbers fell below the number predicted. During the study period negative values were recorded in three years (1991, 1994, and 1996), suggesting that not only did no Kittiwakes recruit to the breeding population in these seasons, but that some birds with previous breeding experience did not breed. The results of ongoing modelling studies using empirical productivity measurements confirm that substantial non-breeding by experienced adults probably occurred in these three years. It is striking that these three seasons followed winters in which one of the other seabird species had been involved in a wreck. If the non-breeding years occurred at random during 1990-96, the probability that each followed a wreck year is 0.029. However, this does not allow for the *post hoc* selection of the coincidence and suggests that non-breeding may be linked to adverse conditions occurring much earlier in the year.

In this study a very high level of effort was put into finding marked birds and this commitment was reflected in very high resighting rates for all the species. Consequently estimates of return rate i.e. the proportion of birds known to be alive in year  $t$  that were actually seen in year  $t + 1$ , were only slightly below the calculated survival rate which had been adjusted for resighting effort. In the context of obtaining a simple and rapid measure of annual survival, simple return rates provided a reasonable indication of relative changes in adult survival and a rapid means of identifying any serious problems.

The overall aim of the JNCC's Seabird Monitoring Programme, is to ensure that sufficient high quality data are collected, both regionally and nationally to 1) enable the conservation status of seabirds to be assessed; 2) monitor aspects of the health of the wider marine environment; and 3) provide sound advice relevant to the conservation needs of breeding seabirds. In this

context the estimation of adult survival rates is a key objective because population changes of seabirds are more sensitive to variations in this parameter than either juvenile survival or breeding success. In addition, reductions in adult survival are predicted to occur only when conditions have deteriorated markedly (Cairns 1987). The results presented in this paper for five species of seabirds breeding on the Isle of May provide evidence both of marked reductions in annual survival, presumably associated with adverse conditions during the winter, and of a sustained decline in Kittiwake survival. At present the reason for this decline is completely unknown. However, given the current concern about the potential impact of the industrial sandeel fishery on the North Sea ecosystem, particularly for small surface-feeding seabirds like Kittiwakes, in areas such as south-east Scotland where there is a large inshore fishery, establishing the cause of the decrease should be high on the conservation agenda.

#### ACKNOWLEDGEMENTS

This work was carried out under a contract placed by JNCC with the Institute of Terrestrial Ecology (Natural Environment Research Council). We thank Scottish Natural Heritage for permission to work on the Isle of May NNR, their wardens who have counted Kittiwake nests the last few years and the many people who have helped ring and resight birds over many years.

#### SAMENVATTING

##### *OVERLEVING VAN VOLWASSEN KUIFAALSCHOLVER, ZEEKOET, ALK, PAPEGAAIDUIKER EN DRIETEENMEEUW OP ISLE OF MAY, 1986-96*

*Op Isle of May bedroeg de jaarlijkse overleving van volwassen vogels tussen 1986 en 1996 82.1% voor Kuifaalscholver Stictocorax [Phalacrocorax] aristotelis, 95.2% voor Zeekoet Uria aalge, 90.5% voor Alk Alca torda, 91.6% voor Papegaaiduiker Fratercula arctica en 88.2% voor Drieteenmeeuw Rissa tridactyla. Kuifaalscholvers, Alken en Papegaaiduikers kenden ieder een enkel jaar met buitengewoon hoge sterfte, maar deze jaren vielen niet samen. In tegenstelling tot deze soorten nam de jaarlijkse overleving van Drieteenmeeuwen significant af in de tijd en er waren aanwijzingen dat in sommige jaren een groot deel van de populatie geheel van broeden afzag. Ook het gemiddelde broedsucces van Drieteenmeeuwen nam af in de tijd, hetgeen aanleiding gaf tot grote zorg voor de toekomst. Het stuk gaat verder in op methodische aspecten, zoals dat bij een voldoende groot aantal ringaflezingen, de jaarlijkse terugkeer op de kolonie (het percentage vogels waarvan dus vaststaat dat ze na een jaar nog in leven zijn) op jaarbasis een goede indicatie kan geven van de adulte overleving.*

#### REFERENCES

- Aebischer N.J. 1995. Philopatry and colony fidelity of Shags *Phalacrocorax aristotelis* on the east coast of Britain. *Ibis* 137: 11-18.
- Aebischer N.J. & Coulson J.C. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology* 59: 1063-1071.
- Bourne W.R.P. 1994. The 1994 Seabird Wreck in north-east Scotland. *Scottish Bird News* 35: 2.
- Bourne W.R.P. 1996. Birds washed up in Grampian early in 1996. *Scottish Bird News* 43: 6.

- Brindley E. 1994. National Beached Bird Survey, February 1994. Seabird Group Newsletter 69: 2-4.
- Burnham K.P. in press. Random effects models in ringing and capture-recapture studies. *J. Agricult. Env. Studies*.
- Cairns D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5:261-271.
- Coulson J.C., Thomas C.S., Butterfield J.E.L., Duncan N., Monaghan P. & Shedden C. 1983. The use of head and bill length to sex live gulls (Laridae). *Ibis* 125: 549-557.
- Croxall J.P. & Rothery P. 1991. Population regulation of seabirds: implications of their demography for conservation. In: Perrins C.M., Lebreton J.-D. & Hiron G.J.M. (eds): *Bird Population Studies*: 272-296. Oxford University Press, Oxford.
- Danchin E. & Monnat J.-Y. 1992. Population dynamics modelling of two neighbouring Kittiwake *Rissa tridactyla* colonies. *Ardea* 80: 171-180.
- Erikstad K.E., Anker-Nilssen T., Barrett R.T. & Tveraa T. 1998. Demography and adult survival in some Norwegian seabird populations. *NINA Oppdragsmelding* 515: 1-15.
- Fairweather J.A. & Coulson J.C. 1995. The influence of forced site change on the dispersal and breeding of the Black-legged Kittiwake *Rissa tridactyla*. *Colonial Waterbirds* 18: 30-40.
- Golet G.H., Irons D.B. & Estes J.A. 1998. Survival costs of chick rearing in black-legged kittiwakes. *Journal of Animal Ecology* 67: 827-841.
- Harris M.P. 1979. Measurements and weights of British Puffins. *Bird Study* 26: 179-186.
- Harris M.P. & Wanless S. 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. *Ibis* 137: 192-197.
- Harris M.P. & Wanless, S. 1996. Differential responses of Guillemot *Uria aalge* and Shag *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study* 43: 220-230.
- Harris M.P. & Wanless S. 1997. Breeding success, diet and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. *ICES Journal of Marine Science* 54: 615-623.
- Harris M.P., Heubeck M. & Suddaby D. 1991. Results of an examination of Puffins *Fratercula arctica* washed ashore in Shetland in winter 1990-91. *Seabird* 13: 63-66.
- Harris M.P., Wanless S. & Barton T.R. 1996. Site use and fidelity in the Common Guillemot. *Ibis* 138: 399-404.
- Harris M.P., Buckland S.T., Russell S.M. & Wanless S. 1994. Year- and age-related variation in the survival of adult European Shags over a 24-year period. *Condor* 96: 600-605.
- Harris M.P., Freeman S.N., Wanless S., Morgan B.J.T. & Wernham C.V. 1997. Factors influencing the survival of Puffins *Fratercula arctica* at a North Sea colony over a 20-year period. *Journal of Avian Biology* 28: 287-295.
- Harris M.P., Wanless S., Rothery P., Swann R.L. & Jardine D. 2000. Survival of adult Common Guillemots *Uria aalge* at three Scottish colonies. *Bird Study* 47: 1-7.
- Lack D. 1966. *Population Studies of Birds*. Clarendon Press, Oxford.
- Lebreton J.-D., Burnham K.P., Clobert J. & Anderson D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.
- Lloyd C.S. & Perrins C.M. 1977. Survival and age of first breeding in the Razorbill (*Alca torda*). *Bird-Banding* 48: 239-252.
- Ollason J.C. & Dunnet G.M. 1978. Age, experience and other factors affecting the breeding success of the fulmar, *Fulmarus glacialis*. *Journal of Animal Ecology* 47: 961-976.
- Poole J., Smith S., Perrins C.M., Birkhead T.R. & Thompson K.R. 1998. Seabird monitoring on Skomer Island in 1996. JNCC Report, No 277. Joint Nature Conservation Committee, Peterborough.
- Potts G.R., Coulson J.C. & Deans I.R. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology* 49: 465-484.

- Pradel R. & Lebreton J.-D. 1993. User's Manual for Program SURGE Version 4.2. Centre d'Ecologie Fonctionnelle et Evolutive, C.N.R.S., Montpellier, France.
- Snow B.K. 1963. The behaviour of the Shag. *British Birds* 56: 77-103.
- Swann B. & Butterfield D. 1996. The 1996 Moray Firth beach bird surveys. *Scottish Bird News* 43: 4-5.



Shags (photo C.J.Camphuysen).

*Appendix I. Summary of models fitted to capture-resighting data using SURGE 4.2. The Sex effect is additive on a logistic scale. A Year x Sex interaction implies a different pattern of annual survival for males and females, i.e. non-parallel changes on a logistic scale.  $n_p$  denotes the number of parameters that can be estimated.*

Model notation	$n_p$	Model description	
		Survival	Resighting
1. $(\phi_{s \cdot t}, p_{s \cdot t})$	46	Year, Sex, Year x Sex interaction	Year, Sex, Year x Sex interaction
2. $(\phi_{s+t}, p_{s \cdot t})$	36	Year, Sex	Year, Sex, Year x Sex interaction
3. $(\phi_{s \cdot t}, p_{s+t})$	36	Year, Sex, Year x Sex interaction	Year, Sex
4. $(\phi_t, p_{s \cdot t})$	35	Year	Year, Sex, Year x Sex interaction
5. $(\phi_{s \cdot t}, p_t)$	35	Year, Sex, Year x Sex interaction	Year
6. $(\phi_s, p_{s \cdot t})$	26	Sex	Year, Sex, Year x Sex interaction
7. $(\phi_{s \cdot t}, p_s)$	26	Year, Sex, Year x Sex interaction	Sex
8. $(\phi_{s+t}, p_t)$	24	Year, Sex	Year
9. $(\phi_t, p_{s+t})$	24	Year	Year, Sex
10. $(\phi_t, p_t)$	23	Year	Year
11. $(\phi_s, p_t)$	14	Sex	Year
12. $(\phi_t, p_s)$	14	Year	Sex
13. $(\phi, p_t)$	13	Constant	Year
14. $(\phi_t, p)$	13	Year	Constant
15. $(\phi, p)$	2	Constant	Constant

*Appendix II. The three most parsimonious models with lowest values of the Akaike Information Criterion (AIC). Model numbering and description as in Appendix I.*

Species	Model	$n_p$	AIC
Shag	9. ( $\phi_t, p_{s+t}$ )	24	1962.98
	10. ( $\phi_t, p_t$ )	23	1963.23
	8. ( $\phi_{s+t}, p_s$ )	24	1963.56
Guillemot	14. ( $\phi_t, p$ )	13	2382.70
	12. ( $\phi_t, p_s$ )	14	2384.40
	10. ( $\phi_t, p_t$ )	23	2390.22
Razorbill	12. ( $\phi_t, p_s$ )	14	724.38
	14. ( $\phi_t, p$ )	13	725.00
	5. ( $\phi_{s+t}, p_t$ )	35	729.08
Puffin	9. ( $\phi_t, p_{s+t}$ )	24	1191.27
	10. ( $\phi_t, p_t$ )	23	1192.05
	8. ( $\phi_{s+t}, p_s$ )	24	1193.49
Kittiwake	10. ( $\phi_t, p_t$ )	23	1616.00
	9. ( $\phi_t, p_{s+t}$ )	24	1617.29
	8. ( $\phi_{s+t}, p_t$ )	24	1617.74

*Appendix III. Summary of likelihood ratio tests for differences in survival and resighting probabilities based on comparison of models for the null hypothesis ( $H_0$ ) and an alternative hypothesis ( $H_A$ ). Year effects tested after allowing for a sex effect and sex effects tested after allowing for year effects. Corresponding tests ignoring year and sex effects give very similar results. See Appendix I for model description. Statistical significance: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ , based on the chi-squared distribution with 1 and 10 degrees of freedom for sex and year effects.*

Species	Survival		Resighting	
	Year effects $H_0$ : Model 6 vs. $H_A$ : Model 2	Sex effects $H_0$ : Model 4 vs. $H_A$ : Model 2	Year effects $H_0$ : Model 7 vs. $H_A$ : Model 3	Sex effects $H_0$ : Model 5 vs. $H_A$ : Model 3
Shag	318.22 ***	0.20	52.39 ***	0.77
Guillemot	37.02 ***	0.12	12.71	0.14
Razorbill	27.54 **	0.20	52.39 ***	0.77
Puffin	22.92 *	0.54	65.95 ***	2.79
Kittiwake	34.16 ***	0.15	25.87 **	0.51

*Appendix IV Estimates of annual survival (%) based on a model with time-dependent survival and resighting probabilities. Out-of-range estimates are set to 100%. All birds includes unsexed individuals.*

Shag	Estimated survival % (SE)		
	Males	Females	All birds
Year			
1986	92.7 (3.0)	93.1 (2.9)	92.9 (2.1)
1987	88.3 (3.9)	86.1 (3.9)	87.2 (2.8)
1988	85.8 (4.2)	93.2 (3.6)	89.5 (2.7)
1989	92.6 (3.2)	86.0 (4.2)	88.7 (2.7)
1990	90.1 (3.7)	85.5 (4.2)	88.0 (2.7)
1991	81.9 (4.3)	83.6 (3.9)	82.5 (3.0)
1992	80.8 (4.6)	77.4 (4.8)	79.0 (3.4)
1993	14.7 (3.9)	15.1 (4.9)	14.9 (2.7)
1994	84.6 (1.0)	100.0 (-)	92.8 (5.3)
1995	96.2 (2.3)	95.4 (2.7)	95.7 (1.8)
1996	92.1 (2.8)	91.3 (2.7)	91.8 (2.2)
Mean	81.8 (6.9)	82.4 (7.0)	82.1 (6.9)

Guillemot	Estimated survival % (SE)		
	Males	Females	All birds
Year			
1986	100.0 (-)	98.4 (1.1)	99.4 (0.6)
1987	92.7 (1.9)	94.0 (1.9)	92.7 (1.4)
1988	94.6 (1.7)	98.7 (0.9)	96.5 (1.0)
1989	96.4 (1.4)	97.0 (1.4)	96.7 (1.0)
1990	90.6 (2.2)	94.4 (1.8)	92.1 (1.4)
1991	96.9 (1.3)	94.3 (1.8)	95.7 (1.1)
1992	98.4 (0.8)	95.5 (1.6)	97.1 (0.9)
1993	95.7 (1.4)	93.5 (1.8)	94.8 (1.1)
1994	95.5 (1.4)	95.4 (1.5)	95.4 (1.1)
1995	92.0 (1.9)	92.6 (1.9)	91.6 (1.4)
1996	97.1 (1.3)	94.0 (1.8)	95.0 (1.1)
Mean	95.4(0.9)	95.3 (0.6)	95.2 (0.7)

Razorbill	Estimated survival % (SE)			
	Year	Males	Females	All birds
	1986	93.7 (4.8)	100 ( - )	96.8 (3.1)
	1987	92.1 (4.4)	93.1 (4.6)	90.4 (3.5)
	1988	92.6 (4.4)	100 ( - )	94.9 (2.9)
	1989	79.4 (6.6)	87.1 (6.0)	82.6 (5.0)
	1990	86.2 (6.3)	96.5 (3.7)	89.5 (4.3)
	1991	100 ( - )	93.6 (4.6)	96.0 (2.7)
	1992	91.0 (5.1)	96.8 (3.2)	94.2 (3.8)
	1993	90.5 (5.9)	98.1 (3.3)	93.8 (4.2)
	1994	85.7 (7.3)	93.1 (6.4)	92.1 (5.5)
	1995	76.4 (8.6)	69.8 (9.2)	73.0 (6.4)
	1996	96.6 (4.7)	88.5 (8.4)	92.4 (6.1)
	Mean	89.5 (2.1)	92.4 (2.6)	90.5 (2.1)

Puffin	Estimated survival % (SE)		
Year	Males	Females	All birds
1986	91.4 (5.2)	100 (-)	91.8 (3.6)
1987	98.0 (3.8)	95.3 (4.5)	92.8 (3.8)
1988	92.0 (6.6)	95.3 (4.6)	93.2 (4.2)
1989	91.0 (7.7)	91.7 (0.7)	85.3 (5.8)
1990	88.3 (4.5)	84.9 (1.6)	79.0 (3.3)
1991	95.7 (2.0)	97.7 (1.7)	96.0 (1.4)
1992	97.1 (1.6)	95.8 (2.0)	93.2 (1.7)
1993	99.1 (0.9)	98.3 (1.5)	96.4 (1.3)
1994	97.5 (1.6)	91.8 (2.8)	93.5 (1.7)
1995	93.9 (2.3)	95.7 (2.3)	93.2 (1.8)
1996	95.7 (2.1)	93.3 (2.9)	93.2 (1.8)
Mean	94.5 (1.0)	94.5 (1.2)	91.6 (1.5)

Kittiwake	Estimates survival % (SE)		
Year	Males	Females	All birds
1986	98.7 (1.2)	98.5 (1.4)	98.9 (0.9)
1987	90.9 (3.2)	93.3 (3.5)	91.8 (2.2)
1988	94.9 (2.7)	92.5 (3.9)	95.4 (1.8)
1989	89.1 (4.1)	85.1 (5.3)	86.3 (2.7)
1990	92.2 (4.0)	90.2 (4.9)	90.5 (2.6)
1991	90.3 (4.5)	81.8 (5.8)	85.6 (2.9)
1992	85.6 (5.2)	88.4 (4.9)	86.5 (3.0)
1993	85.3 (5.3)	89.2 (4.3)	86.8 (3.1)
1994	80.7 (6.4)	83.5 (5.0)	84.2 (3.6)
1995	79.8 (6.3)	87.4 (4.8)	80.7 (3.7)
1996	83.7 (5.5)	88.2 (4.9)	83.0 (3.6)
Mean	88.3 (1.8)	88.9 (1.4)	88.2 (1.7)



*Appendix V Estimates of annual resighting probability (%) based on a model with time-dependent survival and resighting probabilities. All birds includes unsexed individuals.*

Shag	Estimated resighting % (SE)		
	Males	Females	All birds
1986	-	-	-
1987	96.8 (2.0)	95.1 (2.4)	96.0 (1.6)
1988	87.3 (4.2)	85.6 (4.2)	86.6 (2.9)
1989	89.1 (3.9)	83.3 (4.6)	86.2 (3.0)
1990	85.9 (4.1)	78.5 (4.8)	81.7 (3.2)
1991	90.7 (3.6)	94.2 (2.8)	91.8 (2.2)
1992	89.3 (3.7)	96.9 (2.1)	92.3 (2.1)
1993	100 (-)	100 (-)	100 (-)
1994	100 (-)	81.7 (11.8)	90.2 (6.9)
1995	100 (-)	79.8 (10.2)	87.9 (6.8)
1996	96.9 (2.1)	96.9 (2.6)	96.7 (1.5)
1997	98.7 (1.3)	100 (-)	99.3 (0.8)
Mean	94.1 (1.7)	90.1 (2.5)	91.8 (1.8)

Guillemot	Estimated resighting % (SE)		
	Males	Females	All birds
1986	-	-	-
1987	99.4 (0.6)	99.1 (0.8)	99.2 (0.7)
1988	100 (-)	98.6 (0.9)	99.3 (0.5)
1989	97.0 (1.3)	97.9 (1.1)	97.4 (0.9)
1990	98.2 (1.0)	97.3 (1.3)	97.8 (0.8)
1991	98.8 (0.8)	98.6 (0.9)	98.7 (0.6)
1992	97.8 (1.1)	97.4 (1.1)	97.7 (0.8)
1993	99.5 (0.6)	97.5 (1.2)	98.3 (0.7)
1994	98.9 (0.7)	98.8 (0.8)	98.9 (0.5)
1995	97.4 (1.1)	97.6 (1.1)	97.0 (0.8)
1996	96.3 (1.3)	98.2 (1.0)	97.3 (0.8)
1997	97.2 (1.2)	97.4 (1.2)	97.4 (0.8)
Mean	98.3 (0.4)	98.0 (0.2)	98.0 (0.2)

Razorbill	Estimated resighting % (SE)		
	Males	Females	All birds
1986	-	-	-
1987	92.0 (5.3)	100 (-)	95.9 (3.9)
1988	97.0 (2.9)	96.2 (3.6)	96.8 (3.0)
1989	96.4 (3.4)	96.7 (3.2)	96.4 (2.6)
1990	100 (-)	88.0 (6.2)	94.1 (3.3)

<b>Razorbill</b>	Estimated resighting % (SE)		
Year	Males	Females	All birds
1991	92.0 (5.3)	87.2 (6.6)	89.9 (4.3)
1992	96.9 (3.1)	86.2 (6.4)	90.6 (3.7)
1993	96.2 (3.7)	90.0 (5.2)	93.5 (3.7)
1994	91.0 (5.9)	85.7 (6.5)	86.4 (4.5)
1995	94.6 (5.1)	85.2 (7.4)	87.5 (5.6)
1996	89.5 (6.8)	94.5 (5.2)	90.9 (4.4)
1997	87.5 (8.1)	86.7 (8.8)	81.8 (6.8)
Mean	93.9 (1.1)	90.6 (1.6)	91.3 (1.4)

Puffin	Estimated resighting % (SE)		
Year	Males	Females	All birds
1986	-	-	-
1987	74.1 (8.3)	100 (-)	83.5 (4.7)
1988	73.1 (8.2)	88.3 (7.4)	76.1 (5.4)
1989	87.0 (6.8)	94.5 (5.2)	84.3 (4.8)
1990	62.3 (10.3)	87.8 (7.7)	65.5 (6.6)
1991	98.0 (1.9)	100 (-)	92.1 (2.4)
1992	100 (-)	98.7 (1.3)	95.4 (1.5)
1993	96.9 (1.5)	98.9 (1.1)	93.9 (1.6)
1994	99.0 (1.0)	96.7 (1.8)	95.4 (1.4)
1995	94.8 (2.1)	95.3 (2.2)	92.8 (1.8)
1996	98.9 (1.1)	95.0 (2.4)	96.5 (1.3)
1997	94.8 (2.5)	95.6 (2.3)	95.0 (1.6)
Mean	89.0 (4.0 )	95.5 (1.3)	88.0 (3.0)

Kittiwake	Estimated resighting % (SE)			
	Year	Males	Females	All birds
	1986	-	-	-
	1987	100 (-)	96.2 (2.5)	97.8 (1.2)
	1988	96.9 (2.0)	89.6 (4.3)	93.8 (2.0)
	1989	95.0 (2.7)	95.3 (3.5)	93.6 (2.1)
	1990	85.7 (4.6)	87.5 (5.2)	87.1 (2.8)
	1991	84.2 (5.1)	96.9 (3.0)	89.4 (2.6)
	1992	89.3 (4.5)	100 (-)	91.5 (2.5)
	1993	86.2 (5.2)	89.1 (4.9)	85.3 (3.2)
	1994	90.0 (4.6)	93.5 (3.6)	86.2 (3.1)
	1995	77.9 (6.8)	87.0 (4.9)	80.0 (3.8)
	1996	91.3 (4.6)	87.2 (4.8)	88.2 (3.2)
	1997	96.7 (3.1)	90.0 (4.7)	92.6 (2.9)
	Mean	90.3 (2.0)	92.0 (1.4)	89.6 (1.5)