Population and breeding dynamics of European Shags *Phalacrocorax aristotelis* at three major colonies in Shetland, 2001–15

Martin Heubeck[1*], R. Mick Mellor[1], Sheila Gear[2] and Will T. S. Miles[3]

**Correspondence author. Email: martinheubeck@btinternet.com*

[1] *SOTEAG, Aberdeen Institute of Coastal Science and Management, University of Aberdeen, Aberdeen AB24 3UE, UK;*

[2] *Foula Heritage, Magdala, Foula, Shetland ZE2 9PN, UK;*

[3] *Fair Isle Bird Observatory Trust, Fair Isle, Shetland ZE2 9JU, UK.*

Abstract

In the 1998–2002 *Seabird 2000* census, Shetland held 19% of the British and Irish breeding population of European Shags *Phalacrocorax aristotelis* (32,300 apparently occupied nests - AON), and the three largest colonies in Shetland (Fair Isle, Sumburgh Head and Foula) together held 44% of the total for the county. Subsequent monitoring at these colonies recorded substantial decreases in population size in 2004–05, 2008 and 2011–13. This paper describes European Shag population and breeding dynamics at these three colonies for the period 2001–15, using annual monitoring data for six demographic parameters. Demographic changes were characterised by major reductions in breeding population size (AON), timing of breeding getting later, and considerable reductions in the percentages of nests that progressed to incubation and to hatching, and in overall breeding success. The 2004 and 2005 breeding seasons were exceptionally poor in Shetland but also at colonies elsewhere in north and east Scotland, apparently reflecting large-scale scarcity of sandeel *Ammodytes* prey. There was no such Scotland-wide (or Shetland-wide) uniformity in these breeding parameters in 2008 or 2011–13, when local food availability within foraging ranges of colonies appeared to be the main driver of European Shag breeding performance in Shetland. At Fair Isle, Sumburgh Head and Foula, breeding was markedly early in 2014 and 2015, and percentage incubation, percentage hatching and overall breeding success were all high. However, population sizes at these colonies remained low in 2014–15, with a combined deficit of c. 2,600 AON in comparison with the *Seabird 2000* census figures. Possible mechanisms driving this situation, for example persistent non-breeding, emigration, or high mortality are evaluated. Given the high colony fidelity of European Shags once established as breeders, it is assumed these 'missing' birds are dead. Support for this assertion comes from the Shetland beached bird survey which indicated high mortality in late winter in 2003, 2011 and 2014, in the latter two years associated with prolonged gales. European Shag has recently been added to the UK Red list because of severe population decline, and continued (indeed enhanced) monitoring and ringing of the species is to be encouraged.

Introduction

European Shags *Phalacrocorax aristotelis* (hereafter 'Shag') breed colonially along rocky coasts of the northeast Atlantic and the Mediterranean Sea. Although they build substantial nests, monitoring changes in breeding numbers and their breeding success is complicated by their asynchronous, lengthy and often variable breeding season, such that even a well-timed single count of nests is likely to record only about 75% of nesting attempts in a given year (Harris & Forbes 1987). In some years a substantial proportion of adults do not breed, which can result in an abrupt drop in nest numbers relative to previous years, and non-breeding can persist for several successive seasons (Aebischer 1986; Aebischer & Wanless 1992; Harris & Wanless 1996; Wanless & Harris 2004). Abrupt drops in counts of nests have also been recorded following oil spills (Heubeck 1997), weather-related winter mortality events (Harris & Wanless 1996; Harris *et al*. 1998; Frederiksen *et al*. 2008), or mortality events during the breeding season (Coulson *et al*. 1968).

The *Seabird 2000* census recorded 32,306 apparently occupied nests (AON) of Shag in Britain and Ireland in 1998–2002, an estimated 40–45% of the world population (Wanless & Harris 2004). The largest concentration was in Shetland, which held 19% (6,147 AON) of the British and Irish total. The three largest colonies in Shetland, at the remote islands of Foula (2,277 AON; then the largest colony in Britain and Ireland, and one of the largest in the world) and Fair Isle (663 AON), and at Sumburgh Head at the southern tip of Mainland Shetland (270 AON), together held 44% of the Shetland total (Figure 1). At all three colonies, however, numbers had declined between the 1985–88 *Seabird Colony Register* and *Seabird 2000* censuses, by 5% at Foula, 40% at Fair Isle, and 44% at Sumburgh Head.

Shag breeding success has been monitored at Fair Isle since 1986, Sumburgh Head since 1988, and Foula since 1997, and by 2000 each colony had averaged relatively high values of 1.42 ± 0.06 SE, 1.20 ± 0.08 SE, and 1.13 ± 0.22 SE chicks fledged per AON, respectively (Mavor *et al*. 2002). There was relatively low success at Fair Isle and Sumburgh Head in 1990, when the local abundance of Lesser Sandeels *Ammodytes marinus* was low (Walsh *et al*. 1991; Wright & Bailey 1993; Monaghan *et al*. 1997), and at Sumburgh Head and Foula in 2000, when nests were washed away by heavy seas in mid June (Mavor *et al*. 2001). Otherwise, Shags in Shetland seemed less susceptible to the food-related breeding failures experienced by species such as Black-legged Kittiwake *Rissa tridactyla* and Arctic Tern *Sterna paradisaea* (Monaghan *et al*. 1989; Harris & Wanless 1990; Monaghan *et al*. 1997; Heubeck *et al*. 1999), and by 2000 no major non-breeding events had been recorded at Fair Isle, Sumburgh Head or Foula.

This situation changed dramatically in 2004, when Shags largely deserted Foula during the breeding season (Mavor *et al*. 2005). In 2008, a similar crash in breeding numbers and a major breeding failure occurred at Fair Isle (Shaw *et al*. 2008). Then, in 2011, extensive non-breeding first became evident at Sumburgh Head (Heubeck & Mellor 2012; JNCC 2014).

Figure 1. Map of Shetland showing locations of the Fair Isle, Sumburgh Head and Foula colonies, and other standard coastal sections where counts of European Shag *Phalacrocorax aristotelis* nests were made in 2001–15 (see Appendix 2, where counts at South Havra and St Ninian's Isle (Section 5) are pooled).

Accordingly, this paper documents Shag population and breeding dynamics at these three Shetland colonies in 2001–15 using annual monitoring data for six demographic parameters, namely breeding population size (counts of AON), breeding phenology (median date chicks were first recorded at nests), the percentage of nest-building pairs that laid (percentage incubation, used as a measure of non-breeding), the percentage of incubating nests at which young were recorded (percentage hatched), the percentage of nests at which young were recorded from which at least one chick fledged (percentage fledged), and breeding success (chicks fledged per incubating nests). We quantify, test and compare temporal patterns of change in these parameters between and within the three colonies, make comparisons with Shag population changes recorded elsewhere in Shetland, and examine beached bird survey data from Shetland for evidence of abnormal mortality during this period.

Methods

Study colonies: Fair Isle is 5 km long and 2 km wide and has a highly indented coastline, mainly of cliffs that rise to 180 m in the north and west of the island. It is one of the four 'UK Key Monitoring Sites' in the JNCC Seabird Monitoring Programme and annual monitoring is conducted by Fair Isle Bird Observatory staff and volunteers. Sumburgh Head is characterised by 20–90 m high cliffs, Shag nests are mostly visible from vantage points on the cliffs, and annual monitoring is carried out by full-time University of Aberdeen staff. Foula is 5.5 km long and 4 km wide, has low cliffs along the east coast (up to 50 m) but much higher cliffs along the west side (to 380 m), and until at least 2000 c. 90% or more of the island's Shags nested along the base of these high cliffs in boulder fields that are difficult to access (Furness 1981; Heubeck *et al*. 2014). Seabird monitoring on Foula is conducted annually by SG (island resident), while Scottish Natural Heritage staff have conducted whole-island counts. Overall, the three colonies differ in topography, ease of access to and/or visibility of Shag nesting sites, and in manpower available for monitoring (Table 1), and it is acknowledged that these factors influenced data collection and quality.

Population size monitoring: Logistical constraints meant that complete census counts (combining observations from land and sea) were not carried out annually at each site. During 2001–15 four such counts were made at Fair Isle, one at Sumburgh Head, and two at Foula (neither of which included a search of the main boulder fields). For analyses we therefore used counts of AON that provided the largest consistent annual sample size for each colony: at Fair Isle, a single count at five population monitoring plots distributed around the island; at Sumburgh Head, a single count from land of all nests visible from the cliff-top, which in 2007 recorded 88% of the total colony; at Foula, the number of AON recorded in breeding success plots on the check closest to 10 June (Table 1).

Breeding success plots: For the other five parameters we used data from breeding success plots, which were monitored using marked photographs and standard methodology (Walsh *et al*. 1995). At Fair Isle, five plots were contiguous along a

section of 20 m high cliff on the east side of the island, sheltered from swell from all directions except E (Table 1). At Sumburgh Head, plots were spread around the headland and included nest sites exposed to swell from NE through S to W. At Foula, plots were located in cliff and boulder habitat in the southeast of the island, some of which were exposed to swell from NE through E to S. At each colony, observers recorded the status of individually numbered nest sites as 'trace', 'well built but empty', or 'apparently incubating/brooding' (the latter two categories equate to AON), brood sizes when seen clearly, and the approximate size of chicks as they developed. The timing and frequency of checks varied between the colonies and years, largely due to manpower constraints (Table 1).

Breeding phenology: The date that incubation was first seen and the date that a chick was first seen were recorded for nests in each year at each colony. In most years some birds were recorded as incubating on the first check at each colony. Because checks began earlier at Sumburgh Head, at this colony (but not the others) we could calculate the annual median date that incubating nests were first recorded as such. This correlated significantly with the median date that chicks

Table 1. Details of European Shag *Phalacrocorax aristotelis* monitoring at the study colonies, 2001–15.

	Fair Isle	**Sumburgh Head**	**Foula**
Whole colony counts	AON: from land & sea in 2001 (663), 2003 (732), 2008 (235), 2013 (204).	AON: from land and sea in 2007 (250); annually from land in early to mid June.	AON: incomplete censuses from land & sea in 2007 (248) & 2015 (48).
Population monitoring plots & % of colony	AON: single annual count in 5 plots; 22% in 2001, 16% in 2003, 23% in 2008, 10% in 2013.	—	—
Breeding success plots & % of colony	5 plots; 8% in 2001 & 2003, 14% in 2008, 5% in 2013.	13 plots in 2001–07, 16 in 2008–15; 53% in 2007.	8 plots 2001–07, 9 in 2008–11, 10 in 2012–15; in 2001, 3% of 2000 count.
Mean date of first check	30 April ± 1.3 SE days	8 April ± 0.6 SE days	1 May ± 3.3 SE days
Mean check frequency	6.7 ± 0.23 SE days	5.1 ± 0.10 SE days	13.7 ± 0.81 SE days

Table 2. Correlation coefficients between colonies for five European Shag *Phalacrocorax aristotelis* breeding parameters. Significant ($P < 0.05$) relationships are in bold.

	Fair Isle vs Sumburgh Head	**Fair Isle vs Foula**	**Sumburgh Head vs Foula**
Number of AON	**r = 0.637, P = 0.011**	**r = 0.660, P = 0.007**	**r = 0.763, P = 0.001**
% incubation	r = 0.081, P = 0.774	r = 0.055, P = 0.846	**r = 0.843, P < 0.001**
Median hatching date	r = 0.442, P = 0.099	r = 0.257, P = 0.355	**r = 0.803, P < 0.001**
% hatched	r = 0.252, P = 0.356	r = 0.223, P = 0.425	r = 0.465, P = 0.081
% fledged	r = 0.163, P = 0.563	r = 0.467, P = 0.079	r = 0.008, P = 0.978
Breeding success	r = 0.397, P = 0.143	r = 0.419, P = 0.121	r = 0.375, P = 0.168

were first recorded at nests at Sumburgh Head ($r = 0.934$, $df = 13$, $P < 0.001$), so we used the latter metric (median hatching date) to compare timing of breeding between the three colonies. However, we acknowledge potential cross-colony sources of bias in this method: differences in the frequency of checks at the three colonies, the exclusion of nests that failed during incubation or around hatching (newly hatched chicks are difficult to confirm), and low sample sizes in some years.

Percentage incubation, percentage hatched, percentage fledged and breeding success: The percentage of all sites with nest material at which incubation was recorded was the only consistent metric available as a measure of non-breeding. Clutch size was rarely determined and so the percentage of incubating nests at which chicks were recorded (percentage hatched) was used as a proxy for hatching success. Similarly, brood sizes were usually only determined accurately once chicks were well grown, so we used the percentage of hatched nests at which one or more chicks fledged as a proxy for fledging success. Breeding success was expressed as chicks fledged per nest at which apparent incubation was recorded on one or more checks (Walsh *et al*. 1995). Details are given in Appendix 1. In some cases, our analyses of raw data revealed errors in previous calculations, and some values differ from those reported or published previously.

Population size monitoring away from the three focal colonies: Standard stretches of cliff coastline, chosen because they held substantial numbers of breeding Shags in the 1985–88 census, were surveyed opportunistically during June by inflatable boat, which allowed access to caves and narrow cliff indentations (Figure 1, Appendix 2). We distinguished between trace, empty and active nests (Walsh *et al*. 1995), although this is less easy to determine accurately from the sea than from land. One large colony (No Ness) was counted annually from land.

Beached bird surveys: Data were collected using established, standard methods (Heubeck 2006). Surveys were conducted monthly on 28 km of beaches of the outer coastline of Shetland facing the North Sea and the Atlantic Ocean, and on 21 km of more sheltered inner coastline.

Statistical tests: Simple correlations between parameters and colonies were carried out using standard methods and all analyses were performed using R version 2.15.0.

Results

Population size and percentage incubation: Numbers of AON changed across years in a broadly similar pattern, with significant positive correlations between the three colonies (Figure 2, Table 2), although some differences were apparent from 2008 on. At Fair Isle and Sumburgh Head, AON counts decreased between 2001–05, but then in 2006–07 rose back to levels just slightly lower than in 2001; this decrease was accompanied by a clear reduction in percentage incubation at Sumburgh Head, but not at Fair Isle. A large reduction in AON at Foula between 2002 and 2005 was accompanied by a marked dip in percentage incubation, but by 2006–07 numbers of AON were half those in 2001.

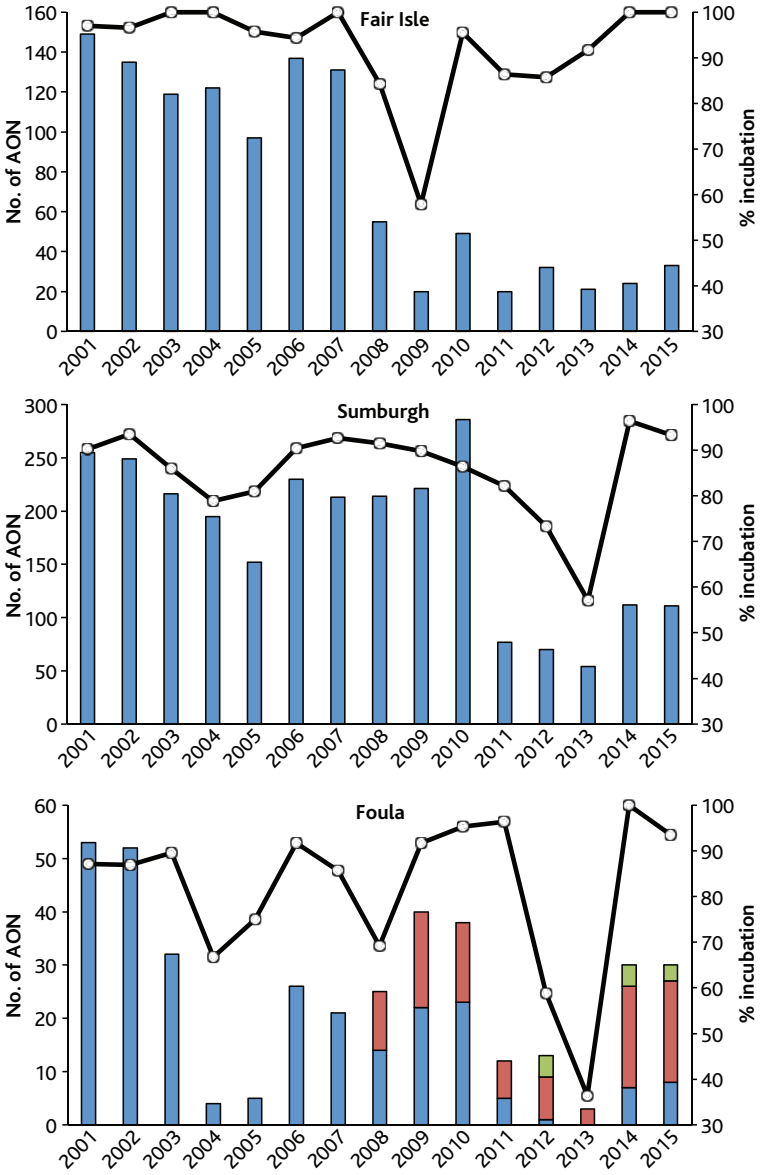

Figure 2. Counts of European Shag *Phalacrocorax aristotelis* AON as filled bars at Fair Isle (population monitoring plots), Sumburgh Head (whole colony counts from land), and Foula (breeding success plots on the check closest to 10 June; additional plots were added in 2008 (red) and 2012 (green)). The percentage of nests that progressed to incubation (% incubation) in breeding parameter plots is shown as open circles with solid line with values denoted on the right-hand y-axis.

A large decrease in AON at Fair Isle in 2008–09 was accompanied by the only marked dip in percentage incubation at this colony; however, percentage incubation returned to 96% in 2010, when the number of AON was 63% lower than in 2007, and to 100% in 2014 and in 2015, when the number of AON was 78% lower than in 2001. The most recent whole-island count, of 204 AON in 2013, was 72% lower than in 2013 and 69% lower than in 2001 (Table 1). Numbers of AON at Sumburgh Head remained stable in 2006–09, increased by 29% in 2010, but crashed in 2011–13 as the percentage incubation declined progressively. By 2014–15, percentage incubation had returned to 93–96%, but numbers of AON were 56% lower than in 2001. At Foula, numbers of AON in the original eight breeding success plots remained

rather stable in 2006–10 (but with a dip in 2008, when the percentage incubation also fell), but also crashed in 2011–13, with none recorded on 16 June 2013. By 2014–15, the percentage incubation had returned to > 90%, but there were only 8 AON in these original plots on 14 June 2015, 85% fewer than in 2001. Numbers of AON and percentage incubation correlated significantly at Sumburgh Head, but not at Fair Isle or Foula (Table 3), which is unsurprising given the greater variation in the former at those colonies in years when the latter was 90–100%.

The greatest uncertainty over current (2014–15) breeding numbers is at Foula, where access to key boulder fields on the west coast was prevented by rocks being too wet for safety in 2007, and by rockfalls in 2015 (Table 4). The most recent search of these from land was in June 2005, when 18 AON were found in an area of the Wick of Mucklebruik (one observer; N. Ratcliffe pers. comm.) that held 604 AON in June 2000 (three observers; Harvey *et al*. 2000). Furthermore, these boulder fields have since been inspected at least annually from the sea and very few Shags have been seen; only 37 birds were counted along the entire west coast of the island on 19 May 2014 (SG pers. obs.), and virtually none were visible in an extensive set of photographs of these boulder fields taken on 21 June 2014 (Heubeck *et al*. 2014).

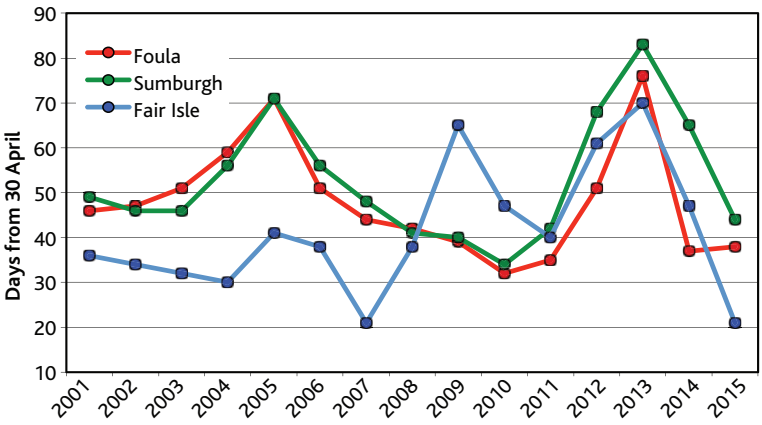

Figure 3a. The median dates (1 May = 1) on which European Shag *Phalacrocorax aristotelis* chicks were first recorded at nests in study plots at Fair Isle, Sumburgh Head and Foula. Sample sizes ≤ 5 nests with chicks: Fair Isle 2008 (3), 2009 (5) & 2013 (4); Foula 2004 (2), 2005 (1), 2012 (5) & 2013 (2).

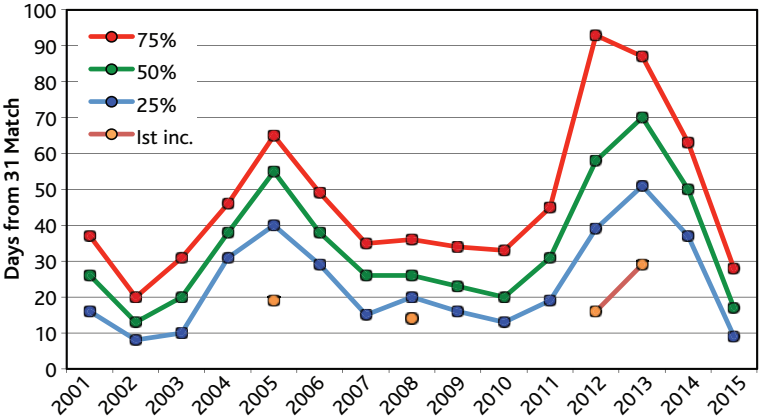

Figure 3b. The dates (1 April = 1) by which 25%, 50% and 75% of apparently incubating European Shag nests were first recorded in study plots at Sumburgh Head. If none were incubating on the first visit, the date of first recorded incubation is shown.

Breeding phenology: Median hatching date varied by 49 days at Fair Isle and Sumburgh Head, and 44 days at Foula (Figure 3a). Despite differences in sample sizes and frequency of checks, there was a highly significant correlation between these dates at Sumburgh Head and Foula, but not between either of these colonies and Fair Isle (Table 2), where median hatching dates were 10–30 days earlier during 2001–07 (Figure 3a). Number of AON at Fair Isle and Sumburgh Head and percentage incubation at all three colonies were higher on average in years when breeding was early (i.e. there was a negative correlation with median hatching date; Table 3). At Sumburgh Head, the interval between 25% and 75% of active nests having first been recorded as incubating ranged from 12 days in 2002 to 54 days in 2012, and was significantly correlated with median first incubation date (r = 0.728, P = 0.002) and median hatching date (r = 0.622, P = 0.013), i.e. laying was less synchronous in years of later laying.

Percentage hatched, percentage fledged and breeding success: There was no significant correlation between colonies in percentage hatched, percentage fledged or breeding success (Table 2), although year-to-year changes in breeding success were rather similar in 2001–07 (Figure 4c). However, differences in timing of breeding may have obscured similar pressures operating at the same time of year at different colonies, but at different stages of the breeding cycle. Breeding success was the same at Fair Isle and Sumburgh Head in 2004, but at Fair Isle median chick date was 26 days earlier (Figure 3a), percentage hatched was markedly higher but percentage

Table 3. Correlation coefficients between five European Shag *Phalacrocorax aristotelis* breeding parameters at Fair Isle (FI), Sumburgh Head (SH), and Foula (FO). Significant (P < 0.05) relationships are in bold.

		% incubation	Median hatching date	% hatched	% fledged	Breeding success
Number of AON	FI	r = 0.486, P = 0.066	**r = -0.598, P = 0.019**	r = 0.487, P = 0.066	r = -0.206, P = 0.461	**r = 0.518, P = 0.048**
	SH	**r = 0.556, P = 0.031**	**r = -0.627, P = 0.012**	**r = 0.781, P = 0.001**	r = -0.059, P = 0.835	**r = 0.721, P = 0.002**
	FO	r = 0.415, P = 0.124	r = -0.251, P = 0.366	r = 0.364, P = 0.183	r = -0.195, P = 0.487	r = 0.262, P = 0.309
% incubation	FI		**r = -0.624, P = 0.013**	**r = 0.532, P = 0.041**	r = -0.349, P = 0.202	**r = 0.586, P = 0.022**
	SH		**r = -0.663, P = 0.007**	**r = 0.856, P < 0.001**	r = -0.295, P = 0.286	**r = 0.835, P < 0.001**
	FO		**r = -0.773, P = 0.001**	**r = 0.560, P = 0.030**	r = -0.102, P = 0.718	r = 0.507, P < 0.054
Median hatching date	FI			r = -0.408, P = 0.131	r = -0.139, P = 0.622	r = -0.408, P = 0.131
	SH			**r = -0.632, P = 0.012**	r = -0.172, P = 0.539	**r = -0.619, P = 0.014**
	FO			**r = -0.665, P = 0.007**	r = -0.351, P = 0.199	**r = -0.558, P = 0.031**
% hatched	FI				r = -0.393, P = 0.147	**r = 0.753, P = 0.001**
	SH				r = -0.396, P = 0.144	**r = 0.960, P < 0.001**
	FO				**r = -0.732, P = 0.002**	**r = 0.916, P < 0.001**
% fledged	FI					**r = 0.749, P = 0.001**
	SH					**r = 0.530, P < 0.042**
	FO					**r = 0.780, P < 0.001**

Table 4. Census counts of European Shags *Phalacrocorax aristotelis* (AON) on Foula by recording section, 1976–2015. Sources: 1976 (Furness 1981), 1987 (Furness 1987), 2000 (Harvey *et al*. 2000), 2007 & 2015 (SNH unpublished data).

Section (main nesting habitat used or available)	1976	1987	2000	2007	2015
1. N. Hiora Wick/Strem Ness cliffs (cliff)	28	21	42	4	6
2. NE. Ruscar (low rocks)	0	0	0	0	0
3. E. Da Gaads (boulders & cliff)	72	96	27	3	4
4. E. Ham (low rocks)	0	0	0	0	0
5. SE. Heddlicliff (boulders & cliff)	554	189	213	84	13
6. S. South Ness (boulders & cliff)	161	53	96	41	7
7. SW. Noup & Mucklebruik (boulders)	1,930	1,850	1,720	102*	14**
8. W. Da Scrodhurdins (boulders)	430	120	106	2*	4**
9. NW. North Banks (boulders)	50	12	0	0	0
10. N. East Hoevdi (cliff)	0	0	0	12	0
11. N. Da Logat (cliff)	132	67	73	10	0
Total	3,357	2,408	2,277	258*	48**

* The 2007 figures exclude boulder fields and grassy slopes which were searched for nests in 1976, 1987 and 2000 (865 AON counted in 2000) but could not be accessed, two inaccessible areas where 100 AON were estimated in 2000, and two other inaccessible boulder fields where 156 AON were estimated in 2000 by multiplying counts of adults x4.

** Coverage in 2015 was very similar to that in 2007.

fledged was markedly lower (Figure 4). At least 136 chicks were recorded in 48 monitored nests at Fair Isle and large numbers were ringed elsewhere on the island, but most died when well-grown and only 37 survived to fledging; by mid July "many colonies were littered with dead and dying chicks" and post-mortem examination of seven collected on 13 July confirmed starvation as the primary cause of death (Shaw 2005). At Sumburgh Head, most breeding failures in 2004 occurred in late June and early July, but mainly at late incubation, or possibly early chick stage but before chicks were large enough to be seen and the nest recorded as having hatched. There were marked differences in 2008 in all three parameters at Sumburgh Head and the other two colonies, after which the sample size monitored at Fair Isle was much reduced (Appendix 1). Percentage fledged was relatively high at all three colonies in 2013 among the few pairs that hatched young, presumably involving either the highest quality adults and/or using high quality nest sites. Percentage hatched and breeding success then increased markedly in 2014 and 2015 at all three colonies, although chick survival at Foula in 2015 was affected by rain and heavy swell (Figure 4).

Percentage hatched correlated positively with numbers of AON at Sumburgh Head (the largest sample sizes throughout), decreased as median hatching date became later at Sumburgh Head and Foula, and correlated positively with percentage incubation and breeding success at all three colonies (Table 3). Unsurprisingly, percentage fledged correlated positively with breeding success at all three colonies, but of the other parameters, the only significant correlation was (positive) with percentage hatched at Foula.

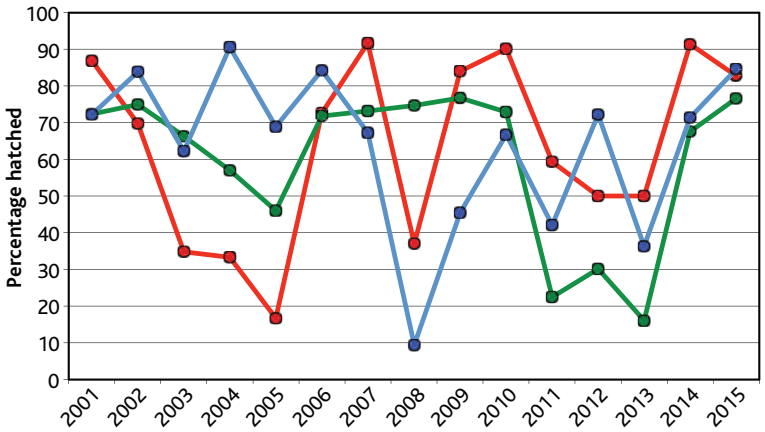

Figure 4a. The percentage of European Shag *Phalacrocorax aristotelis* nests at which incubation was recorded and chicks were known to have hatched (percentage hatched) at Fair Isle (blue), Sumburgh Head (green) and Foula (red). Sample sizes ≤ 5 incubating nests: Foula 2013 (4).

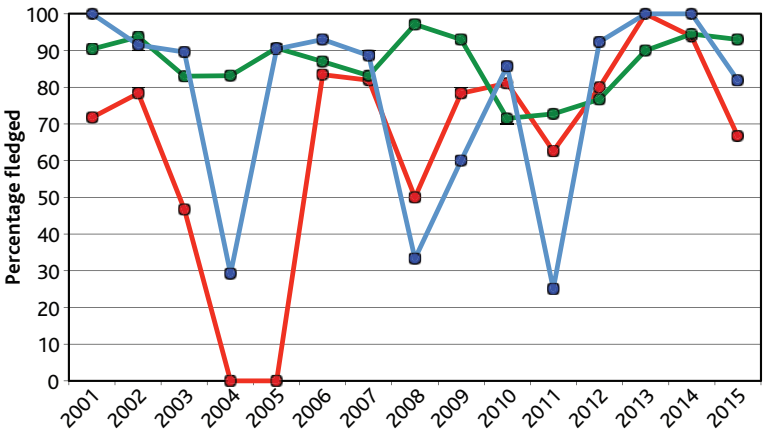

Figure 4b. The percentage of European Shag nests at which chicks were known to have hatched and at least one chick subsequently fledged (percentage fledged) at Fair Isle (blue), Sumburgh Head (green) and Foula (red). Sample sizes ≤ 5 nests with chicks hatched: Fair Isle 2008 (3), 2009 (5) & 2013 (4); Foula 2004 (2), 2005 (1), 2012 (5) & 2013 (2).

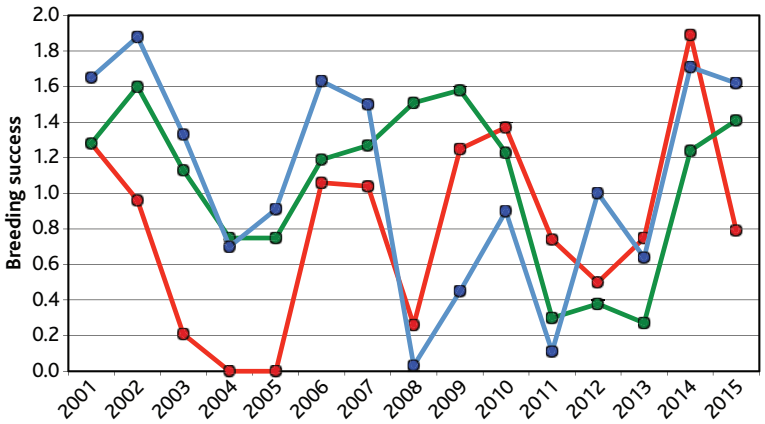

Figure 4c. European Shag breeding success (chicks fledged per laying pair) at Fair Isle (blue), Sumburgh Head (green) and Foula (red). Sample sizes ≤ 5 incubating nests: Foula 2013 (4). Nests with young were washed away by heavy seas at Sumburgh Head in 2006 and 2010, and at Foula in at least 2015.

Population size estimates away from the three focal colonies: At west coast colonies counted in 2004 (Figure 1; Appendix 2: Areas 1 & 3), the number of nests (including trace nests) was 22% lower than in 2001/02, a similar decrease to that at Sumburgh Head (2002–04 decrease = 25%), and while the percentage active

(apparently incubating/brooding or chicks seen) was slightly low, non-breeding was clearly not occurring on the scale at Foula that year. Nor was there evidence in 2006 of any large increase in the number of nests that might have occurred had adults from Foula settled to breed at the nearest colonies around Mainland Shetland. In contrast to Sumburgh Head and Foula, the number of nests in 2012 (Areas 3–5: 553) were similar to those along the same coasts in 2009 (557), although the percentage active was slightly lower in 2012 and it was a late season with chicks seen in only six of 465 active nests. The few nests counts made in 2014 (Areas 4–5) were 11% lower than in 2009 (48% lower at Sumburgh Head), although the number of nests at Papa Stour (Area 2) was 27% lower than in 2006.

In contrast to west coasts, changes in southeast Mainland in 2007–15 (Figure 1; Appendix 2: Areas 6–8) closely mirrored those at Sumburgh Head (Figure 2). The number of nests at No Ness (Area 7) increased by 36% between 2007 (150) and 2010 (204), the same percentage as at Sumburgh Head, but then crashed in 2011–12 (91–54). Between Virkie and Mousa (Areas 6–8), the number of nests in 2013 (136) was 72% lower than in 2010 (484) with a low percentage active; by 2015, the percentage active had returned to > 90% but the number of nests (262) remained 46% lower than in 2010.

The situation further north on the east coast of Shetland was less similar, although data are limited. Counts of AON at Noss (Area 9) were relatively low in 2011–14 (63–76) but by 2015 (99) were similar to those in 2009–10 (97–102). At southeast Yell (Area 10), the number of nests in 2013 (137) was 22% lower than in 2009 although a high percentage were active. Breeding success was monitored at southeast Yell in 2012–15 at a similar effort to that at Sumburgh Head. The number of nests in plots ranged from 33–44, percentage incubation remained high (82–95%), median date of first recorded incubation was earlier than at Sumburgh each year, by 13, 45, 11 and 8 days, respectively, percentage hatched ranged from 53% (2012) to 82% (2014), and breeding success was 0.72, 0.92, 1.56 and 0.80, respectively.

Beached bird surveys: There were two obvious peaks and one lesser one in the seasonal occurrence of Shags on beaches, all in January–April: 2003 (60 adults, 35 immatures, 11 not aged); 2011 (50 adults, 52 immatures, 6 not aged); 2014 (41 adults, 16 immatures, 4 not aged). In these years the number of birds found was, respectively, 4.9, 5.1 and 2.8 times higher than the average for the 12 other late winter periods (Figure 5). The 2003 mortality persisted through February–April, was not obviously associated with prolonged stormy weather, and large numbers of Common Guillemots *Uria aalge* (552) and Razorbills *Alca torda* (189) were also found dead, mainly adults (Heubeck 2004). Shag mortality in 2011 mainly occurred in March and followed persistent south-easterly gales in the second half of February (Heubeck & Mellor 2012), while that in 2014 mainly occurred in February, after persistent gales that month. Following such prolonged gales, beached bird surveys may underestimate seabird mortality relative to calmer periods, due to the vast quantities of beached kelp concealing some carcasses and preventing others from washing ashore, and to

scavenging larids and corvids being more attracted to the greater number of dead birds on the shore and floating in the sea. There was no significant ($P < 0.05$) correlation between the annual number of Shag corpses per km in January–April and any of the six breeding parameters at any of the three colonies. During 2001–15 only three out of 1,029 (0.3%) Shags found dead were recorded as oiled.

Discussion

The 2004 breeding season for seabirds in Britain and Ireland was described as the (then) least productive on record for a range of species, particularly at colonies on the east coast of Scotland and in the Northern Isles (Mavor *et al*. 2005). On the Isle of May, southeast Scotland, where the most detailed studies of breeding Shags have been made in the UK, the return rate of Shags was near normal but many did not breed, the nest count dropped by 29%, the proportion of sandeels fed to chicks was low, and breeding success on the island and at nearby St Abb's Head averaged 0.29 chicks fledged per nest; the situation on the Farne Islands, northeast England, was similar with a 16% drop in numbers of AON and success of 0.27 (Harris *et al*. 2004; Rideout 2004; Walton *et al*. 2004). Not only were sandeels apparently scarce over a wide area of the north-western North Sea in 2004, but in the Firth of Forth (at least) their energy content was low (Wanless *et al*. 2005). The desertion of Foula by Shags in 2004 following low hatching and breeding success there in 2003, and the mass starvation of well-grown chicks at Fair Isle, were therefore seen at the time as at the extreme end of a spectrum of response to a widespread problem over the abundance and possibly the nutritional quality of sandeels that year. The 2005 breeding season was equally poor for Shags in north and southeast Scotland, although the situation was complicated by a wreck of birds in early 2005 in northeast Britain that greatly reduced adult survival and may have left surviving individuals in poor condition (Mavor *et al*. 2006; Frederiksen *et al*. 2008). Shetland

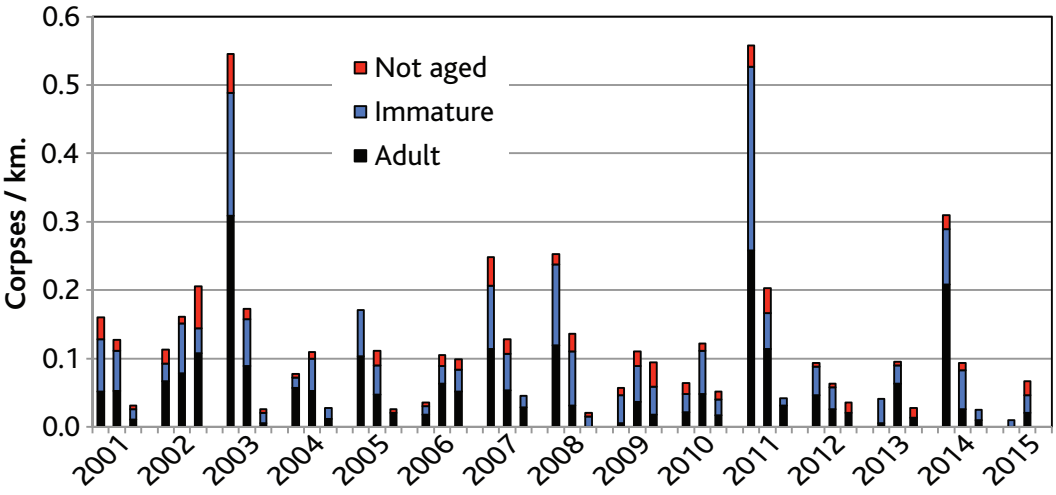

Figure 5. The number of European Shags *Phalacrocorax aristotelis* found dead (per km surveyed) on beached bird surveys in late winter/spring (January–April), summer (May–August), and autumn/early winter (September–December), 2001–15. N.B. 2015 data to August only.

was on the fringe of this wreck (Figure 5), although two Shags ringed at Fair Isle, one as a chick in 1983 and the other as an adult in 1984, were found dead in the Moray Firth in January/February 2005. However, when percentage incubation and breeding success at Foula returned to higher levels in 2006–07 the number of AON in plots was c. 50% lower than in 2001–02, and despite incomplete coverage of the boulder fields (see Figure 6) the whole-island count in 2007 indicated a major reduction in breeding numbers had occurred since 2000 (Figure 2, Table 4).

There was no such widespread pattern in 2008, when numbers of AON and breeding success at Fair Isle crashed. Shags at the Isle of May had an early season, percentage incubation was 100%, and despite a low proportion of sandeels in the chick diet (48% of biomass) breeding success (1.90) was the highest on record (Newell *et al*. 2013). While median hatching date was similar and relatively early at the three focal Shetland colonies (although noting that chicks were recorded in only three nests at the Fair Isle plots), percentage hatched, percentage fledged and breeding success were high at Sumburgh Head but low at Foula. When percentage incubation and breeding success at Fair Isle increased again in 2010, the number of AON in the population and breeding success plots was only 40% of that in 2007. Similarly, while average Shag breeding success at Scottish colonies in 2011–13 was relatively low, these figures will have been depressed by the very low values reported from Shetland, and in 2013 success averaged 1.63 in Orkney and 1.77 in north Scotland (JNCC 2014), while Shags at the Isle of May maintained above average breeding success throughout 2011–13 (www.ceh.ac.uk/sci_programmes/IsleofMay/Long-TermStudy). Such broad geographic disparities, as well as those within Shetland (e.g. the difference in nest counts between southwest and southeast Mainland in 2012 (Appendix 2), and the 45-day difference in timing of laying between Sumburgh Head and southeast Yell in 2013), suggest that variable food availability within foraging range of colonies may have been a crucial determinant of Shag breeding performance within Shetland during 2008–13.

In the 1980s and early 1990s Shag chicks at Fair Isle, Sumburgh Head and Foula were fed almost exclusively sandeels, with gadids (mainly Saithe *Pollachius virens*) forming the bulk of the remainder and forming a substantial component of the diet of non-breeders at Sumburgh Head in at least one year (Furness 1982; Harris & Riddiford 1989; Wright & Bailey 1993). This accords with studies at the Isle of May during the same period (Harris & Wanless 1991, 1993). At Foula, Shag chick regurgitates and pellets contained exclusively sandeels in 1996–2001, but also many small gadid otiliths in 2002, when there was extensive brood reduction, and in 2003 when few broods hatched (Furness 1993–2003; Figure 4a). There are no data on Shag diet at the three focal colonies in the late 2000s and 2010s, and it is unknown whether the percentage of gadids fed to chicks has increased, as has been the case for Common Guillemots at Fair Isle and Sumburgh Head (Heubeck 2009). However, Shags at other Scottish colonies are capable of successful breeding in years when the percentage of sandeels fed to chicks has been relatively low (Swann *et al*. 2008; Newell *et al*. 2013).

Tracking studies have shown that breeding Shags do not feed far from their colony, so it is extremely unlikely that there would be any inter-colony overlap in the foraging ranges of established breeding adults at Fair Isle, Sumburgh Head and Foula. At the Isle of May, mean maximum foraging range in 14 years (1987–2010) was 8.4 km, with an exceptional 17.7 km in one other year (Wanless *et al*. 1991; Bogdanova *et al*. 2014). At Puffin Island, Anglesey, maximum distance averaged 3.6 km for males and 4.6 km for females in 2010–12 (Soanes *et al*. 2014). At Fair Isle in 2010–14, breeding birds rarely foraged far (< 10 km) from the island (RSPB, unpubl.). At Sumburgh Head, Shags foraged up to 10 km from the colony in 1990, a year of low sandeel abundance, but largely within 5 km in 1992 when sandeels were more abundant (Wright & Bailey 1993; Monaghan *et al*. 1997). There have been no tracking studies at Foula, but observations suggest Shags mostly feed to the east of the island, in tide races close to the island or at shallow reefs and shoals up to 10 km offshore (Furness 1981, 1993–2003). Shags breeding on the west coast of Foula therefore mainly have to commute around the south end of the island to reach feeding grounds, in movements that in July 1993 involved c. 9,000 birds per 24 hours flying both east and west. In the 1990s it was noted during ringing visits that brood sizes on the west coast tended be lower than on the east coast, and it was assumed this was a consequence of higher foraging effort of west coast adults (Furness 1993–2003). Although some boulder fields may since have become less suitable for breeding through wave action (Heubeck *et al*. 2014), distance to foraging grounds may be the most plausible explanation for the near-desertion of the former Shag colonies on the west coast of Foula by 2014–15.

Non-breeding by experienced adults in years when local conditions are unfavourable is well known in various phalacrocoracid species (see Aebischer & Wanless (1992) and references within). At the Isle of May, nine non-breeding years in the 1970s, 1980s and 1990s were characterised by reduced numbers of AON, late laying, low breeding success, a return to previous breeding numbers, and no evidence of reduced survival among non-breeding adults (Aebischer & Wanless 1992; Harris *et al*. 1994; Harris *et al*. 1998; Wanless & Harris 2004). In 1993, when only half of birds with previous breeding experience bred (the incidence of breeding was highest in the youngest age classes), the number of AON fell by 56%, first egg date was 30 days later than average, and breeding success was 0.21 fledged per pair. A weather-related wreck of Shags then occurred in February 1994, which resulted in overwinter mortality of adults being 5–6 times the previous 30-year mean. Birds of middle age that bred in 1993 survived less well than those which abstained from breeding; breeding numbers therefore did not 'recover' in 1994, and while first egg date was late that year, other breeding parameters were within the normal range (Harris & Wanless 1996; Harris *et al*. 1998). On the west coast of Scotland, non-breeding years at Canna in 1976 and 1986 (Swann *et al*. 1994), and at the Sanda islands in 1991, 1995 and 1997 (Wanless & Harris 2004) were all single-year events with recoveries in the number of AON the following breeding season. The main distinguishing feature of the events in Shetland, if they simply involved years of non-breeding, is therefore the lack of a recovery in the number of AON in the years

when a return to high percentage incubation and earlier laying suggested most adults were in good enough condition to breed, namely at Foula in 2006–07, at Fair Isle in 2010, and at both these colonies and at Sumburgh Head in 2014–15.

With no Shetland Shags having been individually colour-ringed and therefore identifiable in the field before 2014, one can only speculate on what has happened to the breeders 'missing' from Fair Isle, Sumburgh Head and Foula between 2001 and 2015. In total these amounted to some 2,600 pairs, about 8% of the *Seabird 2000* population figure for Britain and Ireland. Studies at the Farne Islands and the Isle of May found that once established in a breeding colony, individuals may change mate and move nest site at a relatively fine scale between years, but very few (< 1%) then emigrated to breed elsewhere (Potts 1969; Aebischer 1995; Aebischer *et al*. 1995; Barlow *et al*. 2013). Given this, and the high percentage incubation in Shetland in 2014 and 2015, one might have expected these 'missing' birds to have bred had they been alive in the spring of those years, but the continued low counts of AON at the three focal colonies indicate this was largely not the case. Whether breeding Shags have recently shown reduced fidelity to some colonies in Shetland is unknown, but there have been no obvious, substantial increases in AON since 2004 in any time-series of counts, other than in 2010 at Sumburgh Head and in southeast Mainland (Figure 2, Appendix 2). At that time, we speculated whether this could have involved birds from Fair Isle, either movement of established breeders or recruitment of first-time breeders, but there was no evidence to support or refute this. Other possibilities are that Shags that formerly bred at Foula and Fair Isle could have redistributed themselves around Shetland unnoticed amongst colonies that otherwise would have been in decline, have moved out of the archipelago altogether, or have died.

Food availability, foraging conditions (including weather effects), and foraging effort in late winter are also important determinants of timing of breeding and the extent of non-breeding in Shags, both of which can in turn influence breeding success (Aebischer & Wanless 1992; Daunt *et al*. 2014). Although large numbers of Shags winter in Shetland, ringing recoveries indicate their normal winter range extends south to Orkney and northeast mainland Scotland, with a median recovery distance from ringing site of c. 80 km in February/March for birds of all ages (Galbraith *et al*. 1986; Harris & Swann 2002). Recoveries during oil spills have shown that some birds ringed at Fair Isle, Sumburgh Head and Foula winter together in the same local areas in Shetland, and therefore experience similar weather and foraging conditions (Heubeck & Richardson 1980; Heubeck 1997). However, there has been no comparative analysis of dispersal patterns of birds from these colonies, where large numbers of Shags have been ringed as chicks but very few as breeding adults. There are only four recoveries in winter (defined as recovery dates from 1 November–15 March; 1961–2014) of Shags ringed as breeding adults at Fair Isle, three individuals found elsewhere in Shetland and one in the Moray Firth. Including birds ringed as chicks at Fair Isle and recovered in their second winter or older (but excluding two found in Germany and two in Norway) gives 52

winter recoveries, seven (14%) at Fair Isle itself, 18 (35%) elsewhere in Shetland (perhaps biased by the five found on intensive beach searches of south Mainland during the January 1993 *Braer* oil spill), 17 (33%) in Orkney, and ten (19%) further south in Scotland, all but one on North Sea coasts. Fair Isle lies equidistant between Mainland Shetland and the northernmost Orkney island, and given the relative distances involved it is reasonable to propose that a higher percentage (c. 60%) of Shags breeding there move south in winter than do those breeding at Sumburgh Head and Foula, and that there is greater overlap (around Shetland) in the winter distribution of birds from the latter two colonies, at which timing of breeding and percentage incubation correlated highly significantly (Table 2). Individual Shags breeding at the Isle of May show consistent migration strategies and high site fidelity across winters (Grist *et al*. 2014). If the same applies to Shetland breeders, one could speculate whether wintering in the generally shallower waters of the Orkney archipelago or the Moray Firth conveys any difference over wintering around Shetland, that could be carried-over into the next breeding season, e.g. in terms of higher percentage incubation (Figure 2) or earlier laying (Figure 3a). Certainly, the timing of mortality events suggests that weather and foraging conditions vary across the potential winter range of Shetland breeders, with relatively few Shags found dead in Shetland in early 2005 or 2013 (Figure 5), years of wrecks in eastern Scotland and when the return rate of Isle of May breeders was low, and with the converse situation in 2003 and 2011 (JNCC 2015).

Figure 6. Foula: the safest access to the boulder fields of Mucklebruik is down the narrow cleft called da Sneck o' da Smaalie (left); once outside da Sneck, progress is difficult if the smooth slabs of rock are wet (right). 8 August 2008. © *Sheila Gear*.

The changes described above in the population dynamics of Shags in Shetland may have involved a complex interaction of factors, including the colony where individuals recruit to breed, the particular years in which they attempt breeding, and where they spend the winter. In these circumstances, and given that Shag has recently been assigned to the UK's Red list of Birds of Conservation Concern because of a severe decline in population size (Eaton *et al*. 2015), it would seem prudent to maintain the current level of monitoring of colonies and coastlines, complete the census of coastlines not surveyed since 1998–2002, and maintain or increase the level of ringing of chicks and adults at colonies.

Acknowledgements

Seabird monitoring on Fair Isle was funded by Fair Isle Bird Observatory Trust, with contributions from the Joint Nature Conservation Committee; thanks to all Fair Isle Bird Observatory staff members and volunteers in 2001–15 for data collection. SOTEAG monitoring is funded by the Sullom Voe Association Ltd; thanks to all who assisted with boat surveys, especially Billy Fox, Paul Harvey, Roger Riddington, Newton Harper and George Lamont Williamson. Afra Skene, Jonathan Swale and Glen Tyler (Scottish Natural Heritage), and Paul Harvey (Shetland Biological Records Centre) provided details of counts on Noss and Foula, while Rory Tallack and Andy Webb helped produce the figures. Drafts of the manuscript were greatly improved by comments from Mike Harris, Sarah Wanless and Andy Webb, and by referees Francis Daunt and Svein-Håkon Lorentsen.

References

Aebischer, N. J. 1986. Retrospective investigation of an ecological disaster in the Shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. *Journal of Animal Ecology* 55: 613–629.

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., Potts, G. R. & Coulson, J. C. 1995. Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. *Ibis* 137: 19–28.

Aebischer, N. J. & Wanless, S. 1992. Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. *Bird Study* 39: 43–52.

Barlow, E. J., Daunt, F., Wanless, S. & Reid, J. M. 2013. Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European Shags *Phalacrocorax aristotelis*. *Ibis* 155: 762–778.

Bogdanova, M. I., Wanless, S., Harris, M. P., Lindström, J., Butler, A., Newell, M. A., Sato, K., Watanuki, Y., Parsons, M. & Daunt, F. 2014. Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: implications for marine spatial planning. *Biological Conservation* 140: 292–299.

Coulson, J. C., Potts, G. R., Deans, I. R. & Fraser, S. M. 1968. Exceptional mortality of Shags and other seabirds caused by paralytic shellfish poisoning. *British Birds* 61: 381–404.

Daunt, F., Reed, T. E., Newell, M., Burthe, S., Phillips, R. A., Lewis, S. & Wanless, S. 2014. Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. *Ecology* 95: 2077–2083.

Eaton, N., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D. & Gregory, R. 2015. Birds of Conservation Concern 4: the population status of birds in the UK, Channel Islands and Isle of Man. *British Birds* 108: 708–746.

Frederiksen, M., Daunt, F., Harris, M. P. & Wanless, S. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* 77: 1020–1029.

Furness, R. W. 1981. Seabird populations of Foula. *Scottish Birds* 11: 237–253.

Furness, R. W. 1982. Population, breeding biology and diets of seabirds on Foula in 1980. *Seabird Report* 6: 5–12.

Furness, R. W. 1987. 'Assessment of the status of seabirds on the island of Foula, Shetland'. Unpublished report, University of Glasgow.

Furness, R. W. 1993–2003. 'Seabird studies in Foula'. Unpublished annual reports, University of Glasgow.

Galbraith, H., Baillie, S. R., Furness, R. W. & Russell, S. 1986. Regional variations in the dispersal patterns of Shags *Phalacrocorax aristotelis* in northern Europe. *Ornis Scandinavica* 17: 68–74.

Grist, H., Daunt, F., Wanless, S., Nelson, E. J., Harris, M. P., Newell, M. Burthe, S. & Reid, J. M. 2014. Site fidelity and individual variation in winter location in partially migratory European shags. *PLoS One* 9: e98562.

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. *The Condor* 96: 600–605.

Harris, M. P. & Forbes, R. 1987. The effect of date on counts of nests of Shags *Phalacrocorax aristotelis*. *Bird Study* 34: 187–190.

Harris, M. P. & Riddiford, N. J. 1989. The food of some young seabirds on Fair Isle in 1986–88. *Scottish Birds* 15: 119–125.

Harris, M. P. & Swann, B. 2002. European Shag (Shag) *Phalacrocorax aristotelis*. In: Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M. & Baillie, S. R. (eds.) *The Migration Atlas: movements of the birds of Britain and Ireland*: 139–142. Poyser, London.

Harris, M. P. & Wanless, S. 1990. Breeding success of British Kittiwakes *Rissa tridactyla* in 1986–88: evidence for changing conditions in the northern North Sea. *Journal of Applied Ecology* 27: 172–187.

Harris, M. P. & Wanless, S. 1991. The importance of the lesser sandeel *Ammodytes marinus* in the diet of the Shag *Phalacrocorax aristotelis*. *Ornis Scandinavica* 22: 375–382.

Harris, M. P. & Wanless, S. 1993. The diet of Shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. *Bird Study* 40: 135–139.

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. & Elston, D. A. 1998. Age-related effects of a nonbreeding event and a winter wreck on the survival of Shags *Phalacrocorax aristotelis*. *Ibis* 140: 310–314.

Harvey, P. V., Swale, J., Upton, A. J., Gear, J. & S., Adam, M., Churchhill, G., Gillham, K. & Skene, A. 2000. 'A census of the seabirds of Foula - June 2000'. Unpublished Report, SNH Lerwick.

Heubeck, M. 1997. The Direct Effect of the *Braer* Oil Spill on Seabird Populations, and an Assessment of the Role of the Wildlife Response Centre. In: Davies, J. M. & Topping, G. (eds.) *The Impact of an Oil Spill in Turbulent Waters: The* Braer: 73–90. The Stationery Office, Edinburgh.

Heubeck, M. 2004. 'SOTEAG ornithological monitoring programme 2003 summary report'. Unpublished report to SOTEAG, Aberdeen.

Heubeck, M. 2006. The Shetland beached bird survey, 1979–2004. *Marine Ornithology* 34: 123–127.

Heubeck, M. 2009. Common Guillemot *Uria aalge* chick diet and breeding performance at Sumburgh Head, Shetland in 2007–09, compared to 1990–91. *Seabird* 22: 9–18.

Heubeck, M., Gear, S. & Harris, M. P. 2014. A photographic resurvey of seabird colonies on Foula, Shetland. *Scottish Birds* 34: 291–302.

Heubeck, M. & Mellor, M. 2012. 'SOTEAG ornithological monitoring programme 2011 summary report'. Unpublished report to SOTEAG, Aberdeen.

Heubeck, M., Mellor, R. M., Harvey, P. V., Mainwood, A. R. & Riddington, R. 1999. Estimating the population size and rate of decline of Kittiwakes *Rissa tridactyla* breeding in Shetland, 1981–97. *Bird Study* 46: 48–61.

Heubeck, M. & Richardson, M. G. 1980. Bird mortality following the *Esso Bernicia* oil spill, Shetland, December 1978. *Scottish Birds* 11: 97–108.

JNCC 2014. Seabird Population Trends and Causes of Change: 1986–2013 Report (http://www.jncc.defra.gov.uk/page-3201). Joint Nature Conservation Committee. Updated August 2014. Accessed 31 August 2014.

JNCC 2015. Seabird Population Trends and Causes of Change: 1986–2014 Report (http://www.jncc.defra.gov.uk/page-2877). Joint Nature Conservation Committee. Updated October 2015. Accessed 31 October 2015.

Mavor, R. A., Parsons, M., Heubeck, M. & Schmitt, S. 2005. *Seabird numbers and breeding success in Britain and Ireland, 2004*. JNCC, Peterborough (UK Nature Conservation, No. 29).

Mavor, R. A., Parsons, M., Heubeck, M. & Schmitt, S. 2006. *Seabird numbers and breeding success in Britain and Ireland, 2005*. JNCC, Peterborough (UK Nature Conservation, No. 30).

Mavor, R. A., Pickerell, G., Heubeck, M., & Thompson, K. R. 2001. *Seabird numbers and breeding success in Britain and Ireland, 2000*. JNCC, Peterborough (UK Nature Conservation, No. 25).

Mavor, R. A., Pickerell, G., Heubeck, M. & Mitchell, P. I. 2002. *Seabird numbers and breeding success in Britain and Ireland, 2001*. JNCC, Peterborough (UK Nature Conservation, No. 26).

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. *Journal of Animal Ecology* 58: 261–274.

Monaghan, P., Walton, P., Austin, G., Burns, M. D., Turner, C. M. & Wright, P. J. 1997. Sub-lethal effects of the *Braer* oil spill on seabirds. In: Davies, J. M. & Topping, G. (eds). *The Impact of an Oil Spill in Turbulent Waters: The* Braer: 91–105. The Stationery Office, Edinburgh.

Newell, M., Harris, M. P., Quinn, L., Wanless, S. & Daunt, F. 2013. *Isle of May seabird studies in 2008*. JNCC Report, No. 475d.

Potts, G. R. 1969. The influence of eruptive movements, age, population size and other factors on the survival of the Shag (*Phalacrocorax aristotelis* (L.)). *Journal of Animal Ecology* 38: 53–102.

Rideout, K. J. 2004. 'St Abb's Head NNR seabird report 2004'. Unpublished Report, National Trust for Scotland.

Shaw, D. (ed.) 2005. *Fair Isle Bird Observatory Report for 2004*. Fair Isle Bird Observatory Trust, Fair Isle.

Shaw, D. N., Davies, S., Ward, M., Hughes, R. D. & King, P. 2008. 'Fair Isle seabird studies 2008'. Unpublished FIBOT report to JNCC.

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Milligan, G. & Green, J. A. 2014. Factors affecting the foraging behaviour of the European shag: *implications for seabird tracking studies*. *Marine Biology* 161: 1335–1348.

Swann, R. L., Aiton, D. G., Carruthers, J., Graham, R. J. & Ramsay, A. D. K. 1994. An analysis of Shag *Phalacrocorax aristotelis* ring recovery and breeding success data during a period of population change on the Isle of Canna. *Seabird* 16: 50–56.

Swann, R. L., Harris, M. P. & Aiton, D. G. 2008. The diet of European Shag *Phalacrocorax aristotelis*, Black-legged Kittiwake *Rissa tridactyla* and Common Guillemot *Uria aalge* during the chick-rearing period 1981–2007. *Seabird* 21: 44–54.

Walsh, P. M., Halley, D. J., Harris, M. P., del Nevo, A., Sim, I. M. W. & Tasker, M. L. 1995. *Seabird monitoring handbook for Britain & Ireland*. JNCC / RSPB / ITE / Seabird Group, Peterborough.

Walsh, P. M., Sears, J. & Heubeck, M. 1991. *Seabird numbers and breeding success in 1990*. Nature Conservancy Council CSD Report No. 1235.

Walton, P. M., Dawson, N. & Steel, D. 2004. 'Breeding birds of the Farne Islands 2004'. Unpublished Report, The National Trust.

Wanless, S. & Harris, M. P. 2004. European Shag *Phalacrocorax aristotelis*. In: Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. (eds.) *Seabird Populations of Britain and Ireland*: 146–159. Poyser, London.

Wanless, S., Harris, M. P. & Morris, J. A. 1991. Foraging range and feeding locations of Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 133: 30–36.

Wanless, S., Harris, M. P., Redman, P. & Speakman, J. R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.

Wright, P. J. & Bailey, M. C. 1993. *Biology of Sandeels in the Vicinity of Seabird Colonies at Shetland*. Fisheries Research Report No. 15/93. SOAFD Marine Laboratory, Aberdeen.

Appendix 1. European Shag *Phalacrocorax aristotelis* breeding parameters at monitored colonies: the date range and number of visits made, the number of nest sites recorded only as trace (Tr.) or well-built but empty (AON), the number of incubating nests (Inc.) and the percentage of all nests which progressed to incubation (% Inc.), the percentage of incubating nests at which chicks were recorded (% H.), the percentage of nests at which chicks were recorded from which a chick(s) fledged (% Fl.), the median date chicks were first recorded at each nest (M. ch.), the number of chicks fledged (Ch.), sum breeding success (Succ.: chicks fledged/Inc., * = many nests washed out at chick stage), and mean brood size at fledging (B.S.). At each colony, not all plots were occupied in every year.

Fair Isle (5 plots 2001–15)

Year	Dates & Visits	Tr.	AON	Inc.	% Inc.	% H.	% Fl.	M. ch.	Ch.	Succ.	B.S.
2001	30/04–25/08 (17)	1	1	65	97.0	72.3	100.0	05/06	107	1.65	2.28
2002	30/04–10/08 (16)	2	0	56	96.6	83.9	91.5	03/06	105	1.88	2.44
2003	28/04–18/08 (17)	0	0	61	100.0	62.3	89.5	01/06	81	1.33	2.38
2004	06/05–26/07 (15)	0	0	53	100.0	90.6	29.2	30/05	37	0.70	2.64
2005	30/04–06/08 (15)	1	1	45	95.7	68.9	90.3	10/06	41	0.91	1.46

2006	26/04–29/08 (19)	2	1	51	94.4	84.3	93.0	07/06	83	1.63	2.08
2007	24/04–31/07 (15)	0	0	52	100.0	67.3	88.6	21/05	78	1.50	2.52
2008	24/04–18/07 (13)	5	1	32	84.2	9.4	33.3	07/06	1	0.03	1.00
2009	30/04–28/08 (15)	4	4	11	57.9	45.5	60.0	04/07	5	0.45	1.67
2010	06/05–04/08 (14)	0	1	21	95.5	66.7	85.7	16/06	19	0.90	1.58
2011	22/04–05/07 (16)	3	0	19	86.4	42.1	25.0	09/06	2	0.11	1.00
2012	10/05–03/09 (22)	3	0	18	85.7	72.2	92.3	30/06	18	1.00	1.50
2013	03/05–11/09 (22)	1	0	11	91.7	36.4	100.0	09/07	7	0.64	1.75
2014	03/05–12/08 (17)	0	0	14	100.0	71.4	100.0	16/06	24	1.71	2.40
2015	02/05–29/09 (26)	0	0	13	100.0	84.6	81.8	21/05	21	1.62	2.33

Sumburgh Head (13 plots 2001–07, 16 plots 2008–15)

Year	Dates & Visits	Tr.	AON	Inc.	% Inc.	% H.	% Fl.	M. ch.	Ch.	Succ.	B.S.
2001	09/04–10/09 (32)	14	6	185	90.2	72.4	90.3	18/06	237	1.28	1.96
2002	08/04–27/08 (31)	3	10	188	93.5	75.0	93.6	15/06	300	1.61	2.27
2003	07/04–23/08 (29)	17	9	160	86.0	66.3	83.0	15/06	180	1.13	2.05
2004	06/04–16/08 (29)	22	14	135	78.9	57.0	83.1	25/06	101	0.75	1.58
2005	13/04–18/09 (29)	17	10	115	81.0	46.1	90.6	10/07	86	0.75	1.79
2006	10/04–11/09 (28)	14	3	160	90.4	71.9	87.0	25/06	191	1.19*	1.91
2007	06/04–10/09 (31)	10	2	153	92.7	73.2	83.0	17/06	195	1.27*	2.10
2008	07/04–07/09 (31)	12	6	182	91.5	74.7	97.1	10/06	274	1.51	2.08
2009	04/04–20/09 (34)	17	4	185	89.8	76.8	93.0	09/06	293	1.58	2.22
2010	07/04–09/08 (27)	23	12	222	86.4	73.0	71.4	03/06	274	1.23*	2.09
2011	04/04–16/08 (30)	20	11	142	82.1	22.5	72.7	11/06	43	0.30	1.79
2012	09/04–17/09 (34)	21	14	96	73.3	30.2	76.7	07/07	36	0.38	1.57
2013	08/04–05/10 (38)	15	27	56	57.1	16.1	90.0	22/07	15	0.27	1.67
2014	09/04–21/09 (31)	2	2	108	96.4	67.6	94.5	04/07	133	1.23	1.90
2015	06/04–25/08 (25)	5	3	111	93.3	76.6	92.9	13/06	157	1.41	1.99

Foula (8 plots 2001–07, 9 plots 2008–11, 10 plots 2012–15)

Year	Dates & Visits	Tr.	AON	Inc.	% Inc.	% H.	% Fl.	M. ch.	Ch.	Succ.	B.S.
2001	18/05–30/08 (7)	7	2	61	87.1	86.9	71.7	15/06	78	1.28	2.05
2002	17/05–31/07 (5)	1	7	53	86.9	69.8	78.4	16/06	51	0.96	1.76
2003	16/05–16/08 (6)	5	0	43	89.6	34.9	46.7	20/06	9	0.21	1.29
2004	17/05–14/07 (5)	1	2	6	66.7	33.3	0.0	28/06	0	0.00	-
2005	16/04–26/07 (8)	1	1	6	75.0	16.7	0.0	10/07	0	0.00	-
2006	20/04–03/08 (9)	3	0	33	91.7	72.7	83.3	20/06	35	1.06	1.75
2007	26/04–04/08 (8)	3	1	24	85.7	91.7	81.8	13/06	25	1.04	1.39
2008	15/04–14/08 (9)	3	9	27	69.2	37.0	50.0	11/06	7	0.26	1.40
2009	18/04–12/08 (9)	2	2	44	91.7	84.1	78.4	08/06	55	1.25	1.90
2010	03/05–08/08 (9)	1	1	41	95.3	90.2	81.1	01/06	56	1.37	1.87
2011	21/04–26/07 (11)	0	1	27	96.4	59.3	62.5	04/06	20	0.74	2.00
2012	12/05–02/09 (12)	4	3	10	58.8	50.0	80.0	20/06	5	0.50	1.25
2013	10/05–30/08 (11)	3	4	4	36.4	50.0	100.0	15/07	3	0.75	1.50
2014	28/04–27/08 (13)	0	0	35	100	91.4	93.8	06/06	66	1.89	2.20
2015	20/04–25/07 (9)	1	1	29	93.5	82.8	66.7	07/06	23	0.79	1.81

Appendix 2. Counts of European Shag *Phalacrocorax aristotelis* nests (trace, empty, and active, i.e. apparently incubating or containing chicks) made from the sea or from land along standard stretches of coastline away from the three focal colonies. The percentage of nests that were active (i.e. apparently incubating/brooding or chicks seen) and the count date are given. Counts at Noss were the combined total of AON on two dates (n.c. = no count). See Figure 1 for locations.

West Shetland	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**
1. Muckle Roe (sea)		**76**		**63**		**62**			**93**		**67**				
		97%		83%		89%			94%		58%				
		8/6		10/6		7/6			23/6		9/6				
2. Papa Stour (sea)		**360**				**299**								**218**	
		96%				93%								92%	
		13/6				28/6								22/6	
3. Vaila to Skelda Ness (sea)	**407**			**308**		**426**	**304**		**390**			**399**			
	97%			80%		97%	97%		94%			87%			
	15/6			11/6		27/6	21/6		9/6			20/6			
4. Kettla Ness (sea)		**58**	**51**				**57**		**51**			**51**		**45**	
		97%	96%				89%		94%			82%		80%	
		6/6	16/6				9/6		11/6			27/6		23/6	
5. St Ninian's Isle & South Havra (sea)							**102**		**116**			**103**		**103**	
							93%		91%			70%		86%	
							9/6		11/6			27/6		23/6	

East Shetland	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**
6. Virkie to Troswick (sea)	**169**	**175**	**122**		**114**	**149**			**165**	**167**			**61**	**91**	**108**
	96%	92%	89%		86%	93%			96%	96%			38%	91%	93%
	9/6	12/6	12/6		20/6	4/6			13/6	16/6			26/6	15/6	19/6
7. No Ness (land)	**144**	**122**	**117**	**103**	**124**	**139**	**150**	**138**	**167**	**204**	**91**	**54**	**49**	**89**	**89**
	90%	84%	82%	87%	83%	97%	95%	94%	95%	95%	87%	48%	47%	87%	93%
	30/5	15/6	6/6	15/6	14/6	13/6	22/6	13/6	18/6	9/6	13/6	12/6	10/6	12/6	16/6
8. Mousa (sea)			**71**		**94**				**109**	**113**			**26**	**52**	**65**
			90%		89%				86%	97%			62%	94%	100%
			12/6		20/6				21/6	22/6			25/6	16/6	20/6
9. Noss (AON; sea)	**69**	**55**	**47**	**74**	**89**	**92**	**83**	**96**	**97**	**102**	**66**	**63**	**76**	**67**	**99**
	12/6	21/6	9/6	11/6	14/6	16/6	n.c.	7/6	9/6	15/6	5/6	20/6	8/6	6/6	29/6
	14/8	23/7	8/7	6/7	10/7	25/7	15/7	17/7	n.c.	n.c.	4/7	31/7	10/7	7/7	14/7
10. Southeast Yell (sea)		**151**		**134**		**143**			**176**				**137**		
		99%		95%		99%			99%				91%		
		21/6		29/6		16/6			22/6				19/6		