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Isle of May seabird studies in 1999

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1. Summary

1. In general, 1999 was a poor season for Isle of May seabirds, with many species breeding late and/or unsuccessfully. Only fulmars (and terns which are not included in this monitoring scheme) had a good breeding season.

2. Shags had a poor year. Many failed to breed and those that did laid late. Overall breeding success (0.33 chicks per incubated nest) was low.

3. Breeding of kittiwakes was late, about 17% of pairs did not complete a nest and many pairs, which did breed, failed during incubation. The average breeding success of 0.20 chicks per completed nest was an order of magnitude better than it was in 1998. However, far too few young are now being reared to keep the Isle of May population stable.

4. Guillemots, razorbills and puffins had one of their worst seasons since monitoring started on the Isle of May, with breeding success estimated at 0.66, 0.52, and 0.58 chicks per egg laid respectively.

5. Fulmars had a good year, with breeding success estimated at 0.47 chicks per incubating pair.

6. Far fewer than normal colour-ringed shags returned (65.8% of those known to be alive in 1998). It is probable that survival between 1998 and 1999 was very low. Return of kittiwakes was also low (73.1%). In addition, few of the birds not seen in 1998 were sighted in 1999 confirming previous concern that survival between 1997 and 1998 had been very low. Survival of guillemots was slightly below the long-term average (return rate 90.2% compared with the long-term mean of 94.8%). However at this stage we cannot exclude the possibility that some birds may have taken a year off. Razorbill and puffin return rates (86.9% and 88.2% respectively) remain moderately high and continue the trend of year to year fluctuations which have been apparent since intensive monitoring began on the Isle of May.

7. A comparative analysis of long term changes in adult survival rates of seabirds on the Isle of May indicated that over the period 1986-96, the average adult survival of shags was 82.1%, of guillemots was 95.2%, of razorbills was 90.5%, of puffins was 91.6% and of kittiwakes was 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 the kittiwake also declined which, given the low breeding success in recent years, gives cause for concern for the Isle of May population. With the current high level of resighting achieved by studies on the Isle of May, it is clear that year-by-year return rates provide a reasonable indication of relative changes in adult survival.

8. Sandeels predominated in the diet of puffins, razorbills, shags and kittiwakes in 1999. In contrast, guillemots mainly fed their young small sprats and unusually, numbers of gadoids were also brought ashore. There was evidence that guillemots and puffins were having problems raising chicks in 1999 with fledging weights of these species being well below the long term average.

9. Following the ELIFONTS study there is an excellent chance that independent estimates of sandeel availability will continue to be collected in the Firth of Forth area. It is therefore essential that seabird productivity and dietary monitoring also continues to enable a quantitative description of the functional relationships between predator performance and prey availability be determined.

2. Background

1. The Joint Nature Conservation Committee (JNCC) has a responsibility to advise on certain aspects of the condition of the natural marine environment. Seabirds are one of the more important components of this environment, and Britain has internationally important populations of several species. JNCC has designed a programme that will allow the numbers and breeding success of selected species of seabirds to be monitored at a range of colonies throughout the UK. In addition, selected colonies have been targeted for more detailed monitoring of reproductive performance and annual survival rates. These selected colonies are geographically spread in order to give as full a coverage as possible of British waters and the Isle of May NNR is the designated site in eastern Britain.

2. The Centre for Ecology and Hydrology (CEH), formerly the Institute of Terrestrial Ecology (ITE) has a long-term interest in seabirds on the Isle of May. Since 1986, CEH has received NCC-CSD/JNCC support for a more formalised seabird monitoring programme. Long-term studies on numbers, breeding success, adult survival, and chick food are under way on up to eight species. Due to the long period of immaturity and high annual survival rates of seabirds, it is essential that continuity of these long-term studies is maintained. As part of its Seabird Monitoring Programme, JNCC has a contract with CEH to:

   a) ensure that the breeding success of fulmars *Fulmarus glacialis*, shags *Phalacrocorax aristotelis*, kittiwakes *Rissa tridactyla*, guillemots *Uria aalge*, razorbills *Alca torda* and puffins *Fratercula arctica* is monitored;

   b) monitor adult survival of kittiwakes, guillemots, razorbills and puffins. Monitoring of shag adult survival was also included up to March 1994, was then excluded for the 1994 season, but was reinstated in May 1995;

   c) assess food of young shags, kittiwakes, guillemots, razorbills and puffins;

   d) undertake special studies on species agreed between the nominated officer and the contractor.

3. Soon after the Seabird Monitoring Programme (SMP) on the Isle of May was initiated, the Danish industrial sandeel fishery started to use the fishing grounds on the Wee Bankie, Marr Bank and Scalp Bank. These lie 30-50 km east of the island and are known to be important fishing grounds for many seabirds during the breeding season. Considerable concern has been expressed about the potential impact of this fishery on the seabirds in the area and the SMP is providing key information on temporal changes in productivity for the Isle of May seabird community.

4. This long-term approach has been complemented by a short-term multi-disciplinary EU funded project (ELIFONTS) which collected detailed data for the 1997 and 1998 seasons on the diet and productivity responses of avian, mammalian and piscivorous predators in the Firth of Forth. This work is currently being written up but it seems clear that, in combination with the long term data available from the SMP, it will greatly increase our understanding of the predator/ prey relationships in this system and thus improve the quality of advice on possible management options that take account of wildlife as well as commercial requirements.

3. Methods

3.1 Breeding success

The standardised methods used involved minimal disturbance of birds and are described in detail in Walsh *et al.* (1995).

3.1.1 Fulmar: the positions of apparently incubating birds in ten areas were marked on photographs on 27 and 30 May and 2 June. At sites where birds appeared to be incubating on all three visits, or where an egg was seen, breeding was assumed to have occurred. These sites were checked again on 9 July (to determine which eggs had hatched), and on 20 August (by S. Lewis) when the large chicks present were assumed to fledge successfully.

3.1.2 Shag: the positions of nests in 14 areas were marked on photographs and the state and contents of these nests were checked weekly from 21 March until 23 August when breeding had finished.

3.1.3 Kittiwake: the positions of nests in 15 areas were marked on photographs and the presence or absence of an incubating bird, or the number of young present at each was noted. Initial checks were made on 26 May and 6 June. The first check of chicks was on 22 July, the day the first fledged young on the island was seen. A follow up check was carried out on 26 July to determine the status of broods that were classed as having small or medium sized chicks on 22 July.

3.1.4 Guillemot and razorbill: daily checks of the state of breeding of numbered nest-sites in five study plots were made from permanent hides.

3.1.5 Puffin: samples of 50 burrows where an egg could be felt were staked in each of four areas on 3 May (earlier checks indicated that most pairs had laid by this date). The staked burrows were re-checked on 4 July (when chicks were near fledging). All large young present at this time were assumed to fledge successfully. Empty burrows where there were many droppings, moulted down and feather sheaths were also assumed to have been successful.

3.2 Adult survival rates

Adult survival rates were based on sightings of individually colour-ringed birds and therefore, strictly speaking, are return rates. The areas in which birds were originally marked were checked regularly throughout the season and adjacent areas were searched from time to time in an attempt to pick up birds that had moved. Searches were also made of the whole island for birds that had moved out of the study areas. These latter searches are very time consuming, and superficially unrewarding, but are essential if accurate estimates of survival are to be obtained. Observations on the survival of adult puffins are concentrated at Little Hole (where most burrows are individually numbered). The area used for monitoring survival of adults kittiwakes has been expanded to include Cornerstone and nearby cliffs since the overall reduction in kittiwake numbers on the island has resulted in there now being insufficient birds nesting at Tarbert and at Low Light to keep the numbers colour-ringed at the required levels.

3.3 Food of chicks

Food regurgitated by young shags, young kittiwakes and adult kittiwakes feeding young, and loads of fish dropped by adult puffins caught in mist-nets were collected. Given the paucity of shag regurgitates in 1999, pellets were also collected from around shag nests. The regurgitates and food loads were weighed, fish identified and, where possible, measured (total length to tip of tail). Fish otoliths were extracted from regurgitates and identified and the lengths of the fish from which they came were calculated using regressions derived from the otoliths of fish of known length collected from birds on the island in 1999 or published works. Records were kept of fish brought to young guillemots and razorbills during two all-day watches and opportunistically on most other days. Uneaten fish were collected from breeding ledges to confirm identifications and size assessments.

4. Results

4.1 Breeding success

Species accounts are given in Tables 1-4 and a comparison with recent years' results is shown in Table 5 and Figure 1.

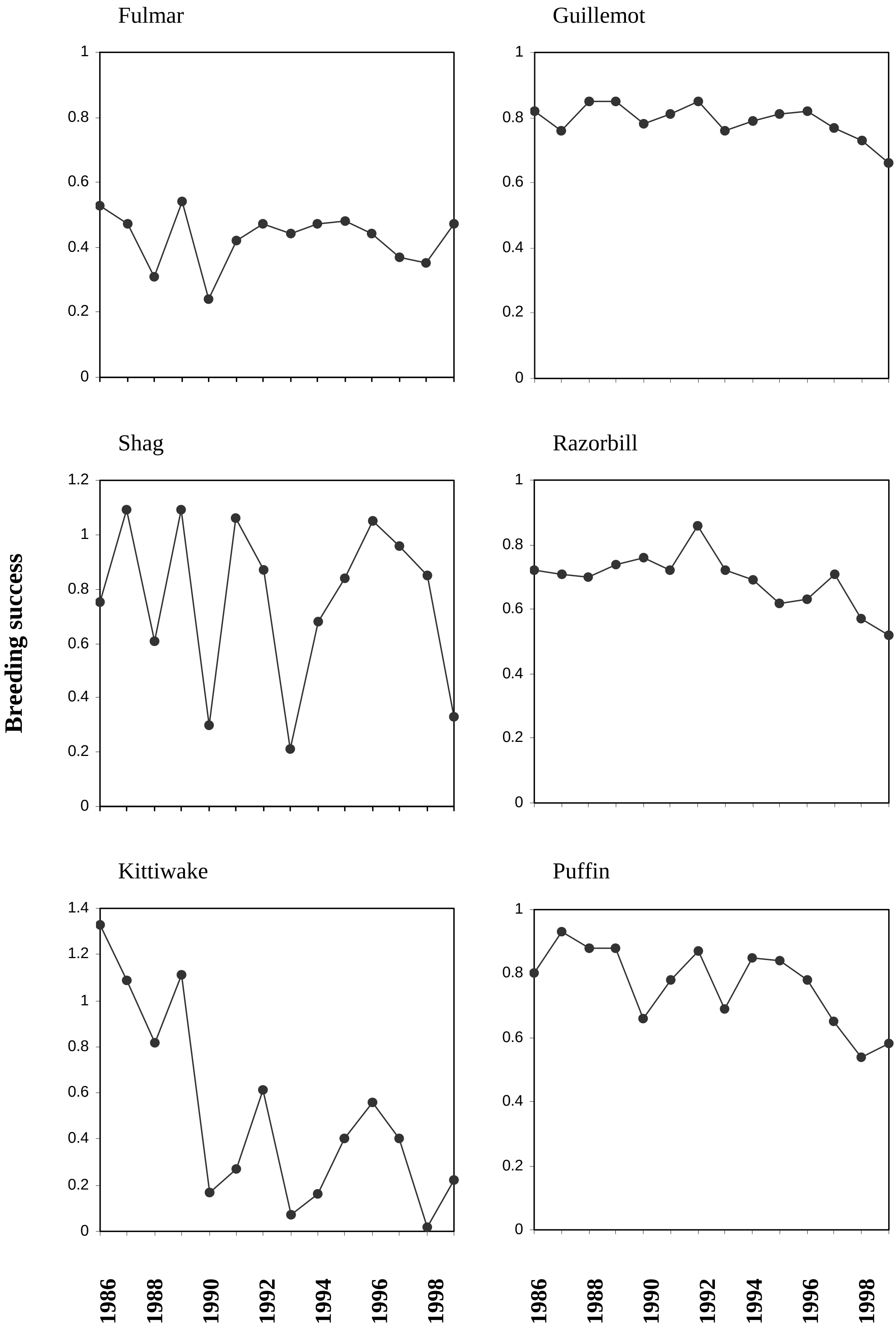
4.1.1 Fulmar: the first egg was seen on 15 May. Breeding success was 0.47 young per incubating pair (Table 1); the highest figure since 1995 but within the 95% Confidence Intervals for the 1989-98 long term average (mean 0.42, CI=0.36-0.48). The methods used are not designed to determine when breeding attempts fail, but it appeared that hatching success was high and that most losses occurred during chick stage

4.1.2 Shag: 1999 was an unusual season. The number of adults present was much lower than in recent years and many of those that were present showed little nesting activity. The first egg was found on 23 April, but this had been laid on bare rock and was lost by the following day. The first proper clutch was not initiated until 1 May. Of 80 nests built in the 14 study plots, 58 later had adults apparently incubating. This is the lowest total recorded during the monitoring scheme, being 11% and 22% lower than the two previous lowest estimates in 1994 and 1993 respectively. A total of 19 young fledged from 58 nests, an average of 0.33 chicks per laying pair (Table 2). This estimate is preferred to that calculated from the mean of estimates for individual plots (0.21 ± 0.07) as nine plots held five or fewer nests and were mostly unsuccessful (Table 2). The estimated success was well below the 95% Confidence Intervals for the 1986-98 average (mean 0.80, CI=0.62-1.01).

4.1.3 Kittiwake: breeding started later than normal (Table 13), with the first egg not recorded until 16 May. The first egg hatched on 13 June and first young fledged on 22 July. In all, 17% of pairs present did not complete the building of a nest and a high number of breeders failed during incubation. The mean clutch-size was 1.99 eggs. Conditions appeared to improve during the latter part of the season and thus the growth of those young that survived past the early chick stage appeared normal and most chicks near fledging looked healthy. The percentage of chicks that were neglected was slightly lower than the long-term average (5% of broods of one and 25% of broods of two compared with long term averages of 11% and 31% respectively – Table 11). One pair at South Horn reared three young – a highly unusual event over the last 5-10 years on the Isle of May.

Breeding success in 1999 was an order of magnitude greater than in 1998 (Table 3) but was still poor with the 616 pairs that built good nests raising a maximum of 137 young (0.22 young per pair). The mean success of the 15 study plots was 0.20 with the highest success (0.51) being recorded at the Cornerstone plot (Table 3).

Figure 1 Breeding success (young reared per pair breeding) of seabirds on the Isle of May 1986-99



4.1.4 Guillemot: the first egg was laid on 23 April. The median laying dates in the earliest and latest areas followed were 8 and 13 May, two and six days earlier than in 1998. The first young left on the night of 15/16 June. Breeding success (0.66 young leaving per pair laying) was the lowest recorded (Tables 4 and 5, Figure 1), and was well below the 95% Confidence Interval for the previous 18 seasons (0.78-0.82). The previous lowest breeding success was 0.73 which was recorded in 1998 and 1984. As in 1998, losses during the chick period (19%) were higher than the normal rate (5-6%) and weights of chicks near fledging were the lowest since observations began in 1983.

4.1.5 Razorbill: timing of breeding was normal for the Isle of May, with the first egg being laid on 30 April. Breeding success (0.52 young leaving per pair laying) was, as in the guillemot, the lowest recorded since studies began (Tables 4 and 5, Figure 1) and was also below the 95% Confidence Interval for the previous 17 seasons (0.65-0.73). As usual, most losses occurred at the egg-stage, but survival to fledging of those chicks that did hatch was also low (79%).

4.1.6 Puffin: the first adults carrying fish were seen on 23 May, but the first young fledged on 27 June which indicates that some young must have hatched slightly earlier than this. Back-calculating from this figure indicates that laying commenced in the second week of April. The overall success rate (0.58 chicks fledged per egg laid) was one of the lowest since records began (Tables 4 and 5, Figure 1). Rainfall was not as great as in 1998 and, although some burrows did become flooded, this was not considered to be the cause of the low nesting success. The available evidence suggests that adults had difficulty in providing sufficient food. Food quality of loads brought to chicks was low with only 52% of the biomass being composed of sandeel and concurrent studies showed that provisioning rates were lower than normal.

Vegetation growth in the puffin breeding areas was much more vigorous than for several years. This helped to reduce soil erosion in many areas, but the stability of certain areas, particularly south Burrian remains poor.

4.2 Adult survival

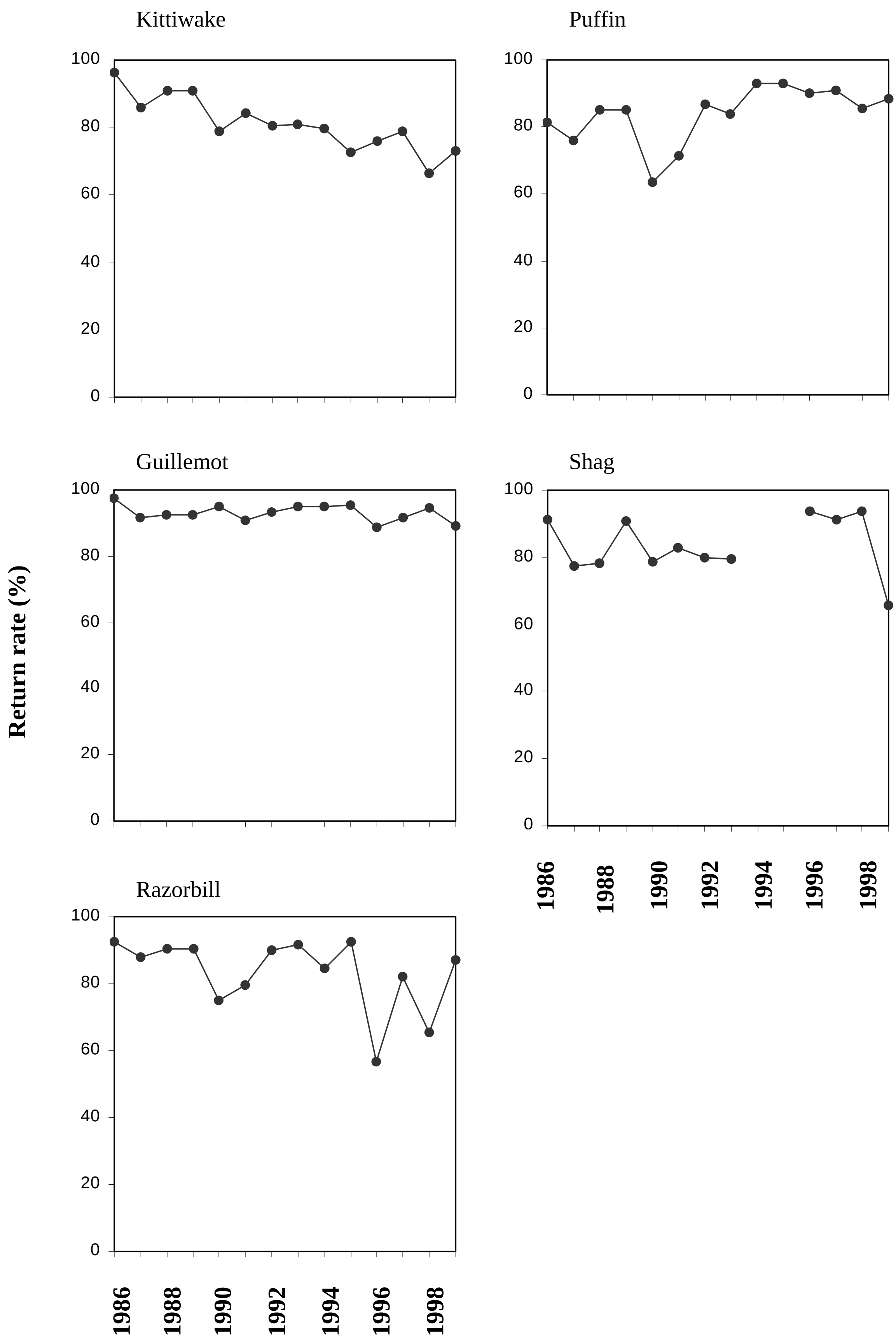
4.2.1 Survival 1998-99

Not every adult alive is seen each year and thus the return rates in 1999 of birds seen in 1998 – 73.1% for kittiwake, 90.2% for guillemot, 86.9% for razorbill, 88.2% for puffin and 65.8% for shag must be treated as minimum estimates of survival. The results are compared with similar figures from earlier years in Table 6 and Figure 2.

The return rate of colour-ringed shags in 1999 was the lowest recorded except following the wreck in early 1994 (Table A1.1). No birds were reported from other colonies despite searches being made at the Farne Islands (M. P. Harris, National Trust Wardens), St. Abb's Head (K. Rideout and D. McCafferty) and other islands in the Firth of Forth (F.Daunt). It is too early to assess whether birds not seen in 1999 have died or have taken a year off attending colonies, but ringing recoveries of immature shags were much higher than normal during the 1998-99 winter which suggests that mortality of older birds may also have been higher.

The return rate of adult guillemots (90.2%) was slightly lower than in recent years (excepting 1995-96). Allowing for an average of 1-2% of birds not seen in any year returning in later years, the survival between 1998 and 1999 appears to be lower than the long-term average of 94.8%

Figure 2 Annual return rates of adult seabirds on the Isle of May 1986-99



The return rate of kittiwakes (73.1%) was higher than in 1998 (66.2%), but was still substantially lower than the values of 80-90% recorded prior to 1994. Only eight birds that were not seen in 1998 were seen in 1999 and it appears that mortality was high between the 1997 and 1998 breeding seasons.

The return rate of puffins (88.2%) was slightly higher than in 1998, but remained below the long-term average of 91.6%.

The return rate of razorbills (86.9%) was higher than in the last three years. As no new birds were colour ringed between 1995 and 1998 the lower return rates recorded during this period were due to birds not being seen rather than having died.

During 1999 an additional nine shags, 24 kittiwakes, 18 puffins, four razorbills and 14 guillemots were colour-ringed.

4.2.2 Analysis of long-term survival data

During the year two major analyses of the survival of Isle of May seabirds using data collected under the JNCC monitoring programme were completed. These will be formally published in *Atlantic Seabirds* and *Bird Study* in due course. Summaries of the results are presented in Appendices 1 and 2, but details of the methodology and models used are omitted.

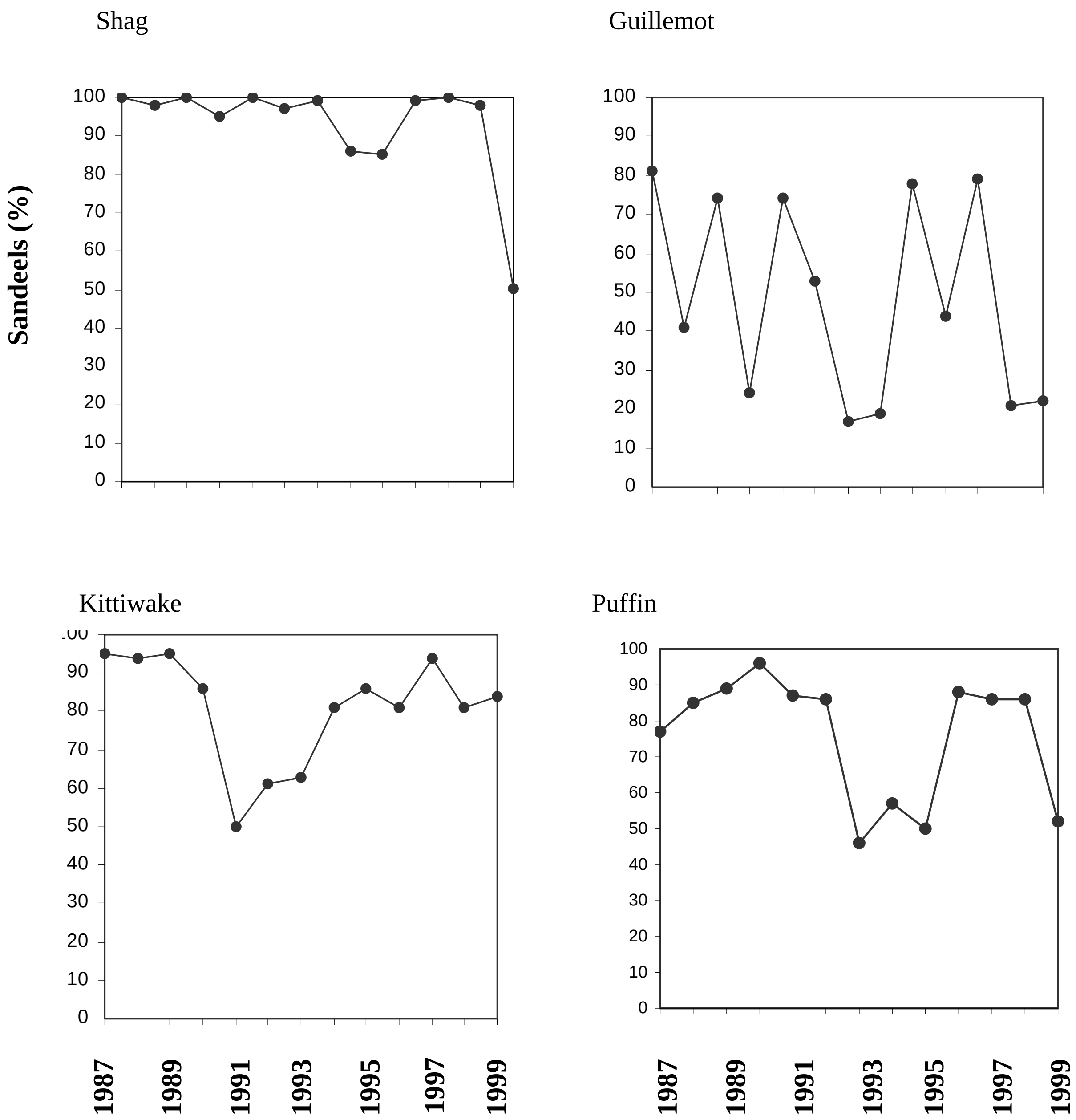
4.3 Food of young

The low breeding population coupled with the low breeding success meant that few shag chicks were available for sampling and only five regurgitations were collected (Table 7). Of the two July samples one contained sandeels older than group-0 and the other one was composed entirely of sprats 7-10cm long. All three samples in August contained 0-group sandeels 8-9 cm long; one of the three also contained older sandeels. To increase the sample size for this species we therefore also collected pellets from around nests and then extracted otoliths and other hard parts from these. Pellets have disadvantages when describing diet since small otoliths are often completely digested. However, of 32 pellets collected at nests between 3 and 15 July, 17 (53%) contained otoliths from sandeels, 13 (41%) from Gadidae, five (16%) from Cottidae, five (16%) from Gobiidae and four (13%) from Pleuronectidae. Comparative rates of occurrence of these fish families in three previous breeding seasons were 87-97% for sandeels, 16-25% for Gadidae, 5-11% for Cottidae, 3-10% for Gobiidae, and 9-22% for Pleuronectidae. Thus there was evidence that in 1999 sandeels contributed less, and hence other groups more, to the diet of shags than in other years (Figure 3 and Table 12).

Sandeels were the commonest food (95% by number of 6,521 otoliths) of young kittiwakes (Table 7). Approximately 93% of the sandeels in regurgitates were 0-group fish 4-8 cm long (n = 5,932 otoliths examined). Sandeels contributed 84% by weight of the diet during the breeding season whilst clupeids (mostly sprat) contributed 11%. Five whiting, two *Trisopterus* sp., one small Gadidae probably cod, and one long rough dab were presumably trawler discards. A single regurgitate contained mainly small pelagic crustacea.

As in 1998 the majority (68%) of 1,035 fish delivered to young guillemots brought in were Clupeidae 9-11cm long (Table 8). Of 13 clupeids retrieved from birds or picked up on breeding ledges, twelve were sprat (8-12cm) and one a herring (15cm). Sandeels accounted for 26% of food delivered to young and were mostly 7-10cm long. Unusual numbers (61 or 6% of total) of gadoids, apparently mostly whiting, were brought to chicks. One small squid was recorded. In biomass terms clupeids made up 75% of the diet, sandeels 22% and gadoids 3%.

Figure 3 Percentage of sandeels (by weight) in the diet of young seabirds on the Isle of May, 1987-99



The average weight of a prey item (calculated from lengths) was 5.4 g. This was rather low compared to the long-term average of 7.5g (18 years). Concurrent studies showed that the feeding frequency was also depressed with the result that the daily intake of food by young was much reduced. Not unexpectedly chicks at fledging age were substantially under-weight.

Most loads of fish brought to razorbill chicks were made up of several small or medium sandeels (Table 9).

Sandeels made up 75% by number of the diet of young puffins (Table 10) but the proportion in biomass terms was only 52%. Most sandeels were 0-group with a mean length of 58 mm; only 28 (1.9%) were longer than 10cm. Many of the Clupeidae were small, and thus difficult to identify, but the bulk appeared to be sprat. The mean load size of 7.99g was significantly below normal (mean of 26 years = 9.3g) and, due to their small size, the number fish per load (10.4) was among the highest recorded.

5. Conclusions

The pattern of productivity and behavioural responses shown by Isle of May seabirds in 1998 and 1999 have been strikingly similar to those recorded in Shetland during the period of reduced sandeel availability during the late 1980s and in 1990. Inspection of the time series data on breeding success on the Isle of May indicates that, with the exception of fulmar and shag, productivity is currently lower than at any time since monitoring began (Figure 1). It has been suggested that seabirds in the south-east of Scotland should be better buffered against changes in sandeel availability than those in Shetland because they have access to alternative prey, notably small clupeids and gadoids. Dietary monitoring carried out for the SMP has shown that these alternative prey have been utilised in recent years by some of the seabirds, particularly guillemots (Figure 3). However compensation is clearly incomplete and the quantity and/or quality of chicks produced by most species has been reduced (Figure 3). The only monitored species to show above average productivity in 1999 was the fulmar, which is not thought to feed on sandeels to any large extent in this area.

One of the key objectives of the EU funded ELIFONTS study was to provide an independent measure of sandeel availability at a spatial and temporal scale appropriate to avian predators in the area. There is an excellent chance that this parameter will continue to be monitored in June each year. It is therefore essential that seabird productivity and dietary monitoring continue on the Isle of May to enable a quantitative description of the functional relationship between predator performance and prey availability to be determined.

6. Acknowledgements

We are extremely grateful to JNCC for an additional contribution to allow the intensive sampling of kittiwake diet to be continued in 1999. Darren Hemsley and Sue Lewis of Scottish Natural Heritage, and Francis Daunt, Suki Finney, David Hammond, Liz Humphreys, Sheila and Debbie Russell, Mark Newell, Tom and Ann Dudney provided help during the 1999 field season.

7. Additional papers on Isle of May seabirds published or in press since publication of the 1998 report

Daunt, F., Wanless, S., Harris, M.P., & Monaghan, P. 1999. Experimental evidence that age-specific reproductive success is independent of environmental effects. *Proceedings of the Royal Society of London* B:266: 1489-1493.

Finney, S.K., Wanless, S., & Harris, M..P. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. *Journal of Avian Biology* 30: 23 – 30.

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Harris, M.P., Wanless, S. & Rothery, P. *in press*. Adult survival rates of shag, guillemot, razorbill, puffin and kittiwake on the Isle of May 1986-96. *Atlantic Seabirds*. (See Appendix 1)

Harris, M.P., Wanless, S., Rothery, P., Swann, R.L.& Jardine, D. *in press*. Survival of Common Guillemots *Uria aalge* at three Scottish Colonies. *Bird Study* (See Appendix 2)

Wanless, S., Harris, M.P. & Greenstreet, S.P.R. 1998. Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. *ICES Journal of Marine Science* 55: 1141-1151.

Wanless, S., Finney, S.K., Harris, M.P., & McCafferty, D.J. *in press*. The effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the blue-eyed shag and the European Shag. *Marine Ecology Series*

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Tables

Table 1 Breeding success of fulmars on the Isle of May in 1999

Area	Incubating birds	No. probably hatched	Young fledged
1. Cleaver	9	9	3
2. Pilgrim's Haven	2	2	2
3. Cornerstone	7	7	2
4. Loch (S)	42	38	10
5. Greengates	26	20	23
6. Horse Hole	5	5	4
8. Tarbet	18	14	9
9. Low Light	6	3	1
Totals	**115**	**98**	**54**
		Overall mean	**0.47 fledged/ pair**

Notes:

No pairs bred in plot 7 (Rona) and 10 (Colm's Hole) in 1999.

Incubating birds were those sitting tight on three chicks or where an egg was seen. Chicks present on 20 August were assumed to have fledged. The final check was made by S Lewis.

Table 2 Breeding success of shags on the Isle of May in 1999

Area	Total Incubated	Other nests	Young fledged 1	Young fledged 2	Young fledged 3	Total young fledged	Mean young fledged per incubated nest
3. Maidens	8	1	0	1	0	2	0.25
4. South Horn	0	0	0	0	0	0	0
5. Chatterstanes	0	0	0	0	0	0	0
15. Pigrims Haven (S)	6	3	0	1	0	2	0.33
6. Colony A	0	0	0	0	0	0	0
7. South Face	0	0	0	0	0	0	0
8. Mill Door (N)	5	2	1	1	0	3	0.60
9. Nill Door (S)	4	2	0	1	0	2	0.50
10. Bishop's Cove	0	0	0	0	0	0	0
16. Horse Hole	11	5	1	3	0	7	0.64
17. North Horn	10	2	0	1	0	2	0.20
12. Tarbet	3	2	0	0	0	0	0
18. Low Light	9	4	0	0	0	0	0
14. Colm's Hole	2	1	1	0	0	1	0.50
Total	**58**	**22**	**3**	**16**	**0**	**19**	**0.33**

Mean of areas ± se **0.21 ± 0.07**

Table 3 Breeding success of kittiwakes on the Isle of May in 1999

Area	Completed Nests	Trace nests	Other pairs with site	Fledged young per completed nest			Total young produced	Fledging success per completed nest
				0	1	2		
1. Cleaver	31	1	6	29	2	0	2	0.06
2. Pilgrim's Haven	20	1	4	14	4	2	8	0.40
3. South Face	27	0	3	20	7	0	7	0.26
4. Colony 4	63	7	7	53	10	0	10	0.16
5. Cornerstone	68	3	4	38	25	5	35	0.51
6. Loch (S)	46	4	15	45	1	0	1	0.02
7. Loch (N)	81	5	2	66	12	3	18	0.22
8. Greengates	38	4	5	31	6	1	8	0.21
9. Bishop's Cove	50	1	9	34	10	6	22	0.44
10. Horse Hole	4	0	0	4	0	0	0	0
11. Iron Bridge	39	2	2	32	6	1	8	0.21
12. Rona	28	0	0	25	3	0	3	0.11
13. Tarbet	84	14	18	75	8	1	10	0.12
14. Low Light	19	2	1	19	0	0	0	0
15. Colm's Hole	18	0	3	14	3	1	5	0.28
Total	**616**			**499**	**97**	**20**	**137**	
							Mean ± se	**0.20 ± 0.04**

Table 4 Breeding success of auks on the Isle of May in 1999

Species	Area	Pairs laying	Young hatched	Young 'fledged'	Young leaving/pair
Guillemot	Dense	282	229	185	0.66
	Hide/White Ledge	97	78	65	0.67
	Colony 4	235	185	163	0.69
	South	48	40	30	0.63
	Cornerstone	208	164	137	0.66
	Mean ± se				**0.66 ± 0.01**
Razorbill	Hide/White Ledge	19	16	11	0.58
	Colony 4	46	22	24	0.52
	South	14	7	5	0.36
	Cornerstone	63	49	40	0.63
	Mean ± se				**0.52 ± 0.06**
Puffin	Lady's Bed	47	?	19	0.40
	Kirkhaven	46	?	28	0.61
	Burrian	45	?	30	0.67
	Rona	43	?	27	0.63
	Mean ± se				**0.58 ± 0.06**

Table 5 Breeding success (young reared per pair breeding) of seabirds on the Isle of May, 1989-99

Species	1989	1990	1991	1992	1993	1994
Fulmar	0.54 (93)	0.24 (66)	0.42 (100)	0.47 (129)	0.44 (121)	0.47 (122)
Shag	1.09 (234)	0.30 (154)	1.06 (187)	0.87 (181)	0.21 (80)	0.68 (74)
Kittiwake	1.11 (1327)	0.17(1095)	0.27 (1172)	0.61 (1062)	0.07 (1034)	0.16 (861)
Guillemot	0.85 (757)	0.78 (748)	0.81 (754)	0.85 (745)	0.76 (797)	0.79 (775)
Razorbill	0.74 (97)	0.76 (100)	0.72 (104)	0.86 (105)	0.72 (119)	0.69 (134)
Puffin	0.88 (164)	0.66 (176)	0.78 (153)	0.87 (184)	0.69 (182)	0.85 (189)

Species	1995	1996	1997	1998	1999
Fulmar	0.48 (126)	0.44 (135)	0.37 (136)	0.35 (120)	0.47 (115)
Shag	0.84 (131)	1.05 (105)	0.92 (109)	0.85 (125)	0.33 (58)
Kittiwake	0.40 (874)	0.56 (825)	0.40 (822)	0.02 (683)	0.20 (616)
Guillemot	0.81 (805)	0.82 (786)	0.77 (842)	0.73 (852)	0.66 (870)
Razorbill	0.62 (143)	0.63 (140)	0.71 (132)	0.57 (134)	0.52 (142)
Puffin	0.84 (180)	0.78 (173)	0.65 (166)	0.54 (179)	0.58 (181)

Notes:

The number of pairs followed is given in brackets. Details of methods, etc. can be found in this and previous reports to JNCC.

Table 6 Annual return rates of adult seabirds on the Isle of May 1987-99

Species	No. seen in 1998	No. alive in 1999	Return rate (%) 1998-99	1997-98	1996-97	1995-96	1994-95
Kittiwake	134	98	73.1	66.2	78.7	75.8	72.7
Guillemot	379	342	90.2	94.6	91.8	88.9	95.6
Razorbill	23	20	86.9	65.5	82.1	56.6	92.6
Puffin	204	180	88.2	85.5	90.7	90.1	93.0
Shag	161	106	65.8	93.6	91.1	93.6	?

			Return rate (%)				
Species	1993-94	1992-93	1991-92	1990-91	1989-90	1988-89	1987-88
Kittiwake	79.5	80.8	80.7	84.2	78.7	90.9	86.0
Guillemot	95.0	95.0	93.3	91.0	94.9	92.4	91.5
Razorbill	84.5	91.5	89.8	79.6	75.0	90.5	88.1
Puffin	93.1	84.0	86.8	71.4	63.3	85.2	76.1
Shag	?	79.6	79.9	82.8	78.7	90.9	86.0

Notes:

Only birds which had definitely bred in 1998 or earlier are included.
Directly comparable figures for earlier seasons are given. These have not been corrected for missing birds seen in later years, and for some species may severely under-estimate actual survival rates.
These figures should not be used for population dynamics calculations without consultation with M.P. Harris.
Details of earlier estimates are given in previous reports to NCC-CSD/JNCC.

Table 7 Food of young kittiwakes and shags on the Isle of May in 1999

	Kittiwake	Shag
No. of regurgitations	179	5*
Range of dates	13 June- 2 July	8 July & 5 August
Total weight (g)	3048	166
% regurgitations with sandeels	90	80
with Gadidae	9	20
with Clupeidae	28	20
% (by weight) of sandeels in sample	84	75
% (by numbers) of sandeels in sample	95	91
Lengths of majority of sandeels (cm)	4-8	8-9cm
Other remains identified	Whiting (5 fish, 14 -18cm) *Trisopterus* (2 fish, 10cm) small Gadidae possibly Cod (12 fish, ca. 10-14cm) Long Rough Dab (1 fish, 7cm) small pelagic Crustacea (1 sample)	Sprat (14 otoliths,7 -10cm) Dragonet (1 fish, 25cm) Flatfish (1 fish, 6cm) Gadidae (1 fish, small)

Notes:

Samples were colected from chicks or adults during the chick rearing period.
Counts and lengths of fish were based on otoliths retrieved from the regurgitations.
*See text for information on the diet of shags assessed by pellets.

Table 8 Food of young guillemots on the Isle of May in 1999

	Number of sandeels				Number of Clupeidae				Number of Gadidae		
	minute	**small**	**medium**	**large**	**minute**	**small**	**medium**	**large**	**small**	**medium**	**large**
Mean length (cm)	6	10	13	15	6	9	11	15	5	8	12
All day watches											
20 June	0	44	89	3	6	137	97	7	21	9	2
27 July	0	12	6	0	1	82	8	2	5	1	0
Other records											
2 June – 11 July	11	78	17	6	6	306	51	5	11	11	1
Total	11	134	112	9	13	525	156	14	37	21	3

Notes:

Lengths were based on visual estimates against the bird’s bill checked by samples of dropped fish collected from the breeding ledges.
1 small squid was brought in on 26 June.

Table 9 Food of young razorbills on the Isle of May in 1999.
Figures are numbers of loads of various types of food

	Single sandeel			Several sandeels				Clupeidae	Gadidae
	large	**medium**	**small**	**large**	**medium**	**small**	**tiny**		
All day watches									
20 June	7	1	0	5	7	10	2	8	2
27 July	0	1	1	0	3	3	0	1	0
Other records									
9 June – 2 July	0	0	0	1	3	1	0	5	0
Total	**7**	**2**	**1**	**6**	**13**	**14**	**2**	**14**	**2**

Table 10 Food of young puffins on the Isle of May, 31 May to 10 July 1999

	Sample size	**Mean**	**se**
a) Load weight (g)	213	7.99	0.25
b) Fish/load	213	10.37	0.44
c) Numbers and lengths of fish (mm)			
Sandeels *Ammodytes* sp.	1473	57.6	0.31
Clupeidae	382	62.6	0.52
Cod *Gadus morhua*	54	50.2	1.18
Whiting *Merlangius merlangus*	6	47.5	1.69
Rockling	11	32.3	1.39
Saithe *Pollarchius virens*	21	51.8	3.18
Gadidae	13	48.5	2.29
Squid *Alloteuthis sp.*	3	61.3	13.60

Note:

Almost all of the Clupeidae category were small sprat.

Table 11 Percentage of kittiwake broods of one and two chicks which had no adults present during daily checks in the middle of the day

Year	One young	Two young
1986	1	7
1988	31	66
1989	13	32
1990	21	45
1991	2	13
1992	13	28
1993	12	31
1994	1	19
1995	3	14
1996	7	27
1997	14	42
1998	23	63
1999	5	25

Notes:

Figures are based on 50-200 broods in the same areas each year and are the means of daily checks made between the dates the first neglected chick was noted and the start of fledging in the areas. (Details of methods are given in Wanless & Harris, *Scottish Birds* 15 (1989):156-161).

In 1999 checks were made between 1 and 22 July.

Table 12 Percentage of sandeels (by weight) in the diet of young seabirds on the Isle of May, 1987-99

	1987	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
Shag	100	98	100	95	100	97	99	86	85	99	100	98	<50
Kittiwake	95	94	95	86	50	61	63	81	86	81	94	81	84
Guillemot	81	41	74	24	74	53	17	19	78	44	79	21	22
Puffin	77	85	89	96	87	86	46	57	50	88	86	86	52

Notes:

Dates and sample sizes can be found in the contract reports for the respective years.
Sandeels also made up the bulk of the food of young razorbills in most years, but it is extremely difficult to assess proportions in terms of biomass.

Table 13 Kittiwake first-egg dates and clutch-sizes on the Isle of May, 1986-99

Year	**First date egg seen**	**Mean clutch-size (eggs)**
1986	9 May	no data
1987	4 May	no data
1988	6 May	no data
1989	27 April	2.04
1990	2 May	1.82
1991	6 May	1.86
1992	30 April	1.83
1993	4 May	1.78
1994	17 May	0.86
1995	16 May	1.61
1996	24 May	1.13
1997	10 May	2.03
1998	13 May	1.46
1999	16 May	1.99

Note:

1999 data collected by E. Humphreys.

Appendices

Appendix 1 Adult survival rates of shag, guillemot, razorbill, puffin and kittiwake on the Isle of May 1986-96. M.P. Harris, S. Wanless & P. Rothery.

A1.1 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 population 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 (eg 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 Procellariformes) compared to those with lower adult survival rates and higher reproductive rates (eg gulls and shags). Therefore, from a conservation perspective, adult survival rate is clearly a key parameter to measure and this fact was recognised by the UK Joint Nature Conservation Committee (JNCC) which has a statutory responsibility to advise on certain aspects of the marine environment. Thus one of the aims of their Seabird Monitoring Programme, which started 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 which have been ringed as chicks with conventional metal rings and subsequently been retrapped and/or recovered (eg 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 checked visually. Thus the number of sites in the UK where survival data are collected is much lower then the total where reproductive output is monitored. Moreover, in general, obtaining adult survival rates requires a considerable commitment both within and between seasons and consequently survival monitoring has largely been restricted to the main (key) JNCC sites. This section presents a detailed analysis of adult survival rates of shag, common guillemot, razorbill, and puffin at one of these sites, the Isle of May, between 1986 and 1996.

A1.2 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 1,600 pairs of shags, 11,500 pairs of guillemots, 1,900 pairs of razorbills, 21,000 pairs of puffins and 6,900 pairs of kittiwakes (personal counts). 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 individuals marked at the end of each summer. This target was exceeded in all cases except the razorbill. From 1987 onwards thorough and widespread searches for these marked individuals were carried out both where we had ringed them and elsewhere on the island.

Annual survival and resighting probabilities were estimated using 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 (Aebischer 1995, Fairweather & Coulson 1995, Harris *et al.* 1996, Lloyd & Perrins 1977). 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 a separate pattern of annual variation in survival and resighting for males and females. 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.

Tests for trends in annual survival used a random effects model (Burnham 1999), with a linear trend on a logistic scale plus a random year effect, i.e. $\log [S_t /(1 – S_t)] = a + bt + \varepsilon_t$, 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 1999).

Survival between two years is referred to by the former year, i.e. 1995 refers to survival between the 1995 and 1996 breeding seasons. The number of birds ringed in the study were as follows: shag (246 males, 238 females, 3 unsexed), guillemot (302, 269, 28), razorbill (56, 44, 20), puffin (129, 118, 127) and kittiwake (122, 126, 111).

A1.3 Results

A1.3.1 Survival

Annual estimates of survival are given in Table A1.1. Guillemot survival appeared fairly stable (92% - 99%). Shag survival was extremely low in 1993 (15% compared with an average of 89% for the other 10 years) whereas puffin survival was poor in 1990. Razorbill survival was relatively low in 1995 (73% compared with a long-term average of 91%).

In contrast with the other species, survival in the kittiwake declined significantly during the period from 99% in 1986 to 83% in 1996 (Burnham’s (1999) 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 none of the other pairwise correlations between species approached statistical significance.

In all species, the survival calculated for any given year was significantly correlated with the return rate, i.e. number of birds actually seen in the second year / number of birds actually seen in the first year (all $r > 0.78$, $P < 0.005$). 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.

A1.3.2 Resighting probability

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 except for guillemot, but differences between sexes were not statistically significant for any species.

Table A1.1 Survival of adult seabirds on the Isle of May 1986-96

Year	Shag	Guillemot	Razorbill	Puffin	Kittiwake
1986	92.9	99.4	96.8	91.8	98.9
1987	87.2	92.7	90.4	92.8	91.8
1988	89.5	96.5	94.9	93.2	95.4
1989	88.7	96.7	82.6	85.3	86.3
1990	88.0	92.1	89.5	79.0	90.5
1991	82.5	95.7	96.0	96.0	85.6
1992	79.0	97.1	94.2	93.2	86.5
1993	14.9	94.8	93.8	96.4	86.8
1994	92.8	95.4	92.1	93.5	84.2
1995	95.7	91.6	73.0	93.2	80.7
1996	91.8	95.0	92.4	93.2	83.0
Mean	**82.1**	**95.2**	**90.5**	**91.6**	**88.2**

A1.4 Discussion

A1.4.1 Interspecific and temporal effects

Comparisons of survival rates of the various seabird species monitored on the Isle of May with those recorded elsewhere in Europe, indicated broadly similar overall values (Table A1.2). 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 and consequently 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 when they are closely related and/or apparently have similar life history or feeding strategies.

Comparison of these colony-based adult survival estimates with records of birds washed up on beaches show 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 1997a). 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. 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, to judge from our survival estimates and the fact that ten guillemots ringed on the Isle of May and old enough to breed were reported dead, some adults were probably involved because the figures for 1995 were the lowest recorded during the study. The magnitude of the reduction in survival shown by guillemots (91.6% compared to the 11-average of 95.2%) was, however, much less than for razorbills (73.0% compared to 90.5%).

In a 34-year study of kittiwakes at North Shields, Aebischer & Coulson (1990) found significantly higher survival in females (81.1%, 95% confidence interval: 80.1% - 83.4%), than in males (78.3%, 95% CI: 76.4% - 80.0%) – a difference of 3.5%. However, this difference is not statistically significant 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.

Table A1.2 Some estimates of long-term adult survival rates of adult shag, guillemot, razorbill, puffin and kittiwake in Europe

Species	Place	Years	Adult Survival	Source
Shag	Isle of May	1986-96	82.1	This study
	Isle of May	1967-92	87.8*	Harris *et a1*. 1994
	Farne Islands	1962-70	82.8	Potts *et al*. 1980
Guillemot	Isle of May	1986-96	95.2	This study
	Isle of May	1982-95	94.8*	Harris *et al*. (in press)
	Canna	1983-95	92.4	Harris *et al*. (in press)
	Colonsay	1984-95	96.7	Harris *et al*. (in press)
	Skomer	1972-93	93.4	Poole *et al*. (1995)
	Hornøya, Norway	1989-96	95.8	Erikstad *et al*. (1998)
Razorbill	Isle of May	1986-96	90.5	This study
	Skomer, Wales	1972-93	90.7	Poole *et al*. (1996)
Puffin	Isle of May	1986-96	91.6	This study
	Isle of May	1973-92	93.6*	Harris *et al*. (1997)
	Skomer	1972-93	91.3	Poole *et al*. (1996)
	Røst, Norway	1990-96	92.7	Erikstad *et al*. (1998)
	Hornøya, Norway	1991-96	86.0	Erikstad *et al*. (1998)
Kittiwake	Isle of May	1986-96	88.2	This study
	North Shields	1954-84	80.1	Aebischer & Coulson (1990)
	North Shields	1987-92	79.0	Fairweather & Coulson (1995)
	Skomer	1978-94	88.4	Poole *et al*. (1996)
	Brittany, France	1980-85	80.8	Danchin & Monnat (1992)
	Hornøya, Norway	1990-95	80.3	Erikstad *et al*. (1998)

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

While results for razorbill, puffin, guillemot and shag indicate that survival rates were generally high and that poor survival years only occurred about once every ten years, a radically different pattern was shown by kittiwake where survival 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 1997b, 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. 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. It is striking that these three seasons followed winters in which one of the other seabird species has been involved in a wreck. If the non-breeding years occurred at random during the 1990-96 period, the probability that each followed a wreck year is 0.029. This suggests that non-breeding may be linked to adverse conditions occurring much earlier in the year but does not provide conclusive proof since it does not allow for the post hoc selection of the coincidence.

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 rapid means of identifying any serious problems.

A1.5 Conclusions

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 only predicted to occur 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 associated with adverse conditions during the winter, and of a sustained decline in survival in kittiwakes. 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 southeast Scotland where there is a large inshore fishery, establishing the cause of the decrease should be high on the conservation agenda.

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Appendix 2 Survival of adult common guillemots at three Scottish colonies. M.P. Harris, S.Wanless, P. Rothery, R.L. Swann & D. Jardine

A2.1 Introduction

The collection of demographic data on birth and death rates is of key importance to the understanding of life history characteristics and population trends. In general, collection of the former is logistically more straightforward than the latter and thus studies which examine geographic variation in the reproductive success of a species are commoner than those which compare survival rates in different areas. The disparity is particularly evident in species such as cliff-nesting seabirds where estimating breeding success is relatively simple but catching and marking large samples of adults and/or chicks in order to estimate survival is much more difficult. Furthermore, although recording which birds are present in subsequent years appears to be relatively straightforward, in practice it is often difficult to locate and identify individuals. Recent developments in the analysis of survival data now provide a way of overcoming these sampling difficulties (Lebreton *et al.* 1992, Prévot-Juliard *et al.* 1998).

The common guillemot *Uria aalge* is a widespread and common species in the colder parts of the Atlantic and Pacific Oceans. There are numerous reports of large numbers of birds being found oiled, drowned in fishing nets or washed ashore dead for no obvious reason but few detailed studies of survival rates (Bourne 1976, Underwood & Stowe 1984, Evans & Nettleship 1985, Harris & Wanless 1996, Mead 1974, Birkhead & Hudson 1977, Birkhead & Perrins 1997, Sydeman 1983, Harris & Wanless 1995). Here we present estimates of the survival of breeding adults from three Scottish colonies derived from long-running field studies and comprehensive capture-recapture analysis of ringed individuals. The three colonies considered are all long established and currently hold substantial numbers of breeding guillemots (3,500-15,000 pairs). One colony (the Isle of May) is in the North Sea off the southeast coast of Scotland, the other two (Canna and Colonsay) are in the Sea of the Hebrides and Firth of Lorn, respectively, off the west coast of Scotland. Recent studies and analysis of the retraps and recoveries of guillemots indicate that, although during the first few years of life individuals move widely, once birds have recruited into the breeding population, there is little, if any, overlap in the areas used outside the breeding season between birds from colonies on the east and west coasts of Scotland (Halley & Harris 1993, Baillie *et al.* 1994). Hence breeding birds on the Isle of May are effectively geographically isolated from those breeding on Canna and Colonsay.

There is also an east/west split in the nature of the studies that have been carried out on this species in Scotland. Guillemots on the Isle of May have been the focus of an intensive study since 1982, and previous, though less refined estimates of adult survival have been published (Harris & Wanless 1995). In contrast studies at the two west coast colonies have been less intensive and no survival estimates are available for either colony, or indeed for any other colony in western Scotland. From a conservation point of view this lack of information on survival rates is a cause for concern because large numbers of guillemots, perhaps 25% of the British and Irish population, breed in the region and are currently considered to be potentially at risk from a variety of anthropogenic effects e.g. overfishing, tanker traffic, oil development, introduced predators (Lloyd *et al.* 1991).

The aims of this analysis were, therefore, to determine overall survival estimates for breeding guillemots at each of these colonies, make inter-colony comparisons of the values and investigate any implications of differences in data collection on the estimation of survival probabilities for this species.

A2.2 Methods

A2.2.1 Study areas and data collection

The analysis is confined to birds known to have bred at least once. Most were breeding when ringed; those which had been marked as chicks or immatures are not included in the data set until the year that they were first recorded as breeding (termed for convenience the year of marking). The colonies concerned were:

1) Isle of May, Firth of Forth (56°11'N, 2°34'W). Observations were made on a total of 625 individually colour-ringed individuals throughout each breeding season 1982-97. The initial ringed sample consisted of 101 birds colour-ringed in 1982. In later years the numbers of colour-ringed birds known to be alive in any summer averaged 334 (se = 18). Birds were initially caught by noose or crook, or by mist-netting during the winter. Otherwise birds were not handled but, for consistency with the other studies, we refer to resightings in subsequent years as recaptures.

2) Canna, Inner Hebrides (57°03'N, 6°35'W). Breeding areas were visited once each summer 1983-97 when adults were caught by hand or crook. A total of 3,140 ringed breeding adults were handled, the initial sample in 1983 was 125 birds and the subsequent average was 516 (se = 61).

3) Colonsay, Inner Hebrides (56°05'N, 6°10'W). A single visit was made to catch breeding adults by noose or crook once each summer 1990-97. Caught birds were temporarily marked to prevent recapture that day. A total of 382 breeding adults was handled, the initial sample in 1990 was 27, and the subsequent annual average was 113 (se = 16).

Survival between year *n* and year *n+1* is expressed as that of year *n* e.g. 1984 refers to the survival between the 1984 and 1985 breeding seasons. Where a range of years is given, e.g. 1983-95, this is survival from the summer of 1983 to the summer of 1996.

A2.2.1 Statistical analysis

Analysis was undertaken using the package SURGE (Lebreton *et al.* 1992) to fit different models to the data which allow survival or recapture to vary between years or to remain constant. Tests for annual differences in survival or recapture were carried out by comparing the fit of different models (as measured by the deviance). The goodness-of-fit of a model was measured by the Akaike Information Criterion (AIC) which allows for the number of parameters being estimated (Lebreton *et al.* 1992).

Previous studies have found evidence of apparent low survival of birds the year following initial marking (Prϑvot-Julliard *et al.* 1998). We therefore compared the proportion of birds subsequently recaptured (a) which had been recaptured on at least one previous occasion, and (b) which were captured for the first time (i.e. were newly marked) by using TESTS3.SR in the package RELEASE (Burnham *et al.* 1987) and a chi-square test for a 2x2 table. The individual tests were then combined by summing the chi-square values for each occasion. For the Isle of May, the mean annual proportions of guillemots subsequently recaptured were 0.95 (recaptured before) and 0.96 (newly marked) after marking. None of the individual chi-square values was statistically significant and the overall value was well within the limits expected by chance ($\chi^2_{14} = 8.13$, $P = 0.88$). For Canna, the mean proportions recaptured were 0.64 (recaptured before) and 0.57 (newly marked). The chi-square values were statistically significant in eight of the 12 years ($P < 0.05$), and overall ($\chi^2_{13} = 61.39$, $P < 0.001$). The effect on Colonsay was similar to that on Canna with mean proportions of 0.83 (recaptured before) and 0.58 (newly marked), and statistically significant chi-square values in four of the six years and overall ($\chi^2_{6} = 33.97$, $P < 0.001$). At these two colonies there was, therefore, strong evidence of a consistently higher subsequent recapture rate for those birds with a previous capture history so we fitted models allowing for heterogeneity in the survival and recapture rates with the years divided into two types: (a) the year following marking of an individual and (b) two or more years since marking.

A2.3 Results

A2.3.1 The effect of time since marking on estimates of survival

For guillemots on the Isle of May, no effect of time since marking was detected for either survival or recapture but there was strong evidence for annual differences in survival. Among birds on Canna, there was a significant effect of time since initial marking on both survival and recapture but no differences in annual survival for two or more years since marking. For Colonsay, there was an effect of time since first marking on survival, but not on the recapture probability; no differences in annual survival were detected.

The effect of allowing for time since marking on the estimated annual survival probabilities is shown in Table A2.1. For the Isle of May, the estimated mean survival in the first year after capture was 96.4% (se = 0.8) compared with 94.8% (se = 0.6) after two years or more, with little evidence for a difference. In contrast for Canna and Colonsay, there was a large difference in the survival probabilities between the two periods, which were consistently and markedly lower in the year following marking. For Canna the estimated survival in the first year after marking was 81.6% (se = 2.9) compared with 93.9% (se = 1.2) after two years or more. The corresponding values for Colonsay were 72.7% (se = 2.7) and 97.1% (se = 2.9), respectively.

A2.3.2 Overall survival estimates

There are several ways to calculate an average survival estimate for birds in each of the colonies and to some extent the choice depends on the most appropriate model for the data.

A2.3.2.1 Isle of May

Since no effect of time since first capture was detected we used the model in which survival and recapture were both time-dependent and the arithmetic mean of the estimates for 1982-95 with standard error calculated from year-to-year variation. The mean survival was 94.8% (se = 0.6). The estimated survival using a model which assumed constant survival was 94.7% (se = 0.3). Although the estimates are virtually identical, the standard error for the latter will be too small because it does not incorporate the random year-to-year variation.

The analysis in Table A2.1 ignores the correlation between successive estimates arising from the sampling errors of the capture-recapture analysis and assumes no long term trend. However, correlations were relatively small and no trend was detected (test for linear time trend on logistic scale: $\chi^2_1 = 0.39$, $P = 0.53$).

The variation in the survival estimates is the sum of (a) the actual annual variation in survival (process variation) and (b) sampling variation associated with the capture-recapture method. The process variation was therefore estimated from the observed year-to-year variation in the estimates after subtracting the sum of the sample variances provided by SURGE as 0.00027. The corresponding coefficient of variation in the survival rates was then 0.016/0.948, or 1.7%.

A2.3.2.2 Canna

Adult survival was best estimated for the period two or more years after marking since this avoids the bias arising from heterogeneity. The arithmetic mean for adult survival between 1983 and 1995 was 93.9% (s.e. = 1.2). Since no significant annual differences in survival were detected, an alternative approach was to use a model with constant survival for two or more years after marking, but allowing for heterogeneity in recapture; this gave 92.6% (s.e. = 0.5). The reduction in standard error rests on the assumption of constant survival and was therefore likely to be understated.

A similar analysis, which ignored the problem of heterogeneity gave an arithmetic mean survival of 92.8% (s.e. = 1.3) and constant survival of 91.4% (s.e. = 0.3). Ignoring heterogeneity had relatively little effect on survival estimates.

Table A2.1 Estimates of annual survival probabilities (s.e.) based on a model with an effect of time since first capture on survival and recapture. Standard errors for individual estimates reflect sampling errors of the capture-recapture analysis. Standard error for the overall mean was based on variation between individual estimates. Out-of-range survival estimates are set to 100% .

Year	Isle of May		Canna		Colonsay	
	$x = 1$	$x = 2$	$x = 1$	$x = 2$	$x = 1$	$x = 2$
1982	93.1 (2.5)	-	-	-	-	-
1983	96.9 (2.0)	94.7 (2.3)	96.3 (3.5)	-	-	-
1984	91.0 (3.1)	94.7 (1.8)	100.0 (-)	100.0 (-)	-	-
1985	94.3 (3.7)	92.5 (1.7)	73.9 (4.0)	90.5 (4.1)	-	-
1986	100.0 (-)	99.2 (0.6)	81.4 (4.6)	93.2 (5.1)	-	-
1987	95.0 (2.8)	92.4 (1.5)	91.2 (6.2)	97.0 (4.7)	-	-
1988	93.3 (6.2)	97.0 (1.0)	90.8 (4.0)	91.5 (4.0)	-	-
1989	96.7 (3.2)	96.5 (1.1)	83.9 (3.4)	86.5 (3.7)	-	-
1990	100.0 (-)	91.7 (1.5)	78.9 (3.7)	90.4 (3.2)	76.2 (9.4)	-
1991	97.6 (2.3)	95.2 (1.2)	81.4 (4.2)	98.0 (3.4)	73.0 (7.6)	100.0 (-)
1992	100.0 (-)	97.0 (1.0)	73.6 (4.7)	92.4 (3.7)	79.8 (7.1)	100.0 (-)
1993	94.7 (3.4)	94.8 (1.1)	77.0 (6.0)	93.9 (4.0)	68.2 (6.7)	85.6 (5.7)
1994	97.1 (2.9)	94.6 (1.2)	67.4 (7.6)	93.6 (5.7)	77.3 (8.2)	100.0 (-)
1995	100.0 (-)	91.8 (1.4)	65.4(18.1)	100.0 (-)	61.9 (7.5)	100.0 (-)
Mean	96.4 (0.8)	94.8 (0.6)	81.6 (2.9)	93.9 (1.2)	72.7 (2.7)	97.1 (2.9)

A2.3.2.3 Colonsay

We use the model assuming constant survival for two or more years from marking, but allowing for an effect of year on recapture; this estimated mean survival as 96.4% (s.e. = 2.2). A similar estimate based on a model with constant survival and time-dependent recapture gave 89.8% (s.e. = 1.6). The arithmetic mean is unsuitable because survival for two or more years was estimated at 100% or more. On Colonsay allowing for heterogeneity makes a substantial difference to estimated survival.

A2.3.2.4 Comparison between colonies

None of the pairwise differences in annual survival between the colonies were statistically significant (paired *t*-tests, P = 0.47-0.6, n= 6-14) nor were there any significant correlations between colonies: Isle of May - Canna (r = -0.28; P = 0.38, n = 13), Isle of May - Colonsay (r = -0.04, P = 0.95, n = 6), Canna - Colonsay (r = 0.29, P = 0.64, n = 6).

A2.4 Discussion

In a previous simple analysis based on return rates (the percentage of birds from year *n* known to be alive in year *n+1* without any allowance being made for recapture effort), the minimum overall survival rate for guillemots on the Isle of May between 1982 and 1992 was estimated as 94.9% (s.e. = 0.6) (Harris & Wanless 1995). The survival estimate for the same period obtained using SURGE was only marginally higher than this (95.0%, s.e. = 0.7), a reflection of the very high mean annual recapture rate (0.996) achieved on the Isle of May. In contrast, studies on Canna and Colonsay have been much less intensive as indicated by the markedly lower recapture rates (0.36 and 0.42, respectively) and hence the disparity between simple return rates and survival estimates derived using SURGE would be expected to be much greater.

The analyses presented in this section represent the first estimates of adult survival for the common guillemot in northwest Scotland, an area of high conservation concern for this species. Our results indicate that survival rates of adult guillemots at these colonies (93.9% on Canna, 96.4% on Colonsay) are as high as those on the Isle of May (94.8%) in the North Sea and also on Skomer in the southern Irish sea (93.4%). Thus, within Britain there is currently no evidence of significant geographic differences in common guillemot survival rates. In a wider context the results also indicate that adult survival rates of guillemots at Atlantic colonies are similar to those in the Pacific (93.7% (Sydeman 1983). This contrasts with the situation in the kittiwake *Rissa tridactyla,* another cliff nesting seabird with a widespread distribution, where there is evidence of consistently lower adult survival rates for birds at Atlantic colonies (83% p.a.) than for birds at Pacific colonies (93%) (Hatch *et al.* 1993, *Hatch et al.* 1994, Golet *et al.* 1998). Hatch *et al.* 1994, suggested that the survival rate of adult kittiwakes is determined primarily by conditions in the nonbreeding season and that Pacific kittiwakes from different colonies may have similar high survival rates because they share common wintering areas. Such cannot be the case in the common guillemot.

While we found no evidence of significant inter-colony differences in overall survival rates, we did find differences in survival rates in relation to previous capture history between the colonies. Thus survival probability in the year following initial marking was significantly lower for birds from Canna and Colonsay but no effect was apparent on the Isle of May. Lower survival estimates following initial marking have previously been recorded for common guillemots on Skomer and in several other species of seabird e.g. black-headed gull *Larus ridibundus* and black guillemot *Cepphus grylle* (Prevot-Julliard *et al.* 1998, Birkhead & Perrins 1997, Frederiksen 1998). In guillemots the effect has been attributed to birds moving site following the disturbance associated with catching, particularly if large numbers of adults were involved (Birkhead & Hudson 1977, Hatchwell & Birkhead 1991). This conclusion is consistent with our study where the effect was apparent at the two colonies where data were derived from recaptured adults but no difference was detected on the Isle of May where data come from resightings. It seems fair to assume that the lower survival immediately following marking was not due to a higher mortality but was an artefact caused by some birds being harder to capture.

An important assumption in most capture-recapture models is that all individuals have the same recapture probability (Golet *et al.* 1998). In general, breeding guillemots show a high degree of site fidelity. However, one source of variation in recapture probability has already been mentioned, namely response to moderate levels of disturbance with some birds being intolerant of disturbance. Particularly in studies where birds are recaught rather than resighted, a movement of only a few metres can mean that a bird is no longer available to be retrapped. In a study where recaptures are derived from visual sightings of birds such small scale movements are likely to be less of a problem although larger scale movements may result in birds no longer being in view.

An additional source of error which again is potentially more serious in studies where birds are recaught is the finding that in any year between 5% and 10% of adults with previous breeding experience do not breed, and moreover that this effect is not random but rather that a few individuals are responsible for most of the nonbreeding (Harris & Wanless 1995). These non-breeders are readily observed since they spend a considerable amount of time in the colony but are very unlikely to be retrapped during large scale ringing operations.

Although intensive population studies of birds produce valuable data on a wide range of biological parameters, by their nature they demand long-term commitment in terms of time and money. It is becoming increasingly difficult to gain such continuing support. The studies on Canna and Colonsay are based on single annual visits to colonies, yet with the analytic techniques now available they have produced robust estimates of survival rates. It is unrealistic to expect such one-off sampling to detect any but the most dramatic annual variation in survival rates; the fact that our analysis failed to detect any on Canna and Colonsay does not mean that there were none. We encourage others ringing seabirds on a regular basis to assiduously collect retrap data and subject their results to detailed statistical analysis.

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