SEABIRD 14

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S. Wanless

CONTENTS

Cover vignette of Manx Shearwater by B. Zonfrillo

Growth of Black Guillemot *Cepphus grylle* chicks in Shetland in 1983-84

P. J. Ewins

INTRODUCTION

Young Black Guillemots *Cepphus grylle* are completely independent once they have left the nest (Harris & Birkhead 1985; Ewins 1986), so one might expect their growth rates and fledging condition to be more crucial to subsequent survival than for auk species having some degree of post-fledging parental care (see Gaston 1985).

Although I have no data on post-fledging survival, this paper provides the first published growth parameters for Black Guillemots nesting in the UK. I also examine several factors which may have influenced chick growth. Elsewhere, chick growth has been documented in Denmark (Asbirk 1979), Iceland (Petersen 1981), in the USSR in the Barents and White Seas (Belopol'skii 1957; Bianki 1967), and in North America (Winn 1950; Cairns 1981, 1987). The Shetland data were collected in 1983-84, at colonies experiencing relatively favourable conditions for foraging and breeding (Ewins 1986). Therefore, given the recent major reductions in breeding success of many seabird species in Shetland and some other parts of Scotland, associated with declining availability of sandeels (Ammodytidae) (eg. Walsh *et al.* 1990), these results may serve as a baseline against which subsequent feeding ecology and growth parameters can be compared.

STUDY AREA AND METHODS

This study was carried out in 1983 and 1984 on the low-lying, uninhabited island of Mousa (60°00'N, 1°10'W), 1 km off the east coast of the Shetland mainland. Over 150 pairs of Black Guillemots bred on the island, in accessible colonies (designated A, B, C, etc.), amongst piles of sandstone boulders and slabs scattered around the 8-km coastline. Large stocks of sandeels occurred in the shallow waters around Mousa and during the study these waters supported an industrial sandeel fishery (Warburton 1983), as well as large numbers of foraging seabirds. Otters *Lutra lutra* were the only mammalian predators on Mousa. (The island also hosted large numbers of breeding Storm Petrels *Hydrobates pelagicus*, Arctic Terns *Sterna paradisaea*, Arctic Skuas *Stercorarius parasiticus*, Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus*). Observations were made throughout the chick period in both study years.

To minimize disturbance nests were usually inspected between 1200 and 1700 GMT, when colony attendance was lowest (Ewins 1985). Colony visits never exceeded 30 minutes, and were curtailed in cold and wet conditions, especially during the early chick period, to allow adults to return to brood small chicks. In both study years nests were inspected daily around the anticipated hatching date, and in the 7-10 days prior to chicks fledging, but in the intervening period chicks were measured at 3-day intervals.

In broods of two chicks (designated as 'b2' as opposed to single chick broods, 'b1'), the first to hatch (referred to as the a-chick) was given a small spot of nail varnish on the dorsal down. The second chick to hatch was termed the b-chick. This permitted individual identification during the first week, whereafter a numbered ring could be fitted to the chicks. Day 0 for a chick was taken as the first afternoon it appeared, although some could have hatched the previous evening. 'Fledging' was taken to mean nest leaving, although the young were probably incapable of sustained flight then (Petersen 1981). The fledging period was the total time spent by a chick in the nest, Particularly thorough searches were made when chicks were due to fledge, since some occasionally moved to nearby cavities.

At each nest visit the wing length and weight of chicks were measured. Some chicks could not

be caught on every visit due to the nature of their nest cavities, but their presence was assessed by use of a torch and small mirrors. Wing lengths were measured to the nearest mm with a stoppered rule, using the maximum flattened chord technique (Svensson 1984). For small chicks the fluffy tips to the remiges were excluded. Wings of freshly-dead immatures collected on beaches between August and February were measured in the same way. Chicks were weighed with pesola balances, accurate to 1 g.

Observations of fish delivered to chicks were made for a sample of 20 nests in colony A (which contained ca.40 nests in both years). These hide observations were made at all times of day, and totalled 1647 chick-hours in 1983 and 2024 chick-hours in 1984. Fish lengths were estimated in relation to the distance from the adult's bill tip to the rear of its head. This "head-bill index" proved to be a more reliable standard measure than bill length, and for 10 breeding adults on Mousa was 85.3 ± 2.0 mm. With binoculars it was usually possible to identify the species (or at least the family) of fish delivered (see Ewins 1990).

Wet weight: length regression equations were calculated for some common prey types, from live specimens caught in benthic traps set around the island (Appendix I). Sandeel measurements were made on a sample of freshly-caught fish aboard a fishing boat. Using the above parameters the average weight of fish delivered per unit time could thus be calculated for chicks of known ages. Energy equivalents (kJ g^{-1} wet weight) given by Harris & Hislop (1978) and (Dunn 1975) were used in the estimation of chick energy intakes: sandeels = 6.5; blennies = 5.87; gadids = 4.52 (mean of values for *Pollachius virens, P. pollachius* and *Merlangius merlangus*); other species = 5.83 (mean of values for rocklings, cottids and flatfish species).

Kleptoparasitism of delivery attempts was studied during hide watches at various times of day at intervals throughout the chick period. These observation periods ranged from 1-3 h long and totalled over 225 h during the two study years. Most observations were made at colony A, and colony B (which supported ca.20 nests, scattered amongst the colony of Herring and Lesser Black-backed Gulls), but some data were collected at other colonies experiencing lower rates of piracy. A fish was scored as lost by a Black Guillemot even if it was not recovered by the kleptoparasite. For further details see Ewins (1986).

Meteorological data were for Lerwick, 16 km north of Mousa (Lerwick Met. Station records). Average sea-surface temperatures were recorded by D. Wheeler at Fair Isle, 50 km south of Mousa.

Means quoted are arithmetic means, usually given ± 1 standard deviation. The number of degrees of freedom is usually subscripted to the statistic. The term significant is used only in the statistical sense, significance being accepted at the 0.05 level. Statistical methods follow Sokal & Rohlf (1981).

RESULTS

The timing of hatching and fledging

In 1983 hatching spanned a period of about 5 weeks, from 23 June to 26 July, with a median hatching date of 9 July (n=107). In 1984 the median hatching date fell 2 days earlier, on 7 July (n=135), again with a range of about 5 weeks (21 June to 27 July). The median fledging date on Mousa was 13 August in 1983 (n=93, range 26 July to 25 August), and 12 August in 1984 (n=114, range 26 July to 29 August).

The mean fledging period in 1983 was 36.0 ± 2.4 d (n=83, range 32-43 d), and 36.1 ± 2.8 d (n=105, range 32-53 d) in 1984. There was no significant difference in the fledging period of a- and b-chicks for any colony or year, or between chicks in broods of one or two, or between years for the same brood size. In 93 two-chick broods (data combined for both years since there were no significant differences between years) chicks hatched on average 0.91 ± 0.58 d apart. Chicks hatched one day apart in 70% of these nests, on the same day in 18%, and 2 days apart in 12%. In 63 broods for which the hatching order was known, the a-chick fledged first in 27 (43%), the b-

chick in 25 (40%), and in 11 (18%) the chicks fledged on the same day. The longest interval was 12 days, involving a runt chick in colony B which received little food until its sibling fledged. Despite regular hide watches at colonies during the late nestling period, no chicks were seen to depart for the sea during daylight; their absence the following day inferred that they left during the hours of darkness.

TABLE I. CHICK SIZES AT HATCHING (DAY 0).

		1983		1984	
		b1	b2	b1	b2
Weight (g)	mean	29.5	31.5	32.4	32.7
	sd	3.3	3.9	3.7	4.0
	n	4	18	5	29
	range	27-34	25-39	26-35	24-40
Wing (mm)	mean	18.3	18.9	19.3*	19.6*
	sd	0.5	0.9	0.5	0.9
	n	4	19	6	28
	range	18-19	17-20	19-20	18-21

Significant differences between years: * = P<0.02

Growth statistics

The average wing length and weight of chicks on the day of hatching are given in Table I. Both parameters were greater in 1984 than 1983, but the differences were only significant for wing length. In both years a-chicks hatched slightly heavier than b-chicks, but the data were pooled since the differences were non-significant. The pattern of wing growth was very similar in the two years, and in chicks from different brood sizes, and was sigmoid in form (Fig. 1). The mean wing length on the day of 'fledging' in 1983 (135 ± 4.3 mm, n=73, range 127-147 mm) was not significantly different from that in 1984 (134.7 ± 4.7 mm, n=89, range 121-151 mm; t_{160} = 0.71, N.S.). The wings of post-fledging immatures found freshly dead on beaches in Shetland and Orkney appeared to continue growing, at least until mid September (Fig. 2). Despite many hours observing recently fledged immatures in various parts of Shetland, the first sustained flights were not recorded until late September (at least 4 weeks after the median 'fledging' date). Further, wings of 14 immatures between September and June of the following summer were significantly shorter on average than those of 64 Shetland breeding adults (154 ± 3.3 mm and 161.8 ± 3.4 mm respectively, t_{76} = 7.41, P<0.001), indicating that wings continue growing slightly until birds reach breeding age.

Growth curves for weight were of a generally similar sigmoid form in both years, but weight recession prior to fledging was evident from this form of data presentation only in 1984 (Fig. 3). For chicks 6-21 days old, the growth curve was essentially linear. In both years growth rates of chicks older than 21 d were lower for those in broods of two, than in single-chick broods. To permit comparison with growth rates in other alcid studies the steepest tangent was fitted by eye to these growth curves. In both years maximum (weight) growth occurred in chicks about 10-11 days old, and the gradients of these tangents indicated daily increments of 15.7 g in 1983, but 18.0 g in 1984. When daily weight increments (DWIs) were calculated for individual chicks in colony A, and averaged for 5-d age categories, average DWIs were also greatest for chicks 10-14 d old, and

Figure 1. Wing growth curves for Black Guillemot chicks in Shetland. The mean ± s.d. and sample size is given for each chick age, according to brood size.

greater in 1984 than in 1983. Average DWIs calculated in this way were higher than those obtained from the fitted tangent to the growth curve for the whole island, being 17.0 g/day in 1983 and 19.9 g/day in 1984 (Table II).

Figure 2. Post-fledging wing growth in Black Guillemots, determined from wing lengths of 14 fresh corpses found in Shetland and Orkney. The arrow indicates mean wing length at fledging, the open circle the median fledging date for 1983-84, and the dashed line the mean wing length of immatures in Shetland between September and June.
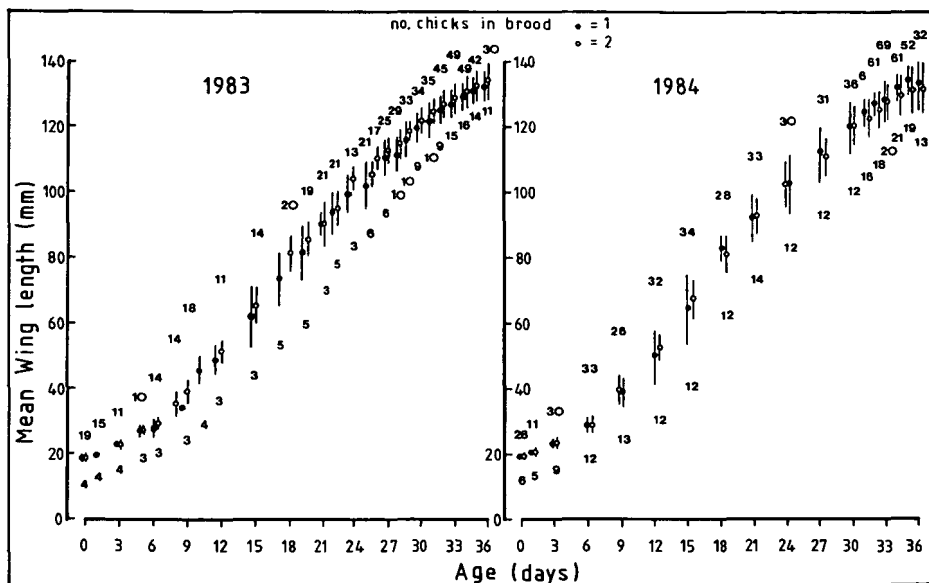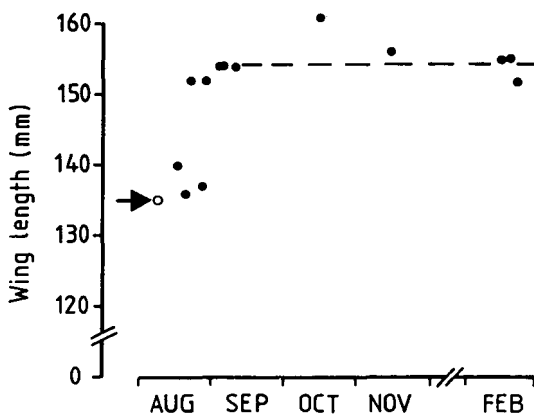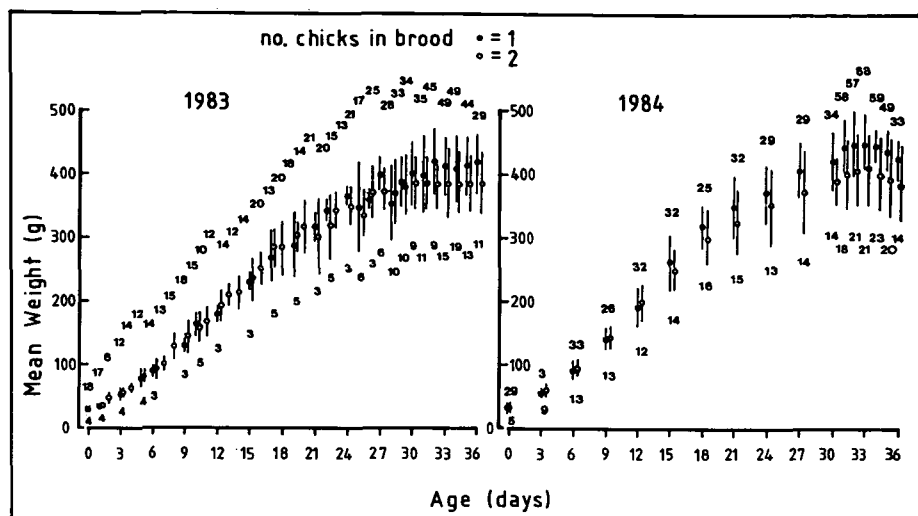
Figure 3. Weight growth curves for Black Guillemot chicks in Shetland. The mean ± s.d. and sample size is given for each chick age, according to brood size.

TABLE II. AVERAGE DAILY WEIGHT INCREMENT (Av. DWI) (g) AND MEAN WEIGHT GAIN PER g OF FISH DELIVERED, FOR CHICKS OF DIFFERENT AGES IN COLONY A IN 1983 AND 1984.

	1983		1984		Mean weight gain (g) per g fish delivered	
Chick age (d)	Av. DWI	(n)	Av. DWI	(n)	1983	1984
0-4	8.1	(22)	8.3	(19)	.633	.487
5-9	15.3	(20)	16.8	(23)	.495	.438
10-14	17.0	(21)	19.9	(32)	.278	.242
15-19	15.4	(22)	18.0	(21)	.212	.177
20-24	13.6	(27)	10.3	(31)	.167	.076
25-29	6.5	(51)	8.5	(43)	.061	.050
30-34	0.4	(103)	0.5	(87)	.004	.003
35-39	-3.7	(66)	-7.4	(39)	−.049	−.091

(n) is the sample size for the number of increments in each age category.

Peak weights were reached, on average, 3 days prior to fledging, but for individual chicks this varied between 0 and 9 days. The mean maximum weight attained by chicks in 1984 was significantly greater than in 1983 (432.7 ± 46.3 g, n=90, and 412.5 ± 41.4 g, n=68, respectively; t_{156} = 2.84, P<0.01). There was no significant difference between years in the mean number of days on which chicks were handled (11.1 ± 6.0 d and 11.3 ± 5.6 d respectively, t_{216} = 0.21, P = 0.8), so any effect of researcher disturbance was unlikely to account for the observed differences in growth rates [such effects on fledging weights have been noted in *Uria* species, by Harris & Wanless (1984) and Gaston (1985)]. Breeding adults, post-laying, were also significantly heavier in 1984 than in 1983 (Ewins 1989), so these mean peak weights of chicks represented 106% of adult weight in 1983 and 105% in 1984. Despite the indication from the overall growth curves of a

difference between years in the degree of weight recession prior to fledging, when chick weights were analysed according to the number of days prior to fledging, average declines were evident over the last 3 days in the nest, of 6.8% in 1983 and 6.6% in 1984 (Fig. 4). For all chicks combined, the mean weight at fledging was significantly higher in 1984 (404.2 ± 43.8 g, n=88) than in 1983 (384.5 ± 34.1 g, n=73) (t_{159} = 3.13, P<0.01). These fledging weights represented 98% and 99% of the respective average adult post-laying weights. In the preceding analyses weights of chicks from different brood sizes were combined, since there was no significant difference between the two years in the proportion of b1 to b2 chicks measured (G-tests, P>0.1). However, single chicks, especially in 1984, were usually significantly heavier at peak weight and at fledging than those having siblings (Table III). In 2-chick broods none of these weight parameters differed significantly between a- and b-chicks.

TABLE III. PEAK WEIGHTS AND FLEDGING WEIGHTS (g) OF CHICKS IN BROODS OF 1 AND 2, IN 1983 AND 1984.

		1983		*1984*		*Sig. difference*
		b1	*b2*	*b1*	*b2*	*between years*
Peak weight	Mean	429.7 *	406.0	465.5 ***	422.6	b1: *, b2: *
	s.d.	45.0	38.6	39.3	45.2	
	n	16	51	19	67	
Fledging weight	Mean	392.3	382.2	428.2 ***	396.0	b1: **
	s.d.	43.2	30.9	30.5	44.5	
	n	17	56	23	66	
	range	319-493	311-466	378-466	240-484	

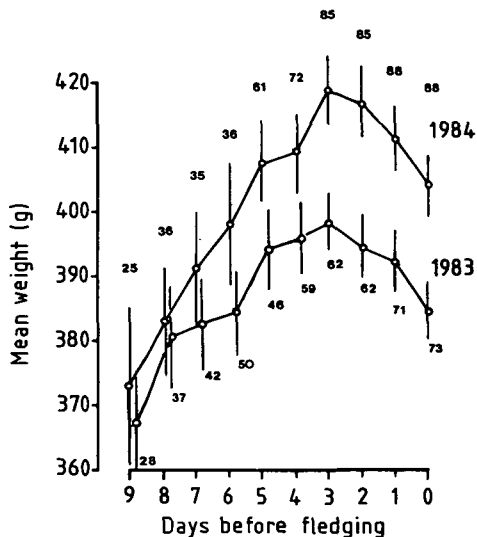Significant differences (t-tests) are denoted by: * P<0.05, ** P<0.02, *** P<0.001.

Figure 4. Changes in mean chick weights in the 10 days prior to fledging in 1983 and 1984. Data from all nests have been combined. Mean ± s.e. and sample size is given for each chick age category.

For 25 nests having the same brood size in the two study years, and at which no mate or pair change was known to have occurred between years (determined by observations of colour-ringed adults), chicks were significantly heavier at fledging in 1984 than in 1983 (paired t-test, $t_{32} = 5.24$, P<0.0001).

Factors affecting chick growth parameters

Egg weight, hatching interval, brood size and timing of breeding
Fresh egg weight was significantly correlated with day 0 chick weight in both years ($r_{17} = 0.54$, P<0.02 in 1983; $r_{20} = 0.60$, P<0.01 in 1984), and with fledging weight in 1984 ($r_{15} = 0.51$, P=0.01), but in 1983 the relationship was non-significant, though still positive ($r_{14} = 0.12$, P=0.67). It might be expected, a priori, that a longer hatching interval in 2-chick broods would give the a-chick greater advantage over the b-chick, particularly when food was scarce. However, for the two study years, when the b-chick hatched within a day of the a-chick it fledged on average 1-2 days later and 1-6 g heavier than the a-chick. But, with a hatching interval of 2 days the b-chick fledged on average 19 g lighter than the a-chick. Single chicks reached significantly higher peak weights, and fledged heavier than those in 2-chick broods (significant only in 1984 though) (Table III; Fig. 3). There were significant negative correlations between fledging weight and fledging date for single chicks and those in 2-chick broods in both years (1984 results only are shown in Fig. 5). To investigate the suggestion of Belopol'skii (1957) that young hatched later in the season have shorter fledging periods, I performed a correlation analysis for fledging period and hatching date. In neither year were significant relationships found ($r_{105} = 0.09$ in 1983, and $r_{105} = 0.15$ in 1984).
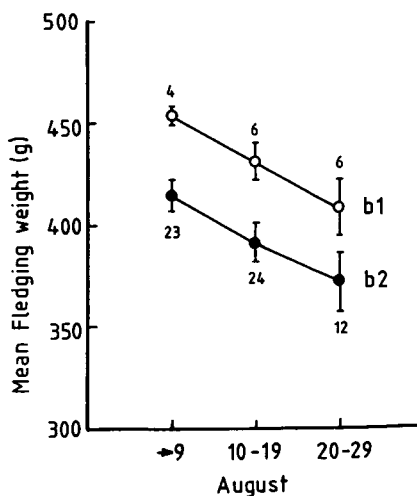
Figure 5. Fledging weights (mean ± s.e., with sample sizes) of chicks in broods of 1 and 2 fledging at different stages of the season in 1984. Correlation analyses carried out on the actual data were significant for both b1 chicks ($r_{14} = -0.52$, P<0.05) and b2 chicks ($r_{57} = -0.41$, P<0.01).

Weather and sea conditions
Weather conditions during the nestling stage were assessed using the daily means of hourly mean wind speeds and the minimum day-time air temperature. These two parameters, along with sea-surface temperatures, were thought to be good indicators of environmental conditions likely to affect food availability, foraging success and energy balance of adult Black Guillemots at this

stage. For the period between median hatching date and median fledging date, the mean daily wind speed was significantly higher in 1983 than in 1984 (12.2 ± 5.3 vs. 9.8 ± 3.3 knots, t_{71} = 2.26, P=0.03). In this period mean daily wind speed exceeded 15 knots on 12 days in 1983, but only on 4 days in 1984. Mean minimum day-time air temperature was significantly lower in 1983 than in 1984 (10.5 ± 1.7°C vs. 11.1 ± 0.7°C, t_{71} =2.19, P=0.03). The average July sea-surface temperature was unusually high (12.3°C) in 1983, compared with a more normal figure (11.2°C) in 1984 (based on an inspection of data from 1980-85). Therefore, reduced chick growth parameters in 1983 were associated with cooler and windier weather conditions, and a warmer sea surface during the chick stage.

Food provisioning: quantity and quality
Chicks of all ages gained, on average, more weight per day in 1984 than in 1983, but put on less weight per gram of fish delivered, particularly in the later stages of the season (Table II). These differences were associated with a greater proportion of fish species of lower energy equivalent in the chick diet in 1984 (notably more gadids and butterfish *Pholis gunnellus*), as opposed to sandeels (Ewins 1986, 1990). At colony A the mean hourly provisioning rates (per chick) were higher for all chick age categories in 1984 than in 1983 (Fig. 6), although the difference was only significant for chicks in the 25-29 d age group (t_{15} = 3.04, P<0.01).
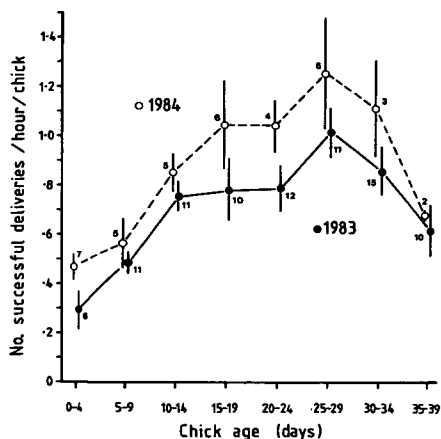
Figure 6. Mean hourly delivery rates of fish delivered to chicks of different ages at colony A in 1983 and 1984. For each age class the mean and standard error are given, with the number of separate observation periods at least 2 hours long from which the data were taken.

Kleptoparasitism
The mean duration of the fledging period in colonies experiencing higher rates of kleptoparasitism (mainly from Arctic Skuas, Herring Gulls and Lesser Black-backed Gulls) was not extended significantly in either year. However, in colony B (which experienced the highest rates of kleptoparasitism), b-chicks took, on average, 1.3 days longer to fledge than a-chicks in 1983, and 2.3 days longer in 1984 (although these differences were not statistically significant). For both single chicks and those with siblings, there was a significant negative correlation between fledging weight and the mean % of delivery attempts at a given colony which lost fish as a result of kleptoparasite activity (Fig. 7).

Figure 7. Mean fledging weights (± s.e., with sample size) of chicks in broods of 1 (open circles) and 2 (filled circles) chicks, in colonies experiencing differing rates of kleptoparasitism (given as the mean % of delivery attempts losing fish as a result of kleptoparasite activity). The correlations (performed on the actual data points for 1983 and 1984 data combined) were significant for both b1 (r = - 0.36; $F_{1,38}$ = 5.7, P=0.02) and b2 (r = - 0.19; $F_{1,120}$ = 4.65, P=0.03).
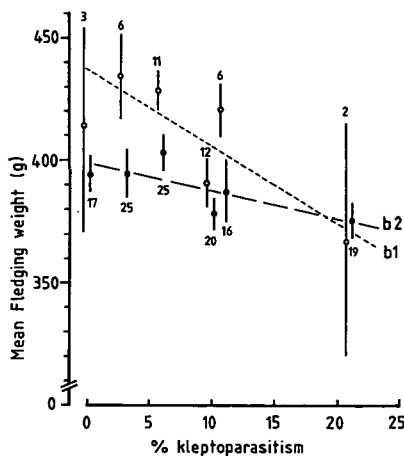
DISCUSSION

The rates of weight increase for chicks in both years are amongst the highest recorded for Black Guillemots, or any auk species (Sealy 1973; Gaston 1985; Cairns 1987), indicating that feeding conditions were relatively good on Mousa during this study. In most bird species the response to nutrient deficiencies in the diet of chicks is usually reduced rates of weight increase, and extension of the fledging period (Ricklefs 1979), whilst growth of anatomical features such as wing, tarsus and bill, proceeds independently (Ricklefs 1968). Brood reduction may also occur when food is very scarce, particularly in species hatching chicks asynchronously (Lack 1954).

On Mousa, both the fledging periods and rates of wing growth were similar for chicks in both brood sizes and in 1983 and 1984. Chicks in 2-chick broods were as likely to fledge in 1983 as in 1984 (93.0% vs. 93.5% respectively), providing no evidence for any brood reduction (Ewins 1989), and indicating that feeding conditions were never sufficiently poor during the study years to lead to chick starvation. However, a number of results do suggest that feeding conditions for Black Guillemots on Mousa were better in 1984 than in 1983, resulting in the significantly heavier chicks in 1984. Fresh eggs (and chicks at hatching) were heavier, breeding was earlier, adults were significantly heavier (post-laying), and chick provisioning rates were significantly higher in 1984. Therefore, food may have been scarcer in 1983, possibly throughout the season (see Ewins 1989), but not acutely so during the chick period. In this way, the only parameter affected was the rate of weight increase in chicks. In two "normal" years at a colony in Denmark, chicks fledged at 98-102 % of adult weight (ie. similar to this study), but at only 90% in a year of failing food resources (Asbirk 1979).

Although no precise direct measure of food availability was available, the appearance inshore of large numbers of gadids (probably mostly Norway pout *Trisopterus esmarkii*) in the later stages of the 1984 breeding season, provided large quantities of potential prey (based on personal observations of seabird diets on Mousa, 1982-84). Whilst these fish have a lower energy equivalent than sandeels, their abundance probably more than compensated for the declining

availability of sandeels at this time (Ewins 1990), and so resulted in greater weight consumption and net energy intake by chicks. In an Alaskan study of Pigeon Guillemots *Cepphus columba*, Oakley (1981) also found that diet quality, and not just quantity, exerted a major influence on chick growth. When Puffins on St. Kilda were forced to feed chicks on less-preferred fish (whiting *Merlangius merlangus*), mean fledging weights were lower than when sprats *Sprattus sprattus* (the preferred diet, of higher energy equivalent) were available (Harris & Hislop 1978). Similarly, Yellow-eyed Penguin *Megadyptes antipodes* chicks experienced depressed weight growth rates, fledging weights, and increased mortality when fed prey with low oil (and hence energy) content (Van Heezik & Davis 1990).

Weight decline prior to fledging was not found by Kaftanovski (1951) in Black Guillemots. Although a few Mousa chicks did continue putting on weight right up to the day of fledging, the average weight decline of about 7% agrees well with all other growth studies in this species (Belopol'skii 1957; Asbirk 1979; Petersen 1981). Pre-fledging weight recession is common in chicks of auk species which fledge at near-adult size, and has usually been attributed to reduction of body water content (Gaston 1985). Hudson (1979) suggested that chicks may have to attain some critical wing loading prior to fledging, which could be achieved by such water loss. However, since Black Guillemots are probably incapable of sustained flight at fledging (and probably for up to 2 weeks thereafter), this explanation is not favoured. More likely, the pre-fledging weight recession could be an adaptive reduction of fat deposits, thereby improving the diving capabilities of newly fledged young, which could be important for capturing fish as well as avoiding predators (Harris 1984).

The influence of environmental conditions on chick growth is difficult to assess, since many factors are probably inter-related, and their effects on prey availability are still poorly understood. Calmer and milder weather at the chick stage in 1984 was associated with improved growth parameters, possibly explained by reduced energy expenditure on existence metabolism, by both chicks and adults. However, although conditions were windier and seas rougher during the 1983 chick period, major water turbulence usually extends only a few metres below the sea surface (Sverdrup *et al.* 1942; Harris & Wanless 1985; J. Goodman pers. comm.), and for a species like Black Guillemot which forages mostly in water 10-50 m deep, at least during the breeding season (Piatt & Nettleship 1985; Ewins 1986), excessive turbulence is likely to seriously impede foraging only in very rough sea conditions. Daily provisioning rates of chicks on Mousa did not appear to be related to weather conditions (Ewins 1986), but such effects might only become apparent when food is very scarce, or weather conditions particularly severe (neither was the case on Mousa during this study). Amongst other auks, Birkhead (1976) noted reduced feeding rates of Common Guillemot *Uria aalge* chicks in Wales, associated with rough seas, but no such effect was found in Scotland (Harris & Wanless 1985), nor for Thick-billed Murres *Uria lomvia* in Canada (Gaston & Nettleship 1981).

Oceanographic factors, such as tidal flow, sea surface temperatures, water mixing, and shifts in plankton distribution and abundance are more likely to exert a strong influence on Black Guillemot chick growth via changes in prey availability. This might be particularly so in areas (such as Mousa), where pelagic fish species are important in the chick diet (Ewins 1990). If young gadids experienced higher survival rates in 1984 as a result of lower sea surface temperatures (cf. Dickson *et al.* 1975), this may explain their increased availability to Black Guillemots, resulting in improved chick growth. However, such direct explanations must remain tentative, since there are undoubtedly numerous interactive effects in the North Sea food web, confounded greatly by man's intensive harvesting of many fish stocks.

SUMMARY

Growth of Black Guillemot chicks was studied on the island of Mousa, Shetland, in 1983 and 1984. Maximum rates of weight increase were amongst the highest recorded in this species, or for any other auk,

indicating that feeding conditions were relatively good around Mousa during the study years. Most weight parameters were higher in 1984 than in 1983, associated with greater provisioning rates, earlier breeding, and heavier adults, which all suggested better feeding conditions in 1984. Weather conditions and kleptoparasitism were also important factors, but fluctuations in prey availability, caused by oceanographic changes and food web interactions, probably have the greatest influence on chick growth in Shetland.

ACKNOWLEDGEMENTS

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P.J. Ewins, Edward Grey Institute of Field Ornithology, Dept. of Zoology, South Parks Road, Oxford. OX1 3PS, U.K. (Present address: Canadian Wildlife Service, Canada Centre for Inland Waters, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ontario. L7R 4A6, Canada.).

APPENDIX I. WET WEIGHT (g) : LENGTH (cm) REGRESSION EQUATIONS FOR INSHORE FISH SPECIES AT MOUSA IN 1984.

Fish type	Fish species	No. of fish	Regression
Gadid	*Pollachius virens*	45	$Wt = 0.00977 \, L^{2.96}$
Sandeel	*Ammodytes* spp.	81	$Wt = 0.00063 \, L^{3.57}$
Blenny	*Pholis gunnellus*	31	$Wt = 0.00105 \, L^{3.39}$
"	*Zoarces viviparus*	56	$Wt = 0.00617 \, L^{2.90}$
Rockling	*Gaidrosparus vulgaris*	41	$Wt = 0.00955 \, L^{2.89}$
"	*Ciliata* spp.	59	$Wt = 0.00631 \, L^{3.02}$
Cottid	*Cottus* spp.	61	$Wt = 0.02692 \, L^{2.77}$

Chick diets and food intake of nestling Common Guillemots *Uria aalge:* an inter-colony comparison.

B.J. Hatchwell, T.R. Birkhead, S.F. Goodburn, J.M. Perrins & S.E. Jones

INTRODUCTION

The population of Common Guillemots *Uria aalge* on Skomer Island and at other Irish Sea colonies has increased considerably in the past 20 years (Hatchwell & Birkhead 1991, Lloyd *et al.* 1991), following a long period of decline (Cramp *et al.* 1974, Birkhead & Ashcroft 1975). The reasons for this population change are not clear, but one possibility is that changes in the marine environment have made feeding conditions more favourable. The measurement of food availability is a major problem for seabird biologists because reliable fisheries data are rarely available and may not be applicable. The usual solution is to study the utilization of the marine environment by the seabirds themselves, an indirect sampling method enabling conclusions to be drawn on changes between years and differences between colonies (Furness & Monaghan 1987). Such studies have generally been conducted at geographically distant colonies with the result that there is little information available on local variation in food availability, or at least on local variation in the use of the marine environment by seabirds.

In this paper we present and compare the results of studies on the feeding ecology of guillemots on Skomer and Lundy Islands, two colonies 75 km apart in the southern Irish Sea. We include data on chick diet, provisioning rates, foraging trip durations and fish used in displays.

METHODS

Observations on Skomer (51°40'N 05°15'W) in 1985-87 showed that there was considerable seasonal variation in the composition of chick feeds and display fish, and also in the rate at which chicks were fed (Hatchwell 1988, 1991). Therefore, comparisons presented here include only those data from Skomer that were collected during a period coinciding with the study periods on Lundy (51°10'N 04°45'W). The seasonal variation may have been more closely associated with chick age rather than calendar date (Hatchwell 1991), so the comparison assumes similar timing of breeding at the two colonies. The timing of fledging at the two colonies was similar in 1986 (median fledging dates: Skomer 12 July, Lundy about 11 July), so this assumption seems reasonable.

Observations on Lundy were conducted from 17-28 June 1985 and 6-11 July 1986, at a colony containing 28-34 chicks in 1985 and 11-21 chicks in 1986. In 1985, ten 4-hour watches were made from 1400-1800 h (all times BST). In 1986, there was one watch from 0400-2215 h (dawn-dusk) on 10 July and five 4-hour watches, three from 1400-1800 h, and two from 0445-0845 h. On Skomer, observations were made at a group of up to 75 chicks from early June to mid-July in 1985-87. It was not possible to compare feeding rates at the two colonies in 1985 because an oil spill in June 1985 killed about 5% of adults on Skomer (Hatchwell 1988). In 1986, a dawn-dusk watch was conducted on 9 July and two 0500-0900 h watches and four 1400-1800 h watches were made during the period of study on Lundy. Observations were made using a telescope at distances of 50-100m.

When fish were brought to the colony during feeding watches we recorded the following information: time, breeding site, chick feed or display fish, fish species and size class. Species and size could not be identified for all feeds. Size classes were assigned as follows; Clupeidae: "small" 80-100mm, "medium" 100-120mm, "large" 120-140mm; sandeels Ammodytidae: "small" 80-110mm, "medium" 110-140mm, "large" 140-170mm. Mass and energy value of prey were

calculated from values given by Harris & Hislop (1978). On Skomer some dropped fish were collected from breeding ledges and from parents arriving at the colony. These were identified, weighed and measured, and they closely fitted the predicted length:mass relationships. All identified clupeids were sprats *Sprattus sprattus*, and all identified sandeels were *Ammodytes tobianus*. Harris & Hislop (1978) give length/mass and length/energy value relationships for *Ammodytes marinus* rather than *A. tobianus*, but we assume the same relationships for these two morphologically similar species. There was no significant difference between visual size estimates of feeds and the length of collected fish for either sandeels or sprats (Hatchwell 1991), indicating that visual size estimates were accurate.

During 4 h watches the time of departure of off-duty birds (who remained at the breeding site until departure) was also recorded and the interval between departure and subsequent arrival with a feed was used to measure the duration of foraging trips. Only those trips completed within an observation period were included in the analyses. These estimates of trip lengths are likely to be biased towards shorter trips since only those recorded within a 4 h watch are included: in 1985 the durations of 30% and 28% of trips preceding feeds were determined on Skomer and Lundy respectively, and the equivalent figures in 1986 were 30% and 40%. Although there are drawbacks to this method, compared to the data from dawn-dusk watches the main effect is to shorten the tail of the distribution rather than to create an artificial skew (unpublished data). For example, on Lundy in 1986, the median duration of 84 trips in 4 h watches was 28 minutes and the modal group was 1-20 minutes (Fig. 2), while on the 10 July during a dawn-dusk watch, the median duration of 32 trips was 46 minutes and the modal group was also 1-20 minutes.

RESULTS

Chick diet
The main prey species at both colonies were sandeels and sprats. A small number of Norway pout *Trisopterus esmarkii* (n=6), gadoids (n=2), mackerel *Scombrus scombrus* (n=1), shrimps (n=2) and squid (n=1) were also recorded on Skomer. In both 1985 and 1986 there was a significantly higher proportion of sandeels fed to chicks on Lundy than on Skomer (Table I). In 1985 there was no significant difference in the proportions of small, medium and large fish fed to chicks. However, in 1986, feeds on Lundy were significantly smaller than those on Skomer, with no large prey items recorded (Table I).

TABLE I. SPECIES AND SIZE COMPOSITION OF FISH FED TO YOUNG GUILLEMOTS ON SKOMER AND LUNDY IN 1985 AND 1986.

	1985		1986	
a) Species	Skomer	Lundy	Skomer	Lundy
Sprat	304 (68%)	44 (19%)	251 (91%)	86 (52%)
Sandeel	146 (32%)	190 (81%)	26 (9%)	78 (48%)
	$\chi^2_1 = 144.5$		$\chi^2_1 = 81.2$	
	P<0.001		P<0.001	
b) Size	Skomer	Lundy	Skomer	Lundy
Small	83 (20%)	44 (19%)	13 (5%)	76 (46%)
Medium	217 (51%)	130 (56%)	178 (64%)	88 (54%)
Large	123 (29%)	60 (26%)	87 (31%)	0 (-)
	$\chi^2_1 = 1.2$		$\chi^2_1 = 142.1$	
	NS		P<0.001	

TABLE II. COMPARISON OF FEEDING RATES (MEAN ± SD (NO. OF CHICKS)) ON SKOMER AND LUNDY IN 1986: (a) DAWN-DUSK WATCHES (FEEDS/CHICK/DAY), (b) AFTERNOON WATCHES (FEEDS/CHICK/4h), AND (c) MORNING WATCHES (FEEDS/CHICK/4h). FOR 4 HOUR PERIODS ONLY SIMULTANEOUS WATCHES HAVE BEEN COMPARED BETWEEN COLONIES. ALL TESTS ARE MANN-WHITNEY U TESTS.

	Skomer	*Lundy*	*P*
a) *Dawn-dusk*			
9/10 July	3.00±1.20 (43)	6.00±3.66 (17)	z=3.17 P<0.001
b) *Afternoon*			
6 July	0.87±0.90 (53)	–	
7 July	–	1.85±0.81 (20)	
8 July	0.69±0.63 (45)	1.95±1.28 (21)	z=2.89 P<0.01
9 July	0.65±0.65 (43)	2.10±1.41 (20)	z=4.10 P<0.001
10 July	–	1.12±1.11 (17)	
11 July	0.71±0.75 (35)	–	
c) *Morning*			
6 July	0.96±0.71 (53)	–	
8 July	–	1.76±1.09 (21)	
9 July	1.02±0.56 (44)	–	
10 July	–	2.12±1.54 (17)	
11 July	1.00±0.77 (11)	–	

Feeding rates

In 1986, chicks on Lundy were fed more frequently than chicks on Skomer (Table II). In the dawn-dusk watches the Lundy feeding rate (6 feeds/chick/day) was significantly higher than on Skomer (3 feeds/chick/day). Similarly, during afternoon watches the Lundy feeding rate was significantly higher than on Skomer (Mann-Whitney U Test: $U_{4,4}$=0, P<0.05), and during simultaneous watches on 8 and 9 July, rates were significantly higher on Lundy. There were too few morning watches for comparison. On Lundy, the mean feeding rate in afternoon watches in 1986 (1.76±0.44 feeds/chick/4h, n=4) was significantly higher than in 1985 (0.87±0.18 feeds/chick/4h, n=10; Mann-Whitney U Test: U=1, P<0.01).

The number of feeds in each hour was closely correlated between the two colonies (r_s=0.632, n=18, P<0.01) indicating a similar diurnal pattern of feeding (Fig. 1).
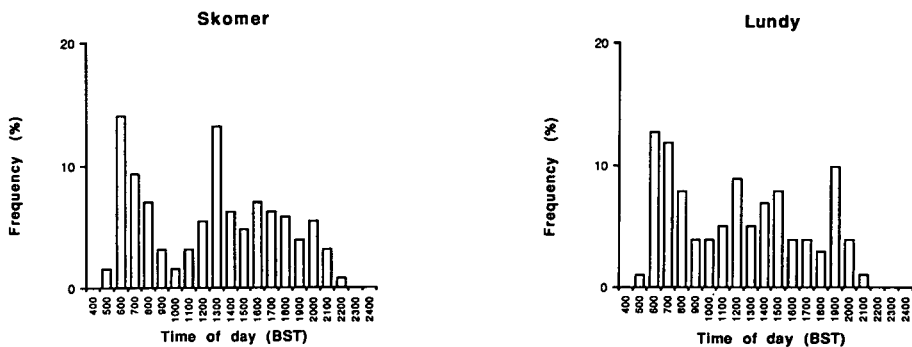
Figure 1. Diurnal distribution of feeds during dawn-dusk watches on Skomer (9 July 1986, n=129 feeds) and Lundy (10 July 1986, n=102 feeds).

Energy intake
Combining data collected on diet and feeding rates during dawn-dusk watches on Skomer and Lundy on 9 and 10 July 1986 respectively, the daily energy intake of chicks at each colony was estimated. The mean energy value of prey items on Skomer was calculated as 109 kJ, compared to only 49 kJ on Lundy. However, chicks were fed more frequently on Lundy, so the estimated daily energy intakes at the two colonies were similar: 296 kJ/chick/day on Lundy and 326 kJ/chick/day on Skomer.

Foraging trips
The distribution of foraging trips recorded on Lundy and Skomer in 1985-86 are shown in Fig. 2. There was no difference in trip durations in morning and afternoon watches in 1986 so data were pooled (Mann-Whitney U tests: Skomer z=1.94, NS; Lundy z=0.37, NS). The duration of foraging trips did not differ between years at the same colony (Mann-Whitney U tests: Skomer z=0.52, NS; Lundy z=1.32, NS), but within years, foraging trips were significantly shorter on Lundy than on Skomer (Mann-Whitney U tests: 1985 z=5.03, P<0.001; 1986 z=4.84, P<0.001; Fig. 2).
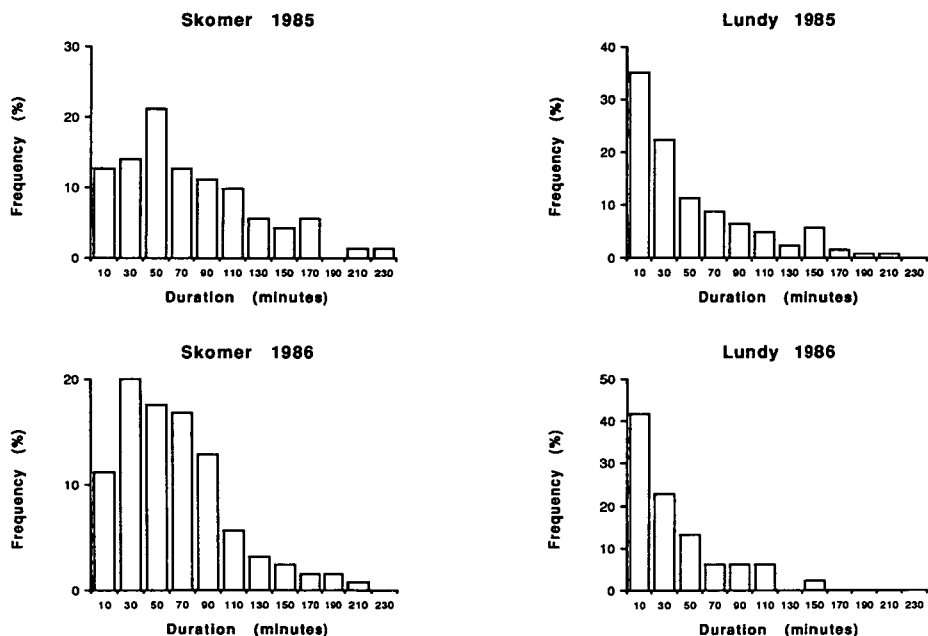
Figure 2. Duration of foraging trips on Skomer and Lundy in 1985 and 1986. Medians (no. of trips recorded): Skomer 1985, 64 minutes (125); Lundy 1985, 26 minutes (77); Skomer 1986, 65 minutes (71); Lundy 1986, 28 minutes (84).

Fish used for displays
The predominant species used in displays were sprats and sandeels, but three Norway pout (Skomer) and one butterfish *Pholis gunellus* (Lundy) were also recorded. The species composition of display fish did not differ between colonies (Table III). The size composition of display fish did not differ in 1985, but as for feeds, there was a significantly higher proportion of small fish used in displays on Lundy than on Skomer in 1986 (Table III).

TABLE III. SPECIES AND SIZE COMPOSITION OF FISH USED IN DISPLAYS ON SKOMER AND LUNDY IN 1985 AND 1986.

	1985		1986	
a) Species	Skomer	Lundy	Skomer	Lundy
Sprat	46 (53%)	11 (38%)	34 (64%)	49 (57%)
Sandeel	40 (47%)	18 (62%)	19 (36%)	37 (43%)
	$\chi^2_1 = 1.5$		$\chi^2_1 = 0.4$	
	NS		NS	
b) Size	Skomer	Lundy	Skomer	Lundy
Small	26 (31%)	12 (41%)	17 (32%)	59 (69%)
Medium	36 (42%)	11 (38%)	28 (53%)	25 (29%)
Large	23 (27%)	6 (21%)	8 (15%)	2 (2%)
	$\chi^2_2 = 1.2$		$\chi^2_2 = 20.3$	
	NS		P<0.001	

Chick feeds and display fish differed in species and size composition. On Skomer, a higher proportion of sandeels and small fish were used in displays than were fed to chicks (Species: 1985 χ^2_1=5.70, P<0.05; 1986 χ^2_1=24.25, P<0.001. Size: 1985 χ^2_2=5.21, NS; 1986 χ^2_2=41.84, P<0.001). On Lundy, the species composition of the two classes of prey differed significantly only in 1985, but display fish were smaller than those fed to chicks in both years (Species: 1985 χ^2_1=4.61, P<0.05; 1986 χ^2_1=0.30, NS. Size: 1985 χ^2_2=7.92, P<0.05; 1986 χ^2_1=10.38, P<0.01).

DISCUSSION

Despite Skomer and Lundy being only 75 km apart, there were marked differences in chick diet, suggesting that there was little overlap in the foraging areas used by birds at the two colonies. In 1986, the mean energetic value of prey on Lundy was less than half that of prey on Skomer, but parents appeared to compensate by bringing prey at a much higher rate, resulting in a very similar daily energy intake of chicks at the two colonies.

The high feeding rates observed at Lundy were presumably facilitated by the relatively short duration of foraging trips (Fig. 2), but a longer series of observations on Skomer in 1986 and 1987 showed no consistent relationship between the two variables (Hatchwell 1988). In addition, feeding rates on Lundy were significantly higher in 1986 than in 1985 even though there was no significant difference in the duration of foraging trips.

Estimates of the distance travelled to foraging areas on the basis of time absent from the breeding site are likely to be very crude because other activities may be performed when away from the colony. However, we can compare such estimates to obtain some idea of how far birds had to travel in order to find food. The median trip durations on Lundy were 26 and 28 minutes (Fig. 2), so with flight speed of 69 km/h (Pennycuick 1987) the foraging distance would be 15-16 km. On Skomer, median trip durations were 64 and 65 minutes (Fig. 2), giving a foraging distance of 37 km. The method for determining foraging trip duration was biased towards shorter trips (see Methods), tending to under-estimate foraging distance. However, the calculations of foraging distance allowed no time for locating and catching fish, and activity recorders indicate that guillemots feeding young spend only 10% of foraging trips in flight (Cairns et al. 1987). Our calculated foraging distances are therefore likely to be considerable over-estimates. Since the colonies are 75km apart these results lend further support to the earlier suggestion (made on the basis of chick diet) that there was little overlap in the foraging areas used by birds at the two colonies.

As reported previously from Skomer (Birkhead 1976, Hatchwell 1988) and from the Isle of May (Harris & Wanless 1985), fish used in displays were smaller than those fed to chicks at both colonies, and on Skomer comprised significantly more sandeels. Parents are under more severe economic constraints when feeding chicks because energetically expensive foraging trips are relatively frequent (Gaston 1985, Cairns *et al.* 1987), so chick feeds should comprise better quality prey than the infrequent displays, whose nutritional value is of little importance since they are often discarded (Birkhead 1976, Harris & Wanless 1985, pers. obs.). However, on Lundy there was no difference in the species composition of feeds and displays in 1986, and in 1985 there was a higher proportion of high energy value sprats used in displays than fed to chicks. The reasons for these results are not obvious, and it is also unclear why the composition of displays did not differ between colonies when there were such marked differences in the composition of feeds.

SUMMARY

The feeding ecology of Common Guillemot chicks at two colonies, Skomer and Lundy Islands, situated 75 km apart in the south Irish Sea was compared over two years. The diet of chicks varied significantly between colonies, with Lundy chicks fed on smaller prey than those on Skomer. However, chicks were fed more frequently on Lundy so the estimated daily energy intake was similar at both colonies. Parents on Lundy made shorter foraging trips than on Skomer. Chick diet and estimated foraging ranges indicated little overlap in foraging areas. Fish fed to chicks were generally of higher quality than those used in display.

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B.J. Hatchwell[1], T.R. Birkhead & S.F. Goodburn, Dept. of Animal & Plant Sciences, P.O. Box 601, University of Sheffield, Sheffield S10 2UQ.
[1] Present address: Edward Grey Institute, Dept. of Zoology, South Parks Road, Oxford OX1 3PS.
J.M. Perrins[2] & S. E. Jones, Dept. of Zoology, University of Bristol, Bristol.
[2] Present address: Dept. of Zoology, University of York, York YO1 5DD.

The diet of Cormorant *Phalacrocorax carbo* chicks in Shetland in 1989

J.D. Okill, J.A. Fowler, P.M. Ellis and G.W. Petrie

INTRODUCTION

Since 1983 several seabird species in Shetland have had difficulty in rearing chicks. These breeding failures have been linked with the availability of sandeels, *Ammodytes* sp. (Heubeck 1989), one of the major prey fish available in Shetland waters (Kunzlik 1989), and have occurred mainly in the surface-feeding and smaller species of seabirds. In contrast, the largest of Shetland's seabirds, the Cormorant *Phalacrocorax carbo* and the Gannet *Sula bassana*, appear to have been unaffected (Martin 1989; Okill 1989).

The diet of the Cormorant has been studied in many places throughout its wide range (Van Dobben 1952, Mills 1965, Mills 1969, West *et al.* 1974, Cramp & Simmons 1977). There has, however, been no previous study in Shetland and this paper presents the results of the analysis of food regurgitated by chicks in the four largest Shetland colonies, in 1989.

In 1989 there were 377 pairs of Cormorant breeding in Shetland (Shetland Bird Report 1989). With the exception of the colony on a small rocky island in Yell Sound all of the Cormorant colonies in Shetland are situated on stacks or steep cliffs off the west coast of Mainland. The population has been declining very slowly since the mid 1970's (Kinnear 1978, Shetland Bird Reports) but brood sizes have remained fairly constant since they were first recorded in 1976 (pers. obs.).

METHODS

The four largest Cormorant colonies (High Holm at St Ninian's Isle, Little Holm in Yell Sound, Clett Stack near Culswick and Muckle Roe) were visited between 18 June and 1 July 1989; the stacks were reached by inflatable boat, then climbed. Chicks of a suitable size were ringed, nests counted and clutch and brood sizes recorded. As Cormorant chicks are approached they often regurgitate food freely from their crops. Larger, undigested fish are usually regurgitated whole whilst well-digested ones are regurgitated as a bolus. These individual regurgitates were collected in plastic bags and subsequently frozen until examination.

Thawed regurgitates were dispersed in dilute alcohol solution contained in white plastic trays (approximately 35 x 23 x 5 cm) and loose disintegrating flesh washed off. Skeletal fragments and otoliths which remained were removed and matched against reference specimens obtained from fresh fish captured in Shetland waters. In some regurgitations intact fish were easily identifiable and furnished additional reference material. Samples of fresh fish were measured to 1.0 mm from the tip of the snout to the ventral lobe of the caudal fin extended backwards; their dissected otoliths were measured with Vernier calipers to 0.01 mm. The relationship between fish length and otolith length was examined by least squares regression, assigning otolith length to the x-variable. The mean length of each matched pair of otoliths was used. Sufficient data was obtained to calculate the regression equations for three fish species, namely:

Sandeel length = (44.01 x otolith length) + 27.92 mm; $n = 230$; SE = 0.05

Saithe length = (29.90 x otolith length) - 30.40 mm; $n = 48$; SE = 0.06

Sea scorpion length = (25 .40 x otolith length) + 22.10 mm; $n = 10$; SE = 3.52

where n is the number of pairs of otoliths measured and SE is the standard error of the slope of the regression line, b. These equations were used to estimate size class frequency distributions of fish in the diet from the lengths of fish recovered from the regurgitations. Because regurgitates consisted of relatively fresh food expelled from the crop rather than non-digestible pellets

TABLE I. FREQUENCY OF OCCURRENCE OF FISH IN CORMORANT CHICK REGURGITATES FROM
FOUR COLONIES IN SHETLAND IN 1989.

Species	Clett Stack	Little Holm	Muckle Roe	High Holm	Total
Saithe *Pollachius virens*	9	18	8	23	58
Pollack *Pollachius pollachius*	–	6	–	–	6
Sandeel *Ammodytes* sp.	1	1	29	4	35
Sea Scorpion *Taurulus buballis*	10	11	9	3	33
Butterfish *Pholis gunnellus*	2	5	–	2	9
Dab *Limanda limanda*	–	2	1	2	5
Flounder *Platichthys flesus*	5	3	3	6	17
Plaice *Pleuronectes platessa*	–	–	2	–	2
Ling *Molva molva*	–	1	3	2	6
Eel *Anguilla anguilla*	–	2	–	1	3
Sea Trout *Salmo trutta*	–	–	–	1	1
Rockling *Gaidropsarus vulgaris*	–	1	–	–	1
15-spined Stickleback *Spinachia spinachia*	–	–	–	1	1
TOTAL	27	50	55	45	177

regurgitated from the stomach, digestion of the otoliths was negligible. Indeed, most otoliths were
found in place within the skull, inacessible to digestive enzymes, in which case the mean length of
the two otoliths was used (Johnstone *et al.* 1990).

RESULTS

Thirteen species of fish (and a single edible crab, *Cancer pagurus* from Clett Stack) were found in
the regurgitates. Apart from sandeel, only 12 (10%) of the regurgitates contained more than a
single specimen of each fish species (7 with 2, 3 with 3 and 2 with 4). In regurgitations from
Muckle Roe 10 contained more than one sandeel (3 with 2, 1 with 4, 1 with 6, 1 with 8, 1 with 9, 2
with 15 and 1 with 16). To simplify the analysis (especially with regard to problems of
independence) frequency of occurrence of fish in regurgitates was examined with saithe and
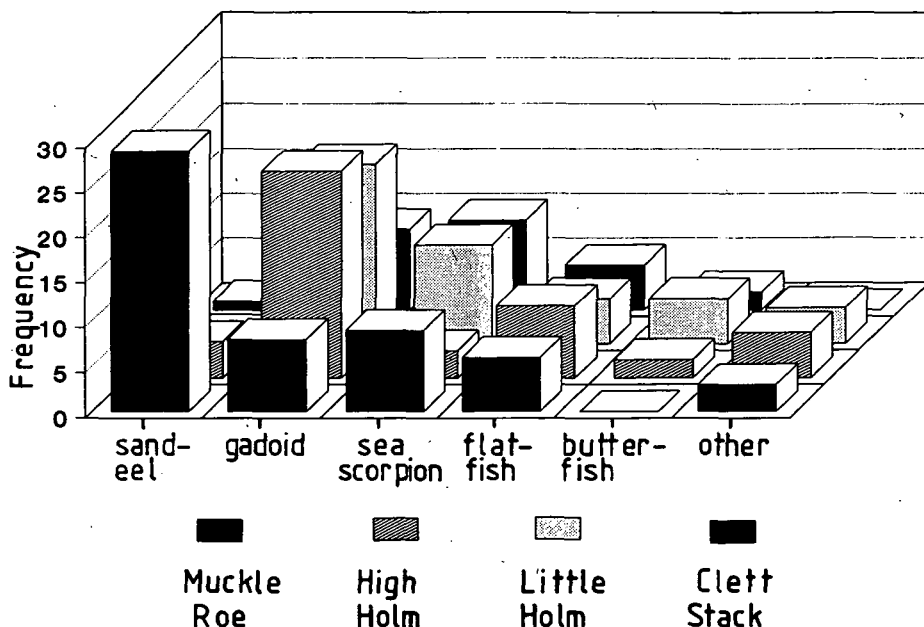
Figure 1. Frequency of occurrence of fish categories in Cormorant regurgitations collected from four colonies in Shetland, 1989.

pollack aggregated as "gadoids"; dab, flounder and plaice as "flatfish"; and ling, eel, sea trout, rockling and 15-spined stickleback as "others". The frequency distribution of fish species from regurgitations from each colony is given in Table I, together with scientific names of each fish species. Figure 1 shows the frequency of each fish category at each colony. There are significant differences in the proportional frequencies of fishes from the different colonies ($\chi^2_{15}=73.53$, P<0.01). Of particular interest are: the high proportion of sandeels in the Muckle Roe sample; the high proportion of butterfish at Little Holm and the low proportion at Muckle Roe; the low proportion of sea scorpions at High Holm; and the higher proportion of gadoids at Little Holm and High Holm and the lower proportion at Clett Stack and Muckle Roe.

The size class frequency distribution of sandeels, saithe and scorpion fish (aggregated from the four colonies) estimated from their average otolith lengths are shown in Figure 2. The modal size class for each species is: sandeel 125-130 mm; saithe 200-210 mm, sea scorpion 170-180 mm. Differences between colonies were minor with the exception of sea scorpions at High Holm; 6 of the 7 fish less than 120 mm were from this colony.

DISCUSSION

Cramp & Simmons (1977) list over 25 fish species (not all of which are present in Shetland waters) known to be taken by Cormorants and the 13 species recorded in this study reflects the Cormorant's catholic diet and the range of habitats in which it can feed. The relative proportions of the prey fishes in the diet of the chicks varied considerably between the four colonies, however the samples were collected on single visits to the colonies so may reflect daily variations. In this study the Muckle Roe colony was the only one with a high proportion of sandeels as part of the chicks'
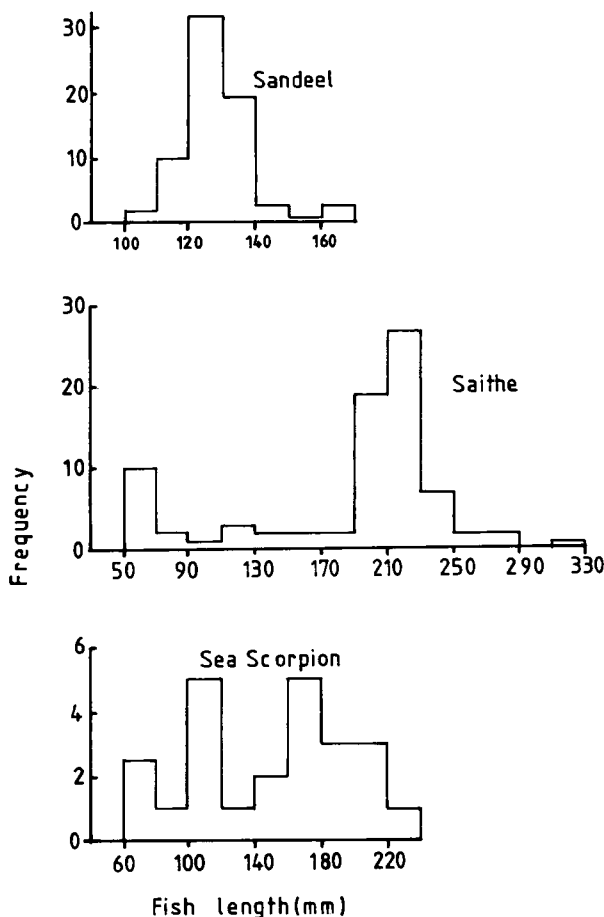
Figure 2. Frequency of size class of sandeels, saithe and scorpion fish in regurgitates from Cormorant chicks in Shetland, 1989.

diet. However during the late 1970s and early 1980s sandeels were often present in regurgitates from the other colonies (pers. obs.) although we have no quantitative data on this.

Sandeels in Shetland waters have recently become scarce (Kunzlik 1989) and the breeding performance of several seabird species is thought to have been reduced as a result. Whilst many Kittiwake, *Rissa tridactyla*, colonies around Shetland failed to produce any young in 1989, some chicks fledged at the colonies in the north west of Shetland (Walsh *et al.* 1990). The Muckle Roe site is the only large Cormorant colony in this area and here chick diet was dominated by sandeels and it is possible that this stock was also taken by the successful Kittiwakes.

It is likely that the different frequencies of prey species recorded at the different colonies reflects the distribution and availability of the prey species in the foraging area of birds from each colony. This was suggested by West *et al.* (1974) for Cormorants in Ireland. However, there is little data

available on the distribution, size or frequency of fish species in Shetland waters, or the preference of Cormorants for shoaling or non-shoaling species.

In addition, the differing calorific values of the prey species may be important in determining which species are taken. Of the main prey species recorded, sandeels have the highest calorific value (Appendix 1). When this species is available in sufficient numbers it is possible that it will be taken in preference to other species. Sandeels were the commonest prey item taken at a colony in east Caithness (MacKay 1988) and represented 41% (n = 27) of the fish in the diet.

The estimated sizes of three of the fish species found in the regurgitates are shown in Figure 2. The sandeels were similar in size to that taken by Bonxies, *Catharacta skua*, on Foula (Furness & Hislop 1981) and to Cormorants in the Caithness study (MacKay 1988) but are larger than those taken by Fulmars, *Fulmarus glacialis*, in Yell (Fowler & Dye 1987). Of the fish measured there is considerable variation in the size of the prey taken. It is noteworthy that the low number of sea scorpions in the High Holm sample were also the smallest of the measured sample.

Cormorants are able to take a wide range of fish species and sizes. Another large seabird in Shetland, the Gannet is thought to have changed its diet in response to food availability (Martin 1989), the diet at Hermaness changing from mostly sandeels in 1981 to mostly herring, *Clupea harengus*, and mackerel, *Scomber scombrus*, by 1988. This species, like the Cormorant, has shown no dramatic decline in its breeding success (Heubeck 1989) and it appears that because of their ability to take fish of a wide variety of species and sizes, Cormorants are better placed to withstand reductions in individual prey species, such as sandeels, than the smaller seabird species.

SUMMARY

Samples of food regurgitated by Cormorant chicks in four Shetland colonies comprised thirteen species of fish of a wide range of sizes and a single edible crab. There was considerable variation in diet between colonies, probably reflecting the local availability of the different prey species. It is thought that the catholic diet of the Cormorant has enabled it to maintain its breeding success when a number of smaller seabird species in Shetland have had poor breeding success due to a reduction in the availability of sandeels.

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J.D. Okill, Heilinabretta, Trondra, Shetland ZE1 0XL.

J.A. Fowler, The David Attenborough Laboratories, Leicester Polytechnic, Scraptoft, Leicestershire LE7 9SU.

P.M. Ellis, Seaview, Sandwick, Shetland ZE2 9HP.

G.W. Petrie, 18 Fogralea, Lerwick, Shetland ZE1 OSE.

APPENDIX 1. ENERGY DENSITIES OF PREY SPECIES OF SHETLAND CORMORANTS.

Energy values given as kJ/g wet weight

Species	*Energy Value*			*Source*
	mean	±*S.E.*	*n.*	
Sandeel (6-20cm)	6.50	± 0.23	8	Harris & Hislop (1978)
Butterfish	5.01	± 0.17	4	D.A.D. Grant unpublished
Saithe	4.29	± 0.13	3	D.A.D. Grant unpublished
Sea scorpion	3.76	± 0.08	4	D.A.D. Grant unpublished
Flounder	2.40	–	–	Prevost 1982

Behaviour and occurrence of Black Guille-mots *Cepphus grylle* in a colony of Pigeon Guillemots *C. columba* on the Chukotka Peninsula, U.S.S.R.

Nikolai B. Konyukhov and Peter J. Ewins

INTRODUCTION

Over the past fifty years there has been considerable debate over taxonomic relationships within the alcid genus *Cepphus* (guillemots). Some have suggested that the genus contains three full extant species, Pigeon Guillemot *C. columba*, Black Guillemot *C. grylle*, and Spectacled Guillemot *C. carbo* (Storer 1952; Kozlova 1957), and this is the current, generally held view. Varying numbers of subspecies have been proposed for the first two species (Salomonsen 1944; Udvardy 1963), whereas others have regarded the Pigeon Guillemot as a subspecies of Black Guillemot (Dement'ev *et al.* 1951; Kartaschew 1960, 1974).

Spectacled Guillemots and the smaller Pigeon Guillemot are confined to the North Pacific, and their breeding ranges overlap in only a few parts of the Sea of Okhotsk and in the Kuril Islands (Ewins *et al.* in press). Pigeon Guillemot skins from the Kuril Islands show considerable reduction in the extent of white in the wing as one proceeds south, towards the breeding range of the all-dark Spectacled Guillemot (pers. obs.), and Kozlova (1957) suggested specific designation of these Kuril Islands birds, as *C. snowi*. The Black Guillemot has a holarctic breeding distribution, being most numerous at high latitudes (Nettleship & Evans 1985), but in the Alaskan waters of Bering Strait small numbers have been recorded from breeding colonies of Pigeon Guillemots (Bedard 1966, and references therein; Sowls *et al.* 1978; Ewins *et al.* in press), and Bedard (1985) has suggested that Black Guillemots may be reinvading the North Pacific (in an evolutionary sense) from further north. In this paper we report on Black Guillemots occupying nesting habitat within large colonies of Pigeon Guillemots along the western side of the Bering Strait, on the southern side of the Chukotka Peninsula in the USSR, and provide the first documentation of interactions between these two closely-related species in an area of sympatry.

STUDY AREA AND METHODS

All observations were made by NBK during the course of detailed studies from 1988 to 1990 of Pigeon Guillemots and other alcids at colonies in the vicinity of Cape Ulyakhpen on the southern side of the Chukotka Peninsula, at approx 64°23'N, 173°54'W (Fig. 1). The cliffs in this area were up to 200m high, often comprising large stretches of loose rock and talus, and hosted large numbers of breeding seabirds, notably Fulmars *Fulmarus glacialis*, Horned Puffins *Fratercula corniculatus*, Tufted Puffins *Lunda cirrhata*, Parakeet Auklets *Cyclorrhynchus psittacula*, Crested Auklets *Aethia cristatella*, Least Auklets *A. pusilla*, and Pigeon Guillemots (at least 2,900 birds along a 350 m stretch of cliffs).

Observations at the main colony of Pigeon Guillemots were carried out between late May and early September in each of the three study years, and about 60 hours in total was spent recording Black Guillemot activities. Most guillemots frequented large piles of boulders and scree towards the base of the cliffs. Observations were made with 12 x magnification binoculars from amongst the rock piles, at a distance of c.30 m from the nests, which did not appear to disrupt the normal pattern of behaviour of the birds under observation. Unfortunately the nature of the nesting habitat made inspection of the nest-cavities impossible. All observations refer to guillemots seemingly in
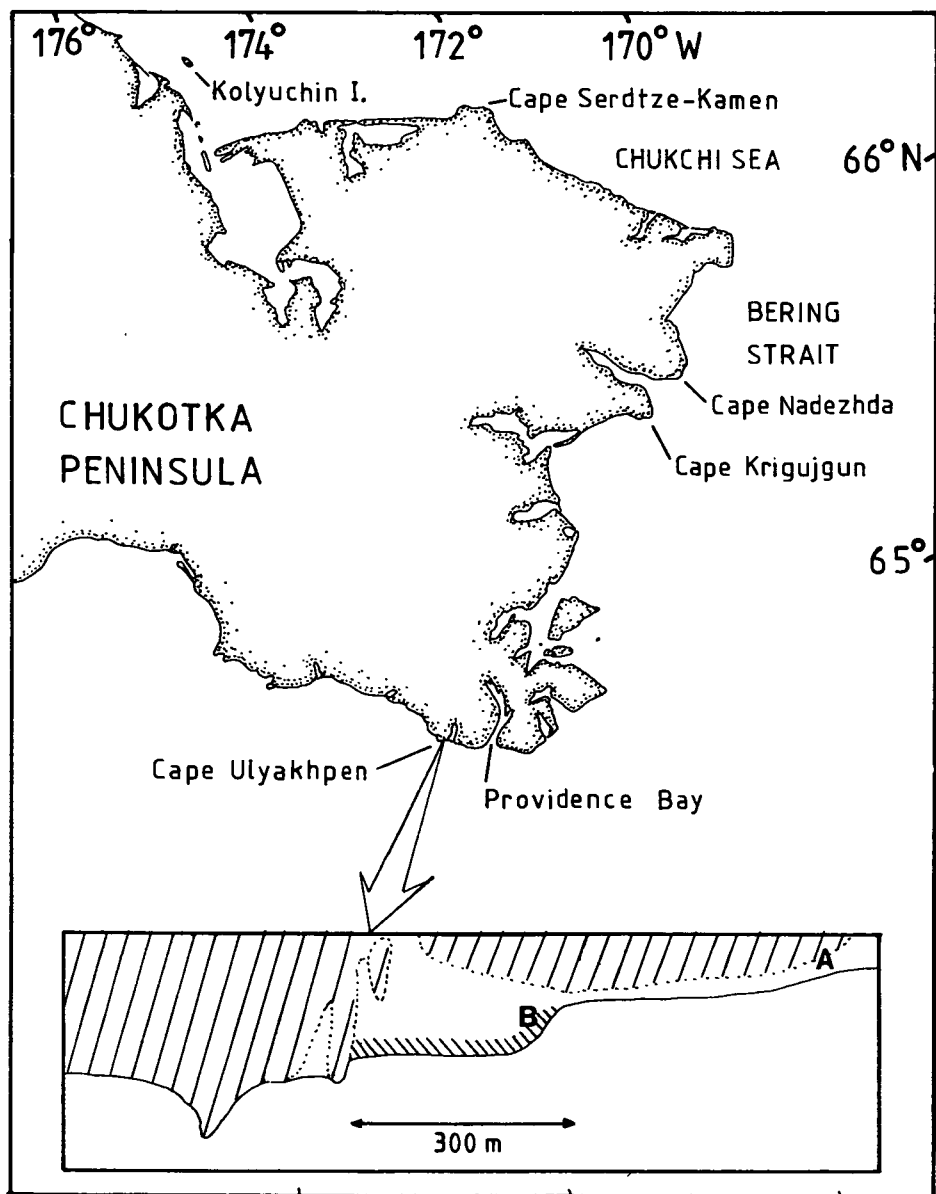
Figure 1. The location of Cape Ulyakhpen and other sites on the Chukotka Peninsula mentioned in the text.
/// Cliffs; \\\ main auklet colony. A, B represent Black Guillemot site locations.

adult plumage, ie. lacking the worn and abraded remiges and duller body plumage characteristic of immatures (1-year-olds) and sub-adults (2-3-year-olds usually) during the early to middle stages of the breeding season (Cramp 1985; pers. obs.).

OBSERVATIONS

Chronology

In 1988 a Black Guillemot in adult breeding plumage was located on 8 July, and again for over 4 hours on 17 July, in potential breeding habitat on cliffs towards the eastern end of the Pigeon Guillemot colony (site A on Fig. 1). No other guillemot was seen associating with this individual on these dates.

In 1989, what was presumably the same individual was present most mornings between 9 June and 12 August (up to 5 hours per morning), at a perch beside a suitable-looking nesting crevice at site A, amongst boulders and approximately 10 m above the beach. This bird frequently defended the nest area from approaching Pigeon Guillemots. The first sighting of a Pigeon Guillemot occurring with this Black Guillemot at site A was on 10 June. The laying peak for 2-egg clutches occurred in mid-late June in each study year. Observations were made of this nest area on 6 dates in July, for a total of nearly 14 hours, and always during the morning peak of colony attendance (0315 h to 1300 h was the range of observation times). Copulation attempts (all unsuccessful) were observed on four occasions, and the Black Guillemot always mounted the Pigeon Guillemot, so we presume that it was a male. Since the behavioural preliminaries were characteristic of a guillemot 'pair' (Drent 1965), we presume that the Pigeon Guillemot was a female. As both birds were usually present at the nest-perch, we suspect that no eggs were laid. On 12 August no birds were present at site A, but a single Black Guillemot was alone on the sea immediately offshore.

In 1990 a Black Guillemot was first seen back on the cliffs on 27 May (presumably the site A male from 1988-89). This time a perch beside a potential nest-crevice about 6 m away from the 1989 site was occupied. A Pigeon Guillemot (possibly the same bird as in 1989) arrived at the site on 4 June. This 'pair' were seen regularly at site A until early August, but there was no evidence of any breeding attempt other than unsuccessful copulation attempts.

On 18 July a second Black Guillemot was discovered occupying a perch about 500 m west of site A (site B on Fig. 1), and located within the main Pigeon Guillemot colony. This bird regularly defended a nest-perch, which was again located close to a potentially suitable nest-crevice, but during a total of over 11 hours of observations on 9 dates between 18 July and 18 August no other guillemot was seen to be tolerated for more than a few minutes at the perch.

A third Black Guillemot, also in adult breeding plumage, was seen ashore in this colony on 3 July 1990, but it did not associate with any particular nest-perch, and interacted little with other guillemots.

Behaviour

The behavioural postures adopted by the (male) Black Guillemot and the (female) Pigeon Guillemot at site A in both 1989 and 1990 appeared to be consistent with those described for these species and sexes by Drent (1965), Preston (1968), Asbirk (1979a), and Nelson (1984). We have followed the terminology of these authors in the displays described below, and indicated these postures by capital letters. We were unable to identify any marked differences between these two individuals or other members of these species in the range or type of behaviours seen. The male Black Guillemot regularly defended the nest-territory (crevice and rocky ledge nest-perch nearby) at site A in both 1989 and 1990, frequently displaying with Upright and Head Turning postures, Lunging and engaging in brief fights, and performing Duet Flights with neighbouring Pigeon Guillemots, but always returning to site A alone. Mutual Billing was never recorded between the mixed 'pair' at site A (this behaviour is characteristic of members of a normal pair, for both

species), but the female Pigeon Guillemot regularly attempted Billing with the male Black Guillemot, who never responded. Copulation attempts were preceded by Circling, involving the male Strutting in an Upright Posture around the female (who was usually sitting, with her tail down). However, in 1990 both birds engaged in Pre-Copulatory Circling, walking slowly around each other with a deliberate high-stepping/Strutting gait. Mounting attempts were usually from behind the female, but occasionally from one side, and on every occasion the female moved aside before any cloacal contact was achieved. This was always followed by both birds preening and then resuming a resting position sitting down.

The Black Guillemot at site B in 1990 always adopted an Upright Posture when a Pigeon Guillemot landed nearby, and usually moved towards an approaching Pigeon Guillemot, which always then flew away. This bird did not seem to engage in Duet Flights.

DISCUSSION

In Alaskan waters of the North Pacific/Bering Strait area, Black Guillemots have now been recorded in small numbers during the breeding season at a few localities (usually supporting Pigeon Guillemot colonies), south to St. Lawrence Island (63°N) (Anderson 1915; references in Bedard 1966; Swartz 1966; Sowls et al. 1978). In Soviet waters in this area, summer records of Black Guillemots are mainly from Kolyuchin Island (Kondratiev 1986), Chaun Bay to Capes Onman and Keleneut (Kozlova 1957; Ewins et al. in press), Cape Nadezhda (latitude = 65°46'N) (Konyukhov in press), and Cape Krigujgun (65°28'N), (pers. obs.). Pigeon Guillemots probably breed only as far north as Cape Serdtze-Kamen (pers. obs.), and there are only two records of stragglers further north (Portenko 1973; Kondratiev et al. 1987). Kozlova (1957) stated that small numbers of sexually immature Black Guillemots occurred in summer in Providence Bay, on the southern side of the Chukotka Peninsula, but it is not clear if this refers mostly to first-year birds, or whether there was any association with potential nesting habitat. Therefore, the Cape Ulyakhpen observations clearly confirm a marked extension of the summer range of adults of this species on the western side of the Bering Strait, as well as providing the first account of social interactions between Black and Pigeon Guillemots in an area of sympatry.

The two Black Guillemots found by Bedard (1966) in a large Pigeon Guillemot colony on St. Lawrence Island appeared not to be casual transients at the colony, and they returned regularly to favoured rock perches after disturbance. When they were shot (July 31) both were found to be females, apparently in adult plumage and in good condition, one having a slightly enlarged oviduct. Unfortunately no further proof of breeding was obtained. Some Black Guillemots move south into the Bering Strait in autumn, presumably to avoid severe ice conditions further north (Ewins et al. in press), and some movement eastwards, from wintering areas along the southern shores of the Chukotka peninsula has been noted in spring at Cape Ulyakhpen, presumably of birds returning to colonies in the Chukchi Sea (pers. obs.). Therefore there is scope for Black Guillemots from high latitude colonies to associate with Pigeon Guillemot colonies at lower latitudes, prior to return movements northwards in the spring. There are some indications that Black Guillemot numbers in Alaska have been increasing in recent decades and that the range expansion has been facilitated by the provision of suitable nest-sites (oil-related industrial debris, derelict buildings, artificial nest-sites) (Divoky et al. 1974; Divoky & Boekelheide 1978; Sowls et al. 1978). Clearly, without more detailed census data it is impossible to determine whether Black Guillemots are indeed expanding their breeding range southwards into the North Pacific, but the above evidence and our observations concur with the idea of a steady but slow '(re)invasion' of these Pacific waters (sensu Bedard 1985).

The behavioural observations are difficult to interpret beyond concluding that the postures noted were all much as given for both species in published behavioural studies (and seen by ourselves) in other parts of their range. It is not clear why the mixed pairing (site A) should have consistently

failed to achieve a successful copulation, since the pre-copulatory circling appeared to be as seen and described for these species (Drent 1965; Asbirk 1979a; pers. obs.). However, the absence of mutual billing between the members of the pair may have been very important, and sufficient to prevent the female from allowing the male to mount. We have assumed that the Pigeon Guillemot was a female, and although we think it unlikely, it is still possible that both birds were in fact males. Drent (1965) observed a number of male-male copulation attempts amongst Pigeon Guillemots in his colony in British Columbia, but in each case there was little if any preliminary behaviour, rather a male would simply rush up to another bird and attempt to copulate, always unsuccessfully. Since the site A pair spent considerable time engaged in pre-copulatory behaviour we suspect that the sexes were different. Another possibility is that the female Pigeon Guillemot was not yet sexually mature, and although her feathers did not appear unduly worn, she could conceivably have been as young as 2 or 3-years-old, even in 1989. *Cepphus* guillemots can breed at 3 years of age (exceptionally at 2), but 4-5 is probably a more typical age for a first breeding attempt (Asbirk 1979b; Cramp 1985).

On the basis of these observations we are unable to determine precisely what, if any, behavioural isolating mechanism might operate to prevent pairing of Black and Pigeon Guillemots in areas of sympatry. Pigeon Guillemots are slightly larger than Black Guillemots, but there is some overlap in body size and wing length. Otherwise, the biology, social behaviour and plumage of these two species are very similar. The dark bar within the white wing patch of adult Pigeon Guillemots may be important though, since it makes the wing look more like that of an immature Black Guillemot: in Iceland, Aevar Petersen (pers. comm.) found that marking this white patch on adult Black Guillemots resulted in their being attacked and chased away by unmarked adults, in much the same way that immatures are driven from nesting areas (pers. obs.). In conclusion, there are still no proven cases of interbreeding between Black and Pigeon Guillemots. A more detailed behavioual study may reveal subtle but important differences which separate the two species, but clearly the North Pacific also currently offers some exciting opportunities for investigating the evolutionary forces which have led to speciation amongst the *Cepphus* guillemots.

SUMMARY

At least three separate adult Black Guillemots frequented a large Pigeon Guillemot colony on the southern shores of the Chukotka peninsula, USSR, at various stages during the breeding seasons of 1988-1990. Two Black Guillemots, probably both males, defended suitable nesting sites, and one seemed to be paired with a female Pigeon Guillemot for much of two seasons, although all copulation attempts were unsuccessful. Behavioural postures adopted by the members of the mixed pairing appeared to be very similar and consistent with published accounts, and it remains uncertain whether any behavioral isolating mechanisms exist between these two species. These observations confirm a marked southwesterly extension of the summer range of Black Guillemots in adult plumage and may reflect a gradual reinvasion of the North Pacific by individuals from higher latitudes.

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Nikolai B. Konyukhov, Laboratory of Bird Ecology, IAEME, 1st Kotelnichesky per., 10, Moscow, 109240, U.S.S.R.

Peter J. Ewins, Canadian Wildlife Service, Canada Centre for Inland Waters, 867 Lakeshore Road, P.O. Box 5050, Burlington, Ontario, L7R 4A6, Canada.

33

Phthiraptera of petrels and skuas from Gough Island, South Atlantic Ocean

R.W. Furness and R.L. Palma

INTRODUCTION

Ectoparasites occur widely on seabirds and have been studied by a number of authors. The population dynamics of feather lice (Insecta: Phthiraptera) found on auks was studied by Eveleigh & Threlfall (1976). There have been many studies of systematics (e.g. Edwards 1961, Price & Clay 1972, Palma & Pilgrim 1983, 1984, 1988), host specificity, frequency distribution on hosts, population age-structure and dynamics of feather lice from a wide variety of species of Procellariiformes from South Orkney Islands (Fowler & Price 1987), Scotland (Fowler & Miller 1984, Fowler & Palma 1986, Fowler & Furness 1987, Fowler & Hodson 1988) and Wales (Fowler & Shaw 1989). Phthiraptera can be valuable in throwing light on phylogenetic relationships and geographic origins of birds because particular species of Phthiraptera tend to be found only on one or a few closely- related species of hosts (Rothschild & Clay 1952, Timmermann 1965, Pilgrim & Palma 1982, Zonfrillo 1988, in press).

Gough Island, in the centre of the South Atlantic Ocean (40°S 10°W) is a small island about 15 km long, but has enormous populations of many species of procellariiform birds, and many of them (and some at neighbouring Tristan da Cunha with which Gough Island forms an extended archipelago) are endemic subspecies or endemic species (Swales 1965). The procellariiform taxa breeding on the island are Wandering Albatross *Diomedea exulans exulans*, Yellow-nosed Albatross *D. chlororhynchos*, Sooty Albatross *Phoebetria fusca*, Southern Giant Petrel *Macronectes giganteus*, White-chinned Petrel *Procellaria aequinoctialis*, Grey Petrel *P. cinerea*, Great Shearwater *Puffinus gravis*, Little Shearwater *P. assimilis elegans*, Broad-billed Prion *Pachyptila vittata vittata*, Atlantic Petrel *Pterodroma incerta*, Great-winged Petrel *P. macroptera*, Soft-plumaged Petrel *P. mollis mollis*, Kerguelen Petrel *Lugensa brevirostris*, White-faced Storm-petrel *Pelagodroma marina marina*, White-bellied Storm-petrel *Fregetta grallaria leucogaster*, Grey-backed Storm-petrel *Garrodia nereis*, and Common Diving-petrel *Pelecanoides urinatrix dacunhae* (taxa follow Swales 1965 updated by Harrison 1983 and Turbott 1990). Most of these birds breed on the lower slopes of the island, and many are burrow-nesters. The numbers present on a small area of land are staggering, with many tens of millions of birds visiting the burrows at night (Swales 1965). Furthermore, most species that use burrows appear to compete for the same burrows on a small part of the island around the coastal clifftop fringe where the ground is covered in deep dry and fibrous peat, rather than showing clear species segregation into different burrowing habitats (Swales 1965, pers. obs.) and so there is enormous opportunity for the transfer of ectoparasites between species. In addition to the large numbers of petrels and shearwaters, some 3000 pairs and a further 3000 nonbreeding Tristan Skuas *Catharacta skua hamiltoni* share the same habitat and feed almost exclusively on the burrow-nesting petrel immatures and adults captured on the surface at night, and on adults and chicks dug out of burrows (Furness 1987).

In view of the extremely high nesting density of seabirds on Gough Island and common use of burrows by several species, one might expect high incidence rates (the mean number of lice per bird) of feather lice and the occurrence of the same species of lice on a variety of hosts. However, because lice are highly host specific the latter is not so, but the information on the lice found on the endemic seabird forms on Gough Island may be of value in assessing relationships between these populations and others elsewhere.

This paper reports the identities and numbers of Phthiraptera obtained from a variety of seabirds from Gough Island in 1985. The birds were caught and deloused by Furness and the lice identified by Palma.

METHODS

Between 30 October and 16 November 1985 burrow-nesting Procellariiformes and skuas were attracted at night to a hand- held quartz-halogen spotlight powered by a 9v motorcycle battery. All birds sampled were caught with a hand-net on the ground on a densely-burrowed area of the lower slopes of Gough Island close to the weather station in the south-east corner of the island. An attempt was made to sample a variety of species but sample sizes reflect to some extent the relative abundances of the different species in that area. Each bird captured was examined in the hand and only adult birds were retained for delousing. Birds were taken individually to the laboratory and deloused in a plastic bucket (approx. 8l) for 20 min, as described by Fowler & Cohen (1983). The anaesthetic used was 15 cm³ of chloroform and the bucket was kept at laboratory temperature (ca. 20°C) to ensure rapid removal of lice. The high temperature causes the chloroform to evaporate quickly and to diffuse through the feathers. After the removal of the bird, lice were picked from the bucket using a fine dissection paintbrush and insect forceps, and were stored in 70% alcohol. No magnification was used to aid searching for lice in the bucket and so some first instars may have been missed. Lice on the head and neck regions would not be sampled by this method.

Because of the time taken to capture, transport, delouse, release the bird and sort the lice, it was not possible to delouse more than three or four birds per night. Lice were also taken by hand-sorting through the head and neck feathers of one adult Wandering Albatross caught at its nest. Altogether, lice were collected from 11 Soft-plumaged Petrels, 10 Broad-billed Prions, 7 Atlantic Petrels, 4 Common Diving-petrels, 4 White- faced Storm-petrels, 1 White-bellied Storm-petrel, 4 Tristan Skuas, 3 Kerguelen Petrels, 3 Great Shearwaters, and 1 Little Shearwater. Identifications were made by R.L. Palma by comparisons with a reference collection in the National Museum, Wellington, N.Z. All the specimens from this study are kept in that collection.

RESULTS

Lice were collected from all seabird species examined. The extraction efficiency of the method is not known and so numbers removed from individual birds represent an unknown proportion of the total ectoparasite burden. The lice removed were from the body and wings and not from the head of the birds, which was not subjected to hand-sorting except for the Wandering Albatross. Two of three Kerguelen Petrels processed gave no lice, but every other bird produced at least one louse and up to 125. Some 24 species of feather lice were identified, representing 12 different genera.

TABLE I. SUMMARY STATISTICS FOR FEATHER LOUSE INFESTATION OF SEABIRDS AT GOUGH ISLAND

Seabird species	Number deloused	Number with lice	Lice per bird mean	range	Number of louse species	Number of each louse species as percentage of the total lice present
Kerguelen Petrel	3	1	4.7	0-14	1	100
Little Shearwater	1	1	27	–	2	70, 30
Great Shearwater	3	3	14.3	9-25	3	40, 37, 23
White-bellied Storm-petrel	1	1	8	–	2	88, 12
Common Diving-petrel	4	4	9.5	6-17	3	68, 29, 3
White-faced Storm-petrel	4	4	17.0	7-34	2	94, 6
Broad-billed Prion	10	10	49.4	4-125	4	99, 0.5, 0.2, 0.2
Atlantic Petrel	7	7	27.3	9-85	4	48, 33, 18, 1
Soft-plumaged Petrel	11	11	52.0	23-84	5	42, 37, 19, 2, 0.2
Tristan Skua	4	4	40.2	10-68	2	99, 1

TABLE II. INFESTATION RATES AND MEAN NUMBERS OF LICE EXTRACTED PER BIRD FOR
DIFFERENT SPECIES OF FEATHER LICE AND SEABIRDS ON GOUGH ISLAND.

Louse	Host	Number deloused	Incidence rate	Infestation rate mean	variance
Docophoroides brevis	Wandering Albatross	1	100	5.0	–
Bedfordiella unica	Kerguelen Petrel	3	33	14.0	–
Halipeurus mundae	Little Shearwater	1	100	19.0	–
H. gravis gravis	Great Shearwater	3	100	3.3	6.3
H. falsus pacificus	Common Diving-petrel	4	75	2.8	7.6
H. pelagicus	White-faced Storm-petrel	4	100	16.0	116.0
H. pelagicus	White-bellied Storm-petrel	1	100	1.0	–
H. procellariae	Atlantic Petrel	7	71	9.0	108.0
H. procellariae	Soft-plumaged Petrel	11	100	21.9	186.3
Trabeculus mirabilis	Little Shearwater	1	100	8.0	–
T. hexakon	Great Shearwater	3	100	5.3	24.3
T. schillingi	Atlantic Petrel	7	86	4.9	20.8
T. schillingi	Soft-plumaged Petrel	11	100	9.7	61.4
Austromenopon stammeri	Broad-billed Prion	10	20	0.2	–
A. popellus	Atlantic Petrel	7	29	0.4	0.6
A. popellus	Soft-plumaged Petrel	11	64	1.0	1.0
A. fuscofasciatum	Tristan Skua	4	25	1.0	–
A. elliotti	Common Diving-petrel	4	25	0.2	–
Naubates harrisoni	Great Shearwater	3	100	5.7	4.3
N. prioni	Broad-billed Prion	10	100	49.0	1623.8
N. pterodromi	Atlantic Petrel	7	100	13.0	195.7
N. pterodromi	Soft-plumaged Petrel	11	100	19.3	87.6
Pelmatocerandra setosa	Common Diving-petrel	4	75	6.5	43.7
Saemundssonia marina	White-faced Storm-petrel	4	25	1.0	–
S. desolata	Broad-billed Prion	10	10	0.1	–
Haffneria grandis	Tristan Skua	4	100	40.0	732.7
Ancistrona sp.	Broad-billed Prion	10	10	0.1	–
Longimenopon sp.	Soft-plumaged Petrel	11	9	0.1	–
Philoceanus sp.	White-bellied Storm-petrel	1	100	7.0	–

The numbers of feather lice of each species, age class and sex collected from each bird are shown
in Appendix 1. Excluding the single Wandering Albatross, 1615 feather lice were extracted from
the total of 48 birds.

Broad-billed Prions and Tristan Skuas had a large number of lice per bird but a low species
diversity, whereas Soft-plumaged Petrels were host to both large numbers and a wide species
diversity of lice. Kerguelen Petrels were noticeably lacking in lice (Table I).

Despite the fact that many seabirds (especially prions, Soft-plumaged Petrels, Atlantic Petrels,
Little Shearwaters, Common Diving-petrels and storm-petrels) were sharing a common nesting
habitat, breeding at unusually high density, and often co-occurring in burrows, there was a
remarkable lack of shared louse species (Table II). Only two seabird species were common hosts to
several louse species; the Atlantic Petrel and its congener the Soft-plumaged Petrel were both host
to *Naubates pterodromi, Halipeurus procellariae, Trabeculus schillingi* and *Austromenopon
popellus*. Furthermore, the abundances of these lice on the two host species were very similar
(Table III). Tristan Skuas carried two species of feather louse. *Haffneria grandis* was numerous on

all four birds processed but no species of *Haffneria* was found on any of the procellariiforms. One specimen of *Austromenopon fuscofasciatum* was found on one of the skuas. Although *Austromenopon* occurred on Common Diving-petrels, prions, Soft-plumaged Petrels and Atlantic Petrels, those birds carried different species of *Austromenopon* (Table II).

Sample sizes were too small to attempt the construction of frequency distributions. However, except for the very rare louse species, the variance:mean ratios were statistically significantly greater than unity (Table II) indicating that lice were contagiously, rather than randomly, dispersed among their hosts (p<0.05, chi² tests for random dispersion). This observation is in accordance with previous studies on seabird ectoparasites where a negative binomial has been shown to be the underlying model of dispersion (Fowler & Price 1987).

TABLE III. FREQUENCIES OF FIVE DIFFERENT GENERA OF FEATHER LICE AMONG THE TOTAL COMMUNITY OF LICE ON ATLANTIC PETRELS, SOFT-PLUMAGED PET- RELS AND KERGUELEN PETRELS AT GOUGH ISLAND.

Genus of louse	Atlantic Petrel	Soft-plumaged Petrel	Kerguelen Petrel
Naubates	48%	37%	0%
Halipeurus	33%	42%	0%
Trabeculus	18%	19%	0%
Austromenopon	1%	2%	0%
Bedfordiella	0%	0%	100%
Total number of lice	191	572	14
Number of birds	7	11	3

DISCUSSION

The samples of seabirds from Gough Island showed Phthiraptera infestation rates (% of hosts infected) of 100% except in the case of the Kerguelen Petrel, with some 20-50 lice on most individual birds. These incidence rates and infestation rates are very similar to those reported for Manx Shearwaters *Puffinus puffinus* in Wales where all 240 birds sampled carried lice with a mean of 53 per bird (Fowler & Shaw 1989). Fowler & Price (1987), Fowler & Miller (1984) and Fowler & Hodson (1988), who used exactly the same delousing method, found infestation rates and incidence rates of feather lice of 98% and 5.8 per bird for British Storm-petrels *Hydrobates pelagicus*, 85% and 6.6 per bird for Wilson's Storm-petrels *Oceanites oceanicus*, 80% and 2.7 per bird for Northern Fulmars *Fulmarus glacialis* and 63% and 1.5 per bird for Leach's Petrels *Oceanodroma leucorhoa*, which are rather lower figures than found among the seabirds on Gough Island, except for the Kerguelen Petrel. These data may suggest that feather lice are less frequent on storm-petrels than on the larger procellariiforms, and there seems to be a hint of this in our data (Table I). Alternatively, the high infestation and incidence rates of lice on Gough seabirds may reflect the particularly high nesting densities of seabirds there. The Kerguelen Petrel is something of an exception in this regard in that it nests rather thinly on the wet upper slopes of the Gough mountains. It is the only burrow-nester in that habitat on Gough since almost all the other species occupy the relatively restricted area of dry and flatter peatland on the coastal clifftop fringes.

The high degree of host-specificity of the many feather louse species is clear evidence of their inability to colonise alternative hosts since the Gough Island seabirds come into physical contact frequently on the surface, and nonbreeders in particular often enter burrows tenanted by other species. Furthermore, the 3000 pairs of skuas must kill about one million burrowing procellariiforms each year (Furness 1987). Since they leave the carcasses of their kills within their territories over the area occupied by burrowing birds, some tens of millions of feather lice must be

left on dead hosts each year and may attempt to locate a new host. Most birds killed by skuas are prions, storm-petrels, Soft-plumaged Petrels or Atlantic Petrels, and a few Kerguelen Petrels, Common Diving-petrels and shearwaters are also taken (Furness 1987). Despite most of these prey having dozens of feather lice on them, it would appear that these abundant lice of petrels are unable to thrive on the skua eating the petrels. Lice from petrels must transfer onto skuas on Gough but clearly skuas are not satisfactory hosts for them to become established.

The close similarity between the feather lice of Soft-plumaged Petrels and Atlantic Petrels suggests a recent evolutionary divergence between the species. By contrast, the Kerguelen Petrel has a rather different louse association with one species of *Bedfordiella* and no *Naubates, Halipeurus, Trabeculus* or *Austromenopon* on the three specimens we processed. The Kerguelen Petrel is very similar in superficial appearance to the two *Pterodroma* species and used to be classified in that genus, but recently it has been put into a genus of its own (*Lugensa*), more closely related to the fulmarine petrels, largely on the basis of its unique intestinal morphology (Imber 1985). This classification is also supported by evidence from feather lice. As we found on birds from Gough Island, Kerguelen Petrels collected elsewhere have carried *Bedfordiella* but no *Naubates, Halipeurus,* or *Trabeculus* (Timmermann 1965, Pilgrim & Palma 1982, Palma & Pilgrim 1983), although *Austromenopon popellus* has been found on Kerguelen Petrels where they share the same nesting habitat as White-chinned Petrels, and Imber (1985) suggested that this may be the result of a secondary infestation on Kerguelen Petrels.

Fowler & Shaw (1989) found that adult lice outnumbered nymphs on Manx Shearwaters and that the sex ratio among adults was near unity. In the samples from Gough, sex ratio was close to 1:1 for every louse and seabird combination (Appendix 1). Adults considerably outnumbered nymphs for every species except *Haffneria grandis* where 39 adults and 121 nymphs were extracted from skuas. Nymphs outnumbered adults on each of the four skuas processed, suggesting that *Haffneria* was at a seasonal peak of breeding when the birds were sampled in November (Marshall 1981).

It would appear to be a characteristic of *Austromenopon* that both incidence and infestation rates are low. Of the 13 birds from which this genus of louse was extracted, nine provided only one specimen, three provided two and one gave three. By contrast, *Naubates, Halipeurus* and *Trabeculus* tended to show comparatively high infestation rates and large numbers per infected host (Table II).

SUMMARY

In November 1985, 1620 feather lice of 24 species were extracted from 49 seabirds of eleven species. Despite high nesting densities and predatory interactions most species of lice were found on only a single host species. Kerguelen Petrels, recently separated from the genus *Pterodroma*, had a very different louse fauna from the sympatric *Pterodroma* species. Soft-plumaged and Atlantic Petrels were the only species to share nearly identical louse communities. With the exception of the Kerguelen Petrel, louse infestations rates and incidence rates were high on all species examined, and lice were dispersed contagiously through the host populations.

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Robert W. Furness, Applied Ornithology Unit, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, U.K. and Percy FitzPatrick Institute of African Ornithology, University of Cape Town, South Africa and Ricardo L. Palma, National Museum of New Zealand, Wellington, New Zealand

APPENDIX 1. LIST OF FEATHER LICE COLLECTED FROM GOUGH ISLAND SEABIRDS IN NOVEMBER 1985. NUMBERS ON EACH BIRD ARE ADULT MALES, ADULT FEMALES, NYMPHS I, NYMPHS II, NYMPHS III.

Seabird	Wandering Albatross *Diomedea exulans exulans* (endemic subspecies)
Louse	*Docophoroides brevis* (Dufour, 1835)
Numbers	Bird 1: 0, 2, 0, 3, 0.

Seabird	Great Shearwater *Puffinus gravis* (species breeding almost confined to Tristan archipelago)
Louse	*Naubates harrisoni* Bedford, 1930
Numbers	Bird 1: 1, 2, 0, 3, 2.
	Bird 2: 0, 1, 2, 0, 2.
	Bird 3: 1, 1, 1, 1, 0.

Louse	*Halipeurus gravis gravis* Timmermann, 1961
Numbers	Bird 1: 1, 1, 1, 3, 0.
	Bird 2: 0, 0, 1, 0, 0.
	Bird 3: 0, 1, 0, 1, 1.

Louse	*Trabeculus hexakon* (Waterston, 1914)
Numbers	Bird 1: 7, 4, 0, 0, 0.
	Bird 2: 2, 1, 0, 0, 0.
	Bird 3: 0, 2, 0, 0, 0.

Seabird	Little Shearwater *Puffinus assimilis elegans*
	(subspecies largely restricted to Tristan archipelago)

Louse	*Halipeurus mundae* Edwards, 1961
Numbers	Bird 1: 7, 8, 2, 2, 0.

Louse	*Trabeculus mirabilis* (Kellogg, 1896)
Numbers	Bird 1: 4, 4, 0, 0, 0.

Seabird	Kerguelen Petrel *Lugensa brevirostris*
	(monotypic, S. Atlantic and Indian Ocean)
Louse	*Bedfordiella unica* Thompson, 1937

Numbers	Bird 1: 2, 8, 2, 1, 1.

Seabird	Broad-billed Prion *Pachyptila vittata vittata*
	(S. Atlantic, Indian Ocean, New Zealand)

Louse	*Naubates prioni* (Enderlein, 1908)
Numbers	Bird 1: 24, 32, 14, 29, 26.
	Bird 2: 1, 0, 2, 0, 1.
	Bird 3: 27, 48, 4, 7, 32.
	Bird 4: 12, 13, 1, 11, 3.
	Bird 5: 7, 10, 3, 4, 3.
	Bird 6: 8, 11, 1, 6, 3.
	Bird 7: 10, 16, 3, 7, 8.
	Bird 8: 10, 10, 0, 2, 4.
	Bird 9: 8, 11, 1, 3, 3.
	Bird 10: 20, 19, 0, 3, 9.

Louse	*Austromenopon stammeri* Timmermann, 1963
Numbers	Bird 3: 0, 1, 0, 0, 0.
	Bird 9: 0, 1, 0, 0, 0.

Louse	*Saemundssonia desolata* Timmermann, 1959
Numbers	Bird 7: 1, 0, 0, 0, 0.

Louse	*Ancistrona* sp.
Numbers	Bird 10: 0, 1, 0, 0, 0.

Seabird	Atlantic Petrel *Pterodroma incerta* (endemic species)

Louse Numbers	*Naubates pterodromi* Bedford, 1930

Bird 1:   2, 5, 0, 1, 5.
Bird 2:   0, 3, 1, 1, 0.
Bird 3:   0, 1, 0, 5, 1.
Bird 4:   2, 3, 1, 0, 0.
Bird 5:   1, 1, 0, 0, 0.
Bird 6:   5, 4, 1, 2, 3.
Bird 7:   4, 26, 0, 7, 6.

Louse
Numbers   *Halipeurus procellariae* (J.C. Fabricius, 1775)
Bird 1:   5, 4, 4, 1, 1.
Bird 2:   3, 1, 2, 2, 1.
Bird 5:   2, 0, 0, 0, 0.
Bird 6:   4, 1, 1, 1, 1.
Bird 7:   3, 2, 3, 13, 8.

Louse
Numbers   *Austromenopon popellus* (Piaget, 1890)
Bird 1:   1, 1, 0, 0, 0.
Bird 2:   0, 1, 0, 0, 0.

Louse
Numbers   *Trabeculus schillingi* Rudow, 1866
Bird 1:   2, 2, 0, 1, 1.
Bird 2:   2, 6, 0, 0, 0.
Bird 3:   2, 0, 0, 0, 0.
Bird 5:   0, 1, 0, 0, 0.
Bird 6:   1, 3, 0, 0, 0.
Bird 7:   6, 5, 0, 0, 2.

Seabird   Soft-plumaged Petrel *Pterodroma mollis mollis*
(subspecies largely confined to Tristan group)

Louse
Numbers   *Naubates pterodromi* Bedford, 1930
Bird 1:   5, 5, 1, 1, 3.
Bird 2:   8, 8, 1, 9, 7.
Bird 3:   1, 3, 3, 1, 4.
Bird 4:   2, 2, 5, 6, 6.
Bird 5:   1, 8, 0, 4, 3.
Bird 6:   2, 2, 3, 1, 2.
Bird 7:   0, 5, 0, 2, 4.
Bird 8:   2, 6, 1, 6, 6.
Bird 9:   2, 6, 1, 5, 3.
Bird 10:   1, 8, 0, 2, 5.
Bird 11:   2, 11, 10, 11, 6.

Louse
Numbers   *Austromenopon popellus* (Piaget, 1890)
Bird 2:   0, 1, 0, 0, 0.
Bird 5:   1, 0, 0, 0, 0.
Bird 6:   0, 1, 0, 0, 0.
Bird 7:   2, 0, 0, 0, 0.

	Bird 8:	2, 1, 0, 0, 0.
	Bird 9:	0, 1, 0, 0, 0.
	Bird 11:	1, 1, 0, 0, 0.
Louse	*Halipeurus procellariae* (J.C. Fabricius, 1775)	
Numbers	Bird 1:	4, 1, 1, 0, 0.
	Bird 2:	8, 14, 0, 3, 3.
	Bird 3:	5, 4, 1, 0, 0.
	Bird 4:	12, 9, 4, 9, 5.
	Bird 5:	2, 9, 0, 4, 3.
	Bird 6:	6, 6, 0, 3, 4.
	Bird 7:	8, 9, 1, 2, 1.
	Bird 8:	4, 10, 0, 6, 4.
	Bird 9:	6, 3, 0, 1, 0.
	Bird 10:	14, 15, 1, 11, 11.
	Bird 11:	2, 5, 2, 3, 2.
Louse	*Longimenopon* sp.	
Numbers	Bird 9:	0, 1, 0, 0, 0.
Louse	*Trabeculus schillingi* Rudow, 1866	
Numbers	Bird 1:	1, 0, 0, 0, 1.
	Bird 2:	6, 10, 0, 0, 0.
	Bird 3:	2, 2, 0, 0, 1.
	Bird 4:	4, 0, 0, 0, 2.
	Bird 5:	1, 2, 0, 1, 3.
	Bird 6:	1, 3, 0, 0, 2.
	Bird 7:	0, 1, 0, 0, 0.
	Bird 8:	7, 0, 0, 1, 4.
	Bird 9:	5, 2, 0, 1, 0.
	Bird 10:	7, 1, 1, 0, 7.
	Bird 11:	9, 14, 1, 3, 1.

Seabird	White-bellied Storm-petrel *Fregetta grallaria leucogaster* (S. Atlantic and Indian Ocean)	
Louse	*Halipeurus (Synnautes) pelagicus* (Denny, 1842)	
Numbers	Bird 1:	1, 0, 0, 0, 0.
Louse	*Philoceanus sp.*	
Numbers	Bird 1:	4, 3, 0, 0, 0.

Seabird	Diving Petrel *Pelecanoides urinatrix dacunhae* (endemic subspecies)	
Louse	*Halipeurus falsus pacificus* Edwards, 1961	
Numbers	Bird 1:	1, 3, 0, 0, 0.
	Bird 2:	1, 0, 0, 0, 0.
	Bird 4:	3, 1, 1, 0, 1.

Louse   *Pelmatocerandra setosa* (Giebel, 1876)
Numbers   Bird 1:   1, 1, 0, 0, 0.
                Bird 3:   4, 7, 0, 0, 3.
                Bird 4:   2, 5, 0, 2, 1.

Louse   *Austromenopon elliotti* Timmermann, 1954
Numbers   Bird 4:   1, 0, 0, 0, 0.

Seabird   White-faced Storm Petrel *Pelagodroma marina marina*
                (endemic subspecies)

Louse   *Halipeurus (Synnautes) pelagicus* (Denny, 1842)
Numbers   Bird 1:   1, 3, 1, 2, 1.
                Bird 2:   6, 6, 0, 3, 4.
                Bird 3:   3, 4, 0, 0, 0.
                Bird 4:   12, 18, 0, 0, 0.

Louse   *Saemundssonia marina* Timmermann, 1956
Numbers   Bird 4:   4, 0, 0, 0, 0.

Seabird   Tristan Great Skua *Catharacta skua hamiltoni*
                (endemic subspecies)

Louse   *Haffneria grandis* (Piaget, 1880)
Numbers   Bird 1:   2, 0, 2, 6, 0.
                Bird 2:   4, 6, 10, 26, 11.
                Bird 3:   6, 6, 1, 6, 6.
                Bird 4:   9, 6, 9, 26, 18.

Louse   *Austromenopon fuscofasciatum* (Piaget, 1880)
Numbers   Bird 2:   0, 1, 0, 0, 0.

Temporal and spatial variations in body-weights of Common Terns and Arctic Terns

J.C.A. Craik and Peter H. Becker

INTRODUCTION

Terns are more vulnerable than most other seabirds to changes in food availability. Reasons for this include their small body size, the very limited depth to which they can dive, and the relatively narrow range of prey species of suitable size available near the surface of the water. Moreover, the abundance of small fishes and crustaceans on which terns feed may vary greatly from time to time and place to place (Becker *et al.* 1987), for natural or anthropogenic reasons. Breeding success of terns can be severely affected by such variations (Becker & Finck 1985, Monaghan *et al.* 1989, Mlody & Becker 1991).

The body-weight of breeding Common Terns *Sterna hirundo* varies greatly during the day, largely because of changes associated with feeding, digestion and excretion (Becker & Frank 1990). The body-weight of Arctic Terns *Sterna paradisaea* has repeatedly been shown to decrease during the breeding season (Belopolskii 1957, Bianki 1967, Monaghan *et al.* 1989). In this paper we show that body-weight of breeding terns can also vary significantly between populations and between years.

METHODS

Terns were studied in two coastal areas c. 900 km apart. In 1985, 1989 and 1990, Common and Arctic Terns were studied at 35 single-species or mixed colonies on small islands off the coast of west Scotland (c. 55° to 57°N and 5°40' to 5°50'W) within a north-south linear distance of 140 km. In 1982, Common Terns were studied on the island of Mellum (53°43'N 08°09'E) and in 1987-1989 on the island of Oldeoog (53°46'N 08°00'E); these two islands, c. 10 km apart, are in the southern part of the German Wadden Sea.

In both areas, adult terns were caught during incubation by nest-trapping during June and early July. Most were caught between 0800 and 2000 h. To avoid catching egg-laying females, in Germany trapping was carried out on clutches known to have been incubated for at least ten days. In the Scottish colonies, this rule could not be applied; instead, clutches of three were selected for Common Tern and clutches of two or three for Arctic Tern.

Trapped birds were not sexed. Wing-length was measured to the nearest mm by the maximum chord method. In Scotland, birds were weighed to the nearest g on a Pesola spring balance. In Germany, in 1982 a beam balance was used and in 1987-89 a Pesola spring balance or an electronic balance. Spring balances were calibrated regularly against an electronic balance.

No egg-carrying females were caught in Germany. In Scotland, however, a small number of trapped birds (1.4%) had an egg visibly protruding from the oviduct or a grossly swollen oviduct. Their body-weights (Common Tern N=7: 146, 148, 148, 152, 158, 159, 164; Arctic Tern N=2: 130, 131) were much higher than the normal range for trapped birds and have been excluded from the analysis below.

Data were obtained from seven samples of Common Tern and three of Arctic Tern, the samples differing in country and year of capture (Table I). The significance of differences between these samples was tested by a one-way ANOVA. In cases of significance (P ≤ 0.05) the means of the samples were compared by the multiple range test of Scheffé (Norusis 1986).

TABLE I. BODY-WEIGHTS OF SCOTTISH AND GERMAN COMMON TERNS AND OF SCOTTISH ARCTIC TERNS IN DIFFERENT YEARS.
First line: arithmetic mean ± sd, second line (in brackets): range, third line: no. of birds. As ANOVA showed significant differences between samples (Common Tern: $F_{6,676} = 29.364$, P<0.001; Arctic Tern: $F_{2,184} = 5.553$, P<0.01), means were tested by the multiple range test according to Scheffé (Norusis 1986).

				Body-weight (g)	
Sample	Site		Year	Common Tern	Arctic Tern
A	Scotland		1985	125.7 ± 7.5 b,c,f,g (107 - 141) 65	108.5 ± 6.4 b,c (94 - 124) 62
B	Scotland		1989	121.1 ± 7.1 a,D-G (101 - 142) 291	105.9 ± 6.7 a (90 - 128) 92
C	Scotland		1990	120.7 ± 7.0 a,D-G (107 - 139) 197	104.2 ± 5.5 a (92 - 115) 33
D	Germany, Mellum		1982	127.6 ± 7.5 B,C (113 - 156) 61	-
E	Germany, Oldeoog		1987	131.5 ± 10.8 B,C (104 - 152) 15	–
F	Germany, Oldeoog		1988	134.4 ± 9.4 a,B,C (120 - 150) 18	–
G	Germany, Oldeoog		1989	131.4 ± 9.3 a,B,C (114 - 149) 36	–

A letter following the mean ± sd shows that the two samples differ significantly, e.g. A: P<0.001, a: P<0.01, a: P<0.05.

RESULTS

Common Tern
In Scotland, body-weights in 1985 were significantly higher than in 1989 and 1990 (Table I); values in the two latter years did not differ significantly. In Germany, no significant differences between the samples were found.

In each of the years 1989 and 1990, Scottish birds were significantly lighter than German birds of 1982-89. In 1985, Scottish birds were significantly lighter than German birds on Oldeoog in 1988 and 1989. The highest Scottish value (in 1985) did not differ significantly from the two lower of the four German values (those of Mellum in 1982 and Oldeoog in 1987). Thus Scottish birds tended to be lighter than German birds, but extreme values for the two countries may overlap in certain years.

In Scottish birds, wing-length was slightly but significantly lower in 1989 than in 1985 (Table II). Values did not differ significantly between 1989 and 1990. In German birds, wing-length did not vary significantly between the four years.

Wing-length did not differ significantly between Scotland and Germany except in relation to the single year 1989, when significantly lower values were obtained in Scotland than on Oldeoog in

1987 (Table II). Thus, if wing-length is assumed to be a measure of body size, there was no evidence of permanent or prevalent size difference between the two countries.

Wing-length is a notoriously difficult measurement to standardise. Although all measurements in Scotland were made by the same person, the anomalous value in 1989 may have been due to unconscious variation in measuring technique rather than genuine reduction in size. In any case, a reduction of this small size, even if it were genuine, could not account for the reduction in weight observed in Scotland in 1989, as is shown in the next paragraph.

The relationship between body-weight and wing-length was examined for each year in the Scottish Common Terns. No significant correlations were found, except for Scottish birds in 1990. For these, there was a weak but significant correlation ($r = 0.203$, $N = 197$, $P < 0.01$; $y = 0.253x + 52.366$ where y=body-weight in g and x=wing-length in mm). This equation implies that a decrease in wing-length of 1 mm, such as observed in Scotland between 1985 and 1990 (Table II), would be accompanied by a reduction in body-weight of only 0.253 ± 0.087 (s.e.) g if due to wing-length reduction. The observed decrease in body weight was 5 g, however, and cannot therefore be explained by the small decrease in wing-length.

TABLE II: WING-LENGTHS OF SCOTTISH AND GERMAN COMMON TERNS AND OF SCOTTISH ARCTIC TERNS IN DIFFERENT YEARS.

First line: arithmetic mean ± sd, second line (in brackets): range, third line: no. of birds. As ANOVA showed significant differences between samples in case of the Common Tern ($F_{6,679} = 7.732$, $P < 0.001$), means were tested by the multiple range test according to Scheffé (Norusis 1986). Arctic Tern: $F_{2,186} = 0.339$, N.S.

			Wing-length (mm)	
Sample	Site	Year	Common Tern	Arctic Tern
A	Scotland	1985	271.1 ± 6.1 b	275.0 ± 6.6
			(257 - 286)	(261 - 290)
			69	63
B	Scotland	1989	268.1 ± 6.3 a,e	275.3 ± 5.5
			(251 - 285)	(261 - 292)
			294	93
C	Scotland	1990	269.9 ± 5.7	274.4 ± 5.4
			(250 - 285)	(263 - 282)
			200	33
D	Germany, Mellum	1982	271.1 ± 5.9	
			(260 - 285)	–
			61	
E	Germany, Oldeoog	1987	275.1 ± 8.8 b	
			(247 - 292)	–
			17	
F	Germany, Oldeoog	1988	274.6 ± 4.9	
			(266 - 280)	–
			8	
G	Germany, Oldeoog	1989	270.6 ± 6.6	
			(260 - 287)	–
			37	

A letter following the mean ± sd shows that the two samples differ significantly, e.g. a: $P < 0.01$, à: $P < 0.05$. N.S. not significant.

Arctic Tern

As in the case of Common Tern, the body-weights of Scottish Arctic terns in 1985 were significantly higher than in 1989 or 1990 (Table I). There was no significant difference in weight between 1989 and 1990.

There were no significant differences between the three years 1985, 1989 and 1990 in wing-lengths of Scottish Arctic Terns (Table II). There were no significant correlations between body-weight and wing-length for Arctic Terns, either within any of these three years, or for the three years combined.

DISCUSSION

Common Terns in Germany were generally heavier than those in west Scotland, the means differing by up to 14 g. Since there were no differences in body-size, as judged by wing-length, this significant difference may reflect better feeding conditions in the Wadden Sea. This in turn may be understood in terms of the high productivity of that part of the North Sea and the less productive, more oceanic regime of west Scotland. Marine productivity can vary over comparatively short distances. The Scottish tern colonies were mostly in the Sound of Jura and the Firth of Lorne, water bodies which are less productive (in terms of commercial fisheries) than for example the Firth of Clyde, 80-100 km to the south-east. Breeding terns have a smaller feeding range than larger seabird species (e.g. Pearson 1968) so one would expect that their body conditions would be correspondingly more dependent on local variations in food supply.

The significant daily body-weight fluctuations in adult Common Terns caused by feeding (Becker & Frank 1990) must be considered when interpreting weight data. The method of weighing incubating birds on the nest, which does not involve handling of the birds, was used on Oldeoog in 1985 by Becker & Frank (1990). Common Terns of 16 breeding pairs, weighed after incubation immediately before leaving the nest to feed, showed weights of 131.2 ± 10.3 g (range 105-163, N = 200 feeding flights). This is almost the same range as for nest-trapped birds in the same German study area (Table I). However, mean weights after feeding were 146.7 ± 12.0 g (range 111-174, N as before). Such high body weights were never obtained from nest-trapped birds (Table I). This striking difference probably has two causes. Firstly, most of the terns trapped on the nest would have been sitting for some time, so that food from the last feeding flight would have been digested. Secondly, birds trapped fully-fed may have regurgitated undigested food before or during handling (regurgitation by trapped and/or handled birds was regularly observed).

Body-weights of some of the shot Arctic Terns of both sexes reported by Bianki (1967), and of Arctic Terns recorded automatically during the breeding season by Monaghan *et al.* (1989), were also considerably higher than those found in this study, probably for the reasons just suggested. The much greater body-weights of egg-carrying females of these tern species (see Methods Section above and Nisbet 1977) may explain some of the pronounced decrease in mean weight between the start and end of the breeding season described in Arctic Tern by Belopolskii (1957), Bianki (1967) and Monaghan *et al.* (1989).

The differences in body-weight between 1985 and 1989-90 observed at Scottish colonies in both species, at most 5 g, are small in comparison with the daily weight fluctuations described above (Becker & Frank 1990) and may have been caused by a number of factors. Time of trapping in relation to time of day, tidal cycle or season, proportion of terns from particular colonies, sample sizes and colony age-structure could all have contributed to this result. We must, however, consider the possibility that the difference between 1985 and 1989-90 may reflect a genuine change in body condition in terns in west Scotland, possibly caused by a change in food availability. The same period saw the onset and repeated breeding failure of Arctic Terns and other seabirds in Shetland, 500 km to the north-east (Furness 1987, 1990, Monaghan *et al.* 1989) caused by the decreased availability of sandeels *Ammodytes* spp. The two phenomena may be associated. However, no such repeated breeding failures have occurred in recent years in the tern colonies of

the Scottish and German study areas described in this paper. Occasional years of mass breeding failure associated with food shortage or bad weather are usual in these species. Such mass failure occurred in the Wadden Sea in 1984 (Becker & Finck 1985, Mlody & Becker 1991) and in west Scotland in 1985 (Craik, unpubl. results). In Scotland, therefore, the highest recorded body-weights of incubating adults were recorded in a year of breeding failure. This paradox is perhaps explained by a requirement for fishes of different size or species by incubating adults and by growing chicks. These size classes or species of fish are not necessarily abundant simultaneously; indeed, perhaps one may be abundant when the other is scarce.

The suggestion of reduced food availability for terns in the west Scotland study area requires confirmation, however, both by studies of their food supply and by determination of weight gain during feeding by automatic electronic weighing.

SUMMARY

Body-weights of incubating Common Terns differed significantly between two coastal study areas, one in west Scotland, the other in the German Wadden Sea. Common Terns in Germany were heavier than those in west Scotland in most but not all of the years studied. In Scotland, body-weights of Common Terns and Arctic Terns were significantly lower in 1989 and 1990 than in 1985. None of these variations in weight could be explained by variations in size as measured by wing-length. The most likely explanation of these temporal and spatial variations in weight may be that they reflect changes in availability of food.

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J.C.A. Craik, Scottish Marine Biological Association, Dunstaffnage Marine Laboratory, Oban, Argyll PA34 4AD, Scotland.

Peter H. Becker, Institut für Vogelforschung, An Der Vogelwarte 21, D-1940 Wilhelmshaven-15, Germany.

Non-oiling Guillemot mortality incidents in the Moray Firth, 1983-86

Greg P. Mudge, Colin H. Crooke and Simon J. Aspinall

INTRODUCTION

In February 1983 there was an unusually large wreck of Razorbills *Alca torda* and Guillemots *Uria aalge* in the Moray Firth and along other eastern coasts of Britain (Underwood & Stowe 1984; Jones, Barratt, Mudge & Harris 1984, 1985). Similar incidents involving Guillemots have occurred within the Moray Firth in 1984, 1985 and 1986. This paper documents these incidents, presents information on the age and sex composition, physical condition and origins of the victims, and discusses the underlying reasons for these die-offs.
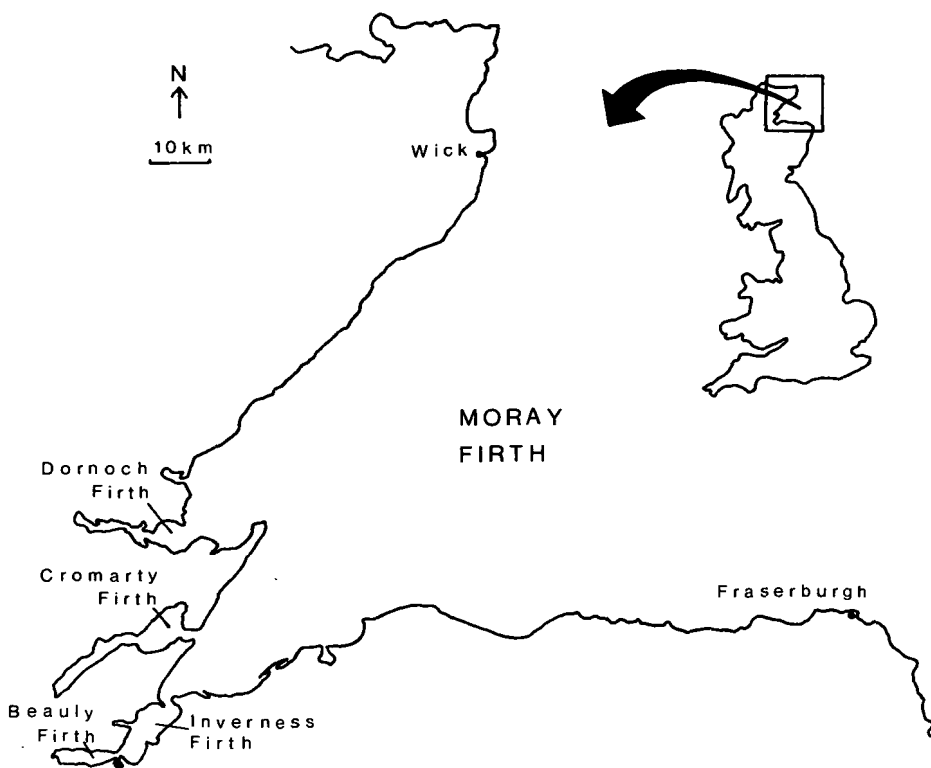

Figure 1. The study area.

METHODS

Basic monitoring of seabird mortality in the Moray Firth (Fig. 1) has been carried out since the early 1970's by regular winter beached-bird-surveys (see Stowe 1982; Heubeck 1987). Surveys were routinely carried out in January, February and March 1972-1988, and also in September, November and December in some years. The lengths of coasts surveyed varied between months and years. The average over the years 1972-88 was 93km in January (range 53-124km), 112km in February (52-194km) and 80km in March (41-119km). "Emergency" surveys were periodically carried out in response to identifiable mortality incidents. All corpses and wings found were identified to species (or species group) and the presence of any oil on the plumage was noted.

During identifiable incidents corpses were collected and subjected to detailed examination following Jones, Blake, Anker-Nilssen & Røstad (1982). Sex was determined by dissection and age was judged from the presence or absence and size of the cloacal bursa. In 1985 and 1986 first-winter birds were distinguished from older birds using wing feather characteristics (Kuschert, Ekelöf & Fleet 1981; Sandee 1984). The size of subcutaneous and abdominal fat deposits were scored on a scale from 0 = no fat up to 3 = thick deposits. The gizzard and crop were removed and contents examined using a binocular microscope. All food items were preserved in alcohol for later identification and measurement. Fish remains were identified to species or species-group by comparing otoliths with a reference collection.
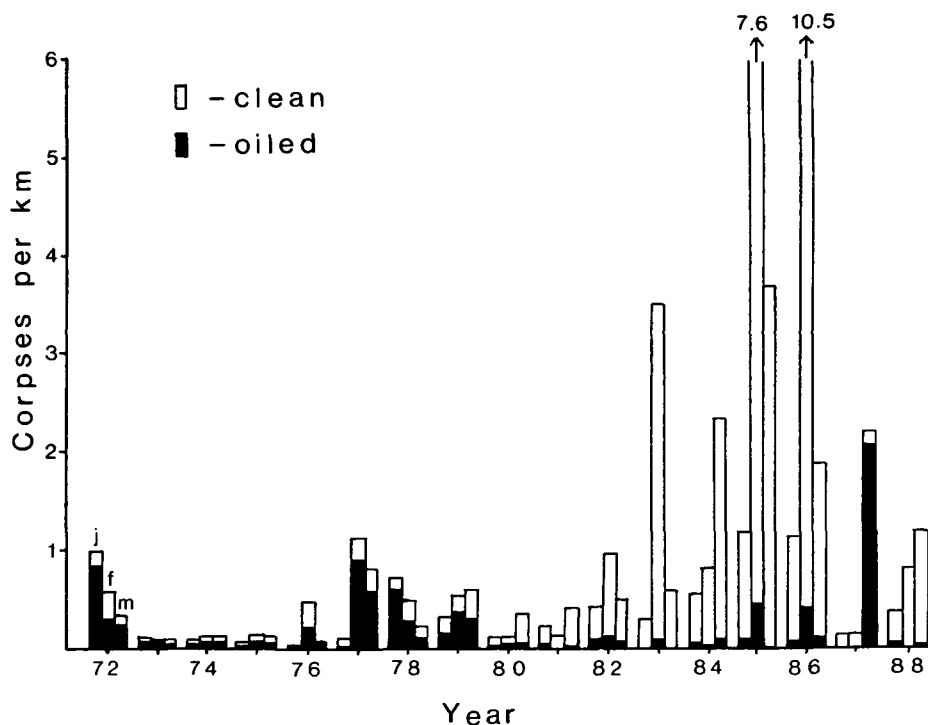

Figure 2. "Densities" and degree of oiling of Guillemot corpses on Moray Firth beaches in January, February and March, 1972-1988.

RESULTS

Beached bird surveys

During the 1970's the "densities" of Guillemot corpses on Moray Firth beaches were generally low with a mean of 0.35 corpse/km and the majority were oiled (Fig. 2). A marked change occurred during the 1980's with a steep increase in the overall density of corpses, peaking in February 1986 at 10.5 corpses/km. The mean corpse density of 1.80 /km recorded in the period 1980-86 was significantly higher than in the 1970s (t_{43}= 2.60, P<0.05). Also there was a marked reduction in the proportion of casualties that had oil on their plumage from 61% overall in the 1970s (N=737) to 4.7% in 1980-86 (N=5143, corrected contingency χ^2 = 1949.5, P<0.001).

Distinct wrecks of largely unoiled Guillemots were recorded in either February or March in each year 1983-86 (Table I) but were not repeated in 1987 or 1988. Corpses were found on beaches throughout the outer and inner firths in 1983, 1985 and 1986, but were concentrated in the Inverness, Beauly and Cromarty Firths in 1984 (62% of corpses). Weather conditions at the time of these wrecks were generally severe with easterly gales (NE round to SE), although this was not the case in 1984.

TABLE I. PLUMAGE, AGE AND SEX OF GUILLEMOT CORPSES.

	No. corpses reported	Corpses per km	Number examined	% in full winter plumage	% with immature-type bursa	% of imms. that were males
Feb 1983	378	3.52	102	56.3	58.0	67.8
Mar 1984	242	2.34	68	88.2	93.0	83.0
Feb 1985	1129	7.55	100	96.0	96.0	60.0
Feb 1986	1981	10.50	96	91.7	85.1	60.8

Corpse examinations

In each incident the majority of casualties were immature males (Table I). The proportion of immatures was significantly lower in 1983 compared to the other three years (χ^2, P<0.001 in each case). In 1985 all birds classed as immatures on bursa were identified as first-winters using wing feather characteristics. In 1986 this was the case for 88% of immatures (75% of the 96 corpses examined). The sex ratio among immatures was significantly different from 50/50 in 1983 and 1984 and nearly so in 1985 and 1986 (Goodness of fit χ^2, 1983 P<0.01; 1984 P<0.001; 1985 and 1986 P<0.10).

TABLE II.BODY WEIGHTS OF IMMATURE GUILLEMOTS.

		N	Mean	SD	Range
Feb 1983	male	26	674.2	72.2	550-855
	female	15	641.7	48.9	550-730
Mar 1984	male	6	665.0	32.7	630-710
	female	2	555.0	–	550-560
Feb 1985	male	52	639.0	57.7	510-860
	female	34	611.2	62.5	490-810
Feb 1986	male	35	644.3	57.5	580-810
	female	25	612.4	49.9	490-710

Corpses whose plumage was oiled or wet were not weighed.

TABLE III. THE SIZE OF SUBCUTANEOUS AND ABDOMINAL FAT DEPOSITS.

		Percent of birds with fat:		
Date	*No. birds examined*	*none*	*thin*	*moderate or thick*
Feb 1983	79	40.5	49.4	10.1
Mar 1984	57	50.8	44.3	4.9
Feb 1985	95	96.8	1.1	2.1
Feb 1986	78	89.7	6.4	3.9

Mean body-weights of casualties were consistently low (Table II) and can be compared with a mean for adult birds at East Caithness colonies in late June of 930g (N=105, GPM & SJA, unpublished). There is little available information on normal body-weights for first-winter birds, although four male net-drowning casualties from the Cromarty Firth in December 1984 averaged 996g and the mean weight of Guillemots killed in gill nets in the southeastern Kattegat (81% first-winters) was 1100g (Peterz & Olden 1987). Subcutaneous and abdominal fat deposits of wreck casualties were either absent or were very thin in the majority of cases (Table III).

A high proportion of birds in each incident contained no food remains at all in the proventriculus or gizzard (Table IV). Even those with items mostly contained just odd fish bones and/or otoliths. The relative abundance of different fish groups varied between incidents, but remains of gadoids were usually the most abundant.

TABLE IV. THE STOMACH CONTENTS OF GUILLEMOT CORPSES.

	No. examined	*% empty*	*% with poly-chaetes*	*% with fish remains*	*% occurrence of fish groups**		
					gadoid	*sandeel*	*clupeid*
Feb 1983	60	c.50	7	48	38	17	31
Mar 1984	53	43	4	53	63	26	26
Feb 1985	93	54	4	44	27	46	36
Feb 1986	68	79	0	21	91	18	0

* - % of birds with identifiable fish remains that contained each species group.

Samples of corpses from the 1983, 1985 and 1986 incidents were examined at various veterinary laboratories. No evidence was found of any problems from pollutants or infectious diseases. Nematode parasites *Contracaecum rudolphii* were present in the proventriculus of some birds with infestation levels varying between 4 and 72% in different incidents. It is possible that this nematode infestation was a contributory factor to the deaths of some birds, but should more realistically be viewed as a manifestation of prolonged poor condition of the birds resulting from food shortage.

Origins of casualties
Of 16 marked birds recovered during these wrecks 12 had been ringed at colonies within the Moray Firth, one came from east Grampian, two from Fair Isle and one from Iceland. This suggests that most casualties were of very local origin in NE Scotland. However, given the large size of the Icelandic Guillemot population and the small ringing effort there, the single Icelandic bird opens some doubts.

Although the relationship between immature wing-length and geographical origin has not been determined for Guillemots, mean wing-lengths were highly consistent between incidents (Table V) indicating similar origins.

TABLE V. WING LENGTHS OF IMMATURE GUILLEMOTS.

Date	Sex	N	Mean	SD	Range
Feb 1983	male	31	199.2	5.5	185-212
	female	18	198.2	5.1	188-205
Mar 1984	male	38	199.2	5.2	189-209
	female	9	199.0	5.5	191-208
Feb 1985	male	57	200.8	4.0	194-212
	female	38	199.5	4.3	190-210
Feb 1986	male	47	200.5	4.0	191-208
	female	31	199.0	4.3	187-207

DISCUSSION

The broad pattern of events described here parallels that recorded in Shetland over a similar period (Heubeck 1987). We know of no previous annual series of non-oiling die-offs of Guillemots in Britain. However, a broadly similar series of events has been recorded by long-term beached bird survey work on the Netherlands coast of the southern North Sea (Camphuysen 1989). Here the densities of guillemot corpses increased dramatically in the early 1980's compared with the 1970's, with peaks in the months of February and March. Immature males predominated among corpses examined during these later incidents, and most birds were severely emaciated. The main difference from the Moray Firth situation in the 1980's was that the majority of corpses in the Netherlands (80-90%) were oiled. However, in most cases the degree of oiling was light and was attributed to chronic oil pollution, perhaps occurring after death (Camphuysen 1989).

The evidence for the Moray Firth in 1984-86, as in 1983 (Blake 1984; Jones *et al.* 1984), is that starvation was the proximate cause of death. Adult Guillemots are present in the Moray Firth in February and particularly in March (Mudge, Aspinall & Crooke 1987) and figure strongly in oiling incidents. Thus 92% of Guillemots killed by oil off the Buchan coast in March 1982 were adults (North 1982) as were 68% from Caithness in December 1984 (GPM &SJA unpublished). Their paucity among wreck casualties is presumably due to them being better able than immatures to cope with food shortage or with factors that make food less easily available. The reason why there should have been a preponderance of males among immature casualties is not known. Either males are more vulnerable than females to starvation or they are more abundant in the area at that time of year.

The wrecks all occurred at the end of the winter and in three out of four cases were associated with periods of strong winds from an easterly quadrant. These conditions may have caused feeding difficulties, but similar conditions earlier in the winters did not result in die-offs. It seems more likely that these weather conditions were simply concentrating the mortalities of young Guillemots that were already weakened due to general food supply problems. A similar conclusion was reached by Blake (1984) concerning the 1983 wreck.

The breeding populations of Guillemots in northern Scotland increased substantially during the 1970's (Stowe 1982; Stowe & Harris 1984) at a time when stocks of herring *Clupea harengus* and sprat *Sprattus sprattus* declined in the northern North Sea (Baxter 1978; Edwards & McKay 1984). In the Moray Firth a large winter fishery for sprat commenced in the early 1960's with a peak catch of over 60,000 tonnes in 1966 (McKay 1983). The fishery collapsed in 1979/80 and was closed in the western half to protect immature herring which were taken as a bycatch.

It is possible, therefore, that a situation was reached in the 1980's where the numbers of Guillemots were too large in relation to the available food supply at a critical period at the end of the winter. Various additional factors may have combined to create this "bottleneck". Sandeels, an important summer food for local birds, are not readily available in the winter so that Guillemots are largely dependant upon clupeids and gadoids (Blake 1984; Blake, Dixon, Jones & Tasker 1985). Sprat shoals, which winter in inshore waters, move in late winter / spring to offshore spawning grounds (Saville 1966; McKay 1983). In February / March there is a large scale return of adult Guillemots from wintering areas in the southern North Sea to the vicinity of breeding colonies in the Moray Firth (Mudge *et al* 1987; Mudge & Crooke 1986). Immatures may accompany these returning adults and/or returning adults may displace resident immatures from feeding areas. The 1983-86 wrecks have certainly been associated in each case with an influx of immature birds into the Inverness, Beauly and Cromarty Firths, but we do not know whether these came from within or outwith the Moray Firth.

The situation subsequently appears to have changed. In 1987 there was no influx of Guillemots into the inner firths and no wreck occurred, although there was a large oiling incident in March. In 1987/88 large numbers wintered inshore in the Moray Firth and in the inner firths, but again no wreck occurred.

ACKNOWLEDGEMENTS

SUMMARY

A series of mortality incidents involving un-oiled Guillemots occurred in the Moray Firth in February/March of each year 1983-1986. Detailed examination of samples of corpses showed that the majority were immature males with low body-weights, empty stomachs and depleted fat reserves. In three of the incidents it appeared that strong winds had concentrated the deaths of young Guillemots that were already weakened due to general food supply problems.

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G.P. Mudge*, C.H. Crooke and S.J. Aspinall**, RSPB, Highland Office, Munlochy, Ross & Cromarty, IV8 8ND.

* Present address: Joint Nature Conservation Committee, Battleby, Redgorton, Perth, PH1 3EW.

** Present address: Joint Nature Conservation Committee, c/o 1 Southampton Road, Lyndhurst, Hampshire, SO43 7BU.

Distribution and population status of the Herring Gull *Larus argentatus* in the Canary Islands

Guillermo Delgado, Aurelio Martín, Manuel Nogales, Vicente Quilis, Efraín Hernández and Octavio Trujillo.

INTRODUCTION

The Herring Gull *Larus argentatus* is widely distributed through much of North America and the Western Palearctic (Vaurie 1965, Harrison 1983, Grant 1986). It occurs on all the archipelagoes of Macaronesia except the Cape Verde Islands, where it is only an occasional visitor (Bannerman & Bannerman 1968). Some 2000 pairs nest on the Azores and it is widespread in small, but unknown numbers on Madeira (Le Grand *et al.* 1984). On the Desertas, Le Grand *et al.* (1984) mentioned a large colony on Chao, as well as some old nests on Deserta Grande and Bugio in 1981, whilst a brief visit to Porto Santo in 1981 found breeding in only limited numbers. It seems to be relatively scarce on the Selvagens where Jouanin (1974) found 10 nests on Selvagem Grande during 1973 and Jensen (1981) estimated the size of the colony at 25-30 pairs, figures which agree with the observations of Hartog *et al.* (1984). On Selvagem Pequeña, Le Grand *et al.* (1984) counted 5-10 pairs.

It is the only gull to nest on the Canaries, although a pair of Slender-billed Gulls *Larus genei* attempted to nest on Fuerteventura in 1976 (Cramp & Simmons 1983). Although the Herring Gull was a relatively common species in the past (Bolle 1855), there are few data on its distribution and breeding. Bolle (1857) mentioned that it nested under bushes on the dunes of Maspalomas (Gran Canaria). Meade-Waldo (1893) stated that it bred on all the islands, and Polatzek (1909) collected a clutch on Fuerteventura. Bannerman (1919) mentioned that the Roques de Anaga (Tenerife) and the Roque del Este (Lanzarote) were once the main breeding grounds, and Volsøe (1951) noted the likelihood of a colony in Los Cristianos (Tenerife). Later, Lovegrove (1971), Le Grand *et al.* (1984) and Martín (1987) contributed more detailed information on other breeding sites, especially those on the eastern islets (north of Lanzarote) and Tenerife.

METHODS

In April and May 1987, a team of seven (F.Santana and ourselves) ornithologists investigated both the major part of the Canary coastline from the land and the sea and inland areas which seemed suitable for nesting gulls.

Wherever possible, we counted nests with and without eggs or small chicks; otherwise we counted adults present. Where colonies were inaccessible or difficult to see, the number of birds was calculated by letting off small rockets in the area, the counts being repeated several times in the larger breeding areas (Nettleship 1976). Where it was possible to count both birds and nests at the same time, the results were very similar (e.g. R. del Este, Pta. Barlovento, Roque Garachico).

RESULTS

Details of counts are given in Table I and location of colonies in Figure 1.

Roque del Este: Thirty nests were found, with a total of 66 birds being observed and an estimated population of 35-40 pairs. Lovegrove (1971) noted *c.* 20 pairs on this small rock in 1970.

Alegranza: We found a colony (35-41 pairs) on the upper outer rim of La Caldera in the west of the island. Bannerman (1914) noted the species as being very scarce and Lovegrove (1971) did not mention the species.

Table I. Details of counts in the main colonies of the Herring Gull in the Canary Islands in 1987; N.C.(no count).

Island	Locality	Colony number	Date	Nests counted	Adults counted	Estimated Pairs
R. del Este		1	10 March	30	66	35-40
Alegranza	La Caldera	2	14 March	23	79	35-41
R. del Oeste		3	22 October	1		1
M. Clara	La Caldera	4	11 March	231	337	235-245
M. Clara	Las Tabaibitas	5	12 March	5	123	70-100
Lanzarote	Macizo Famara	6	21 March	N.C.	913	450-550
Lanzarote	Timanfaya	7	23 March	3	97	50
Lobos	La Caldera	8	29 March	73	133	77-88
Fuerteventura	Pta. Barlovento	9	31 March	290	535	295-305
Fuerteventura	Amanay	10	2 April	153	184	165-175
Fuerteventura	Recogedero	11	3 April	48	97	50-60
Fuerteventura	Mtña. Roja	12	4 April	36	74	49-59
G. Canaria	R. del Herrero	13	8 May	N.C.	435	204-230
G. Canaria	Pta. del Manso	14	8 May	N.C.	156	85-100
G. Canaria	Pta. Las Tetas	15	9 May	N.C.	333	170-190
Tenerife	R. Fuera Anaga	16	12 May	N.C.	348	210-215
Tenerife	Los Cristianos	17	14 May	N.C.	193	100-110
Tenerife	Roque Garachico	18	16 May	42	71	45-50
La Gomera	Pta. Salinas	19	28 April	N.C.	68	50-75
La Gomera	Pta. Gorda	20	28 April	N.C.	121	75-85
La Gomera	Risco Amargura	21	29 April	N.C.	760	400-450
La Gomera	Playa Argaga	22	29 April	N.C.	332	180-212
La Gomera	Puntillas Avalo	23	1 May	N.C.	146	40-60
El Hierro	Roque Gaviotas	24	8 April	4	98	50-60
El Hierro	Bahía de Naos	25	10 April	N.C.	59	30-40
El Hierro	Pta. Lapillas	26	10 April	N.C.	91	45-60
El Hierro	Mta. Cardillos	27	10 April	N.C.	112	60-75
El Hierro	Morro del Paso	28	10 April	N.C.	53	30-40
El Hierro	Roques Salmor	29	13 April	N.C.	67	45-55
El Hierro	El Corral	30	13 April	N.C.	100	45-50
El Hierro	Los Cercaditos	31	1 June	N.C.	150	25-40
La Palma	Roque Tabaibas	32	16 April	6	18	10-14
La Palma	Punta Gaviotas	33	16 April	3	5	3

Roque del Oeste: Sea conditions prevented a landing during the breeding season but the remains of a recent nest were found in August 1987.

Montaña Clara: Some 235-245 pairs were concentrated round the summit of La Caldera, and another 70-100 pairs on the eastern outer slope. Bannerman (1914) observed many gulls on the northeast cliffs in 1913, although he indicated that the species does not breed on the islet. De la Hoz (1961) commented that when the inhabitants of Graciosa visited Montaña Clara to collect shearwater chicks, the gulls were very afraid that theirs chicks would be stolen. Lovegrove (1971) estimated 20 nesting pairs.
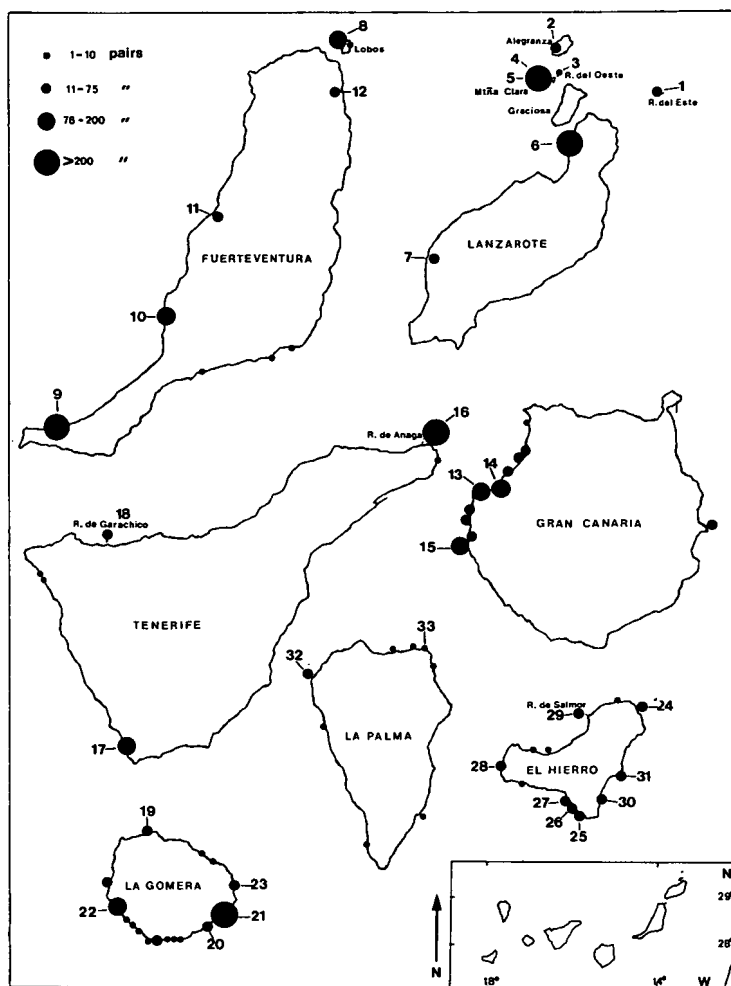
Figure 1. Distribution and estimated colony sizes of the Herring Gull in the Canary Islands in 1987. Colony numbers refer to Table I.

Lanzarote: The most important colony in the Archipelago was on the Riscos de Famara, in the north of the island, with some 450-550 pairs; the presence of this colony was suspected by Bannerman in 1913. Some 50 pairs breed in a recent volcanic "badland" inside the Timanfaya National Park (west of the island).

Lobos: Some 77-88 pairs bred inside the Caldera de la Montaña, where Osborne (1986) observed c. 30 birds in April 1984. A further 11-16 pairs were discovered inland.

Fuerteventura: The population was 574-618 pairs with the main colonies on the western coast, principally the Punta de Barlovento, Jandía (295-305 pairs) and the Punta de las Hendiduras de Amanay (165-175 pairs). On the east coast at Montaña Roja 49-59 pairs nested.

Gran Canaria: The nesting population was 823-950 pairs most on the western coast, from Agaete to the Barranco de Tasartico. The main concentration was between the Roque del Herrero and Paso del Herrero (204-230 pairs) and the area between Las Tetas and Punta de las Tetas (170-190 pairs). There was a small colony (15-17 pairs) on the Roque de Gando (east coast).

Tenerife: The total population was c. 412-438 pairs. The main breeding areas were the Roque de Fuera de Anaga (210-215 pairs), Los Cristianos (100-110 pairs) and the Roque de Garachico (45-50 pairs). Scattered pairs bred close to the Playa de Anosma (7 pairs) and the Acantilado de Los Gigantes (15-16 pairs). Martín (1987) noted a large colony here in 1980-1984, which has now gone, possibly as a result of the almost continuous traffic of pleasure craft in the area.

La Gomera: The total population was 866-1026 pairs. Most pairs were found in the southern half of the island, generally at very scattered sites on the cliffs between San Sebastián and Valle Gran Rey, which mostly had no more than 10 pairs. Some 400-450 pairs were found on the Risco de la Amargura making this one of the most important colonies in the Archipelago. Also, 180-212 pairs breed between the Playa de Argaga and Punta de Iguala. In the northern half, 50-75 pairs bred at Punta de las Salinas, and a few scattered pairs elsewhere.

El Hierro: The Herring Gull was widely distributed but all the colonies were small, El Corral (45-50 pairs), Playa de los Negros (30-40), Los Cercaditos (25-40), Roque de las Gaviotas (50-60) and Roques de Salmor (45-50). Martín & Hernández (1985) estimated c. some 30 pairs at Roque Chico.

La Palma: Despite suitable breeding cliffs, La Palma had only 23-37 pairs, scattered principally along the north coast. The most important site was at Roque de las Tabaibas (Garafía) with 10-14 pairs.

DISCUSSION

During this century the Herring Gull has increased in numbers throughout most of its range during this century (Cramp & Simmons 1983, Carrera & Vilagrasa 1984, De Wit & Spaans 1984, Guyot et al. 1985, Monaghan & Zonfrillo 1986, Beaubrun 1988). This appears to have been due to its ability to colonize new habitats, and the ease with which it exploits new food resources, especially household rubbish and other waste created by man (Cramp & Simmons 1983, Furness & Monaghan 1987).

The few past counts to the population size in the Canaries do not allow us to reconstruct its development during the past few decades. However numbers appear to have increased, eg. Lovegrove (1971) reported c. 20 pairs on Montaña Clara where we found 305-345 pairs in 1987. During 1989 we noted an increase in numbers in two sites on El Hierro: Roques de la Sal and Roque Grande de Salmor. At the first three pairs bred in 1989, with 37 birds being present compared to one in 1987. At the second more than 200 birds were observed in June 1989, compared with the 26 birds counted in 1987.

The apparent increase in numbers in the Canaries has probably been helped by the expansion of the fish (canning and salting) industries. These started in the 1920s and increased until the 1970s when its decline started (García 1970, Santos & Macías 1984). Most factories were on Gran Canaria, with fewer on Lanzarote, Tenerife and La Gomera; although it was on these islands where the population of L. argentatus has remained most numerous up to the present day. At present, the number of factories has been drastically reduced and only a small number remain on Lanzarote and Gran Canaria. Unauthorized rubbish tips are common on all the islands, and these may allow the populations to remain at their current levels.

SUMMARY

A complete survey of possible breeding sites in 1987 found a total of 4000 -4700 pairs of Herring Gulls in the Canary Archipelago. The species was widespread on all islands except La Palma where the population was very reduced. The main colonies were on Montaña Clara (305-345 pairs), Acantilados de Famara, north Lanzarote (450-550 pairs), and Risco de la Amargura, south La Gomera (400-450 pairs).

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Guillermo Delgado, Museo Insular de Ciencias Naturales, Aptdo. de Correos 853, 38080 S/C de Tenerife, Islas Canarias.

Aurelio Martín, Manuel Nogales, Vicente Quilis, Efraín Hernández, Departamento de Biología Animal (Zoología), Universidad de La Laguna, 38206 Tenerife, Islas Canarias.

Octavio Trujillo, Jardín Canario "Viera y Clavijo", Aptdo. de Correos 14, Tafira Alta, 35017 Las Palmas de Gran Canaria, Islas Canarias.

BOOK REVIEWS

HARRISON, C.S. 1990. Seabirds of Hawaii: natural history and conservation. 249pp. $36.50 cloth, $15.95 paper. Cornell University Press, Ithaca and London. ISBN 0 8014 2449 6 (cloth), ISBN 0 8014 9722 (paper).

Craig Harrison is well known for his research on the status and feeding ecology of Hawaiian seabirds and has wide experience of environmental law. He is clearly well qualified to write this volume on the natural history and conservation of the seabirds of Hawaii.

The book is divided into four parts. The first, entitled "The environment and humans" introduces the reader to the Hawaiian archipelago and described what is known as the islands' geology, archaeology and natural history, the characteristics and oceanography of the surrounding seas and the history of man's association with, and exploitation of, the islands. The second part is a review of the comparative biology of Hawaiian seabirds with chapters on origins and adaptations, populations, breeding and feeding ecology and the birds' lives at sea. The third section takes a family by family look at the seabirds describing, for each of the 22 species, their distribution and abundance, behaviour and ecology on sea and land, breeding and conservation. The book concludes with a comprehensive review of the threats facing Hawaiian seabirds both on land and at sea and conservation issues.

Together these sections provide a highly readable overview of a tropical seabird community, with the emphasis on conservation. As a reference work the book's value is somewhat reduced because the author has elected to give selected bibliographies for each chapter at the end of the book, rather than give source references in the text.

The author's enthusiasm and commitment to the area and its seabirds, comes through strongly both in the anecdotes of his experiences in the field, which enliven the natural history sections, and in his diatribe on the political intrigues which currently thwart the implementation of effective wildlife conservation. In his preface Craig Harrison expresses the hope that this book will convey some of the wonders of Hawaii's seabirds and will help to stimulate improvements in the ways humans manage wildlife in Hawaii. For me, he succeeds in his first aim, only time will tell whether his second, and more important, goal will be achieved.

The book is well produced and enhanced by some attractive line drawings, colour and black and white photographs.

Sarah Wanless

LLOYD, C., TASKER, M.L. and PARTRIDGE, K. 1991. The Status of Seabirds in Britain and Ireland. 355pp. £20.00. T. & A.D. Poyser, London. ISBN 0 85661 061 5.

This must be just about the most superfluous review of the year. Can there be any member of the Seabird Group who by now does not own a copy of this excellent book, which reports the results of their labours between 1985 and 1987 in repeating 'Operation Seafarer'? I hope not, because the book is a fitting tribute to the army of data collectors (over 600 individuals), to those who processed and analysed these data, to the authors of the book and to its publishers.

It is a great deal more, however, than the report of a repeat of Operation Seafarer. First, the field work had the benefit of the experience gained during and after this pioneering enterprise. This made it possible to improve the organisation, methods and instructions with considerable improvements in the quality and quantity of the data, leading to more detailed and precise analysis and presentation of results. As a baseline for future work we are now in a most enviable position.

Second, in parallel with the actual field work, went the establishment of the Seabird Colony Register. This ensured that not only the new but also much previous data on seabird status (including all Seafarer data) became part of a single computer-based registry. This alone would have been a landmark achievement.

Third, the book reviews a wealth of data on both historical and recent population trends of British and Irish seabirds. It is therefore a valuable work of reference and interpretation as well as providing a detailed comparison of changes in status over the last 20 years. The introductory chapters, on seabird biology, population regulation and known and potential causes of population change are excellent – clear, concise and well balanced. The first part of the book also contains the vital chapter on the methods of data collection and analysis (together with appendices on the forms and instructions used in both the recent and the Seafarer surveys).

The second part of the book consists of the species accounts, which comprise sections on international distribution and status, census methods and problems, status in Britain and Ireland and reasons for population change. These sections are accompanied with a variety of maps and tables, always including summaries of world and British and Irish populations. One minor irritation is that the source references for the individual elements for the world population estimates are aggregated at the foot of each table, making it nearly impossible to attribute particular data to any specific source; this would have been easily overcome by use of reference numbers.

Otherwise these chapters are written and produced to a high standard. Inevitably some are better than others but all give an adequate picture of current status and recent trends and ideas on possible causes of these in our seabird populations. It is surprising, perhaps, that no explanation is given for the involvement of an additional author (Mark Avery) to write the tern accounts or, conversely, why specialists on other species did not contribute as appropriate.

The book as a whole is a tribute to collaboration. First, and perhaps foremost, within the Seabird Group. This acknowledges the great debt to those, mainly professional, who planned and organised the work and even greater debt to those, mainly amateur, who actually did the field work. The Group can be very proud of the result. Second, between the Seabird Group and the then Nature Conservancy Council. Without the involvement of the latter it is very unlikely that the whole project, including the register and the book, would have been completed successfully. Here the principal debt is to Clare Lloyd who, in 1986, shouldered the triple burden of supervising the field work, inputting the collected data and leading the team charged with production of the book.

We should not lose sight, however, of the fact that way back in 1983, it was the Seabird Group, in developing plans for a seabird site register, which actually got the whole programme underway. This is rather glossed over in the foreword, where the NCC awards itself a disproportionate share of the credit!

The successful conclusion of an enterprise should always lead us to ask: what next? With the Seabird Colony Register we now have an excellent basis for the future and indeed for considerable detailed analysis even now. However, computer database technology evolves rapidly. Should we already be considering how to modify the register so as to ensure compatibility with national and international geographic information systems, whether targeted at landforms, coastlines or protected areas?

Should we be satisfied with a register for Britain and Ireland? Is it time now to extend the concept to the rest of Europe and/or to the full geographical range of the seabird species or sub-species which breed in our area? Is it worth repeating the survey of British and Irish seabirds? If so when? Perhaps the year 2000 is a date to conjure with. Not only does it give plenty of time for planning but it would be about 30 years after Seafarer with the most recent survey almost exactly half way between. By 2000 there should also be quite considerable time series' of data from the current detailed monitoring studies of seabirds. The results of existing studies did not feature much in the present book. Such work, particularly incorporating indices of annual productivity, is the key counterpart to broad scale, intermittent censuses. A comprehensive review in another 5-10 years would be a very appropriate complement to the overall census data.

The important thing is to ensure that seabird enthusiasts should be trying to decide now what actions at national, regional and local scales will be required by the turn of the century, not just to provide a better retrospective assessment of our seabird populations but to permit realistic predictions of their potential trends in what is likely to be an increasingly hostile world.

J.P. Croxall

MARCHANT, S. and HIGGINS, P.J. (Co-ordinators). 1990. Handbook of Australian, New Zealand and Antarctic Birds, Volume 1 Ratites to Ducks; Part A Ratites to Petrels, Part B Australian Pelican to Ducks. 1397pp. £95. Oxford University Press; Melbourne and Oxford. ISBN 0-19-553068-3.

This handbook (which will be known as HANZAB) covers several of the most important of the world's assemblages of seabirds, both in numbers and species. The area surveyed is vast: Australia within the limits of the continental shelf, north to 10°S or the Queensland-New Guinea border, but excluding the eastern end of New Guinea; New Zealand and its islands from the Kermadec Group to Campbell Island; the Antarctic Continent; the subantarctic islands, Marion, Prince Edward, Crozet, Kerguelen, Heard and Macquarie, and islands of the Scotia Arc, South Georgia, South Sandwich, South Orkney and South

Shetland Islands; Cocos-Keeling, Christmas (Indian Ocean), Lord Howe and Norfolk; reefs and islands of the Coral Sea. Volume 1 is so large that is has had to be bound in two parts.

Volume 1 is of enormous importance to seabird biologists as it covers the penguins (14 species), albatrosses (10), fulmars, petrels, prions and shearwaters (53 including 20 *Pterodroma* spp. and 13 *Puffinus* spp.) storm- and diving-petrels (9), pelican (1), gannets and boobies (5), cormorants and shags (19), frigatebirds (3), tropicbirds (2) and darter (1). For good measure, we also get the esoteric emus, cassowaries and kiwis, and the prosaic grebes, herons and allies, and wildfowl. A total of 162 breeding species are treated in great detail while 34 nonbreeding migrants and vagrants receive rather less attention.

HANZAB was inspired by the publication of the first volume of The Birds of the Western Palearctic in 1977. Recruitment of contributors started in 1983 for a similar Handbook of Australian birds. The area of interest gradually expanded and the final limit was reached in 1985 with New Zealand being included. Good progress has, therefore, been made.

The layout follows that of BWP. Species accounts are divided into sections: field identification, habitat, distribution and population, movements, food, social organization, behaviour, voice, breeding and plumages, and related matters. All species currently on the area list are illustrated in 96 very pleasing and uncluttered colour-plates by J.N. Davies. There are many maps, diagrams, drawings of behaviour and sonagrams. All are well executed and the maps are as clear as those in any handbook, perhaps because of the relative lack of data which allows the broad-brush approach and the making of sweeping generalizations easier (especially across the tens of thousands of miles of oceans roamed by pelagic species). The rather limited literature means that it has been possible to include a reference list with each species which makes it so much easier for the reader wanting to quickly check the source than when thousands of citations are grouped at the end of a book. There are appendices of ectoparasites, aboriginal, maori and foreign names.

I have read the accounts of species which I know and am mightily impressed. Doubtless there will be mistakes and errors of omission (although I found all my own rather trivial notes on the birds of this area quoted) but I give unqualified approval to this volume. The Royal Australian Ornithologists Union, the two co-ordinators, their 14 collaborators and 225 contributors and reviewers and the publishers are to be congratulated on this fine publication. The price may seem high but by any standards these two books are exceptional value.

M.P. Harris

WEBB, A., HARRISON, N.M., LEAPER, G.M., STEELE, R.D., TASKER, M.L. and PIENKOWSKI, M.W. 1990. Seabird distribution west of Britain. 282pp. £20.00. Nature Conservancy Council, Peterborough. ISBN 0 86139 676 6.

For the last ten years, the Nature Conservancy Council's Seabirds at Sea Team, based at Aberdeen, has been charting the distribution of seabirds around the coasts of Britain, with the prime aim of identifying when and where concentrations of particular species occur that would be vulnerable to oil pollution. This report represents the results of the third phase, running from 1986-1990, and concentrating primarily upon the Irish Sea and waters off the west coast of Scotland. Altogether, over 19,000 km² of water were examined from ships during journeys totalling over 68,000 km while surveying. It is an enormous achievement and the authors and their colleagues should be congratulated for their dedication in often difficult conditions.

The report first provides a useful summary of the marine environment west of Britain, including the divisions of sea used in the analyses, and their associated oceanographic conditions. This is followed by a review of the survey methods (primarily ships for offshore surveys, and aircraft or land-based watches for inshore waters) and data handling. Bird densities (for the commoner species) are assessed from a 300 metre belt transect with a generalised correction to allow for the inability to see all birds in the transect. No correction, however, was made to flying bird densities although obviously some species will be detectable at greater distances than others, even within a 300 metre band. So far as I can tell, there was no adjustment made for variation in viewing conditions – sea state and glare. Both could have important effects on detectability of auks, divers, and sea duck on the water, and small petrels in the air. Although I can understand the impracticality of obtaining distance estimations for every bird seen, I am not sure why this could not be done for a sample of birds of each species under varying conditions, and the resulting

curves for detectability distances used a basis for deriving species densities.

The main body of the report comprises species by species accounts, with a short literature review of the distribution, population size, breeding biology and diet of each species before their distribution at sea is presented on a seasonal basis. The text is liberally illustrated with maps and large histograms. Where possible, the authors have supplemented their findings with results published in various books/papers, notably the Handbook of the Birds of the Western Palearctic, the BTO Atlas of birds wintering in Britain and Ireland, and the Seabird Group/NCC Seabird Colony Register. A summary is presented for each species, together with conservation implications. The final chapter then summarises by sea area its relative importance to seabirds at different times of the year. The Minch off north-west Scotland is emphasised as of particular importance, as are waters around the major seabird colonies. Other important areas include the Western Irish Sea, North Channel and Sound of Jura, the Sea of Hebrides, some inshore waters (sea lochs and bays), the Firth of Clyde, North-eastern Irish Sea, and the continental shelf break west of Scotland.

Without doubt, this report represents the most comprehensive survey to date of the distribution of seabirds at sea off western Britain. As such it will be of great value to a wide range of people, from birdwatchers eager to see particular species, to conservationists and managers concerned for the protection of vulnerable concentrations. Inevitably, most areas can only be covered once or a few times in any month. Coverage in the central and southern Irish Sea in particular was limited largely to two ferry routes, whilst that of western Ireland seems to be derived primarily from the whale and seabird cruise which I organised between July and October 1980. This does limit the generality of some of the results, since numbers may vary on both a short term basis and from year to year. Thus, an estimate of the numbers of Razorbills using the Minch was estimated at 34,500 birds but with a standard error of 17,000! Surveys we have carried out off south-west and southern Irish coasts in summer and autumn indicate that these areas are much more important for Kittiwakes and Razorbills than indicated from our 1980 cruise alone and in this report. Densities of inshore species such as Shags, Cormorants, divers, grebes and sea duck may also be misinterpreted. Aerial surveys generally gave very different results from land-based surveys, usually producing much lower density estimates. It may be therefore difficult to place too much confidence in those estimates. On the other hand, the authors have been careful to draw upon the findings of others in their evaluation of the overall importance of an area to a particular species. This does beg a question. Bearing in mind the difficulty of making too much out of the precise densities given for various species, and that many of the qualitative results are already present in the literature through specific surveys, would it be better to concentrate upon studying the proximate factors which may lead to concentrations of particular species? If these were better understood, we might be able to predict more accurately where concentrations will occur and how these might vary from month to month and year to year.

Peter Evans

THE SEABIRD GROUP 1991

The Seabird Group was founded in 1966 to circulate news of work in progress on seabirds and to promote research. It is run by an elected Executive Committee and maintains close links with the three major British national ornithological bodies – the British Ornithologist's Union, the British Trust for Ornithology, and the Royal Society for the Protection of Birds. Membership (£10 per annum, £9 if paid by banker's order, £5 for students) is open to all with an interest in seabirds; for details please contact the Membership Secretary (address below) – payment by banker's order helps the Group.

Current Executive Committee The present Committee comprises: Chairman K. Taylor, Secretary M. Heubeck, Treasurer R.W. Furness, Membership Secretary S. Russell, Editor of *Seabird* S. Wanless, Newsletter Editor M. Tasker, also M.P. Harris, P. Monaghan, B. Zonfrillo.

Newsletters and Meetings Three Newsletters are circulated to members each year. They contain all sorts of items including reports on seabird conservation issues and research projects, news from seabird groups in other countries, book reviews, details of meetings, etc. The Newsletter Editor (address below) welcomes contributions from members. The usual venue for the Group's annual meeting is the BTO Ringing and Migration Conference at Swanwick, except when the Group holds its own conference, in which case the meeting is combined with that. Our conferences draw seabird workers from many countries to join in a forum of topical interest. In keeping with our desire to promote work in the field, practical manuals and guidelines evolve from the workshop sessions which cater for specialist topics within the conference theme.

Seabird Group Grants Each year the Group has some money available to help fund research conducted by members. All grant applications should be submitted to the Secretary by the end of February, and will be considered by the Executive Committee by the end of March. Successful applicants are required to submit a typed report, not exceeding 500 words, by the end of October of the same year for inclusion in the Newsletter. A full typed report (in triplicate) must be submitted by the end of the year.

Seabird Colony Register The Seabird Group has always sought to organise and implement national schemes involving the active participation of its membership, now standing at 350 members. The Group membership played a major role in the national Operation Seafarer survey whose results were published in 'The Seabirds of Britain and Ireland' (1974). The Group completed the Seabird Colony Register fieldwork in 1988, in cooperation with the Nature Conservancy Council, and the results were published in the book: 'The Status of Seabirds in Britain and Ireland' in 1991. This register was begun in 1985 to gather together all existing data on breeding seabird numbers in the British Isles, to bring our knowledge of their status up to date by detailed field surveys and to establish a computerised database which can be easily updated in the future. Although this round of survey work has been completed, it is important to continue monitoring of seabird breeding numbers: anyone eager to conduct counts on a regular basis should contact Paul Walsh, JNCC, 17 Rubislaw Terrace, Aberdeen AB1 1XE.

Seabird Journal In November 1984 the Group launched its new-look journal *Seabird*, numbered 7 in deference to its pedigree of Seabird Group Reports 1-6. Our priority is to maintain a high volume and quality of content and the current editor, Sarah Wanless, welcomes offers of papers (see Notice to Contributors, and address below). Members of the Seabird Group receive *Seabird* free of charge; additional copies to members, and any copies to non-members are £10 + 50p postage within the British Isles, £10 + £1 postage overseas. Postage overseas is by surface mail, unless the recipient can make prior provision for air mail. The subscription to Libraries is £15 per copy. To help reduce costs, overseas subscribers are kindly asked to make payment by international money order rather than by cheque. Back issues of *Seabird 11, 12 and 13* are

available at £5 + 50p per copy. There are no cost concessions for multiple orders of *Seabird* and postal charges are additive.

Who to write to While the Seabird Group maintains an accommodation address (c/o RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, England, UK), the following can be contacted directly, as appropriate. Please help the Group by enclosing a stamped addressed envelope for reply.

Secretary (general enquiries about the Group, seabird conservation matters, grants, etc.): Martin Heubeck, Mansefield, Dunrossness, Shetland ZE2 9JH, Scotland, UK.

Membership Secretary (membership renewals, applications and enquiries): Sheila Russell, Clober Farm, Craigton Road, Milngavie, Glasgow G62 7HW, Scotland, UK.

Treasurer (subscriptions, donations, etc.): Dr Robert Furness, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, UK.

Editor of Seabird: Dr Sarah Wanless, c/o Institute of Terrestrial Ecology, Hill of Brathens, Banchory, Kincardineshire AB31 4BY, Scotland, UK.

Newsletter Editor: Mark Tasker, JNCC, 17 Rubislaw Terrace, Aberdeen AB1 1XE, Scotland, UK.

EDITORIAL ACKNOWLEDGEMENTS

NOTICE TO CONTRIBUTORS

Seabird publishes original contributions relating to any aspect of seabird ornithology as full-length papers (preferably not exceeding thirty manuscript double-spaced pages) or short notes. Although a portion of the journal will be of particular interest to UK members, contributions are welcomed on aspects of seabird ornithology from any part of the world so long as they are likely to be of general interest.

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Contributions should be submitted in the same format as used in recent copies of *Seabird,* and this is outlined below:

All submissions, of which *three* copies are required, must be typewritten, on one side of the paper, with double spacing and adequate margins. The approximate position of figures and tables should be indicated in the margin. Authors are advised to consult a recent copy of *Seabird* and follow the conventions for section headings, tables, captions, references, quotation marks, abbreviations etc. The Editor may return without consideration any submission that departs from the *Seabird* form of presentation. Spelling should conform with the preferred i.e. first-cited spelling of the *Shorter Oxford Dictionary.* Details of experimental technique, extensive tabulations of results of computation procedures, etc. are best presented as appendices. A full-length paper must include a summary not exceeding 5% of the total length.

On first mention a bird species should be designated by an English vernacular name drawn from *The Status of Birds in Britain and Ireland,* or from an authorative faunistic work treating the appropriate region, followed by systematic binomial; author and date need be cited only in taxonomic papers. Thereafter only one name should be used, preferably the English one. Capitals should be used for the initial letters of all single words or hyphenated vernacular names (e.g. Great Black-backed Gull, White-eyed Gull) but not in a group name (e.g. gulls, terns). Trinomials should be used only if the subspecific nomenclature is relevant to the topic under discussion. Underlining is used for all words of foreign languages, including Latin, other than those which have been adopted into English. Underlining should also be used for phonetic renderings of bird vocalizations. Underlining is not needed for emphasis.

Measurements should be given in SI (International system of units), but if the original measurements were made in non-SI units, the actual values and units should be given, with SI equivalents inserted in parentheses at appropriate points. Measurements may be given in cm.

Figures and diagrams should be drawn in black ink on white board, paper or tracing material, with scales (for maps), and lettering given in Letraset. In designing drawings, authors are asked to note the page-size and shape of *Seabird;* originals should be 1½-2 times final size. Tables should be typewritten and spaced appropriately. References should be quoted in the text in the format indicated by the following examples: Harris 1980, Cramp & Simmons 1980, Monaghan *et al.* 1980. References at the end of the paper (following acknowledgements) should be given in the following format:

COULSON, J.C. and WOOLER, R.D. 1976. Differential survival rates among breeding Kittiwake Gulls *Rissa tridactyla* (L.). *J. Anim. Ecol.* 45: 205-213.

The author's name should be placed beneath the title of the paper and again at the end, together with the address, after the references.

Twenty-five offprints of each original contribution will be supplied free. Additional copies can be supplied on payment; orders will be required at the time of proof-correction. Reprints of book reviews will only be supplied if a request is submitted with the original copy; in this case the full number will be charged at cost.

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