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YEAR- AND AGE-RELATED VARIATION IN THE SURVIVAL OF ADULT EUROPEAN SHAGS OVER A 24-YEAR PERIOD[1]

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Abstract. Over 13,000 chicks and 1,800 adult European Shags (*Phalacrocorax aristotelis*) were banded at a colony in southeast Scotland between 1963 and 1987. Survival estimates for adults (birds three or more years old) were calculated from subsequent retrapping of these birds back at the colony and recoveries of birds found dead in the colony and elsewhere. The mean annual survival for the period 1967–1992 was estimated at 0.878 (95% C.I. = 0.859, 0.897). European Shags exhibit considerable annual variation in several breeding parameters, but there was no evidence that survival was lower in years when breeding was late or reproductive output reduced. Survival in years when the number of nests in the colony showed a dramatic decline was not significantly lower than normal years. An age-related effect was found indicating that survival declined significantly in birds older than 13 years.

Key words: Phalacrocorax aristotelis; *adult survival; age-related survival; European Shag.*

INTRODUCTION

The majority of seabirds have low reproductive rates and high adult survival. In such species a relatively small change in adult survival can have a marked effect on demography (Croxall and Rothery 1991). Considerable effort has, therefore, been put into obtaining accurate survival estimates for a range of species. As the duration of population studies has increased, it has become possible to investigate some of the sources of variation associated with these estimates, in particular age, sex and year (e.g., Kittiwake [*Rissa tridactyla*; Aebischer and Coulson 1990], Fulmar [*Fulmarus glacialis*; Dunnet and Ollason 1978], European Shag [*Phalacrocorax aristotelis*; Potts 1969, Potts et al. 1980], Wandering Albatross [*Diomedea exulans*; Croxall et al. 1990, Weimerskirch 1992], Puffin [*Fratercula arctica*; Harris and Wanless 1991], Short-tailed Shearwater [*Puffinus tenuirostris*; Bradley et al. 1989]).

The European Shag is a long-lived, colonially nesting seabird endemic to the northeast Atlantic and western Mediterranean. During the breeding season the birds are tame, so it is easy to band large numbers of adults and chicks and obtain information on marked individuals in subsequent years by either recatching them or reading their band numbers using a telescope. Such large-scale banding and retrapping of shags has been carried out at a colony on the Isle of May from the early 1960s to 1992. In an earlier study, Aebischer (1986) attempted to read the band numbers of all shags on the island during a single season (1982). His retrospective analysis indicated that survival was related to age but provided no evidence of any annual or long-term changes in survival even during a period when the number of nests in the colony decreased dramatically. In this paper we use a different method for estimating adult survival which incorporates retraps of live birds, resightings of individually color-banded birds, and recoveries of birds found dead over many years. Our aim was to investigate the relationships between survival and two factors, year and age, over a 24-year period.

METHODS

SURVIVAL INFORMATION

This study is based on the analyses of 3,495 retraps and recoveries from 13,653 chicks and 1,830 adult European Shags banded on the Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W) be-

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tween 1963 and 1987. To avoid bias due to band wear (Aebischer 1983), data from individuals banded with soft aluminum bands have been discarded and only data from birds marked with hard monel bands have been analyzed.

Each season from 1964 to 1992, the band numbers of a sample of breeding shags were read, usually by catching the bird. The annual totals varied greatly but, in general, were low in the 1960s and high in the 1980s (Table 1). The year 1982 was exceptional in that an attempt was made to read the band numbers of all shags on the island (Aebischer 1986). In most years, adult birds were sexed by size and voice when they were banded or recaptured. Mean adult survival rates were estimated for males and females, and for birds banded as adults or as chicks. No significant differences were found. Therefore, data from all individuals were pooled. Our data set contains information from the records of the Isle of May Bird Observatory and Field Station, N. J. Aebischer, J. A. Graves, the British Trust for Ornithology, and ourselves.

We used the methods of Buckland (1982, 1990) which give robust variance and interval estimation for any survival estimate or combination of estimates of interest. Additionally, they allow simultaneous analyses of data from both resightings of live birds and recoveries of dead birds. Ringing recoveries are often age biased but these analyses do not assume that there is no age bias. Annual survival rates were estimated for each combination of estimates of interest. Annual survival rates were estimated for each cohort of birds, where a single cohort comprised birds banded in the same year. Within each cohort, mark-recapture methods gave the survival estimates, and these were combined either by year or by age across cohorts (see Buckland 1982). Variances and 95% confidence intervals were estimated by the bootstrap method (Buckland and Garthwaite 1991). Marking and resighting were assumed to occur over a short time period, whereas deaths occurred throughout the year. We define the start of a new year as 1 July for determining the year of death for a bird found dead. A bird was assumed to become adult and breed for the first time at three years. Therefore, birds banded as chicks were only included in the analysis if they were caught alive on the island aged three or more years old. For convenience, we refer to survival by the initial year, e.g., 1982 refers to survival between 1982 and 1983.

To compare survival estimates, z-tests were used. If two survival estimates, $\hat{\Phi}_1$ and $\hat{\Phi}_2$, were correlated because birds contributed data to both estimates, the variances and covariances were estimated using the bootstrap, and z calculated as:

$$z = \frac{\hat{\Phi}_1 - \hat{\Phi}_2}{\sqrt{[\widehat{\mathrm{var}}(\hat{\Phi}_1) + \widehat{\mathrm{var}}(\hat{\Phi}_2) - 2\,\widehat{\mathrm{cov}}(\hat{\Phi}_1, \hat{\Phi}_2)]}}$$

During the 1980s and early 1990s, about 25% of banded breeding adults were recaught and given unique color-band combinations which made them potentially more easily detectable and identifiable. The presence of many of these birds was recorded before and during the egg-laying period, whereas the bulk of data for non-color-banded individuals came from birds caught when they had chicks. To reduce possible bias in estimates of survival due to heterogeneity of sighting, we carried out separate analyses for color-banded and non-color-banded individuals for each cohort from 1982 onwards. In seven of the nine years for which comparisons were possible, estimates of survival based on color-banded and non-color-banded birds did not differ significantly (Appendix). The difference in 1982 was probably due to unusual trapping effort; the reason for the low survival estimate for color-banded birds in 1990 is obscure. Excluding the 1982 and 1990 estimates, the mean weighted survival of color-banded birds (0.893, CI = 0.864, 0.918) was not significantly higher than that of non-color-banded birds (0.853, CI = 0.797, 0.895). In years with both color-banded and non-color-banded individuals, survival was estimated separately for the two groups. These estimates were combined to give a single survival estimate for each year after weighting by the estimated number of individuals contributing to each estimate.

The estimates of survival depend on the assumption that adult shags which have disappeared have died and not changed colony. Adult shags on the Isle of May are highly faithful to the island. Only three birds banded as adults were known to have bred at other colonies in the period 1963–1992 (compared with 864 which remained). One of these deserted its nest and clutch after it had been caught and was recorded breeding 86 km away on the Farne Islands, Northumberland, later the same season. However, in the following year the bird returned to

TABLE 1. Year specific survival estimates and 95% confidence intervals for adult European Shags on the Isle of May. Also given are the number of birds banded or captured as a breeding adult in an earlier year (including years prior to 1967) and recorded alive on the island in the specified year, the estimated number of birds captured as an adult in an earlier year that were still alive in the specified year, and the estimated probability of recording for those birds. Estimates from 1982 onwards as were obtained by stratifying birds by whether or not they were color-banded (see Appendix).

Year	Banded adults caught (*n*)	Estimate of banded adults alive (*n*)	Estimated probability of capture	Survival	95% confidence interval
1967	7	22	0.32	1.000	(0.840, 1.000)
1968	3	72	0.04	0.782	(0.676, 0.971)
1969	2	74	0.03	0.939	(0.814, 1.000)
1970	2	77	0.03	0.956	(0.835, 1.000)
1971	11	84	0.13	0.946	(0.635, 0.983)
1972	10	197	0.05	0.944	(0.579, 0.994)
1973	3	240	0.01	0.726	(0.630, 0.968)
1974	33	222	0.15	0.894	(0.796, 0.951)
1975	0	304	0.00	0.837	(0.766, 0.903)
1976	5	255	0.02	0.860	(0.776, 0.929)
1977	1	263	0.00	0.882	(0.839, 0.952)
1978	0	238	0.00	0.884	(0.856, 0.960)
1979	32	264	0.12	0.913	(0.713, 0.970)
1980	78	378	0.21	0.870	(0.785, 0.949)
1981	193	462	0.42	0.983	(0.912, 0.993)
1982	673	753	0.89	0.490	(0.433, 0.707)
1983	81	548	0.15	0.734	(0.510, 0.863)
1984	242	548	0.44	0.943	(0.890, 0.967)
1985	359	796	0.45	0.968	(0.882, 0.987)
1986	188	596	0.32	0.780	(0.695, 0.961)
1987	187	587	0.32	0.869	(0.706, 0.942)
1988	217	598	0.36	0.963	(0.802, 0.970)
1989	368	622	0.59	0.747	(0.665, 0.881)
1990	185	480	0.39	0.910	(0.833, 0.954)

breed on the Isle of May. For the purposes of this analysis, movement of adults between colonies was virtually non-existent and the bias negligible.

Relationships between annual survival rate and shag breeding parameters (timing of breeding as indicated by [a] the laying date of the first egg, and [b] the median date of banding of chicks), and an index of breeding success (the average brood size at banding [Potts 1969]) were examined using linear correlation and regression. An annual index of the size of the breeding population came from counts of occupied nests in early June each year (Harris and Forbes 1987). Data were obtained from Aebischer (1986), Aebischer and Wanless (1992) and Isle of May Bird Observatory records.

RESULTS

For birds banded as adults, survival in the year following banding (0.687; SE = 0.022) was significantly lower ($P < 0.001$) than mean survival in subsequent years (0.821; SE = 0.010). In part, this could have been an age effect with some birds only being two (the earliest age of breeding, Potts 1969) or three years old when they were banded. However, the primary cause was likely to be that the first survival estimate for a cohort is particularly susceptible to downward bias arising from heterogeneity in the probability of sighting between birds (Buckland 1982). This might occur because some individuals breed in less accessible sites, spend less time at the nest, usually fail early or breed less frequently (Potts 1969, Aebischer and Wanless 1992). Therefore, estimates of survival in the year following banding were excluded from all subsequent analyses.

Year-specific survival estimates for adult shags are presented in Table 1. Only the 1982 estimate of 0.490 was significantly lower than the overall weighted mean for the 24 years (0.860, CI = 0.842, 0.878). In that season there had been exceptionally high retrapping effort (see Methods) and many birds recorded in 1982 were not re-

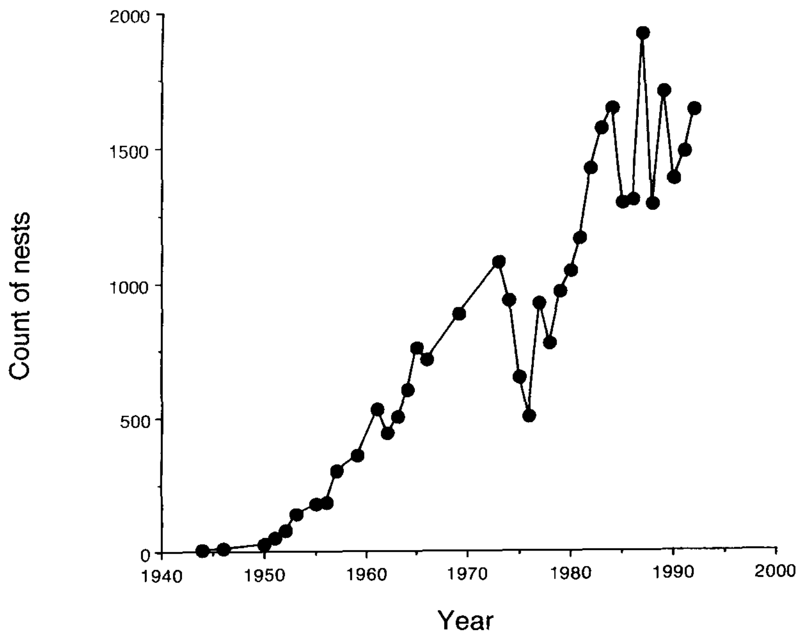

FIGURE 1. Counts of nests of European Shags on the Isle of May 1944–1992.

corded subsequently. Analysis of banding returns gave no indication of unusual numbers of first-year or adult shags dying during the 1982–1983 winter, the limited data from color-banded birds (see Methods and Appendix), and the fact that the count of nests in 1983 was 10% higher than that in 1982 all suggest strongly that this low estimate was due to greater trapping effort, which included the use of a telescope to read the band numbers of individuals nesting in accessible areas, rather than a real reduction in survival. Excluding the 1982 estimate, average survival between 1967 and 1990 was estimated as 0.878 (CI = 0.859, 0.897). Including the 1982 estimate, the estimated average survival was reduced to 0.860 (CI = 0.842, 0.878).

There was no evidence of any long-term change in survival rate during the study period ($r = -0.21$, $n = 23$, $P > 0.05$). Survival was not significantly correlated with timing of breeding (first egg date or median chick banding date) or breeding success (brood size) (all $r < 0.35$, $n = 22$, NS). In years when the counts of nests decreased dramatically (Fig. 1, 1974–1976, 1985–1986) survival was not significantly lower than in normal years (mean survival in five crash years = 0.874, SE = 0.04, 18 normal years = 0.887, SE = 0.11, $t = 0.31$, NS).

There were sufficient known-age birds to examine the effect of age on survival between the ages of three and 20 years (Table 2). Estimated survival of three-year-olds was 0.724 (SE = 0.053), which is not significantly lower than the mean survival estimate for older age classes (0.806; SE = 0.017). There was a suggestion that survival was also lower in four-year-olds before stabilizing at 0.875 (weighted mean; SE = 0.017) between the ages of five and 13 years. Survival then began to decrease so that in the oldest age group (20–21 years), survival was estimated to be only 0.416. The mean survival of birds older than 13 years was estimated at 0.659 (SE = 0.044).

DISCUSSION

Our estimate of a mean annual survival of 0.878 is similar to the previous estimate of 0.854 reported by Aebischer (1986) for Isle of May shags using a different method and over a shorter time period, but slightly higher than the 0.828 estimated for the Farne Islands (Potts et al. 1980). It is also similar to survival rates of other species of cormorant, e.g., 0.88 for the Flightless Cormorant (*Nannopterum harrisi*) in Galapagos (Harris 1979) and 0.899 for the Blue-eyed Shag (*P. atriceps*) at Signy Island, South Orkney Island (Cobley 1989).

TABLE 2. Age specific estimates of annual survival for European Shags banded as chicks between 1963–1987 and reported by the end of 1992.

Age	Estimated number of birds alive at this age	Estimated number alive one year later	Survival	95% confidence interval
3	3,210	2,324	0.724	(0.613, 0.899)
4	2,236	1,814	0.811	(0.635, 0.913)
5	1,699	1,535	0.903	(0.819, 0.939)
6	1,505	1,319	0.876	(0.713, 0.925)
7	1,175	1,074	0.914	(0.793, 0.951)
8	1,021	800	0.784	(0.686, 0.925)
9	728	661	0.909	(0.806, 0.938)
10	613	539	0.879	(0.793, 0.934)
11	491	409	0.833	(0.768, 0.934)
12	391	328	0.840	(0.623, 0.922)
13	319	285	0.892	(0.712, 0.954)
14	279	172	0.615	(0.572, 0.912)
15	170	123	0.727	(0.528, 0.946)
16	122	94	0.771	(0.444, 0.942)
17	91	57	0.625	(0.392, 0.940)
18	57	38	0.663	(0.314, 0.966)
19	34	15	0.452	(0.000, 0.783)
20	11	5	0.416	–

In common with shags and cormorants elsewhere (e.g., Boekelheide and Ainley 1989), shags on the Isle of May exhibit considerable annual variation in several breeding and population parameters (Aebischer 1986, Aebischer and Wanless 1992). In the most extreme cases, the number of nests in the colony decreases dramatically, breeding is significantly later and less successful, and very few birds recruit to the breeding population. Over the last thirty years, two such events have been recorded, in 1974–1976 and 1985–1986 (Fig. 1). Aebischer (1986) found no evidence of reduced adult survival during the 1974–1976 episode. Results from our analysis similarly indicate that the probability of survival was not significantly lower during the crashes which supports the contention that some birds with previous breeding experience must have abstained from breeding in these years (Aebischer 1986).

Studies elsewhere have, however, found evidence of annual difference in survival of adult shags. On the Farne Islands, incidents of paralytic shellfish poisoning caused by toxins produced by a dinoflagellate, reduced survival from 0.828 (n = 9 years between 1962 and 1971) to 0.24 in 1967–1968 and 0.38 in 1974–1975 (Coulson et al. 1968, Armstrong et al. 1978, Potts et al. 1980). Neither of these incidents had any discernible effect on survival of Isle of May shags even though the colonies are only 86 km apart (Coulson et al. 1968, Aebischer 1986, this study).

Potts et al. (1980) found no evidence of any increase in mortality with age among shags on the Farne Islands. In contrast, on the Isle of May, Aebischer (1986) noted that survival from banding to 1982 of the 1965–1971 cohorts was consistently lower than that of subsequent cohorts which was indicative of higher mortality in older birds. Our analysis also indicated that survival in shags was age-related with the effect appearing after birds reached about 14 years. Similar effects have been found in some other seabirds, e.g., the Kittiwake (after 12 years, Aebischer and Coulson 1990), Eider (13 years, Coulson 1984), Short-tailed Shearwater (20 years, Bradley et al. 1989) and Wandering Albatross (27 years, Weimerskirch 1992) and will, as expected (Botkin and Miller 1974), probably be detected by those other long-term studies which have marked sufficiently large numbers of young birds to overcome the inevitable problems of decreasing sample sizes with increasing age.

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APPENDIX. Year specific adult survival estimates for color-banded and non-color-banded European Shags. Data on birds in the year of first capture as an adult are excluded. * Estimates differ significantly ($P < 0.05$).

	Color-banded			Non-color-banded		
Year	Marked birds reported (n)	Estimated probability of survival	95% confidence interval	Marked birds reported (n)	Estimated probability of survival	95% confidence interval
1982	7	0.857	(0.500, 1.000)	619	0.486	(0.429, 0.704)*
1983	16	0.851	(0.670, 1.000)	41	0.730	(0.502, 0.860)
1984	27	0.927	(0.786, 1.000)	154	0.944	(0.891, 0.968)
1985	8	0.972	(0.896, 1.000)	253	0.968	(0.876, 0.988)
1986	40	0.785	(0.664, 0.911)	49	0.780	(0.691, 0.973)
1987	104	0.918	(0.861, 0.971)	14	0.860	(0.672, 0.945)
1988	9	0.917	(0.839, 0.973)	56	0.971	(0.787, 0.979)
1989	94	0.852	(0.774, 0.921)	197	0.729	(0.634, 0.892)
1990	122	0.798	(0.730, 0.872)	18	0.936	(0.840, 0.981)*
Weighted mean 1983–1989		0.893	(0.864, 0.918)		0.853	(0.797, 0.875)