

# SEABIRD 16



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# Do Great Skuas *Catharacta skua* respond to changes in the nutritional needs of their chicks?

J.K. Hill and K.C. Hamer

## INTRODUCTION

Several studies of the responses of seabirds to changes in the availability of prey have recorded an apparent increase in foraging effort in conditions of reduced food supply (e.g. Burger & Piatt 1990, Hamer *et al.* 1993), although this has generally been inferred from changes in colony attendance rather than being measured directly. Perceived increases in foraging effort have been taken to represent an increase in reproductive effort (e.g. Reid 1988, Monaghan *et al.* 1989), although this is confounded by uncertainty as to whether extra time spent foraging represents allocation of resources to chicks or to maintenance of adult body condition. Furthermore, there is little empirical evidence to support the assumption that adult seabirds respond to changes in chicks' nutritional requirements (Harris 1978, Ricklefs 1990) and there is some evidence to the contrary, at least for pelagic species (Shea & Ricklefs 1985, Ricklefs 1992, Hamer & Hill 1993). This has important implications for studies of responses of seabirds to changes in food supply, particularly with regard to the predictions of life history theory concerning reproductive effort (Martin 1987, Hamer *et al.* 1991).

During the 1970s, Great Skuas *Catharacta skua* at the largest British colony, on Foula, Shetland, experienced high annual breeding success and an abundant, energy-dense food supply in the form of sandeels *Ammodytes marinus* (Furness & Hislop 1981). During the 1980s, there was a marked decline in the availability of sandeels in Shetland waters, due to a three to four-fold reduction in sandeel stock biomass and recruitment (Bailey *et al.* 1991). In conjunction with the decline in sandeel stocks, the breeding success of Great Skuas in Shetland declined virtually to zero, mainly as a result of adults spending long periods away from their territories and leaving their chicks unguarded, and so vulnerable to predation by adult conspecifics (Hamer *et al.* 1991). This change in adult territorial attendance was taken to indicate that adults had increased the time spent foraging to provide food for their chicks (Hamer *et al.* 1991). While this was supported by evidence concerning differences in the diets of adults and chicks, the possibility remains that adults may have been spending much of the extra time foraging for themselves rather than for their chicks.

This paper examines the effects of supplementary feeding of Great Skua chicks upon mass growth rates of chicks and territorial attendance of adults. It tests whether supplementary feeding resulted in a decrease in provisioning by adults, and whether any decrease was reflected by an increase in the time adults spent within their territories.

## METHODS

A total of 59 chicks at 33 territories on Foula, Shetland were located between 25 and 28 June 1991 and fitted with monel rings to allow subsequent identification. To control for possible differences in adult quality, related to laying date (Hamer & Furness 1991), territories were chosen only if chicks were less than one week old, as determined from wing length (Furness 1977), on 28 June

(within 10 days of median laying dates in previous years; Hamer & Furness 1991). Chicks were assigned to one of three groups, and between 30 June and 13 July 1991, they received daily supplements of either lipid and protein, water or nothing.

The lipid/protein mixture consisted of 1.3 parts by volume of cod-liver oil mixed with 1 part of an aqueous solution of 40g protein ('Casilan 90') in 100ml water, and had an energy density of approximately 20kJ/ml. We were careful not to overload chicks with lipid, since this tends to congest within the proventriculus, and may reduce feeding capacity (Ricklefs 1992). Accordingly, chicks weighing less than 200g were given 10ml of supplement, chicks weighing between 200g and 300g were given 15ml of supplement and, for every subsequent 100g increase in chick mass, they were given an additional 5ml of supplement. This resulted in a mean ( $\pm$ SD) daily supplement of  $32.8 \pm 15.2$ ml (range 10–45ml), for a mean chick mass of  $497 \pm 202$ g (range 110–890g). We estimated that this provided chicks with approximately 40% of the normal daily energy intake of chicks during conditions of good food supply (34% from lipid, 6% from protein), based upon published data regarding the energy density of adult sandeels (6.5kJ/g wet weight; Harris & Hislop 1978) and the average mass of sandeels fed to chicks per day (5–6 meals, with an average mass per meal of 91g per brood of two chicks; Furness & Hislop 1981).

Chicks in the second treatment group were given volumes of water equal to the volumes of dietary supplement fed to chicks in the first group, according to their mass. This was done in order to control for any effects upon chick feeding of distending the proventriculus with liquid, regardless of its nutritional content. In both groups, supplements were introduced slowly into chicks' oesophagi via a short length of plastic tubing attached to a syringe. Chicks in the third treatment group were handled each day but were not fed anything.

All chicks were weighed at 24h intervals, to the nearest 5g using a Pesola spring balance, to determine daily mass increments. These resulted both from feeding by parents and, for chicks in group 1, from supplementary feeding.

Adult attendance (the number of parents present per territory) was recorded twice a day (during late morning and early evening) at each nest, every day from 25 June to 13 July. This gave an accurate indication of adult attendance (Hamer 1990). The mean number of adults present at each territory was calculated for each of three periods; before manipulation, days 1–7 and days 8–14. Most study territories contained two chicks, and there was no difference between groups in the proportions of territories with broods of one or two chicks ( $\chi^2_2 = 0.36$ ,  $n = 33$ ,  $P = 0.8$ ).

Nine chicks died during the course of the study, due to predation by adult conspecifics. This was in keeping with overall chick mortality at the colony in 1991, which was lower than in any of the previous four years (R.W. Furness & N. Ratcliffe, unpublished data). The timing and rate of chick mortality were similar in the three groups, so that they did not differ in terms of the overall mean number of chicks per territory (calculated as the mean number of chicks per nest per day within each treatment group; ANOVA,  $F_{28,2} = 0.15$ ,  $P = 0.9$ ).

## RESULTS

Chicks were growing rapidly during the period of supplementary feeding, and there were no age differences between treatment groups (see above). Mass growth rates of chicks during the period of supplementary feeding (30 June to 13 July) did not differ between treatment groups (Table I; Kruskal-Wallis one-way ANOVA;  $\chi^2$  with 50 cases = 4.35,  $P = 0.1$ ). Nor was there a difference between groups in adult attendance during the week before manipulation (Table II; one-way ANOVA;  $F_{28,2} = 0.32$ ,  $P = 0.7$ ), or in the first week of supplementary feeding (one-way ANOVA;  $F_{28,2} = 1.96$ ,  $P = 0.2$ ; since these data were not independent, separate analyses were carried out for each period). In the second week of manipulation, adult attendance was significantly higher at nests where chicks had been given supplementary food (Table II; one-way ANOVA followed by Tukey's range test;  $F_{28,2} = 5.17$ ,  $P < 0.02$ ).

TABLE I. MASS GROWTH RATES OF GREAT SKUA CHICKS IN FOOD, WATER AND CONTROL GROUPS.

Group	n	Growth rate (g day <sup>-1</sup> )	
		Mean	S.D.
Food	16	26.7	9.2
Water	18	31.4	10.1
Control	16	37.4	34.0

TABLE II. MEAN NUMBER OF GREAT SKUA ADULTS PRESENT PER TERRITORY DURING THREE PERIODS, FOR FOOD, WATER AND CONTROL GROUPS.

Time period	Group 1 food			Group 2 water			Group 3 control		
	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
Before treatment	9	1.67	0.43	9	1.50	0.50	11	1.61	0.42
Days 1-7	9	1.52	0.18	9	1.35	0.24	11	1.38	0.18
Days 8-14	9	1.60	0.18	9	1.33	0.22	11	1.29	0.27

## DISCUSSION

Mass growth rates are a useful index for comparing feeding rates among chicks of similar ages (Ricklefs *et al.* 1985, Hamer & Hill 1993), and may be used as an indirect measure of food supply (Ricklefs *et al.* 1984). Mass growth rates of chicks in this study did not differ between treatments (Table I). Since the lipid/protein supplements provided approximately 40% of the daily energy intake of well-fed chicks (see above), we would have expected chicks given these supplements to have gained mass significantly faster than chicks in the other two groups, unless supplementary feeding reduced the rate of food supply by parents. Supplementary food may have been digested and assimilated less efficiently than chicks' usual food (Ricklefs 1992), but the receipt of extra lipid and protein in addition to a normal supply of food from parents would still have led to enhanced mass growth. In fact there is an indication that the rate of mass growth of chicks given supplementary food may have been lower than that of chicks in the other two groups, although the difference was not significant, due to large variances in the data (Table I). In the absence of a reduction in feeding by parents, a lower rate of mass growth could result only from supplementary food causing chicks to lose more than 100% of mass gained through feeding. While this is theoretically possible (for instance if supplementary food induced diarrhoea or regurgitation among chicks) we saw no evidence of any such extreme effects. Changes in pH and ionic balance within the gut lumen, produced by oil/protein supplements, may have impaired absorption, but this would not have affected chicks given supplements of water, and these showed similar mass growth rates to chicks in the other two treatment groups (Table I).

Supplementary feeding may fail to enhance mass growth if chicks are already growing at their physiological maximum rate (Harris 1978), but the highest growth rates of chicks in this study (Table I) were slightly below the rate of 43g/day recorded at the same colony during the 1970s (Furness 1983). Mass growth rates of chicks may also vary in relation to brooding by parents, which reduces chicks' energy requirements for thermoregulation (Montevicchi & Vaughan 1989),

but in this study brooding had ceased by the beginning of the period of supplementary feeding. We are therefore confident that the similarity in mass growth rates for chicks in the three groups indicated that chicks given dietary supplements received less food from their parents.

Mass increments of chicks reflect their feeding rates, but these do not necessarily equate with provisioning rates by parents if chicks do not accept all of the food brought back to them. This raises the possibility that the apparent reduction in provisioning rate among chicks given supplementary food resulted simply from their being less able to accept food from their parents. However, chicks given supplements of water gained mass at a similar rate to those given no supplements (Table I). Reductions in chick feeding rate thus appeared to result from our supplying them with nutrients, and not simply from our distending their proventriculi with liquid. Furthermore, a presumed reduction in provisioning rate was accompanied, once chicks were more than two weeks old, by an increase in adult territorial attendance (Table II).

The lack of a difference in attendance prior to the second week of manipulation was probably due to the food requirements of chicks being too small at this stage to affect adult attendance (Furness 1983). These results are in accord with previous studies which recorded lower attendance of adults with artificially enlarged broods or in conditions of reduced food supply only when chicks were more than two weeks old (Furness & Hislop 1981, Hamer *et al.* 1991).

Breeding performance and reproductive effort of Great Skuas are related to adult quality (Hamer & Furness 1991, 1993), and so differences between treatment groups in chick provisioning rate could arise from differences in adult quality rather than differences in experimental manipulation. Although we present no data concerning mass growth rates of chicks before supplementary feeding, there was no difference between treatment groups in adult attendance before manipulation (Table II) or in laying date, which has a close relationship with chick growth and survival in Great Skuas (Furness 1983). Differences between groups in chick provisioning rate and adult territorial attendance thus resulted from differences in supplementary feeding rather than from differences in adult quality.

The results of this study indicate that supplementary feeding of chicks led to a decrease in provisioning by adults, and that this was reflected by an increase in the time which adults spent within their territories. The study was carried out in conditions of relatively good food supply (as indicated by monitoring of sandeel stocks in Shetland waters; Hamer *et al.* 1993), when chick growth rate was close to the maximum recorded at the colony (see above). In conditions of poor food supply, supplementary feeding might be expected to lead to enhanced chick growth, with adults reducing their foraging effort only above a threshold growth rate. The results of this study should perhaps be viewed with some caution, since the sample of chicks was small, and we present no information concerning the effects of supplementary feeding upon solicitation by chicks (Henderson 1975). Nonetheless, the study suggests that reductions in territorial attendance by Great Skuas following a decline in food availability (Hamer *et al.* 1991) were indicative of an increase in reproductive effort. We hope that it also draws attention to the need for further investigation of the regulation of chick-feeding in seabirds.

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#### SUMMARY

Supplementary feeding of Great Skua chicks on Foula, Shetland did not produce any increase in mass growth rates of chicks over a 14-day period. However, territorial attendance of parents whose chicks were given supplementary food was elevated in comparison to control groups during the second week of feeding. These

results suggested that supplementary feeding of chicks led to a decrease in provisioning by adults. This was in accord with the notion that observed reductions in territorial attendance of adults in previous years, following a reduction in food supply at the colony, were indicative of increases in reproductive effort. Nonetheless, there is a need for further investigation of the regulation of chick-feeding in seabirds.

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# Age-related changes in the agonistic behaviour of immature Common Guillemots *Uria aalge*

D.J. Halley and M.P. Harris

## INTRODUCTION

A number of factors have been suggested as influencing the age at which seabirds recruit into the breeding population. These include physiological maturity (Ainley 1978, Hector *et al.* 1986), development of foraging competence (Burger 1990), the acquisition of social skills and intra-pair co-ordination (Nelson 1989, Pickering 1989), and competitive ability to obtain sites and/or mates (Potts *et al.* 1980, Porter & Coulson 1987).

Although at least some Common Guillemots *Uria aalge* are physiologically capable of breeding at age 3, typically birds first breed at age 5-7 (Birkhead & Hudson 1977, Harris, Halley & Swann *in press*). Before breeding, an individual typically spends several years attending the breeding colony. Guillemots both defend nest sites vigorously and nest at extreme densities (up to 20 pairs/m<sup>2</sup>); in some colonies, density of nesting is positively correlated with breeding success (Birkhead 1977). They appear not to form more than transient pairings prior to site acquisition, so that obtaining a good site and a high-quality mate may be correlated (Halley 1992). As pair-bond formation and physiological maturity seem unlikely, therefore, to account for the length of deferred maturity in Guillemots, the underlying factors are presumably foraging competence and/or competitive ability for sites/mates at the colony.

We investigated the agonistic behaviour of individually identifiable immature Guillemots of known age to test whether the pattern of agonistic behaviour was consistent with the second of these hypotheses, i.e. that increased ability to compete at the colony was an influence on the period of deferred maturity in the species.

## METHODS

Fieldwork was carried out during 1990 and 1991 at the colony of c.12000 breeding pairs on the Isle of May (56°11'N, 2°33'W) in the entrance to the Firth of Forth, Scotland. The island is described in detail in Eggeling (1974). Each year since 1983 Guillemot chicks (range: n = 194-581 chicks; see Halley & Harris 1993 for details) have been ringed with BTO metal rings and, in most cases, year-class colour rings. Since 1988 most colour rings have been engraved with a unique number. Birds were classified as 'immature' if they were of known age and did not attempt to breed in the season in which observations were made, or in any previous year.

Behavioural data was collected as five minute samples of ringed focal individuals using the continuous sampling method (Altmann 1974), which involves the recording of data in real time, noting changes in behaviour as they occur. A total of 513 samples were collected in 1990 and 415 in 1991. Samples were recorded on an Epson HX20 microcomputer using a BASIC programme. The data were later transferred to an ORACLE database. Data recorded included the identity of the bird (BTO ring number) and its age, and various behavioural categories including agonistic interactions. Agonistic encounters were defined as the neck-pointing threat display (Birkhead 1978), jabbing with the bill, and full-scale fights. For agonistic encounters, the identity of the opponent was noted (where known), which bird initiated the encounter (focal bird, opponent, or unclear), and the outcome (win, lose, draw). Birds moving away, flying off, or performing any of several appeasement displays (Birkhead 1978) were considered to have lost the interaction. If both birds withdrew simultaneously, or the encounter ended without withdrawal or appeasement, the outcome was scored as a draw.

The presence of immature birds at the colony was not predictable and sampling was therefore haphazard, using birds available at the time. An effort was made to sample as many different individuals as possible. Many birds were sampled more than once in the course of a season; where this occurred, only one sample for each bird was included in statistical calculations of agonistic behaviours (Beal & Khamis 1990). The sample used was selected at random (using random number tables or dice). Data was analysed for differences in frequency between age classes using  $\chi^2$  tests. In most cases sample sizes were small, as agonistic encounters were relatively uncommon, and it was necessary to combine data from more than one age class to allow calculation. Between-years comparisons of the same cohort were made using  $\chi^2$  or Fisher Exact Tests. Where a bird was sampled in both seasons, the sample used was selected at random so that no individual was represented in more than one category. Ringed birds constituted only a small proportion of the immature (and adult) population and all but one agonistic encounter recorded the non-focal bird was unringed. As a result, the age and sex of the opponent was usually unknown (although they appeared to be immatures in almost all cases). Guillemots are sexually monomorphic, and few ringed immatures could be sexed. In consequence, information on the age of opponents or on the role of sex in agonistic encounters was not obtainable.

## RESULTS

In both 1990 and 1991, younger immature cohorts were more likely to be involved in agonistic encounters than older age classes (Fig. 1). Older birds were significantly more likely to start fights than younger birds in 1990, but not in 1991 (Fig. 2), and were also more likely to win fights in both years (Fig. 3). Changes between years in whether cohorts were likely to start and to win agonistic encounters are summarised in Table I. Birds of the 1988 cohort were significantly more likely to start the agonistic encounters they engaged in in 1991 compared to 1990. All other comparisons were not significant.

TABLE I. AGE-RELATED CHANGES WITHIN COHORTS IN THE PROPORTION OF BIRDS INITIATING AND WINNING AGONISTIC INTERACTIONS

Natal Year	1990 <sup>1</sup>		1991 <sup>1</sup>	
	Number of interactions initiated by:		Number of interactions initiated by:	
	focal bird	other bird	focal bird	other bird
1985	6	2	3	2
1986	12	4	6	7
1987	2	7	5	4
1988 <sup>2</sup>	1	2	8	5

	1990		1991	
	Number of interactions won by:		Number of interactions won by:	
	focal bird	other bird	focal bird	other bird
1985	6	2	3	2
1986	12	4	6	7
1987	2	7	5	4
1988	1	2	8	5

<sup>1</sup>Where an individual was recorded in an agonistic interaction more than once in a year, and/or in both years, only one record, selected at random, was used (see text).

<sup>2</sup>Fisher Exact Test,  $p < 0.05$ . All other between-years comparisons n.s.

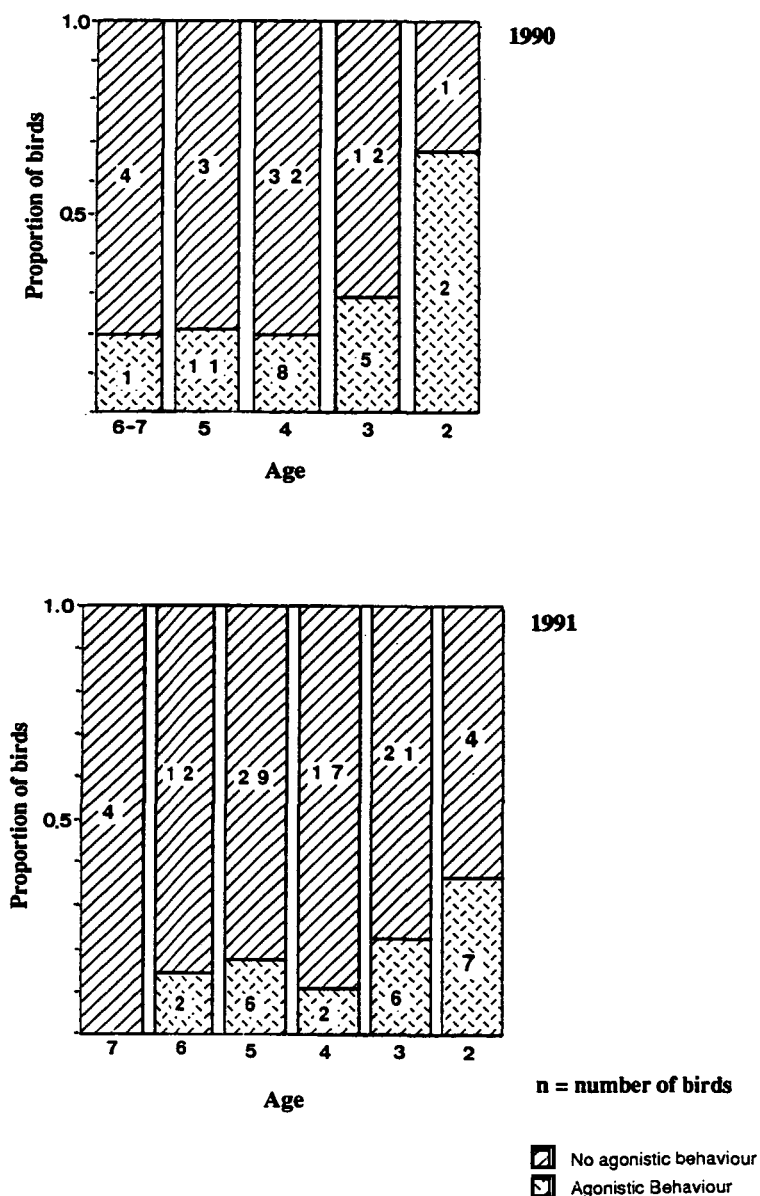


Figure 1. Proportion of known-age immatures involved in agonistic interactions. Differences in proportions related to age were significant in both years (1990:  $\chi^2 = 10.67$ , 2d.f.,  $p = 0.005$ . 5-7 year old and 2-3 year old cohorts combined in calculation. 1991:  $\chi^2 = 6.39$ , 2d.f.,  $p = 0.041$ . 5-7 year old and 2-3 year old cohorts combined in calculation).

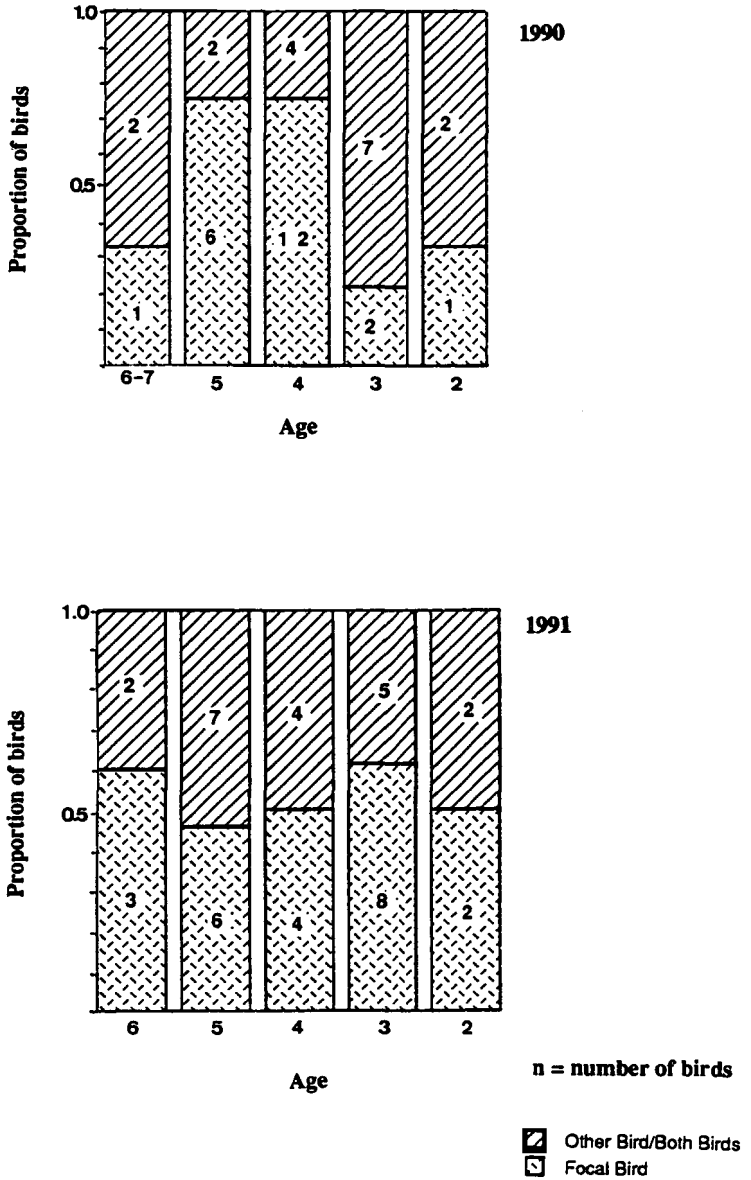


Figure 2. Proportion of known-age immatures initiating agonistic interactions. Differences in proportions related to age were significant in 1990 ( $\chi^2 = 7.30$ , 2d.f.,  $p = 0.026$ . 5-7 year old and 2-3 year old cohorts combined in calculation) but not in 1991 ( $\chi^2 = 0.006$ , 1d.f.,  $p = 0.94$  n.s. 5-6 year old and 2-3 year old cohorts combined in calculation).

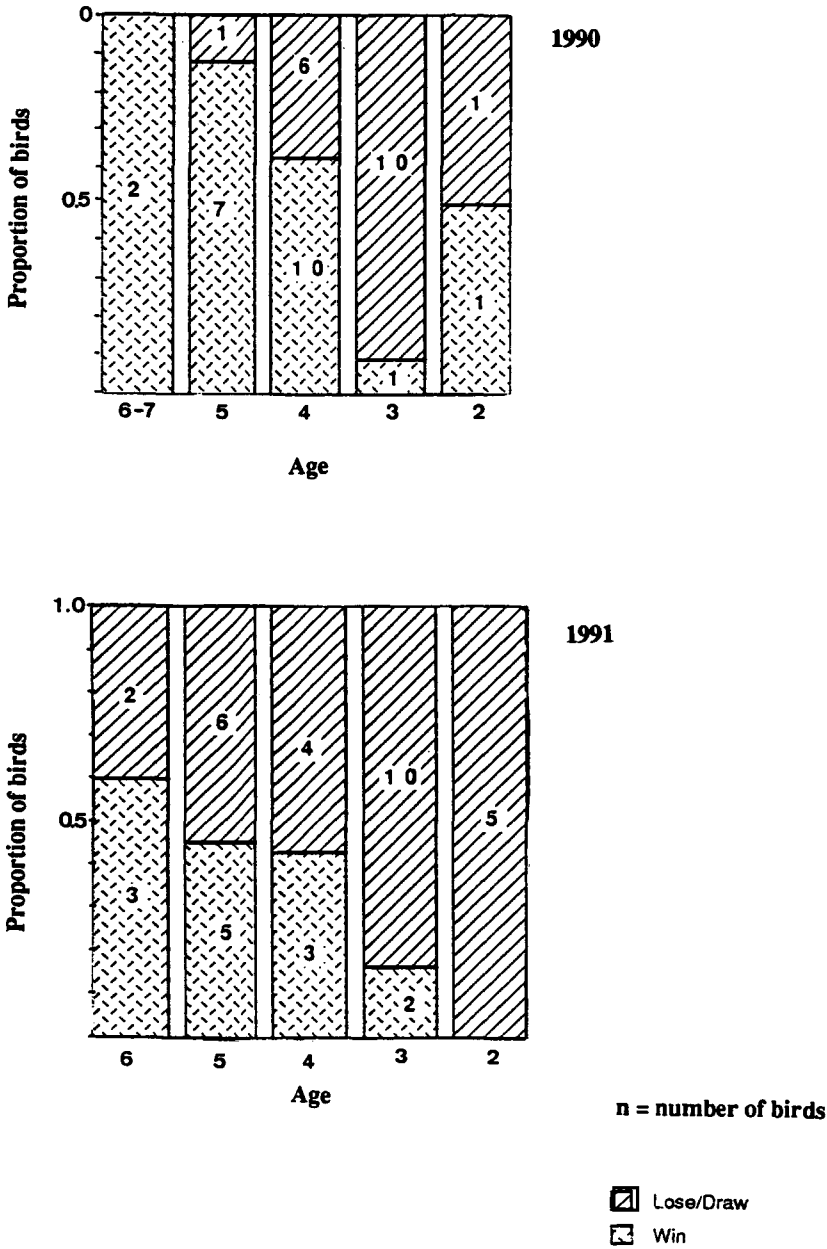


Figure 3. Outcome of agonistic interactions in relation to age in 1990. Differences in proportions related to age were significant (1990:  $\chi^2 = 9.40$ , 2d.f.,  $p = 0.002$ . 5-7 year old and 2-3 year old cohorts combined in calculation. 1991:  $\chi^2 = 4.27$ , 1d.f.,  $p = 0.039$ . 4-6 year old and 2-3 year old cohorts combined in calculation).

## DISCUSSION

Older immatures were more likely than younger birds to start fights and to win them, but were involved in fewer fights overall. Most immature Guillemots remained on top ledges or fringe sites, rather than breeding sites, until the season that they first bred (Halley 1992), suggesting that differences between cohorts in location did not cause the observed pattern of behaviour, and that fights for breeding sites *per se* were not the cause of the differences in agonistic behaviour observed. Guillemots feed at sites remote from the breeding colony, so competition for food or feeding sites can also be excluded.

However, sites where Guillemots could observe breeding areas of the colony were limited. Individual immatures normally occupied a specific site or small area of nonbreeding ledge, overlooking or adjacent to a breeding area of the colony, within and between breeding seasons (Halley & Harris *in prep*). This suggests the possibility that immatures were building a detailed knowledge of a small part of the breeding colony in order to exploit any vacancies in sites/mates which might occur. Of 22 immatures seen in 1990 which bred in 1991, all bred at the subcolony which they attended in 1990, and none on the site which they occupied in the former year (Halley 1992).

The attendance site used by an immature bird would therefore appear to have some value to it, and this value probably increases, up to a point, the greater the time invested at that site. Competition and agonistic encounters over such sites would therefore be expected. Aggressiveness, and competence in agonistic behaviour, will presumably also assist in securing a good-quality site when recruitment is attempted.

In a wide range of seabird species, foraging competence increases with age and birds normally recruit at or just after the age at which they attain adult levels of competence (Burger 1990 for review). This suggests that older birds will be in better physical condition, with higher reserves of energy. Among other things, this would tend to enhance the ability to perform, and to recover from, agonistic interactions. Older birds will also have had, on average, more practice in such behaviours. These factors may account for their greater propensity to start and to win fights.

However, older birds will also have a higher level of motivation to breed, and therefore to compete for sites and mates, than younger birds (Partridge & Harvey 1986). Motivation, physical ability, and practice will tend to be mutually reinforcing, combining as proximate factors producing the observed pattern of behaviour. The tendency of younger birds to be in more fights (because they are attacked more often), and to lose, is consistent with this pattern.

The pattern of agonistic behaviour seen in immature Guillemots is, therefore, consistent with a role as a proximate factor influencing age of first breeding. However, the underlying ultimate reason remains most likely to be the time taken to develop foraging competence, which influences the physical state of the animal, the amount of time it can devote to colony attendance and consequently practice in agonistic interactions, speed of recovery from damage inflicted, and ability to provision offspring (which will affect the cost/benefits of a breeding attempt, and so motivation to breed). Unfortunately, the data available do not permit investigation of the role of sex, or of the influence of the age of the opponent, on the pattern of behaviour. Further information in these areas would be valuable. From the perspective of behavioural ecology, it would also be of further interest to understand the factors underlying the choice of attendance location, and the factors which might induce birds to change it. Possibilities exist for manipulative studies to investigate the nature of this decision-making process.

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### SUMMARY

The agonistic behaviour of individually identifiable immature Common Guillemots was studied in 1990 and 1991 at the Isle of May, Scotland. In both years, younger birds were more likely to be involved in agonistic encounters, but were more likely to lose them, compared to older immatures. In 1990, older birds were more likely to initiate agonistic encounters than younger immatures. The pattern of behaviour is consistent with the hypothesis that competitive ability at the colony is a proximate factor promoting deferred maturity in the species.

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# Courtship behaviour in offshore Kittiwake *Rissa tridactyla* flocks prior to the breeding season

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## INTRODUCTION

The Kittiwake *Rissa tridactyla* is the most oceanic of British gulls *Laridae*, coming to land only in the breeding season (April to August) and nesting colonially on narrow cliff ledges. Previous studies (e.g. Cullen 1957, Daniels & Heath 1984a and b, Coulson & Thomas 1985, Danchin 1987, 1988) have thus concentrated entirely on behaviour at the breeding cliffs. Indeed, it has been widely assumed that the breeding cliffs are the only place where pair interactions occur. For instance, Chardine (1983) states that:

"It is important to note that unlike many other gulls that interact as pairs in "clubs" or in areas other than the nest site the kittiwake returns directly to the nest site upon arrival from wintering areas (Cullen 1957). Thus all pair interactions are likely to occur at the nest site."

Coulson and Thomas (1983) also assume that pair-bonds break down during the winter and are re-formed upon return to the breeding cliffs. They regard individual differences in date of return to the colony as an important mechanism in determining mate choice, first time breeders arriving at the breeding site later than older birds.

The observations reported below show that Kittiwakes are present offshore from the breeding cliffs, in flocks or rafts at least one month before moving collectively to the cliffs. Moreover behavioural interactions within the flocks include many of the aggressive, pair formation and courtship displays described previously (Daniels & Heath 1984, Daniels *et al.* 1984, Danchin 1991). This suggests that in some cases mate choice may begin on the water in the close vicinity of the breeding cliffs.

Surprisingly, this is the first study reporting the behaviour of Kittiwakes on the sea, others have merely mentioned the presence of flocks offshore at the start of the breeding season (Mauder & Threlfall 1975) or the foraging behaviour of Kittiwakes following fishing vessels (Wahl & Heinmann 1979).

## METHODS

The colonies studied were located at Hope's Nose in Devon where there were approximately 200 breeding pairs in 1984, and at Puffin Gully, Lundy, Bristol Channel where there were approximately 220 breeding pairs in 1990. Observations of both the breeding cliffs and the off-shore sea areas were originally commenced in early January through February, but at these times the breeding cliffs were only occasionally visited by solitary immature birds which never stayed for any length of time. Observation was commenced at dawn on both the sea areas and the breeding cliffs but it quickly became apparent that the Kittiwakes were not within observable distance at that time of the year. It was at the beginning of March that the first Kittiwake flocks were observed. Rafts of birds formed off-shore at distances of 150-800m. These rafts were always formed directly in front of the breeding cliffs and although tide and wind moved the raft, it would eventually re-form in the original position.

Observations were made from a vantage point above each breeding cliff with the aid of 10 x 50 binoculars and a 16 x 32 telescope. The binoculars were used for counting the number of birds



comprising the flock, this was done every 15 min throughout the observation period 1000-1700 hours each day. The telescope was used to observe individual behaviour in Kittiwakes in response to the Long-Calling emitted by birds on the sea (aquatic Long-Calling) and the observations of the subsequent behavioural interactions that followed such Long-Calling. The method employed to record behavioural interactions was that of Focal-Animal Sampling (Altmann 1974) i.e. when a calling bird was located, neighbouring birds within a radius of approximately 15m of the calling bird, were scanned, the number of birds responding were noted and their specific responses to the Long Call and the Greeting Ceremony were recorded.

## RESULTS

The dependant measures recorded from each of the two flocks concentrated on (a) the flock size and (b) the behavioural interaction between flock members.

Looking first at the flock size several factors emerged as being important. For instance, the data (shown in Fig 1) suggest that the flock sizes increased with the time of day.

A two-way ANOVA (flock x time) was used to test the significance of this observation and from this it appears that not only was the flock at Puffin Gully significantly larger than the one at Hope's Nose, ( $F_{1,174}=8.11$ ,  $p<0.005$ ), but also, flock size was significantly affected by the time of day ( $F_{28,174}=7.24$ ,  $p<0.0001$ ). A post-hoc contrast revealed that this 'time of day' effect was due to

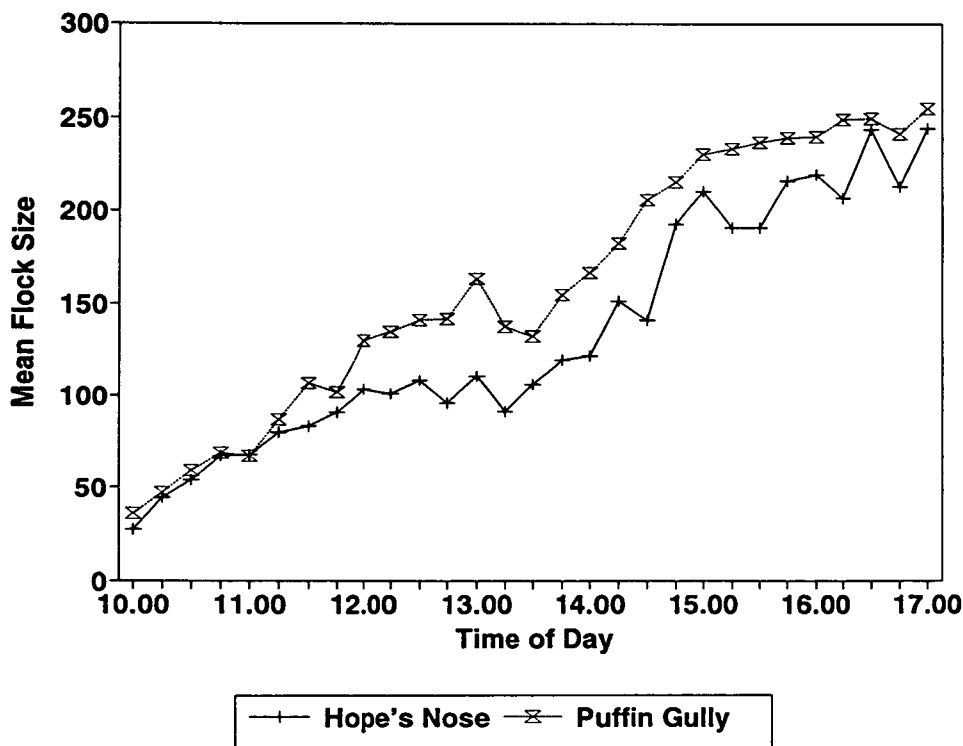


Figure 1. Changes in mean Kittiwake flock size in relation to the time of day at the Hope's Nose and Puffin Gully study sites. The mean flock size increases linearly and significantly throughout the day at both study sites.

a linear increase in flock size throughout the day ( $F(\text{lin})=195.16$ , which exceeds the Scheffé Criterion at  $p<0.0001$ ). The lack of a significant interaction between flock and time of day indicates that this 'time of day' effect is common across the two flocks.

The second important factor to affect flock size was that of 'week' within March. As shown in Fig. 2, it emerged that over the four-week observation period, the size of both flocks increased, and maximum numbers were observed at week 4, 14-16 days before the breeding cliffs were occupied. This suggests that most of the birds had arrived in the vicinity of the breeding-cliffs by this time.

A two-way ANOVA (flock x week) was applied to the raw data from which Fig. 2 is derived in order to assess the significance of this flock increase over weeks. Again, the Puffin Gully flock was found to be significantly larger than the one at Hope's Nose ( $F_{1,224}=7.31$ ,  $p<0.007$ ). Furthermore, the flock size was seen to be significantly affected by the week of the observation period ( $F_{3,224}=36.3$ ,  $p<0.0001$ ). Three post-hoc tests were performed to assess the significance of the linear, quadratic and cubic components of this effect. From this, it is clear that the 'week' effect can be mainly attributed to a linear increase in flock size across weeks ( $F(\text{lin})=69.28$ , which exceeds the Scheffé Criterion at  $p<0.0001$ ), and this accounts for 63.6% of the 'week' effect. The remainder of the variance associated with this 'week' effect is accounted for by a non-significant quadratic effect ( $F(\text{quad})=3.47$ , NS) and a significant, but subsidiary, cubic effect ( $F(\text{cubic})=36.15$ ,  $p<0.0001$ ) 33.2% of the 'week' effect.

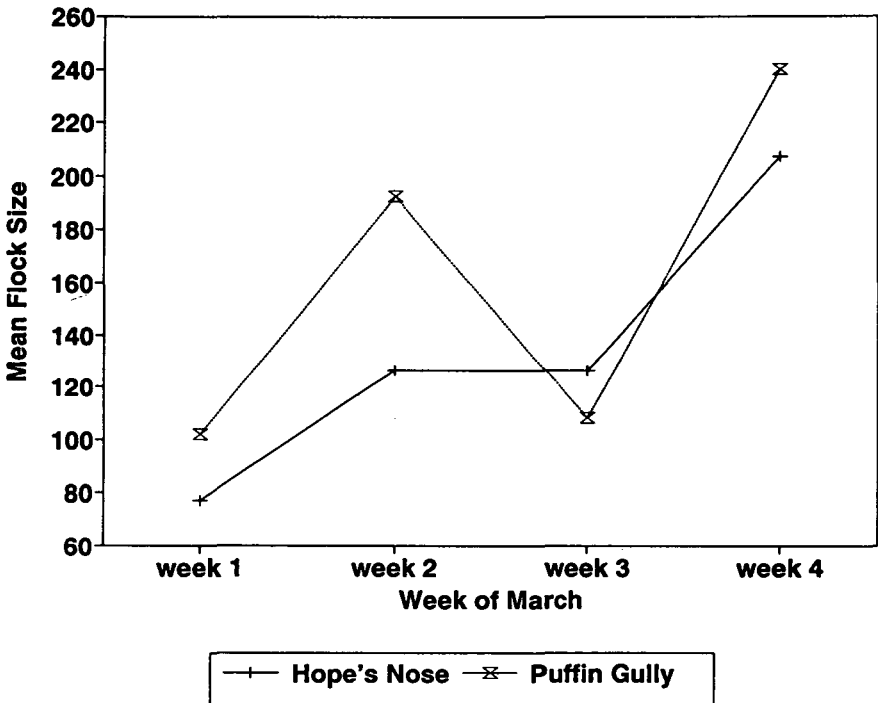


Figure 2. Changes in mean Kittiwake flock size in relation to week of March at the Hope's Nose and Puffin Gully study sites. The mean flock size increases from week 1 to week 4. The Hope's Nose flock shows significant linear increase, whereas the Puffin Gully flock shows a cubic pattern of growth over time.

The two-way ANOVA also revealed a significant interaction of 'flock x week' ( $F_{3,224}=3.22$ ,  $p<0.024$ ). Referring back to Fig. 2 it appears that the flock at Hope's Nose shows a more or less steady increase in flock size across weeks while the flock at Puffin Gully shows a more irregular pattern of flock size across weeks. Six post-hoc test were performed to assess, for each flock, the significance of the linear, quadratic and cubic increase in flock size across weeks. It emerged that the increase in flock size at Hope's Nose was only significantly described by a linear pattern of flock growth across weeks ( $F(\text{lin})=40.74$ ,  $p<0.0001$ ;  $F(\text{quad})=1.3$ , NS;  $F(\text{cubic})=4.48$ , NS), whereas, the increase in flock size at Puffin Gully was best described by a cubic pattern of flock growth across weeks, with a subsidiary but significant linear pattern of growth ( $F(\text{lin})=29.04$ ,  $p<0.0001$ ;  $F(\text{quad})=2.23$ , NS;  $F(\text{cubic})=40.77$ ,  $p<0.0001$ ). While there is a significant linear pattern of flock growth for the Puffin Gully flock, the complex contrast assuming a linear pattern of growth for both flocks is not significant ( $F(\text{lin} \times \text{lin})=0.497$ , NS). Thus it is concluded that the variance accounted for by the 'week' effect and its interaction within the two flocks can be attributed to a linear increase in flock size across weeks at Hope's Nose and a cubic increase in flock size across weeks at Puffin Gully.

Although the Bow-and-Moan display and occasionally Downward Choking were observed to occur spontaneously on the sea, most behavioural interactions within the flock were initiated by the Long-Call (see Daniels & Heath 1984, Daniels *et al.* 1984 and Danchin 1991 for a full description of these displays and others). Therefore, it is these interactions which we quantified. The Long-Call in the off-shore flocks differs in a number of ways from that uttered at the breeding cliffs, where it is predominantly, but not always, emitted upon the return of one of the partners when it forms the basis of the Greeting Ceremony (Wooller 1978, Heath *et al.* 1982). On the sea however, it is notable that Kittiwakes never emit the Long-Call upon landing on the sea and make no immediate attempt at any interaction. The aquatic Long-Call is apparently spontaneous, emitted when the bird is paddling vigorously and turning its body in different directions as if to broadcast the sound more widely. The number of other birds responding to this display is given in Table I.

Of the 401 observations made of the display at Hope's Nose, it can be seen that 26% of the calls elicited no evident response from birds within a radius of approximately 15m from the calling bird whilst a further 13% were countered with aggressive (Attack) replies, the calling bird being pursued and pecked by a single neighbour. Attacks by more than one bird within the 15m radius were never observed. In the remaining cases, birds near the caller (though not necessarily the nearest ones) responded by Long-Calling. Interestingly, in the majority of cases where there was a Long-Call in response, only a single bird responded, even though there were many other birds at the same distance or even closer to the caller. In 165 (41%) cases the original caller and the responding bird paddled towards each other over a distance of 10-20m, other birds in the vicinity playing no part in the interaction. They performed aquatic Greeting Ceremonies in parallel or face-to-face and commenced the mutual rhythmic movements of head and neck (Heath *et al.* 1982, Danchin, 1991) whilst continuing to call. As in the terrestrial Greeting Ceremony, it is often terminated by Upward Choking, though the latter is less vigorous and less pronounced in the

TABLE I. HOPE'S NOSE SITE: NUMBER OF BIRDS (1-5) WHICH RESPOND TO AN AQUATIC LONG-CALL, WITH A LONG-CALL, ATTACK OR NO RESPONSE (NR).

	<i>Long-Call</i>					<i>Attack</i>	<i>NR</i>
	1	2	3	4	5	1	
No.	200	33	9	3	2	50	104
%	50	8	2	0.5	0.5	13	26

aquatic version. Table II shows that 29% of greetings are followed by Head Tossing, the main courtship display in the Kittiwake (Chardine 1983, Daniels & Heath 1984, Danchin 1991) and which later in the season precedes either Courtship Feeding or Copulation (D. Daniels & J. Heath, unpublished data). Occasionally Courtship Feeding did occur on the water but Copulation was never observed. Aquatic Head Tossing, when it occurred commenced immediately after the Greeting Ceremony and continued for up to two minutes.

Bill Dipping is a display hitherto unreported in the literature. It sometimes follows the Greeting Ceremony (38%) when one or both birds dip their bills very rapidly into the water sometimes followed by a rapid shake of the head. This display is obviously peculiar to aquatic Courtship. It is well known that ritualised preening and bathing form the basis of many courtship displays e.g. the *Anatidae* (Lorenz 1951).

The data presented in Table III shows the number of birds which responded to the aquatic Long-Call over the period of the study. Each week exactly 100 observations were made of aquatic Long-Call occurrence and the number of birds responding were counted. As can be seen from Table III as the weeks progress it becomes increasingly likely that only one bird will respond.

Making 100 observations of aquatic Long-Calling during each week, revealed that the most likely outcome of responding to the aquatic Long-Call was the aquatic Greeting Ceremony (Table IV) and this increased in frequency from week 1 to week 4.

Finally, Table V shows the result of using Focal-Animal Sampling to determine exactly which behaviour followed the Greeting Ceremony. There were four extensive possibilities. First the Pre-Departure Call, secondly Head-Tossing, thirdly Bill-Dipping (see above) and last, a category we call no discernible display or NR. As can be seen from the Table, all these displays remain fairly constant over the period of study.

TABLE II. HOPE'S NOSE SITE: TYPES OF BEHAVIOUR WHICH FOLLOW THE AQUATIC GREETING CEREMONY.

	<i>Head Tossing</i>	<i>Bill Dipping</i>	<i>No further behaviour</i>
N	48	62	55
%	29	38	33

## DISCUSSION

It is clear from the data presented above that courtship behaviour in the Kittiwake is not confined to the breeding cliffs. The main courtship displays of this gull, the Greeting Ceremony and Head Tossing have both been observed to occur within flocks on the sea and in the vicinity of the breeding site. These observations bring into question the supposition that Kittiwakes perform all their pair-bonding behaviour within the confines of the breeding cliffs. It is also clear from these data that occupation of the breeding cliffs in these conditions differ from those described by

TABLE III. THE NUMBERS OF BIRDS RESPONDING TO THE AQUATIC LONG-CALL. EACH WEEK A TOTAL OF EXACTLY 100 OBSERVATIONS WERE MADE.

<i>Week</i>	<i>Numbers of birds responding to aquatic Long-Call</i>					
	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>NR</i>
1	57	9	5	1	3	25
2	63	7	1	0	0	29
3	61	11	4	0	0	24
4	76	8	2	0	0	14

Coulson & Thomas (1983). In the colony studied and described by these latter workers the Kittiwakes build nests on the window ledges of warehouses situated on the north bank of the River Tyne some distance from the sea. There, it is said, the Kittiwakes arrive at the breeding site in small groups over the period December to April (Coulson & Thomas 1985).

TABLE IV. TYPE AND FREQUENCY OF BEHAVIOURAL RESPONSE WHICH FOLLOWS AQUATIC LONG-CALLING. 100 OBSERVATIONS WERE MADE EACH WEEK.

Response	Week 1	Week 2	Week 3	Week 4
Greeting Ceremony	48	51	54	63
Long-Calling	13	9	8	7
Attack	14	11	14	16
No Response	25	29	24	14

Kittiwakes live for up to 22 years and tend to retain the same mate over a period of up to seventeen years (Coulson 1972). However, some birds do change mate, either through death of a partner or by "divorce". Asynchronous return to the colony between pairs is considered to be the mechanism for a change of mate (Coulson & Thomas 1983). Furthermore, these workers also note that "divorce" is more common among mates that fail to breed. Such failure perhaps stems from the same incompatibility that results in partners' asynchronous return to the breeding cliffs. At both breeding sites studied here, most if not all members of the colony were present 14-16 days

TABLE V. PUFFIN GULLY SITE: THE TYPES OF BEHAVIOUR WHICH FOLLOW THE AQUATIC GREETING CEREMONY

Week	N	Pre-Departure Call	Head Tossing	Bill Dipping	NR
1	48	2 (4%)	14 (30%)	21 (44%)	11 (22%)
2	51	3 (6%)	19 (37%)	20 (40%)	9 (17%)
3	54	5 (9%)	17 (31%)	21 (39%)	11 (21%)
4	63	5 (8%)	24 (38%)	22 (35%)	12 (19%)

prior to the occupation of the breeding-cliffs. Furthermore, the move to the cliffs was completely synchronised, and all breeding sites were occupied fully by the end of the first week in April. Cullen (1957) in her classic study of Kittiwakes postulated that Kittiwakes, unlike ground-nesting gull species, do not go to neutral ground or to pairing territories prior to the breeding season. Rather, males were said to go directly to the nesting ledges and there advertise for females whilst repelling males using the Downward Choking display. The immediate occupation of a site by male occupation, was attributed to (a) the Kittiwakes "fear of land" and (b) the severe competition for nesting-sites. However, the present study has revealed that Kittiwakes do not return to the breeding cliffs directly, but remain offshore, in flocks, for at least one month prior to synchronised occupation of the cliffs. Although individual male Kittiwakes could have moved to the ledges at any time during that month, none did. Thus, occupation of the breeding cliffs was clearly a "colonial" decision. It is likely that the offshore Kittiwake flock is equivalent to the pre-breeding gathering of ground-nesting Larids on neutral ground. Furthermore it is possible that Kittiwake

partners remain in contact outside the breeding season, as in some passerine species (Witkin & Ficken, 1979) which would obviate any protracted pair-bond formation each and every year. Since pair interactions occur away from the breeding-cliffs, then recognition of partner is a necessary precondition. Individual recognition is the obvious (Wooller 1978, Falls 1982) and occurs through vocal recognition (Wooller 1978). However, exactly how Kittiwakes discriminate between kin and partner is not known and will form the basis of further research.

#### SUMMARY

The behaviour within offshore Kittiwake flocks was observed at two sites in Devon, over a period of a month (March 1984 and March 1990) immediately prior to the birds taking up seasonal residence on the breeding-cliffs. Over these periods of observation the size of both blocks increased significantly throughout the day and over the period of observation.

Within the flocks, single floating birds would emit the aquatic Long-Call whereupon several surrounding birds would respond to the caller, mainly with the Long-Call. Secondly, the calling bird located a responding bird and subsequently displayed interactive behaviours typical of those observed in Kittiwakes on the breeding-cliffs. Once signal sender and responder had located each other and performed the aquatic Greeting Ceremony, subsequent courtship behaviour was observed to occur, the most notable being the Head-Tossing display the main courtship display of the Kittiwake. Interestingly, a heretofore unreported display was observed that of Bill-Dipping, which is obviously peculiar to aquatic courtship. These observations query previous suppositions that Kittiwakes perform all pair-bonding behaviour within the confines of the breeding cliffs. Furthermore, it now seems likely that mate-choice and partner recognition in the Kittiwake begin at sea.

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# Biometrics and seasonal changes in body composition of Common Guillemots *Uria aalge* from north-west Scotland

R.W. Furness, D.R. Thompson and N. Harrison

## INTRODUCTION

Fat and protein reserves in birds vary in relation to migration, breeding and winter conditions. Osborn (1979) reported seasonal changes in protein and fat contents of livers of Starlings *Sturnus vulgaris* whilst a similar study noted seasonal trends in Goshawks *Accipiter gentilis* (Marcstrom & Kenward 1981), and body composition changes in a range of species of waders have been reported (Pienkowski *et al.* 1979, Dugan *et al.* 1981). Changes in total body mass, fat reserves and body water content have been reported in some seabirds (Harris 1979, Coulson *et al.* 1983, Osborn & Harris 1984, Furness 1987). In several cases, changes in total body mass have been interpreted as a measure of changes in body reserves.

In this paper, seasonal patterns in whole body and tissue masses together with fat and water contents are presented for samples of Common Guillemots *Uria aalge* from a non-migratory population. These birds were obtained primarily for dietary studies, but were made available for further study. Here we examine the differences in seasonal samples with particular emphasis on the components fat, protein and stomach contents as determinants of total body mass.

## METHODS

### *Sample collection and treatment*

Common Guillemots were collected on three occasions (27 April, 25 June and 1-2 November, 1988) from the waters surrounding the Summer Isles at the mouth of Loch Broom, north-west Scotland for dietary studies by the JNCC Seabirds-at-Sea Team, and were subsequently made available to us. In all cases, birds were shot, at sea under licence, from a small inflatable boat using a 12-bore shotgun. All collections were made under calm conditions.

Shot Common Guillemots were returned to shore within ca. five minutes and weighed (to 10 g) using a 1500 g Pesola spring balance. No birds were 'water-logged' at the time of weighing, but some variation in fresh body mass would have been attributable to moisture on the plumage. Measurements of bill depth at gonydeal angle (to 0.1 mm), culmen length (to 0.1 mm), head plus bill (from the back of the skull to the tip of the bill, to 1 mm) and wing length (maximum, flattened chord from the carpal joint to the tip of the longest primary, to 1 mm) were made using methods described by Jones *et al.* (1982). In addition, birds were identified as being in summer or winter plumage, details of primary and secondary moult were noted and presence or absence of a brood patch recorded.

The body cavity was opened, the liver carefully removed, placed in a sealed polythene bag and labelled to await further treatments. The crop and gizzard were removed to await dietary examinations. The sex of each bird was determined by internal examination. The length and width of the testes were measured in males (to 0.1 mm) and the length of the bursa, if present, measured (to 0.1 mm). Fresh masses of whole liver were determined in the laboratory (to 0.001 g) and any measurements and sex determinations which could not be obtained in the field (through fading light during the November collection, for example) were performed. One individual, an adult bird from the November collection, could not be sexed unequivocally due to gun-shot damage. All

carcasses and livers were stored deep-frozen at ca.  $-20^{\circ}\text{C}$  prior to further treatments; storage time was less than one month. None of the birds obtained in this study carried a unique metal leg ring.

#### *Body composition analyses*

All tissue masses were accurately determined (to 0.001 g). After removal of ca. 0.5 g (accurately weighed) sections of liver for mercury analysis, the remainder of the liver was weighed again and dried in an oven at  $70^{\circ}\text{C}$  to constant mass. One complete pectoral muscle was removed, weighed fresh, and then dried to constant mass. Livers and pectoral muscles from each bird were individually wrapped in filter paper packets and lipid was extracted with refluxing chloroform in a soxhlet apparatus. A subsample of tissues re-dried and weighed after 24 h and again after 48 h of extraction showed that fat extracted during the second 24 h period represented less than 5% of the total. Nevertheless, all extractions were performed over 48 h.

The remaining carcass (after removal of proventriculus and gizzard, the liver, one complete pectoral muscle and a 0.5 g fragment from the other for mercury analysis, most of the kidneys and ca. 0.1 g of body feathers also for mercury analysis) was weighed fresh and then dried to constant mass at  $70^{\circ}\text{C}$ . It was then crushed to powder inside a cloth bag and fat extracted in a soxhlet apparatus as before. As with liver and muscle tissues, almost all fat was removed within 24 h but extractions were performed over 48 h, one bird in the soxhlet apparatus at a time. After fat extraction, carcasses and tissues were placed in a drying oven at  $70^{\circ}\text{C}$  overnight to remove all traces of chloroform before fat-free dry masses were determined. Amounts of fat and water were obtained by subtraction of fat-free dry masses from dry masses, and dry masses from fresh masses, respectively. Water and fat contents were expressed as indices where the water (or fat) index of a particular tissue or whole bird = water (or fat) mass/fat-free dry mass of that tissue or bird.

#### *Statistical analyses*

Preliminary tests were performed of the goodness of fit of data to normal distributions (Kolmogorov-Smirnov one sample tests). Where fit was good, subsequent analyses were made using parametric statistics. Where data deviated significantly ( $P < 0.05$ ) from normality we used nonparametric statistics. Statistical tests were performed using the SPSS-PC+ package (Norusis 1986, 1988). Throughout this paper, statistical significance is defined as a probability of chance occurrence under the null hypothesis of less than 0.05. Means are presented  $\pm 1$  SE.

## RESULTS

#### *Ages, sex ratio and biometrics of seasonal samples*

All three samples showed a predominance of males, with about twice as many males as females collected (Table I). Although significantly different from a 1:1 sex ratio ( $\chi^2_1 = 11.8$ ,  $P < 0.001$ ), the three seasonal samples were homogeneous ( $\chi^2_2 = 2.1$ , NS). About 20% of the birds sampled were immatures, and this ratio was also homogeneous between seasonal samples ( $\chi^2_2 = 0.05$ , NS; Table I).

TABLE I. SEXES AND AGES OF BIRDS COLLECTED IN EACH SAMPLE

<i>Collection date</i>	<i>Males</i>	<i>Females</i>	<i>Immatures</i>	<i>Adults</i>	<i>Totals</i>
26 April	23	7	6	24	30
25 June	16	11	6	21	27
1-2 November	17	7 (+1*)	5	20	25
Totals	56	25 (+1*)	17	65	82

\* one adult bird from the November collection could not be sexed.



Wing length did not differ between the sexes nor between seasons, but adult wing length (mean 203.3 mm) was longer than that of immatures (mean 198.9 mm;  $F_{1,67}=9.76$ ,  $P<0.01$ ). Bill length did not differ between adults and immatures nor between seasons, but was longer in males (mean 48.6 mm) than in females (mean 47.3 mm;  $F_{1,66}=6.24$ ,  $P<0.05$ ). Head-and-bill length showed the same pattern as bill length (mean 114.2 mm in males, 112.2 mm in females;  $F_{1,66}=7.42$ ,  $P<0.01$ ). Bill depth differed between ages (mean in adults 13.2 mm, immatures 12.3 mm;  $F_{1,65}=24.90$ ,  $P<0.001$ ), between sexes (mean in males 13.1 mm, females 12.9 mm;  $F_{1,65}=4.30$ ,  $P<0.05$ ) and between seasonal samples (mean in spring 13.4 mm, summer 13.2 mm, winter 12.5 mm;  $F_{2,65}=13.72$ ,  $P<0.001$ ). This pattern of seasonal variation would be expected within any Common Guillemot population as this species moults the bill covering plates after breeding (Cramp 1985).

Measurements of wing length, bill length and head-and-bill length were transformed to weighted Z-scores in order to overcome differences due to scale (for example, weighted or Z-score for a given measurement of wing length:  $Z_{\text{wing}} = \text{wing length} - (\text{mean wing length of birds in the sample (collection)/standard deviation of that mean}$ ; Norusis 1986). The three Z-scores were combined for each adult to produce an overall 'size index'. Size indices were homoscedastic (Bartlett-Box  $F=0.703$ , NS) and there was no significant difference between the mean size index of birds from each collection (one-way ANOVA;  $F_{2,59}=0.28$ , NS). These results together with the lack of seasonal variation in mean wing length, bill length or head-and-bill length indicate that the three samples were from the same (local) breeding population of birds, and so allow a comparison of seasonal changes in body composition within a homogeneous population.

#### *Body composition in relation to sex, age and date*

Only four body composition measurements showed statistically significant differences between males and females. Females had a slightly higher mean fat content in the liver ( $1.71 \text{ g} \pm 0.19$ ,  $n=25$ ) compared with males ( $1.41 \text{ g} \pm 0.07$ ,  $n=56$ );  $F_{1,69}=4.60$ ,  $P<0.05$ ). Similarly, mean female

TABLE II. VARIATIONS IN BODY COMPOSITION BETWEEN IMMATURES ( $N=17$ ) AND ADULTS ( $N=65$ ). VALUES ARE MEANS  $\pm$  1 SE.

Parameter	Level in		Statistical comparison	
	immatures	adults		
Food in stomach (g)	$3.24 \pm 0.74$	$21.54 \pm 3.86$	$F_{1,69} = 5.79$	$P<0.05$
Bird fat-free dry mass (g)	$249.01 \pm 4.84$	$262.38 \pm 2.33$	$F_{1,69} = 8.42$	$P<0.01$
Total fat in body (g)	$102.93 \pm 6.55$	$79.31 \pm 4.22$	$F_{1,69} = 7.99$	$P<0.01$
Bird fat index	$0.42 \pm 0.03$	$0.30 \pm 0.02$	$F_{1,69} = 12.01$	$P<0.01$
Total water in body (g)	$653.06 \pm 12.17$	$648.47 \pm 6.40$	$F_{1,69} = 0.17$	NS
Bird water index	$2.63 \pm 0.05$	$2.48 \pm 0.02$	$F_{1,69} = 12.15$	$P<0.01$
Pectoralis fat-free dry mass (g)	$26.12 \pm 0.68$	$27.13 \pm 0.29$	$F_{1,69} = 2.94$	NS
Fat in pectoralis (g)	$2.11 \pm 0.30$	$1.62 \pm 0.10$	$F_{1,69} = 4.86$	$P<0.05$
Pectoralis fat index	$0.08 \pm 0.01$	$0.06 \pm 0.01$	$F_{1,69} = 7.55$	$P<0.01$
Water in pectoralis (g)	$71.22 \pm 1.53$	$74.68 \pm 0.85$	$F_{1,69} = 3.97$	$P<0.05$
Pectoralis water index	$2.73 \pm 0.03$	$2.75 \pm 0.02$	$F_{1,69} = 0.19$	NS
Liver fresh mass (g)	$54.44 \pm 1.83$	$49.53 \pm 0.92$	$F_{1,69} = 7.27$	$P<0.01$
Liver dry mass (g)	$12.23 \pm 0.45$	$10.87 \pm 0.23$	$F_{1,69} = 7.99$	$P<0.01$
Liver fat-free dry mass (g)	$10.73 \pm 0.38$	$9.37 \pm 0.17$	$F_{1,69} = 13.41$	$P<0.001$
Liver fat index	$0.14 \pm 0.01$	$0.16 \pm 0.01$	$F_{1,69} = 0.88$	NS
Water in liver (g)	$42.20 \pm 1.48$	$38.65 \pm 0.76$	$F_{1,69} = 6.18$	$P<0.05$
Liver water index	$3.96 \pm 0.11$	$4.16 \pm 0.08$	$F_{1,69} = 2.71$	NS

TABLE III. STATISTICALLY SIGNIFICANT DIFFERENCES IN BODY COMPOSITION OF BIRDS SAMPLED IN DIFFERENT SEASONS. SAMPLE SIZES FOR ALL COMPARISONS: APRIL N=30; JUNE N=27; NOVEMBER N=25. VALUES ARE MEANS  $\pm$  S.E. VALUES WITH DIFFERENT UPPER CASE LETTERS (A-C) SIGNIFICANTLY DIFFERENT AT  $P<0.05$  LEVEL, STUDENT-NEWMAN-KEULLS RANGE TEST.

Parameter	Mean level			Statistical comparison	
	Spring (April)	Summer (June)	Winter (November)		
Food in stomach (g)	18.3 $\pm$ 4.0 A	4.8 $\pm$ 1.4 A	31.0 $\pm$ 8.4 B	$F_{2,79} = 6.12$	$P<0.01$
Mass at collection (g)	1022.0 $\pm$ 11.9 A	980.0 $\pm$ 14.8 B	1031.0 $\pm$ 14.7 A	$F_{2,79} = 3.78$	$P<0.05$
Total dry mass (g)	331.0 $\pm$ 4.3 A	347.0 $\pm$ 8.7 A	356.0 $\pm$ 7.0 B	$F_{2,79} = 3.38$	$P<0.05$
Total fat-free mass (g)	261.0 $\pm$ 3.5 —	264.0 $\pm$ 3.0 —	253.0 $\pm$ 4.6 —	$F_{2,79} = 1.99$	NS
Total water in body (g)	672.0 $\pm$ 8.0 A	629.0 $\pm$ 9.8 B	644.0 $\pm$ 10.1 B	$F_{2,79} = 5.89$	$P<0.01$
Bird water index	2.58 $\pm$ 0.03 A	2.38 $\pm$ 0.03 B	2.56 $\pm$ 0.05 A	$F_{2,79} = 8.77$	$P<0.001$
Total fat in body (g)	70.4 $\pm$ 4.0 A	82.8 $\pm$ 8.0 A	102.3 $\pm$ 5.3 B	$F_{2,79} = 6.92$	$P<0.01$
Bird fat index	0.27 $\pm$ 0.02 A	0.31 $\pm$ 0.03 A	0.41 $\pm$ 0.02 B	$F_{2,79} = 7.78$	$P<0.001$
Pectoralis fat-free dry mass (g)	27.0 $\pm$ 0.5 —	26.6 $\pm$ 0.5 —	27.2 $\pm$ 0.5 —	$F_{2,79} = 0.33$	NS
Fat in pectoralis (g)	1.3 $\pm$ 0.1 A	1.7 $\pm$ 0.2 AB	2.2 $\pm$ 0.2 B	$F_{2,79} = 7.76$	$P<0.001$
Pectoralis fat index	0.05 $\pm$ 0.01 A	0.07 $\pm$ 0.01 AB	0.08 $\pm$ 0.01 B	$F_{2,79} = 6.23$	$P<0.01$
Water in pectoralis (g)	73.5 $\pm$ 1.4 —	72.2 $\pm$ 1.0 —	76.4 $\pm$ 1.4 —	$F_{2,79} = 2.64$	NS
Pectoralis water index	2.7 $\pm$ 0.02 A	2.7 $\pm$ 0.02 A	2.8 $\pm$ 0.02 B	$F_{2,79} = 5.16$	$P<0.01$
Liver fresh mass (g)	54.2 $\pm$ 1.4 A	48.3 $\pm$ 1.5 B	48.5 $\pm$ 1.2 B	$F_{2,79} = 6.14$	$P<0.01$
Liver fat-free dry mass (g)	9.6 $\pm$ 0.3 —	9.3 $\pm$ 0.3 —	10.1 $\pm$ 0.2 —	$F_{2,79} = 1.97$	NS
Fat in liver (g)	1.7 $\pm$ 0.1 —	1.3 $\pm$ 0.2 —	1.5 $\pm$ 0.1 —	$F_{2,79} = 2.07$	NS
Liver fat index	0.17 $\pm$ 0.01 —	0.14 $\pm$ 0.01 —	0.15 $\pm$ 0.01 —	$F_{2,79} = 2.63$	NS
Water in liver (g)	43.0 $\pm$ 1.1 A	37.7 $\pm$ 1.1 B	36.9 $\pm$ 1.0 B	$F_{2,79} = 9.62$	$P<0.001$
Liver water index	4.5 $\pm$ 0.09 A	4.1 $\pm$ 0.11 B	3.6 $\pm$ 0.05 C	$F_{2,79} = 24.57$	$P<0.001$

liver fat index ( $0.17 \pm 0.02$ ,  $n=25$ ) was significantly higher than that of males ( $0.15 \pm 0.01$ ,  $n=56$ ;  $F_{1,69}=4.80$ ,  $P<0.05$ ). Males had slightly larger pectoral muscle protein masses ( $27.34 \text{ g} \pm 0.33$ ,  $n=56$ ) than females ( $25.99 \text{ g} \pm 0.99$ ,  $n=25$ ;  $F_{1,69}=5.55$ ,  $P<0.05$ ) and larger pectoral muscles when expressed on a dry mass basis ( $29.03 \text{ g} \pm 0.32$ ,  $n=56$ ) compared with females ( $27.78 \text{ g} \pm 0.51$ ,  $n=25$ ;  $F_{1,69}=4.79$ ,  $P<0.05$ ).

Differences in body composition between immatures and adults were more pronounced. Adults had much more food in the stomach, had less total body fat, had lower body fat and water indices, less fat but more water in their pectoral muscle, a lower muscle fat index, adults had smaller livers than immatures (fresh weight, dry weight and fat-free dry weight) and had less water in their livers (Table II).

No statistically significant interactions were detected by two-way ANOVA between sex or age categories and sampling occasions in values of any body composition parameters. Since neither sex ratio nor age ratio differed between sampling dates and parameters all conformed to normal distributions it was possible to analyse body composition changes between seasonal samples by one-way ANOVA. Seasonal samples differed significantly in total (live) body masses, food mass in the stomach, total dry mass, total water and fat contents and indices, fat in the pectoral muscle, pectoral muscle fat and water indices, liver fresh mass, water in the liver and liver water index (Table III). These seasonal changes were quite complex. Although live mass at collection varied significantly between samples and was least in June, this variation could be attributed to differences in the mass of food carried in the stomach, since masses after removal of food did not differ significantly between seasons ( $F_{2,79}=1.43$ ,  $P=0.25$ ). However, while body mass remained the same, composition did vary. The weight of fat increased significantly, from 70.4 g in April and 82.8 g in June to 102.3 g in November, while the body water index fell significantly, from 2.58 in April to 2.38 in June and increased to 2.56 in November. Water and fat levels in liver and pectoral muscle also changed despite the apparent constancy of total body mass (Table III).

Testes dimensions for adult male Guillemots from each of the three collections are presented in Table IV. Testes decreased significantly in size from April to June and November (one-way ANOVA;  $F_{2,40}=56.45$ ,  $P<0.001$ ).

TABLE IV. TESTES DIMENSIONS (LENGTH x WIDTH IN mm) IN ADULT MALES FROM THE THREE COLLECTIONS.

	<i>April</i>	<i>June</i>	<i>November</i>
Sample size	18	12	13
Mean dimensions	33.0 x 13.3	14.9 x 4.5	9.9 x 3.7
Standard deviation	6.6 3.7	2.5 1.6	1.2 0.6

## DISCUSSION

### *Population homogeneity of samples*

Our results show the presence of a consistent proportion (20%) of immatures in the collected samples at each season and a predominance of males. We cannot explain why there were consistently more males than females in the samples. Immatures differed from adults in wing length and bill depth, tending to be smaller. Harris & Wanless (1988) found no difference in wing length between breeding and nonbreeding Common Guillemots caught at the Isle of May. The nonbreeders in their study are likely to have been older than the immature birds in our samples, however, which were identified as young from the presence of a bursa of Fabricius, which in those

species in which it has been studied, is usually retained for less than eighteen months (King & McLelland 1984). Thus for comparisons between seasons and with data collected at colonies we have considered only biometrics of the adult birds.

Although we found no significant difference in wing length between sexes of adults, Harris & Wanless (1988) found that females had slightly longer wings than males at the Isle of May. The difference was so small (about 1%), however, that in four of the five seasonal samples they took, the difference failed to reach statistical significance. However, Threlfall & Mahoney (1980) also noted that female wing length tended to be slightly longer than that of males. In our samples, males were larger than females in bill length, head-and-bill length and bill depth. Although males had larger pectoral muscle fat-free dry mass than females, the sexes did not differ significantly in overall body mass at collection. Harris & Wanless (1988) found that breeding males were heavier than females immediately before breeding and during chick-rearing but not at other times during the breeding period.

Jones (1988) reported details of the well-established clinal variation in Common Guillemot biometrics with latitude (Cramp 1985, Anker-Nilssen *et al.* 1988). Breeding adults from Canna (57°N in north-west Scotland) had a wing length of 193-215 mm (mean 203.8, SD 4.81,  $n=91$ ). Our samples of adults (mean wing length 203.3 mm) were no different in wing length from the Canna birds, but had shorter wings than Common Guillemots from further north (means 206.6 mm from Fair Isle (59°N), 207.3 mm from Foula (60°N) and 207.3 mm from Noss (60°N); data from Jones 1988).

We wished to assess whether any birds from other breeding populations were present in the winter sample. Most Common Guillemot dispersal in winter is to the south of the breeding area so that one would expect any influx to north-west Scotland to lead to an increase in mean size in the winter sample or to an increase in variance in size. Adult Common Guillemot biometrics were normally distributed in each of our samples and means of samples did not differ between seasons except for bill depth where winter birds had shed bill plates. Mean 'size indices' for each collection were not significantly different, nor were the respective variances about those means. When taken together, these findings argue strongly that the same discrete population was being sampled in each season. This result was anticipated since ring recovery data presented by Mead (1974) showed that in winter, Common Guillemots ringed in north-west Scotland remain in the area or disperse south, but that Common Guillemots from Orkney, Shetland or north Scotland were never recovered in north-west Scotland, tending instead to move eastwards to Scandinavia or south into the North Sea. Nor did any Common Guillemots ringed in other areas of Britain or abroad move to north-west Scotland (Mead 1974).

Thus the biometric data indicate that all three seasonal samples were entirely of birds from the same population, from about 57°N. This finding is a prerequisite for comparisons between seasonal samples to assess seasonal variations since it is essential that the samples are derived from the same population.

#### *Body composition: differences between sexes and age classes*

Harris & Wanless (1988) found that both males and females lost weight between late incubation (early June) and fledging of the chick (late June), but that weight lost was recovered by October. Although they also found that nonbreeders were significantly lighter than breeders, they found no relationship between body weight of breeders and their breeding success. However, their study provided only live weights of Common Guillemots and not body composition and so the changes in weight could not be identified as weight of stomach contents, lipid, protein or water, nor due to changes in particular tissues. Our carcass analyses showed that differences between the sexes were very slight. While males had slightly larger pectoral muscle fat-free dry masses and females had higher fat levels in the liver, other parameters were the same between the sexes. Since males may have slightly shorter wings than females, and so higher wing loadings since the sexes do not

usually differ in body mass, the larger pectoral muscle power of males may compensate for their greater wing loading.

The tendency for immatures to have less food in the stomach, to weigh less, but to have larger livers and carry more fat reserves than adults suggests that immatures may compensate for a lower feeding efficiency by carrying larger energy reserves. This would further imply that the adults regulate their fat levels below the amounts they could accumulate because they are less likely to be stressed by adverse conditions and carrying excess fat must reduce fitness. Such a conclusion is in accord with earlier studies of seasonal changes in body composition of Herring Gulls *Larus argentatus* (Coulson *et al.* 1983) and various species of waders (Pienkowski *et al.* 1979, Dugan *et al.* 1981). Since our samples were collected in the morning, the larger mass of food in adults suggests that they may show a more pronounced morning peak in feeding than seen in immatures.

#### *Body composition: seasonal changes*

Although live body mass was less in June than in April or November (in agreement with trends found by Harris & Wanless 1988) this difference was in large part due to differences in the mass of food present in the stomach (Table III). Food-free fresh masses did not differ significantly between samples although they remained less in June than in the other periods. However, body fat tended to increase between April and June while food-free body mass fell (though not significantly). The body water index was 2.58 in April but only 2.38 (significantly less) in June (Table III). Thus the lighter birds in June carried more fat but less water.

The complex seasonal changes in body composition should be taken as a warning of the danger of using changes in live body weight as an index of condition or as a reflection of food availability or the reproductive effort of birds (e.g. Freed 1981, Nur 1984, Monaghan *et al.* 1989). In the case of these Common Guillemots the loss of weight in June is attributable to reduced body water and food mass in the stomach and masks an increase in the amount of body fat which can be detected only by studies of body composition or visible fat stores (Jones *et al.* 1984, Jones *et al.* 1985).

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#### SUMMARY

Seasonal variations in body composition were assessed in Common Guillemots from the north-west of Scotland sampled in spring, summer and winter. Changes in fat and water contents in liver, kidney and muscle tissues were complex. Seasonal differences in fresh masses of whole birds could be explained mainly in terms of the mass of food in the alimentary tract.

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# Mesopelagic fish eaten by Yellow-legged Herring Gulls *Larus argentatus atlantis* in the Azores

K.C. Hamer, D.R. Thompson, A.J. Rundle, S.A. Lewis and F.M. Stewart

## INTRODUCTION

Herring Gulls *Larus argentatus* are highly flexible and opportunistic feeders; their diets have been recorded to include, among other items, marine fish (including discards from fishing boats), marine invertebrates, seabird eggs and chicks, earthworms and domestic refuse (Furness & Monaghan 1987). Yellow-legged Herring Gulls *L. argentatus atlantis* breed throughout the Mediterranean and the south-east region of the North Atlantic Ocean, and have been increasing in number for several decades, at least in the Azores archipelago (Le Grande *et al.* 1984). Despite this, their diets are poorly known, although Mediterranean populations have been recorded feeding upon marine fish (Witt 1974, Borg & Zammit 1987) and those in the Selvagens Islands on seabird eggs (Zino *et al.* 1987) and terrestrial snails (K.C. Hamer unpublished data). This paper provides information concerning the diets of Yellow-legged Herring Gulls in the Azores.

## METHODS

Field-work was conducted at Ilheu Topo, an island of about 20ha, 0.5km from the eastern tip of São Jorge in the centre of the archipelago, where less than 100 pairs of Yellow-legged Herring Gulls breed each year. Regurgitated pellets containing the undigested elements of the gulls' food were collected from the colony between 28 and 30 August 1989, shortly after the end of that year's breeding season. The contents of all pellets were identified in the field, and any sagittal otoliths present were retained and later identified by A.J.R., using keys in Nolf (1985) augmented by otoliths dissected from material at the British Museum of Natural History.

## RESULTS

A total of 510 pellets were collected, of which 89% were fish and 8% were goose-barnacle *Lepas* sp. (Table I). All other food items were present in less than 1% of pellets, and all pellets contained

TABLE I. THE NUMBER AND PERCENTAGE OF PELLETS OF DIFFERENT TYPES IN A SAMPLE OF 510 PRODUCED BY YELLOW-LEGGED HERRING GULLS ON ILHEU TOPO, AZORES IN 1989.

Pellet type	Number of pellets	Percentage of pellets
Fish	447	89.4
Goose-barnacle	41	8.2
Black rat <i>Rattus rattus</i>	4	0.8
Squid	4	0.8
Gastropod mollusc	3	0.6
Unidentified crustacea	1	0.2

Note: Squid were identified from beaks as one species of *Chiroteuthis*, one species of *Taonius* and two individuals in the family Ommastrephidae. Black rats were identified from mandibles, molar teeth and long bones.

TABLE II. THE NUMBER AND PERCENTAGE OF DIFFERENT FISH SPECIES IN A SAMPLE OF 280 OTOLITHS FROM PELLETS COLLECTED ON ILHEU TOPO.

Identification	Number of otoliths	Percentage of otoliths	Habitat and depth
Opisthoproctidae			
<i>Opisthoproctus grimaldii</i>	4	1.4	mesopelagic; 200-600m
Myctophidae			
<i>Myctophum</i> sp.	21	7.5	mesopelagic; 100-1000m
<i>Notoscopelus</i> sp.	1	0.4	mesopelagic; 100-1000m
<i>Protomyctophum</i> sp.	3	1.1	mesopelagic; 100-1000m
<i>Symbolophorus</i> sp.	93	33.2	mesopelagic; 100-1000m
Undetermined	2	0.7	
Macrouridae			
<i>Coelorhynchus</i> sp.	11	3.9	benthopelagic; 140-2000m
<i>Nezumia aequalis</i>	2	0.7	benthopelagic; 140-2000m
Batrachoididae			
Undetermined	1	0.4	coastal, benthic
Trachichthyidae			
<i>Trachichthodes</i> sp.	4	1.4	benthopelagic; deep water
Diretmidae			
<i>Diretmus argenteus</i>	117	41.8	mesopelagic; 500-700m
Berycidae			
<i>Beryx</i> sp.	1	0.4	benthopelagic; 400-600m
Caproidae			
<i>Capros aper</i>	1	0.4	mesopelagic; 100-600m
Gobiidae			
Undetermined; 2 species	2	0.7	
Undetermined Family; 4 species	15	5.4	
Undetermined Order; 2 species	2	0.7	

Note: Data concerning habitats and depth ranges are from Whitehead *et al.* (1984) and Nelson (1984). Where fish have been identified to genus, the depth range given is the maximum covering all species recorded in the North-east Atlantic.

remains of a single food-type. Of 280 complete otoliths, representing 21 species of fish (Table II), 44% were identified to species with certainty. A further 48% were identified to genus, but a lack of described otoliths from Azorean fish prevented further identification. The remaining 8% of otoliths were not identifiable to genus, because of erosion by stomach acid before regurgitation. However, they were separable into ten species (Table II).

Whole otoliths were obtained from 36% of fish pellets. A further 32% (omitted from Table II) contained fragmented otoliths, but apparently included no new species. The remainder contained no otoliths, but mostly had a similar appearance to pellets that contained otoliths, and probably represented the same species. However, 31 pellets (6% of the total), all lacking otoliths, consisted



of very fine bones, probably of horse mackerel *Trachurus picturatus*, a species which has very small otoliths that are likely to be dissolved by stomach acid before regurgitation (Jobling & Breiby 1986).

Three species contributed 83% of otoliths; 42% were *Diretmus argenteus*, 33% were a single species of *Symbolophorus* and 8% a single species of *Myctophum*. These are all mesopelagic fish occurring at depths below 100m (Whitehead *et al.* 1984; Table II). All other fish identified to genus also occur at depths below 100m, and three (*Coelorhynchus*, *Trachichthodes* and *Beryx*) are benthopelagic genera, found mainly on the sea-bed away from the coast (Table II), while the Batrachoididae (toadfish) are characterized by a coastal benthic habitat (Nelson 1984).

## DISCUSSION

Analysis of regurgitated pellets generally underestimates the importance of items that produce little indigestible material (Johnstone *et al.* 1990), while infrequent collection underestimates the importance of foods that result in unstable pellets, since these tend to be broken up and dispersed during periods of bad weather (Furness & Hislop 1981). Although the very low summer rainfall on Ilheu Topo probably reduced the latter source of error, we do not claim that the data in Tables I and II allow a quantitative assessment of the diet of Yellow-legged Herring Gulls at this colony in 1989. However, they do allow an assessment of whether different items were important dietary components.

Almost 90% of pellets were composed of fish (Table I), indicating that they were an important resource for adults at this colony. The true proportion of fish in the gulls' diet may in fact have exceeded this figure, since pellets containing crustacean and molluscan remains were comparatively large and easily visible, while those containing black rat were very durable, and so may have been over-represented.

Horse mackerel, or other fine-boned species, may have been under-represented if their pellets were less stable than those produced from other species, although this did not appear to be the case in the pellets that we obtained. Even allowing for the uncertainties inherent in analysis of pellet samples, it was obvious that mesopelagic fish made a significant contribution to the diets of Yellow-legged Herring Gulls at this colony.

Meso- and benthopelagic fish species may be made available to surface predators as discards from fishing vessels (Hudson & Furness 1988). However, the fishery in the central Azores is very small. Fish could have been eaten by vertically-migrating piscine predators, and entered surface-feeding seabirds when the predatory fish were themselves eaten. However, this should have resulted in pellets containing otoliths of more than one species, which was not the case in this study. Fish in the genera *Symbolophorus* and *Myctophum*, from which 41% of otoliths were derived, are nyctoeipelagic (found in surface waters at night) and so could have been caught by Yellow-legged Herring Gulls feeding nocturnally, as they do in the Mediterranean (Borg & Zammit 1987). However, the other species are not nyctoeipelagic. Otoliths of *D. argenteus* represented 42% of the total; this species is mesopelagic when adult and, although juveniles are found near the surface by day (Whitehead *et al.* 1984), these are less than 1cm long and therefore too small to have produced the otoliths in this sample.

Meso- and benthopelagic species may be driven to the surface by marine predators, particularly tuna (Au & Pitman 1988). Periodic associations between surface-schooling tuna, cetaceans and various seabird species have long been recognized and exploited by fishermen (Evans 1982) but gulls are considered to feed largely independently of fish schools in pelagic waters and to rarely occur with either tuna or cetaceans (Au & Pitman 1988). However, Martin (1986) recorded Yellow-legged Herring Gulls in the Azores feeding in association with Atlantic spotted dolphin *Stenella frontalis* and Cory's Shearwater *Calonectris diomedea*, although on all occasions these three species were feeding upon horse mackerel rather than upon mesopelagic species. Cetaceans and seabirds were reported by fishermen in the Azores to reliably pinpoint feeding tuna, although

these were not present in any of the small number of associations observed by Martin (1986). Hence, the high frequency of mesopelagic fish in the diets of Yellow-legged Herring Gulls at Ilheu Topo suggested that they regularly feed in association with surface-schooling tuna.

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#### SUMMARY

Over 70% of pellets regurgitated by Yellow-legged Herring Gulls in the Azores contained the remains of diurnally meso- or benthopelagic fish species. A third of pellets were of nyctoeipipelagic species, which may have been caught at the surface at night. However most other pellets, including the most abundant type, were of species not normally found at depths less than 100m. These were probably made available to Herring Gulls by the activities of tuna, which drive mesopelagic fish to the surface.

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# Breeding skuas in Orkney: the results of the 1992 census

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## INTRODUCTION

A comprehensive census of breeding Arctic Skuas *Stercorarius parasiticus* and Great Skuas (or Bonxies) *Stercorarius skua* was undertaken in Orkney in 1992 as part of the Royal Society for the Protection of Birds' Orkney and Shetland Skua Survey. Previous surveys in 1974-75 (Everett 1982) and in 1982 (Meek *et al.* 1985) provided baselines against which to measure population and distribution changes.

Orkney holds important numbers of both species. In 1982 the total of 1034 apparently occupied territories (AOTs) represented 37% of the British Arctic Skua population (Evans 1984), and the total of 1652 Great Skua AOTs represented 23% of the British and 13% of the world population of 12,500 pairs (Furness 1987).

Although marked increases were recorded for both species between 1974-75 and 1982, the years since the latter survey have been notable, certainly in Shetland and to a lesser extent in Orkney, for the reduced availability of sandeels *Ammodytes marinus* (Heubeck & Ellis 1986). As both skua species depend, at least in part, on sandeels obtained either directly, or indirectly through kleptoparasitism, their breeding populations might be expected to reflect this situation. In addition, there has been speculation that the predation pressure exerted by Great on Arctic Skuas might influence both the numbers and the distribution of the smaller species (Furness 1977).

## METHODS

All areas of potential skua habitat were visited between 25 May and 10 July 1992, the great majority of visits being made in June. In large moorland areas, transects were walked about 500m apart but in denser colonies transects were closer and it was recommended that observers allowed birds to settle before assessing numbers. The counting unit used was the 'apparently occupied territory' (AOT) (Furness 1982). The positions of all AOTs and 'clubs' of non-breeding birds were plotted on 1:25000 maps. The colour phases of Arctic Skuas were also recorded using the criteria recommended by P.O'Donald (in Meek *et al.* 1985).

To ensure comparability between surveys the major Great Skua colony on Hoy was counted by the same person (BR) using the same methods as in 1982.

## RESULTS

### *Arctic Skua*

The overall total of 1056 AOTs represents a 2% increase on the 1982 total of 1034 AOTs (Table I, Fig.2). Although the overall population has changed little in the period 1982-1992, there has been a marked redistribution of birds within the islands. Islands which showed marked population changes are Westray (+117%), Papa Westray (+59%), West Mainland (+44%), Flotta (+246%) and Hoy (-48%). The losses on Hoy are almost exactly made up for, in numerical terms, by the increases on these four other islands. Forty-four Arctic Skuas were recorded in clubs, the majority on Papa Westray and Rousay with 15 and 12 individuals respectively.

The colour phase of 1890 territorial birds was recorded, 1428 (76%) being melanistic and 462 (24%) being pale (Table II). Exactly the same ratio of melanistic to pale birds was recorded in the sample of 1869 birds in 1982. The ratio of pairings of different phases was also exactly the same in the two census years: 58% melanistic x melanistic, 35% melanistic x pale and 7% pale x pale.

TABLE I. NUMBERS OF APPARENTLY OCCUPIED TERRITORIES OF ARCTIC SKUAS IN ORKNEY IN 1982 AND 1992.

<i>Island</i>	<i>1982</i> <i>(Meek et al. 1985)</i>	<i>1992</i> <i>(Present survey)</i>	<i>% Change</i>
North Ronaldsay	1	1	0
Sanday	25	28	+12
Papa Westray	95	151	+59
Holm of Papay	1	2	+100
Westray	45	98	+118
Eday	101	106	+5
Calf of Eday	22	14	-36
Faray (and Holm)	1	2	+100
Stronsay	44	40	-9
Linga Holm	1	0	-100
Holm of Huip	0	1	+100
Auskerry	2	2	0
Rousay	97	137	+41
Egilsay	1	0	-100
Wyre	3	2	-33
Holm of Scockness	1	0	-100
Eynhallow	19	13	-32
Gairsay	38	31	-18
Sweyn Holm	1	1	0
Shapinsay	NV	10	?
Helliar Holm	NV	1	?
Mainland	67	79	+18
Hoy & South Walls	408	211	-48
Fara	28	20	-29
Cava	NV	1	?
Flotta	26	80	+208
Burray (Hunda)	2	3	+33
South Ronaldsay	7	8	+14
Swona	NV	1	?
Stroma (Caithness)	NV	2	?
Totals	1034	1056	+2

NV = islands not visited during 1982 survey. In 1992 all islands were visited except Rusk Holm where a single AOT was known in 1985.

### *Great Skua*

The overall total of 2018 AOTs represents a 22% increase on the 1982 figure of 1653 AOTs (Table III, Fig.1). The great majority of this overall increase of 365 AOTs is accounted for by the main colony on Hoy where numbers rose by 327 (21%).

Away from Hoy, Bonxie numbers are comparatively small. However, it is noteworthy that numbers on Stronsay and Rousay almost doubled in the ten-year period, to 15 and 31 pairs respectively, while Flotta, Burray and probably Shapinsay were newly colonised during that time.

In 1992 214 Bonxies were found in clubs, the great majority (202) on Hoy (where 92 bathing birds were also recorded), the others being on Papa Westray (4) and Rousay (8). In 1982, 131 were found in nine clubs, again mainly on Hoy (120 in six clubs plus 174 bathers) but with others on Westray (10), Eday (4) and Rousay (8).

TABLE II. COLOUR PHASES AND PAIRINGS OF ARCTIC SKUAS IN ORKNEY IN 1982 AND 1992.

	1982	1992
Total Melanic	1414 (76%)	1428 (76%)
Total Pale	455 (24%)	462 (24%)
Melanic x Melanic	501 (58%)	491 (58%)
Melanic x Pale	299 (35%)	299 (35%)
Pale x Pale	58 (7%)	55 (7%)

TABLE III. NUMBERS OF APPARENTLY OCCUPIED TERRITORIES OF GREAT SKUAS IN ORKNEY IN 1982 AND 1992.

<i>Island</i>	<i>1982</i> <i>(Meek et al. 1985)</i>	<i>1992</i> <i>(Present survey)</i>	<i>% Change</i>
Papa Westray	2	3	+50
Westray	6	10	+67
Eday	6	9	+50
Calf of Eday	4	3	-25
Stronsay	8	15	+88
Auskerry	1	1	0
Rousay	16	31	+94
Eynhallow	1	3	+200
Gairsay	3	2	-33
Shapinsay	NV	1	?
Mainland	25	25	0
Hoy & South Walls	1573	1900	+21
Fara	6	7	+17
Cava	NV	1	?
Flotta	0	2	+200
Burray (Hunda)	0	2	+200
South Ronaldsay	2	3	+50
Totals	1652	2018	+22

NV = island not visited. All islands were visited in 1992 except Rusk Holm which has never held breeding Bonxies in previous years.

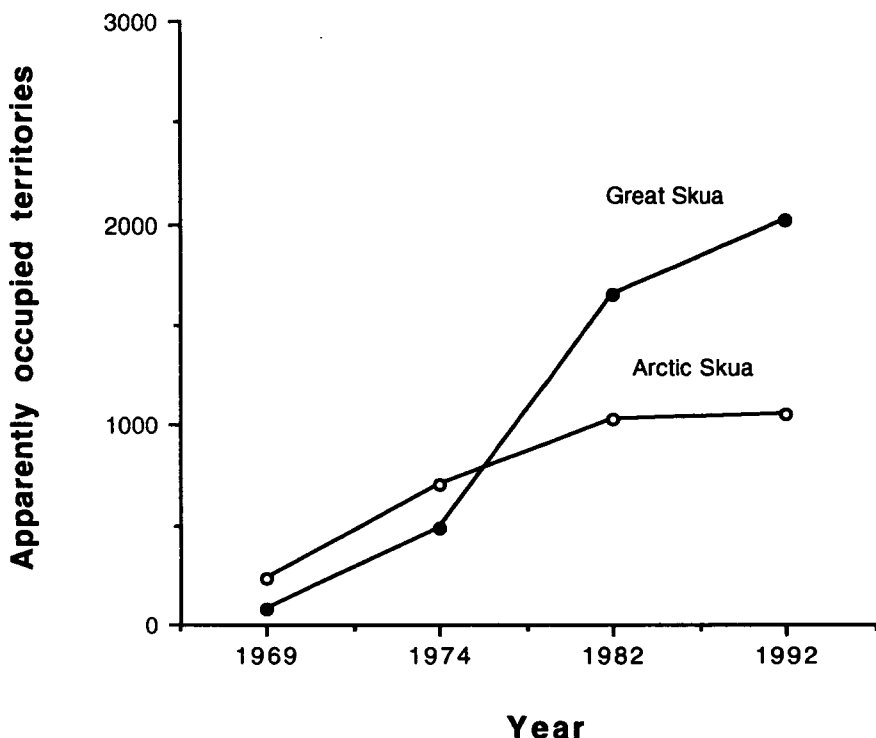


Figure 1. The number of apparently occupied territories of Great Skuas (●) and Arctic Skuas (○) in Orkney, 1969-92.

### DISCUSSION

The Arctic Skua has been known as a breeding species in Orkney since at least the early 19th century but it appears to have remained quite scarce until relatively recently (Meek *et al.* 1985). Population estimates in the 1960s fell in the range 158-269 'pairs' (Cramp *et al.* 1974) but by 1974 numbers had risen to 717 pairs (Everett 1982) and by 1982 to 1034 AOTs (Meek *et al.* 1985). If we assume 'pairs' to be the equivalent of 'apparently occupied territories', the increase between 1974 and 1982 was of the order of 44% and, even allowing for a degree of inaccuracy as a result of incomplete coverage in 1974, the increase of only 2% between 1982 and 1992 represents a marked change in this species' fortunes. Only one new island, Holm of Huip, had been colonised since the 1982 survey while three (Egilsay, Linga Holm and Holm of Scockness) lost their single pairs in the same period. The population growth curve for this species in Orkney (Fig.1) strongly suggests that its numbers may have reached a plateau.

An examination of counts of Arctic Skuas in specific areas in years between 1982 and 1992 throws little light on the timing of the decline in rate of increase. A peak of 160 AOTs was reached on the RSPB's North Hill Reserve on Papa Westray in 1989 falling to 125 in 1991 before rising again in the 1992 survey to 151. A similar 1989 peak (46 AOTs) was reached on the Birsay Moors

Reserve (West Mainland) but on Brings (Rousay) the only other site for which comparable figures are available, numbers climbed from 97 in 1989 to 122 in 1991 before falling to 108 in 1992.

O'Donald (in Meek *et al.* 1985), using data collected during the 1982 Orkney survey, found evidence of assortative mating between the two Arctic Skua colour phases. The results of the present survey, in which both the overall ratio of colour phases and the proportions of different colour phase pairings are virtually identical to those of 1982, indicate that this situation still prevails.

The Great Skua is a relative newcomer to Orkney, nesting first being proved in 1915 (Jourdain 1919). The results of 'Operation Seafarer' (Cramp *et al.* 1974) indicated a total of 87 pairs in 1969 but by 1974 numbers had increased to 485 pairs. By 1982 the figure was 1652 AOTs, an increase of 242% (if 'pairs' equate to 'AOTs') over the previous eight years. The 22% increase since 1982, obviously represents a marked slowing of the rate of increase but not nearly to the extent shown by the smaller species. No counts exist for intervening years which would help to pinpoint the timing of the slow-down. Flotta and Burray (Hunda) were colonised between 1982 and 1992 as, probably, was Shapinsay although this island was not visited during the 1982 survey. No island lost Bonxies having held them in the previous survey. The population growth curve for Bonxie (Fig.1) contrasts markedly with that for Arctic Skua but the slowing of the rate of increase is still obvious. The earlier rapid rate of increase must have been the result of immigration, presumably from Shetland; some Foula-ringed Bonxies chicks are known to be breeding on Hoy (pers.obs.). The present slower rate of increase may reflect both decreased immigration and poorer conditions within Orkney itself. Klomp & Furness (1992) have shown that non-breeding birds in clubs may act as a buffer against population change in the breeding colony. On Foula, numbers of both breeders and non-breeders decreased between 1988 and 1990 but the decline in non-breeders was much greater. They suggest that this was due to increased adult mortality rates leading to increased recruitment to the breeding colony from amongst the club birds. In the main Orkney Bonxie colony on Hoy, distinguishing club birds from bathing birds is difficult because most club sites are also bathing sites. However, in 1982, 120 club and 174 bathing birds were recorded, a total of 294. In 1992, 202 club and 92 bathers were counted, again a total of 294. Numbers of birds attending clubs varies according to time of day and it was not possible to count all clubs at the same time within either year or between years. However, the counts do seem to suggest that numbers of non-breeders are very similar to those recorded ten years ago and that therefore adult mortality and increased recruitment from the clubs may not be so marked as in Shetland.

Everett (1982) considered the various possible threats to breeding skuas in Scotland, peat-cutting activities, moorland fires, oil pollution, human persecution and human disturbance all being listed. Meek *et al.* (1985) considered each of these in the Orkney context and concluded that, although each played some part in controlling skua numbers, none could be considered to be major factors. Today, ten years on, the same conclusion would be reached. Meek *et al.* (1985) did, however, consider one further factor omitted by Everett, the loss of skua breeding habitat as a result of agricultural reclamation of moorland and heathland, hypothesising that some islands might lose their skua populations if the process of agricultural 'improvement' continued. Over much of Orkney, the pressure on heathland and moorland habitat has eased as a result of SSSI designation, reserve acquisition and the marked reduction in the available grant aid for the 'improvement' of these habitats. The fears expressed by Meek *et al.* (1985) have therefore not been realised to any large extent. One island, Sanday, was quoted as an example of a marked reduction in Arctic Skua numbers resulting from habitat loss. Numbers there had fallen from 45 to 25 pairs between 1974 and 1982 as the main breeding area on the Gump of Spurness had been ploughed. In fact the Sanday population has since risen very slightly to 28 AOTs in 1992; 23 AOTs were on the Gump, 13 of these on remaining heathland but 10 located on grassland. This was an unexpected finding: breeding attempts away from heathland or moorland habitat have previously been known in Orkney from only three localities each involving only one or two pairs

(none on improved grassland). Grassland breeding is, however, known from both Foula and Fair Isle (Shetland) (Ewins *et al.* 1988). It would be of great interest to know how the breeding success of grassland pairs compares with those on heathland, both eggs and chicks being presumably more vulnerable to predation in the former habitat.

Perhaps the most important factor influencing seabird numbers is food availability (Ashmole 1963, Lack 1967). No attempt was made to assess this factor in the analysis of the 1982 Orkney survey results but its importance in the northern isles became clear in the mid-1980s as the breeding success of several seabird species, particularly in Shetland (Heubeck & Ellis 1986), declined markedly as sandeels became less readily available. Evidence from Orkney was less clear cut but tern breeding success has been low for a number of years (Walsh *et al.* 1992, pers.obs.). Arctic Skuas are kleptoparasitic upon Kittiwakes *Rissa tridactyla*, terns and auks (Furness 1980; pers.obs.) so that any food shortages experienced by those species, all of which are chiefly sandeel feeders, will indirectly affect the skuas.

The very small increase in Arctic Skua AOTs between 1982 and 1992 may reflect rather poor breeding success during some of this period. No systematic monitoring of Arctic Skua productivity was carried out on Orkney before 1989. Since then, the RSPB has monitored breeding success at several colonies and annual average figures have been between 0.42 and 0.60 young fledged per AOT (Walsh *et al.* 1992). These productivity figures are rather low; for example, on Handa, Sutherland, figures ranged between 1.19 and 1.28 in the same period (Walsh *et al.* 1992). Arctic Skuas first breed at four or five years (Furness 1987). Thus it will take several years before any reduction in breeding success will be reflected in lower numbers of breeding birds. The low breeding success recorded in the period 1989-91 is likely to result in relatively small numbers of birds recruiting into the breeding population from 1993. We would therefore expect to see a continued slowing of population increase, or perhaps a population decrease, on Orkney during the next four or five years, unless there is an influx of birds from elsewhere.

Bonxies will employ piracy but raise their young mainly on sandeels caught themselves (Ewins *et al.* 1988). They are, however, opportunistic feeders, eating a large variety of food, including the eggs, chicks and adults of other birds as well as offal and whitefish discards from the fishing fleet. It is, perhaps, the more catholic nature of the Bonxie's diet which has enabled it to fare better in Orkney over the last decade.

As with Arctic Skuas, there was no systematic monitoring of Bonxie breeding success on Orkney before 1989. Since then, productivity has been monitored by RSPB at between one and three colonies each year on Hoy where breeding success has averaged between 0.80 and 0.96 young fledged per AOT (Walsh *et al.* 1992). These figures are quite high and may help to explain why Bonxies have increased at a more rapid rate than Arctic Skuas in the last ten years.

Another factor potentially affecting the populations and distributions of both skua species is interspecific competition. Predation by Bonxies on newly fledged Arctic Skua chicks is well documented on Noss (Shetland) (references in Ewins *et al.* 1988) and has been observed on Hoy (pers.obs.). Predation pressure on a particular study colony in southern Hoy was so great in 1991 that no Arctic Skua chicks were reared at all (Walsh *et al.* 1992). It is suspected that the decline of the Arctic Skua on Hoy (by 48% between 1982 and 1992) may in large part be the result of competition with the larger species. The redistribution of Arctic Skuas within Orkney, and particularly the considerable growth of the nearby colony on Flotta, which has few breeding Bonxies, lends further credence to this suggestion.

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## SUMMARY

A survey of breeding skuas in Orkney in 1992 revealed totals of 1056 AOTs and 2018 AOTs respectively. These figures represent a 2% increase in Arctic Skua numbers and a 22% increase in Great Skuas since the last full survey in 1982. The ratio of colour phases in the Arctic Skua (76% melanistic and 24% pale) was identical in the two survey years as was the ratio of pairings of different colour phases. Factors affecting the populations of the two species within Orkney are discussed.

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# Manx Shearwaters *Puffinus puffinus* breeding in the Bailiwick of Guernsey, Channel Islands

Mike G. Hill

## INTRODUCTION

Although the Manx Shearwater *Puffinus puffinus* has been recorded at sea off the Channel Islands for many years the species was, until recently, not thought to breed on any of the Islands. The passing birds were assumed to be on migration or feeding movements from the British or French colonies.

Fieldwork in 1989 during the Seabird Colony Register (SCR) survey found shearwaters ashore at burrows, with positive signs of breeding on Little Sark and on Jethou. This caused a re-evaluation of the Manx Shearwater's status in the Channel Islands.

This paper reports the recent investigations in the Bailiwick of Guernsey, which consists of Guernsey, Alderney, Sark, Herm and Jethou (Fig. 1); some background data are also included.

## METHODS

This study combines basic observational fieldwork with systematic assessment of possible nest-burrows using visual clues such as fresh digging, droppings, eggshell and chick feather-down etc. Recorded calls were also played back to burrows during daylight in an attempt to elicit a response from any birds within them.

When possible areas of shearwater activity were identified they were divided into named sub-colonies and the individual burrows given numbers. It was not considered safe to mark burrows on Sark because of the very public location of both colonies, and here sketch maps or photographs were used to help identify burrows. Numbered tags and a measured plan of the colony were used on Jethou.

Visits to both Sark colonies were short and it was necessary to work rapidly to avoid undue public attention. Therefore, taped call playback was used as a quick method of detecting birds within burrows (James & Robertson 1985). Manx Shearwater flight calls were used in 1989. Specific male and female calls (from birds underground) were obtained in 1990 and two microcassette machines were used for a time. The response ratio to either call (Brooke 1990) was not recorded in detail because the primary use of playback during this study was to establish whether or not a burrow was occupied.

## RESULTS

### *Sark (both parts)*

There is one vague record of Manx Shearwaters calling at night near Sark in May 1968 (F.R.G. Rountree in litt.). The birds were possibly off the east coast.

### *Little Sark*

Five or six dead birds were found on the cliff-slopes of Little Sark in late August 1977 indicating that shearwaters were possibly active in the area (D. Parish in litt.). Breeding was not confirmed and no further investigations appear to have taken place until the SCR survey visits in 1989.

Two Manx Shearwaters were found ashore during an overnight trip on 5/6 April 1989, other birds were calling from burrows and in flight. The subsequent observations identified five sub-colonies situated along 300 m of cliff and adjacent land. Visual evidence of occupation was recorded at about 35 burrows; 17 birds responded to taped calls in June and feather-down was

observed at more than 28 burrows in September. Successful breeding was confirmed on 1 September 1989 when a downy fledgling/juvenile was caught. Eleven fledglings were caught in 1989.

Similar observations were made in 1990. Male and female calls were played to 45 burrows in early morning on 3 June 1990. Nothing was heard from 25 of these burrows but 13 birds responded to male calls, six to female and one to both tapes. Twenty-eight fledglings were ringed at the colony during the 1989-92 period.

### *Sark (Big Sark)*

Eight dead Manx Shearwaters were found on the cliff-slopes of Big Sark on 27 June 1990 (J.H. Wood/S.D. Carré pers. comm.). The birds had been killed by a cat *Felis domesticus*. Although flying birds had been heard calling at night nearby earlier in the year (pers. obs.), the dead birds were the first indication of a possible colony site.

The initial overnight visit was on 28/29 June 1990. Of the 40 unidentified burrows tape-tested, more than ten had signs of recent visits and three were occupied by shearwaters; two in daylight. Shearwaters were heard and seen over the colony at night. Further visits to the colony located additional burrows, two of which had fragments of eggshell outside, suggesting breeding attempts. A shearwater was heard over the colony on 11 August 1990, however, the cat had killed 25 adult shearwaters by then and there was no indication of successful breeding.

The cat killed at least ten adult shearwaters in 1991. There were signs of shearwater activity at seven burrows in June and by August five occupied burrows had been located. A downy fledgling was caught at a burrow on the night of 30/31 August 1991, confirming successful breeding at this colony. The Big Sark colony was estimated to total less than ten pairs in 1991 and considered to be in probable danger of extinction. No observations were made in 1992.

### *Jethou Island*

The first positive record of a Manx Shearwater for Jethou was that of a bird calling in flight at night on 16 July 1983 (P.K. Veron pers. comm.). However, it is possible that birds were heard at night as far back as 1977 (J.S. Kendrick in litt.).

The SCR survey visit was made on the night of 24/25 April 1989. Several shearwaters were heard calling in flight. One bird was found ashore at a burrow and another was disturbed on the ground nearby. About ten burrows were located; fragments of thin white eggshell were found outside four burrows and feather-down was seen at one burrow in September. However, no burrow was known to be occupied. Brown rats *Rattus norvegicus* were active in the area and it is probable that predation prevented successful breeding in 1989; feathers and down were found in rat droppings at one burrow.

Male and female calls were played back to 20 burrows on 12 June 1990. Five responded to the male tape (a burrow with two birds responded to both). Fragments of eggshell were found at two burrows and feather-down was seen at three. Birds in two burrows responded to playback on 13 August. However, although breeding seemed probable it was not confirmed during two overnight visits later in August.

Little data was obtained in 1991 but many observations were made during 1992. Seventeen burrows were tape-tested with male or female calls on 2 June 1992. Seven responded to male calls and two to female calls and 12 burrows were probably in use; 11 were known to be occupied at some later stage. Six definite chicks had responded to taped calls of adults by 3 September and feather-down was found at four other burrows. Successful breeding was confirmed on the night of 3/4 September 1992 when two fledgling/juveniles were caught.

Late in 1992 indications of activity were noted at another possible, small sub-colony nearby, but positive signs of occupation were few.

*Burhou Island (off Alderney)*

There are no breeding records for this low turf-covered island which has many rabbits *Oryctolagus cuniculus*, but is free of rats or other mammalian predators. However, Manx Shearwaters seem to have had an interest in the island for a number of years. Birds were heard calling in flight over Burhou in 1949, 1959, 1989 and 1990. Single birds were caught in mist-nets in 1977, 1978 and 1988. The island was searched for signs of fledglings in September 1978 and 1988 without success. A visit from 28-30 April 1989 failed to locate any signs of breeding activity on the island.

*Other sites*

Shearwaters have recently been heard at night off the east coast of Sark and also off Guernsey. Apparently suitable breeding habitat exists in the cliff-zones of all the islands in the Bailiwick, and many of their adjacent rocky islets. Although some areas of Sark have been checked (Hill 1992), it is virtually impossible to survey many of the sites. Little work was carried out on Herm, Brecqhou or Alderney.

Precise details of the colony locations are held by the Seabird Group / JNCC in Aberdeen, Scotland and by the Guernsey Museum.

## DISCUSSION

The dead Manx Shearwaters found on Little Sark in 1977 were thought to have been killed by an escaped ferret *Putorius furo*. At least two of the birds were considered to be adults and no particular significance was attached to the occurrence at that time. Fortunately, a map accompanied Parish's 1977 report (in Hill 1992) and it shows that most of the corpses found in 1977 were in sub-colony areas which had breeding birds in 1989.

The dead shearwaters found on Big Sark in 1990 were killed by a cat, probably from the farm or houses 1 km away. This colony is split into two sub-colonies 200 m apart, both were subject to predation. The colony as a whole was estimated to have once held at least 20 pairs.

Predators other than cats likely to affect the Sark colonies include brown rats, which, although not seen during this survey, are known to be present on Sark. A black rat *Rattus rattus* was seen in runs on the cliff below the Little Sark colony burrows, but as young fledged from these burrows these rats seem to have caused few problems. Hedgehogs *Erinaceus europaeus* were introduced to Sark in 1984 (D. Beaumont pers. comm.). They are apparently thriving, and are now active near the burrows, particularly on Big Sark, which could possibly pose an added threat to nesting birds (Uttley *et al.* 1989). Accidental damage to burrows by tourists seems less of a problem than the rubbish which they have deposited in burrows in some areas.

The Island of Jethou is privately owned and closed to the public. Disturbance and threats have been minimal up to now, and it is hoped that this situation will continue. An attempt was made to control the brown rat population near the chicken runs 250 m from the colony in 1990. Although signs of rat activity at the colony were not noticed during 1992 the action was unlikely to have had much effect on the rat population elsewhere on the island.

Most of the shearwaters in the three colonies were nesting in rabbit burrows, but a few burrows were definitely excavated by the birds themselves, and two or three sites were under boulders. Great Black-backed Gulls *Larus marinus* were nesting within sight of all the colonies, and predation, although not observed, may have occurred. The high density of gulls (375 pairs) nesting on Burhou Island may be one reason why shearwaters have yet to be found breeding on the island.

The origin of the Channel Island shearwaters is not known, but it seems fair to assume that there is a sizeable pool of wandering birds from the large British colonies (Brooke 1990), and that these could be the source of the embryonic colonies in the Channel Islands, rather than some immigration from the small French colonies (Brooke 1990). Although there have been no ringing recoveries in the Channel Islands, a bird ringed on Bardsey has been recovered on Sept-Iles (Siorat

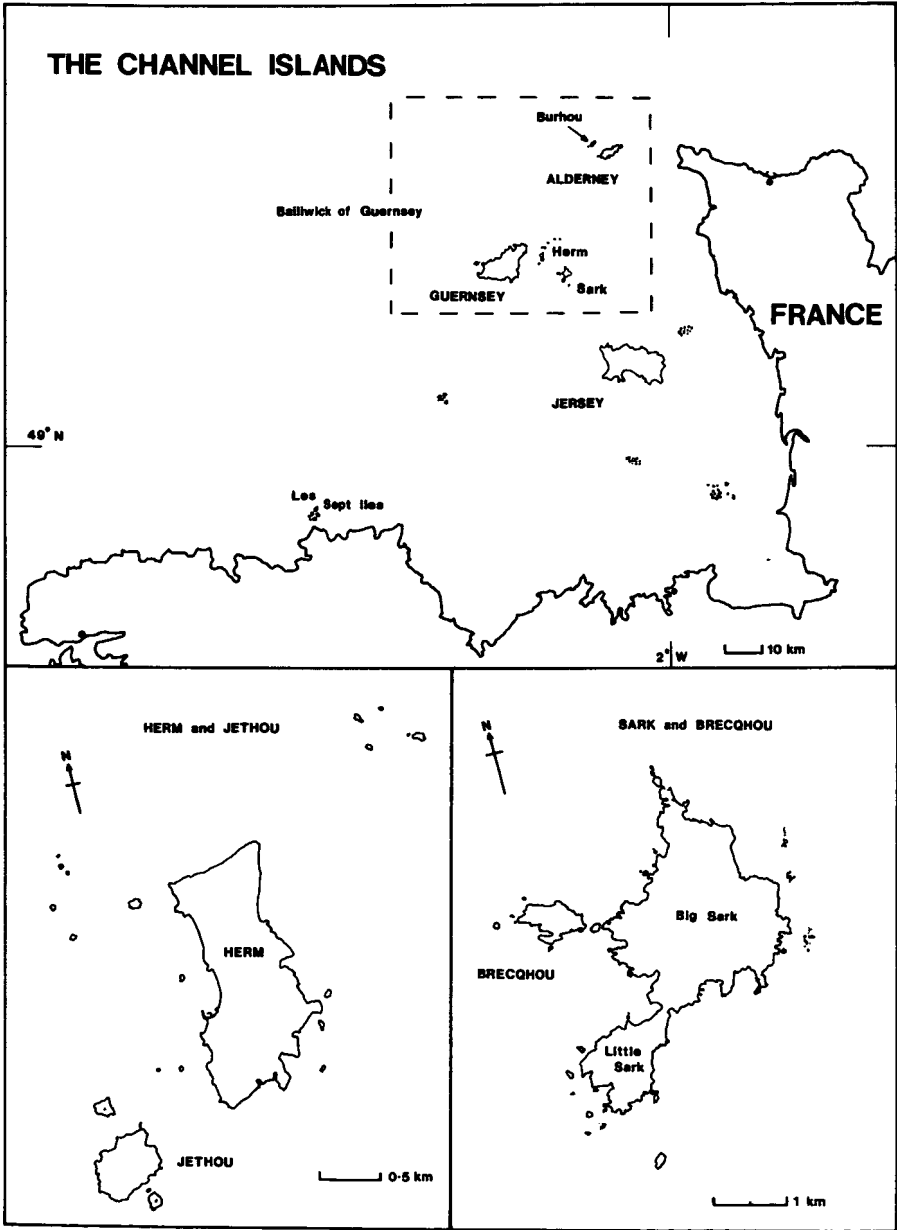


Figure 1. The location of the Channel Islands within the Gulf of St. Malo; Herm and Jethou; Brecqhou and both parts of Sark.

1992). Skokholm birds have also been found there, and at other colonies in Brittany (Brooke 1990).

Manx Shearwaters have clearly had an interest in the Channel Islands for some years and although it is not known when the colonies were established, all three colonies confirmed recently may well have been in existence for a decade or more. There is a strong possibility that other small colonies remain to be discovered in the less accessible cliff areas, headlands and islets, particularly on Sark and Alderney.

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#### SUMMARY

Circumstantial evidence suggests that Manx Shearwaters have had an interest in the Channel Islands since 1968 and possibly before. Shearwaters found dead on Little Sark in 1977 indicated the possibility of a breeding colony but this was not investigated at the time. Potential sites were checked during 1989-92, and breeding was confirmed at three Channel Island colonies. The size of these colonies was estimated to be: Little Sark 30-35 pairs (1990), Big Sark 5-10 pairs (1991), and Jethou Island 10-15 pairs (1992). Predation was either a serious problem or potential threat at some colonies.

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# The effects of disturbance on growth rate and survival of young Razorbills *Alca torda*

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## INTRODUCTION

Daily disturbances in colonies of Guillemots *Uria aalge* is known to reduce survival and growth rate of the chicks (Harris & Wanless 1984, Hatchwell 1989). However, nothing has been published on the effects of disturbance on Razorbills *Alca torda*, which usually breed at a lower density and at less exposed sites than Guillemots. This paper reports on the effect of human disturbance on growth rate, weight at departure and survival of young Razorbills from Græsholmen, Denmark (55°19'N, 15°11'E), in the central Baltic Sea.

## METHODS

In the breeding seasons of 1985 and 1986 three areas on Græsholmen were selected so that each area could be visited without causing disturbance at the others. Areas 1 (1985-86) and 2 (1986) were visited daily around 1800 hours from 5 days before the first egg hatched to the day that the last chick left. These areas are termed Heavily Disturbed Areas (HDA). The knowledge gained of the timing of hatching and chick departure in HDA was used in planning the visits to other areas. Area 2 (1985) was visited every 3-5 days from when the first egg hatched until most chicks had left, and is termed a Moderately Disturbed Area (MDA). However, on two occasions around hatching and around chick departure, MDA was visited on two successive days. From these visits the exact dates of hatching and departure were obtained for 6 MDA chicks. Nests in Area 3 (1985-86) were visited 1-3 times during the chick-rearing season, and this area is termed a Slightly Disturbed Area (SDA). Together the three areas contained about 100 pairs, 28% of the Razorbill population on Græsholmen (see Lyngs 1992). Nest sites (almost all under boulders) were numbered and their contents recorded. An approximate age of SDA chicks was estimated by comparing their wing-length with the wing-length of chicks whose age were known exactly. In HDA and MDA, chicks were considered to have departed successfully if they disappeared overnight at an age of 15 days or more, while in SDA, chicks were considered to have departed successfully if they reached an age of at least 10 days and were not later found dead in the nest. Sixty-three of the 69 (91%) SDA chicks were between 12 and 20 days old (mean  $16.0 \pm SD 2.4$  days) when last visited. In HDA 30 out of 31 (97%) chicks which reached an age of 8 days departed successfully, the last disappeared at the age of 11 days. Investigations in other years confirms this pattern: for example, at 17 sites checked daily in 1984 all 11 chicks which reached an age of 8 days departed successfully.

In 1985 and 1986, 125 and 51 chicks respectively, from Area 3 and other undisturbed areas on the island were measured and weighed once. Chicks from HDA were weighed (to nearest g) daily using a Pesola balance, and maximum wing-length was measured (to nearest mm). Chicks from MDA were weighed and measured on every visit.

Measurements of 68 eggs (maximum length and breadth) from HDA were taken to the nearest 0.1 mm, and egg volume was calculated using Coulson's (1963) equation  $V = klb^2$  ( $V$ =volume in  $cm^3$ ,  $k=0.54$  (Lloyd 1979),  $l$ =length in cm,  $b$ =breadth in cm).

Several studies of alcids have shown that wing growth is relatively independent of nutrition (references in Hatchwell 1989), so I assume that wing growth was independent of level of disturbance.

As there were no significant difference in measurements, weight or day of departure in HDA

chicks from 1985 and 1986, data from the two years have been combined. The mean weights (compared to wing-length) of chicks handled only once in 1985 and 1986 did not differ significantly, so these data have also been combined.

In 1986 all 18 departing chicks from Areas 1 and 2, and 50 of the chicks weighed and measured once (30 chicks from Area 3 and 20 chicks from other undisturbed areas) were ringed with British-made triangular rings (see Lloyd & Perrins 1977). The return of these chicks in later years was documented by reading the numbers using a telescope.

### RESULTS

Combining data from 1985 and 1986, overall breeding success in HDA was significantly lower than in SDA (Table I;  $\chi^2 = 23.6$ , 1 df,  $P < 0.01$ ). Mean hatching success in the two areas was 80% and 86%, respectively, but in HDA 57% of the chicks died or disappeared (93% within 6 days after hatching) compared with 13% from SDA. In 1985 breeding success in MDA and SDA did not differ significantly ( $\chi^2 = 0.03$ , 1 df, ns).

TABLE I. BREEDING SUCCESS OF RAZORBILLS IN DIFFERENT STUDY AREAS ON GRÆSHOLMEN 1985-86.

<i>Area</i>	<i>Pairs</i>	<i>Eggs</i>	<i>Hatched (%)</i>	<i>Departed (%)</i>	<i>Departed chick/pair</i>
Area 1, 1985 (HDA)	26	27	25 (93)	12 (48)	0.46
Area 2, 1985 (MDA)	22	22	21 (95)	15 (71)	0.68
Area 3, 1985 (SDA)	47	47	39 (83)	34 (87)	0.72
Area 1, 1986 (HDA)	31	34	24 (71)	9 (38)	0.29
Area 2, 1986 (HDA)	25	26	21 (81)	9 (43)	0.36
Area 3, 1986 (SDA)	46	46	41 (89)	35 (85)	0.76

Notes: HDA, Heavily Disturbed Area; visited daily.

MDA, Moderately Disturbed Area; visited every 3-5 d.

SDA, Slightly Disturbed Area; visited 3-4 times during chick-rearing period.

Of the 68 eggs measured in HDA, those which produced departing chicks had a mean volume of  $98.0 \pm 6.0 \text{ cm}^3$  (range 83.0-108.1  $\text{cm}^3$ ,  $n = 25$ ), while those where the breeding attempt failed had a volume of  $93.7 \pm 7.6 \text{ cm}^3$  (range 75.0-113.1  $\text{cm}^3$ ,  $n = 43$ ). The difference in mean egg volume between these two groups is statistically significant ( $t = 2.39$ ,  $P < 0.02$ , two-tailed).

There was no difference in the weight/wing-length relationship of chicks from HDA and chicks from slightly disturbed areas (ANCOVA,  $P = 0.35$ , ns; Fig. 1).

Twenty-eight chicks from HDA departed at a mean weight of  $212 \pm 24.2 \text{ g}$  (range 163-253 g), a wing-length of  $82 \pm 6.9 \text{ mm}$  (range 62-94 mm) and at an age of  $20.4 \pm 2.2$  days (range 16-26 days). Comparable data for six MDA chicks were  $212 \pm 30.6 \text{ g}$  (168-249 g),  $78 \pm 4.3 \text{ mm}$  (71-84 mm) and  $18.8 \pm 0.7$  days (18-20 days) respectively. There was no significant difference between the two groups in any of these variables ( $t = 0$ , -1.35 and -1.71 respectively; all ns).



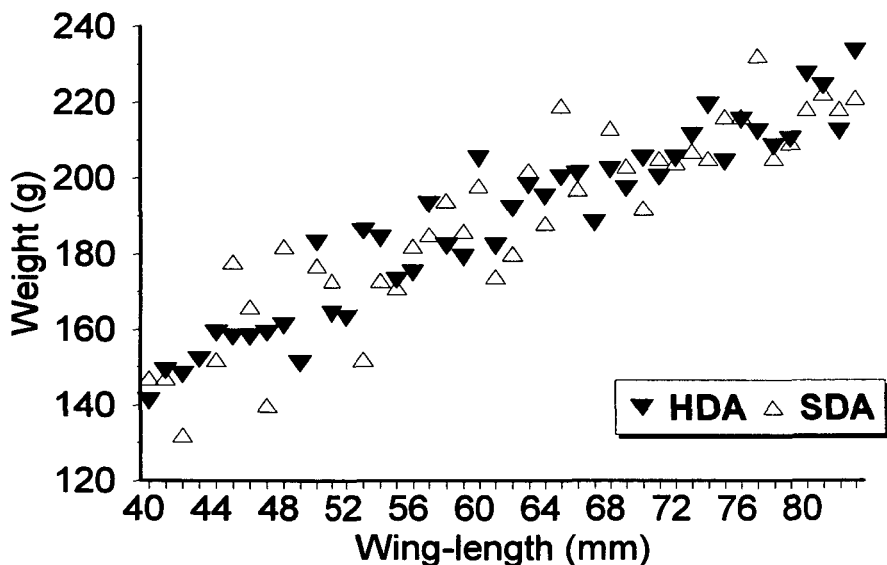


Figure 1. Relationship between mean chick weight and wing-length for daily weighed chicks (HDA; filled triangle; 32 chicks, 311 measurements) and chicks handled once (SDA; open triangle; 176 chicks, 176 measurements). Each point represent 2-13 sample values.

It was not possible to obtain data on weight and age at departure for chicks from SDA. However, as weight and age at departure of chicks from HDA and MDA did not differ significantly, and as there was no difference in the weight/wing-length relationship of chicks from HDA and SDA, it seems reasonable to assume that the daily disturbances did not have any significant negative influence on weight of departure.

Two of the 18 ringed chicks from HDA in 1986 were reported dead at an age of 12 and 13 months, while eight others were controlled on Græsholmen in 1990 and seven of them again in 1992 or 1993. First-year survival was therefore at least 55%, and survival to the fourth and sixth year of life (breeding age) 44% and 39%, respectively. Of the 50 ringed chicks in different SDAs in 1986, two were reported dead at an age of 21 and 51 months, while 22 others were controlled on Græsholmen in 1990 and 20 of them again in 1992 or 1993. First-year survival was thus at least 48%, and survival to the fourth and sixth year of life 44% and 40%, respectively. These findings suggested that post-departure survival was not affected by the daily disturbances in the colony.

#### DISCUSSION

The overall breeding success of HDA Razorbills was significantly lower than that of SDA birds, but growth rate, age and weight at departure and post-departure survival of HDA chicks were not affected. Birds laying smaller eggs were apparently most influenced by the disturbances. As egg size increases with age of the female Razorbill (Lloyd 1979), this suggests that younger breeders are more sensitive to disturbance than older birds.

Harris & Wanless (1984) and Hatchwell (1989) reported that breeding success, growth rate and age at departure of Guillemot chicks were reduced by daily human disturbances. Hatchwell (1989)

proposed that the effect of disturbance might be due to 'reduced provisioning of chicks by parents, increased energy demands for thermoregulation in the absence of brooding, and/or increased energy expenditure due to the stress of being handled'. I made no attempts to quantify these possibilities, but sitting with a chick on my lap who first stared inquisitively at the great world outside its nest and then calmly started preening, I was led to imagine that Razorbill chicks may be less prone to stress than Guillemot chicks, and that this might be due to differences e.g. in nest sites and in the density of breeding birds.

#### ACKNOWLEDGEMENTS

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#### SUMMARY

Daily disturbance of Razorbill sub-colonies resulted in a significantly reduced nesting success, whereas growth rate, weight and age of departure and post-departure survival were not affected.

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# An analysis of Shag *Phalacrocorax aristotelis* ring recovery and breeding success data during a period of population change on the Isle of Canna

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## INTRODUCTION

During the 1970s and early 1980s most of the seabird colonies on the Isle of Canna in the Inner Hebrides grew rapidly (Swann & Ramsay 1984). However, since the mid 1980s seabird numbers have shown little further increase or have declined markedly (Swann 1992). These observations suggest that changes in population dynamics have occurred. This paper uses ringing recoveries and breeding success monitoring data for Shags *Phalacrocorax aristotelis* on Canna collected over a 20 year period. Our aim was to examine whether there was any evidence for differences in these parameters during the period when numbers of Shags were increasing and decreasing on Canna.

## METHODS

Each year between 1974 and 1993 an extensive and detailed count was made of all occupied nests in all colonies on the island in late June/early July. This was mainly done by the same observers each year, helping to maintain consistency. From 1974 to 1984 the trend in the numbers of nests counted was one of increase (see results) since 1984 the trend has been one of decrease.

Between 1961 and 1965, 350 nestling Shags were ringed. Ringing then continued annually from 1969 to 1991 resulting in 9030 nestlings being ringed in that period. In addition between 1977 and 1993, 3109 adults were caught on nests in the breeding colonies, 165 of which had been ringed on Canna as nestlings. From these data return rates of Shags to the island were estimated.

Although Shags sometimes breed at 2 years old (Potts 1969) on Canna most do not do so until older (pers.obs.). Ringing recovery data were divided into three time periods for analysis: 1961-70 (no colony counts available), 1971-81 (birds from these cohorts entered the population during the increase phase) and 1982-91 (birds from these cohorts entered the population while it was decreasing). Only individuals ringed between 1974 and 1981 could be used to examine return rates of adults during the period of growth as prior to 1977 too few adults were caught in the colonies. Birds ringed as nestlings and reported prior to 1 August the following year are referred to as first-year birds, prior to 1 August two years later as second-year birds and so on.

To assess breeding success 60 permanently marked sites were visited at least four times a year during the season (1976-1993) to record clutch size and number of young fledged. All means are given  $\pm 1$  standard deviation.

## RESULTS

### *Breeding numbers*

The number of Shag nests on Canna rose from 856 nests in 1974 at an average rate of 9.0% pa to reach a peak of 1753 nests in 1984 (Fig. 1). Numbers then declined at an average rate of 6.7% pa to 697 nests in 1993. Dramatic decreases of 40% and 74% occurred in 1976 and 1986 respectively. In each case numbers recovered close to pre-crash levels in following years.

### *Ringing recoveries*

There was a significant difference in first year recovery rates between the three time periods with the percentage recovered decreasing during the study (Table I). Recovery rates of birds reported as

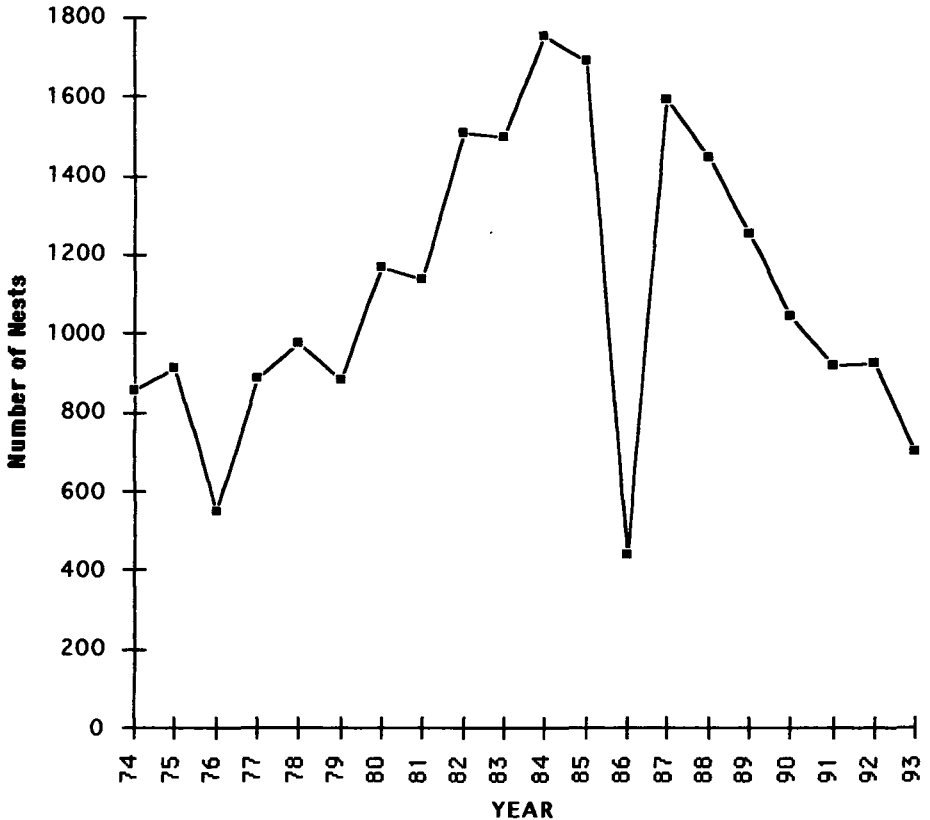


Figure 1. Number of Shag nests counted on Canna 1974-1993.

TABLE I. NUMBER (AND PERCENTAGE) OF CANNA SHAGS RINGED AS NESTLINGS AND RECOVERED IN THEIR FIRST YEAR OF LIFE AND SECOND AND THIRD YEAR.

	<i>no. ringed</i>	<i>no. recovered</i> <i>1st year</i>	<i>no. recovered</i> <i>2nd and 3rd year</i>
1961-70	617	45 (7.3)	12 (1.9)
1971-81	4005	125 (3.1)	26 (0.6)
1982-91	4758	83 (1.7)	24 (0.6) <sup>1</sup>

Note: <sup>1</sup> The 0.6% of birds recovered in their 2nd and 3rd year during the third period was calculated from the 4221 chicks ringed between 1982 and 1990. There was a significant decline in the 1st year recovery rate between each of the three cohort groups ( $\chi^2=23.7$ ,  $df=1$ ,  $p<0.001$  and  $\chi^2=16.94$ ,  $df=1$ ,  $p<0.001$ ). Significantly more 1961-71 birds were recovered in their 2nd and 3rd years than 1971-90 combined ( $\chi^2=14.37$ ,  $df=1$ ,  $p<0.001$ ).

TABLE II. TIMING OF RECOVERY OF FIRST YEAR SHAGS

	1961-70	1971-81	1982-91
August-October	21 47%	35 28%	12 15%
November-February	18 40%	54 43%	42 51%
March-July	6 13%	36 29%	28 34%

Note: No significant difference between 1971-81 and 1982-91 birds ( $\chi^2=5.04$ ,  $df=2$ , ns), but significant difference between 1961-70 and 1971-91 birds ( $\chi^2=12.31$ ,  $df=2$ ,  $p<0.001$ ).

'found dead' showed a similar significant decrease from 4.1% 1961-70 to 1.9% 1971-81 ( $\chi^2=10.237$ ,  $df=1$ ,  $p<0.01$ ) and to 1.4% 1982-91 ( $\chi^2=4.087$ ,  $df=1$ ,  $p<0.05$ ). Recovery rates of 2nd and 3rd year birds ringed in 1971-81 and 1982-88 did not differ significantly but the recovery rate was significantly higher in 1961-70 than in the two later periods combined (Table I).

Of the 724 adults ringed 1974-1981, 8 (1.1%) were recovered within three years of ringing, not significantly different from the 9 of 970 (0.9%) ringed between 1982 and 1989 ( $\chi^2=0.13$ ,  $df=1$ , ns).

There was no significant difference in the timing of recoveries of first year birds between the 1971-81 and the 1982-1991 cohorts (Table II). There was however, a significant difference between these birds and the earlier 1961-70 cohorts, which had more August-October recoveries and fewer March-July ones.

There was no significant change in area of recovery (Table III) or method of recovery (Table IV) between the 1961-70 cohorts and those ringed between 1971 and 1981. There was however, a significant difference between the 1971-81 cohorts and the 1982-91 cohorts with significantly more of the latter recovered further south and significantly fewer shot.

### *Return rates*

From the 1974-81 cohorts 132 chicks were re-caught between ages 3 and 7 years in the colony suggesting that a minimum of 3.7% of young birds had survived to breeding age, this figure compared with only 33 (1.6%) of the 1982-86 cohorts (Table V).

These estimates do not, however, allow for annual differences in catching effort. We attempted to take such variation into account by dividing the number of retraps of each cohort caught in each year by the total number of adults caught in that year and multiplying this value by 1000 (ie. to produce a ratio of the number of birds retrapped per 1000 caught). For each cohort the numbers returning per 1000 in their 3rd-7th years were added together and then further corrected by dividing by the number of chicks ringed to take into account variation in ringing effort. The return rate indices so derived (Table V) suggest that since 1981 less than half as many young Shags are returning to the colony: a return rate of 0.07 (1982-86 cohorts) compared with 0.19 (1974-81 cohorts). This is similar to the results shown by the raw retrap data. A spearman rank correlation showed a significant correlation between the retrap data and the return rate ( $r=0.962$ ,  $n=13$ ,  $p<0.01$ ) indicating that variation in trapping effort had little effect on the overall result. There was no correlation, however, between these return rates and first year recovery rates ( $r=0.185$ ,  $n=13$ , ns) nor between the return rates and the percentage of birds reported as found dead ( $r=0.143$ ,  $n=13$ , ns).

### *Breeding success*

The number of young fledged per nest (Fig. 2) has varied from 0.9 to 2.1 throughout the study (mean  $1.6 \pm 1.07$ ). There was, however, a significant difference between 1976-84 (mean  $1.8 \pm 1.02$  young per nest) and 1985-93 (mean  $1.4 \pm 1.1$  young per nest,  $t=5.132$ ,  $p<0.001$ ).

TABLE III. RECOVERY REGIONS OF CANNA SHAGS IN FIRST YEAR OF LIFE.

<i>Recovery Area</i>	<i>1961-70</i>	<i>1971-81</i>	<i>1982-91</i>
Western Isles	26 58%	81 65%	31 37%
Highlands	11 24%	23 18%	21 25%
Strathclyde	7 16%	21 17%	27 33%
Ireland	1 2%		4 5%

Note: For the chi-square test the Irish records are combined with the Strathclyde ones.

1961-71 v 1971-81 ( $\chi^2=0.88$ , df=2, ns)

1971-81 v 1982-91 ( $\chi^2=16.52$ , df=2,  $p<0.001$ )

TABLE IV. METHOD OF RECOVERY OF FIRST YEAR SHAGS

	<i>1961-70</i>	<i>1971-81</i>	<i>1982-91</i>
Found dead	25 56%	78 62%	66 80%
Shot	13 29%	30 24%	1 1%
Netted	7 16%	16 13%	12 14%
Oiled	0	1 1%	4 5%

Note: Chi-squared tests omit the small numbers reported as oiled.

1961-70 v 1971-81 ( $\chi^2=0.75$ , df=2, ns)

1971-81 v 1982-91 ( $\chi^2=19.69$ , df=2,  $p<0.001$ )

TABLE V. RETURN RATES OF CHICK SHAGS TO CANNA BY AGES 3-7.

<i>year</i>	<i>no. ringed</i>	<i>no. retrapped</i>	<i>% retrapped</i>	<i>no. return per 1000 caught</i>	<i>return index</i>
1974	204	8	3.9%	46.20	0.23
1975	613	10	1.6%	61.34	0.10
1976	441	9	2.0%	45.66	0.10
1977	688	39	5.7%	195.96	0.28
1978	408	11	2.7%	54.92	0.13
1979	393	17	4.3%	94.28	0.24
1980	412	20	4.8%	107.21	0.26
1981	397	18	4.5%	77.12	0.19
1982	455	7	1.5%	31.83	0.07
1983	523	13	2.5%	44.00	0.08
1984	476	10	2.1%	46.92	0.10
1985	464	1	0.2%	7.63	0.02
1986	127	2	1.6%	11.28	0.09
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1974-81	3556	132	3.7%	682.69	0.19
1982-86	2045	33	1.6%	141.66	0.07

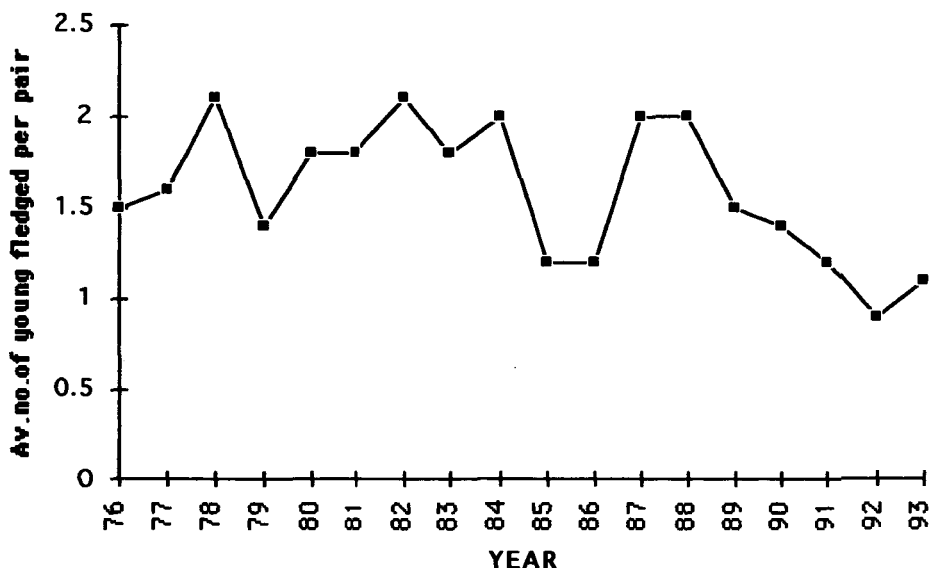


Figure 2. Average number of chicks fledged per pair from study nests on Canna 1976-1993.

### DISCUSSION

Between 1974 and 1984 the breeding population of Shags on Canna doubled since when it has decreased. During this period there were two large crashes in breeding numbers (1976 and 1986). The low breeding success and the rapid recovery in numbers the following year suggest that this may well have been due to large-scale non-breeding of experienced adults as has previously been documented on the Isle of May (Aebischer & Wanless 1992).

Why did Shag numbers start to decline after 1984? One possibility would be an increase in mortality rates. The analysis of ringing recovery data showed no significant changes in the recovery rates between the periods of population growth and subsequent decline of birds aged 2 or 3 years old or of those ringed as adults. First year recovery rates, however, have declined throughout the study period and this has coincided with a decrease in the return index (Table V). No significant correlations were found between a cohorts first year recovery rate and return index. Since 1981 there have been some significant changes in recovery statistics. Notably fewer birds are now being recovered in the Western Isles and reported as shot. A Spearman Rank test on the data in Table VI showed a significant correlation between the % shot and the % recovered ( $r=0.937$ ,  $n=7$ ,  $p<0.001$ ).

The number of birds reported as shot will therefore have inflated past recovery rates. Up to 1981, when it became illegal, large numbers of Shags were shot for eating in the Western Isles. Potts (1969) suggested that the increase in the Shag population of south-east Scotland and north-east England was due to a gradual reduction in persecution. Heubeck *et al.* (1991) suggested that a ban on shooting Guillemots *Uria aalge* in Norway was one factor that resulted in the large population increases witnessed in Shetland in the 1970s. This does not appear to be the case on Canna where shooting pressure was quite high during the period of population increase (see Table VI) and since the cessation of (reported) shooting the population has declined.

TABLE VI. NUMBER OF CANNA SHAGS SHOT COMPARED TO FIRST YEAR RECOVERY RATE.

year	no. ringed	no. recovered	% recovered	no. shot	% shot
1961-65	350	31	8.9	11	36
1969-71	414	16	3.8	3	19
1972-74	456	27	5.9	8	30
1975-77	1742	53	3.0	13	25
1978-81	1660	43	2.6	8	19
1982-84	1454	22	1.5	0	
1985-87	1130	18	1.6	1	6

Recovery rates, of course, do not necessarily equal actual mortality rates. The coastline of much of north-west Scotland where the bulk of Canna shags are recovered, is remote and rocky. Birds that are killed by direct human activities eg. shot or netted are more likely to be reported than birds found dead from natural causes, thus distorting the recovery rate. A separate analysis of those birds reported as found dead during their first year of life showed that the percentage so reported had declined significantly throughout the study period and that there was no significant correlation between return rates and first year 'found dead' rates. The found dead category will include birds that have died from other causes such as shooting. Despite the few recoveries of shot birds amongst the 1982-86 cohorts there was still no significant correlation between the first year recovery and the return index ( $r=0.356$ ,  $n=5$ , ns).

The low first year recovery rate associated with the low return index during the period of decline could suggest high rates of emigration from Canna. Potts (1969) stated that on the Farne Islands, Northumberland the emigration rate of Shags prior to their first breeding attempt at 2 years was 8% and for known breeders was 1%. Aebischer (1986) concluded that emigration from the Isle of May was low. There is no evidence of increasing rates of emigration from Canna. There are no large colonies within 70km. (Lloyd *et al.* 1991). Smaller colonies close to Canna eg. Rum, Eigg have shown no significant changes in numbers.

The decline in Shag numbers on Canna since 1984 has coincided with a significant reduction in breeding output and decline in the rate of young birds returning to breed. The reasons for the decline are not clear. A reduction in food supply in the Minch area around Canna is a possible factor. To investigate long term changes in diet, regurgitations from Shag chicks have been collected on Canna between 1981-1992 (Swann *et al.* 1991, updated). Of the 51 collected up to 1992 the commonest species was sandeel *Ammodytidae* ( $n=35$ ), *Gadidae* (13), Sprat *Sprattus sprattus* (1) Bullrout *Myoxocephalus scorpius* (1) and one sample that was evenly split between sandeel and *Gadidae*. Sample sizes when Shag numbers were increasing were small, with only 15 collected between 1981 and 1984. A further 36 samples were collected between 1987 and 1992. In years of good breeding success (ie. 1.5 or more chicks reared per pair) 25 out of the 29 samples were composed of sandeel, significantly more than the 10.5 out of 22 samples from years with breeding success less than 1.5 chicks per pair ( $\chi^2 = 8.824$ ,  $df=1$ ,  $p<0.01$ ). In the period of colony growth only two years had a fledging success less than 1.5 but since 1984 there have been 7 years where fledging success has been below 1.5 chicks per pair. Hislop *et al.* (1991) showed that sandeels have higher calorific values than *Gadidae*, so that a decrease in the amount of sandeels in the chicks diet could have resulted in the observed reduction in breeding success. Other species such as Manx Shearwater *Puffinus puffinus* and Kittiwake *Rissa tridactyla* have similarly shown declines in breeding performance and numbers since the mid 1980s on Canna (Swann 1992). This may also provide some indirect support to the food shortage hypothesis.

Why fewer first year birds are returning cannot be explained by an analysis of ringing recoveries alone. The ban on shooting has obviously resulted in a decline in reported recoveries. Perhaps after almost 30 years of continual ringing local people are now suffering from 'ring report fatigue' and are now less likely to report a ringed bird than they were in the 1960s and 70s.



## SUMMARY

Between 1973 and 1984 Shag numbers on Canna increased on average, by 9.0% pa and have since declined. The period of decline has been characterised by lower breeding success, lower return rates of birds ringed as nestlings but also lower first year recovery rates. Recovery rates of older birds have remained unchanged. A reduction in shooting pressure since 1981 partly explains the decline in first year recovery rates, but not the decline in breeding numbers. The role of emigration and food supply in these changes are considered.

## ACKNOWLEDGEMENTS

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# Audouin's Gulls *Larus audouinii* in Senegambia

A.J.del Nevo, S.Rodwell, I.M.W.Sim, C.R.Saunders and T.Wacher

## INTRODUCTION

Audouin's Gull *Larus audouinii* is a globally threatened species which breeds on coastal sites in the Mediterranean (particularly western Mediterranean, Collar & Andrew 1988), from the Moroccan coast in the west to Cyprus in the east. Large numbers of adult and immature Audouin's Gulls leave the Mediterranean, passing through the Straits of Gibraltar (Beaubrun 1983), to winter on the Atlantic coast of Morocco (20-45 individuals, Smith 1972, Cramp 1983), with a few thought to move further south (Cramp 1983). Relatively little is known of the status and distribution of Audouin's Gull outside the Mediterranean (De Juana *et al.* 1987) and away from the coast of Morocco. Urban *et al.* (1986) and Gore (1990) cited four records from Senegambia and more recently Baillon (1989) recorded up to 321 in Senegal during 1985. We are aware of only two other records for this species in Senegambia, by Delaporte & Dubois (1990) and Mackrill (1989) who saw 130 and 68 in 1988 and 1989 respectively. Most of the records came from the Saloum Delta (Fig. 1), although Delaporte & Dubois (1990) observed 72 Audouin's Gulls between Mbour and Palmarin. Baillon (1989) recorded the highest counts during December, with smaller numbers present from September to April.

Here we present data which confirm that Senegambia is an important wintering area for this species.

## METHODS

We conducted two surveys, along the entire Senegambian coast from St Louis in northern Senegal to the Allahein River on the southern border of The Gambia, between 2-18 February 1991 and 5 September - 3 October 1992. Roost sites were identified and daily patterns of bird attendance recorded at five sites distributed along the coast during 1991. In 1991 counts of adult and juvenile birds were highest during the late afternoon when birds were at roost. The entire Gambian coast was covered in one day. Counts for Senegal took place over two days. Final estimates represent the highest count at each site. Some double-counting of birds may have taken place but observations of darvic ringed birds suggested that this was probably small. During 1992 most observations were made in the morning and counts are most probably underestimates. At each site observers recorded: the number of birds in each age class (adult, first winter, second winter, third winter; Grant 1986); the number of pairs of legs visible; the number of ringed (metal and darvic rings) birds and the individual ring combination.

## RESULTS

### *Status and distribution*

In February 1991, 531 Audouin's Gulls were counted; 459 (86%) in Senegal and 72 (14%) in The Gambia (Fig. 2). The highest count (350) was on sand shoals at the river mouth next to Joal-Fadiout. Other large flocks included 70 at Sangomar Point and 39 at the mouth of the Allahein River. During September 1992, 276 were seen; all were in Senegal. Most records were from the Sangomar Peninsula, including 200 on 30 September. J. Willsher (pers.comm.) recorded 316 Audouin's Gulls there in October 1992.

*Age composition and movement*

Adult birds dominated both surveys (Table I) and proportionately more adults than first year birds were present during September 1992 than in February 1991. Post-nuptial migration commences in late July (Beaubrun 1983) with the peak of departure three weeks later (Cramp 1983). Our observations are consistent with the view that adult Audouin's Gulls tend to arrive in Senegambia before first year birds; the ratios of first year to adult were 0.1:1 in September and 0.54:1 during February.

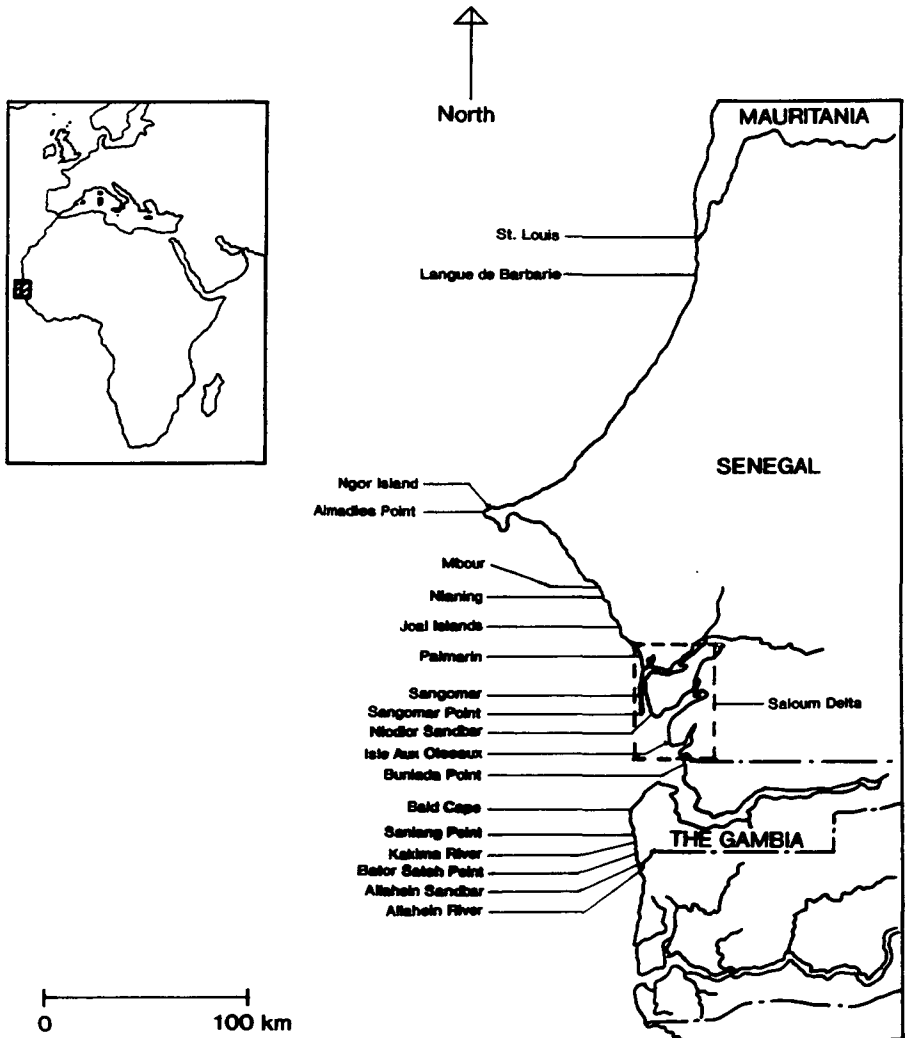


Figure 1. The location of study sites in Senegambia in February 1991 and September 1992.

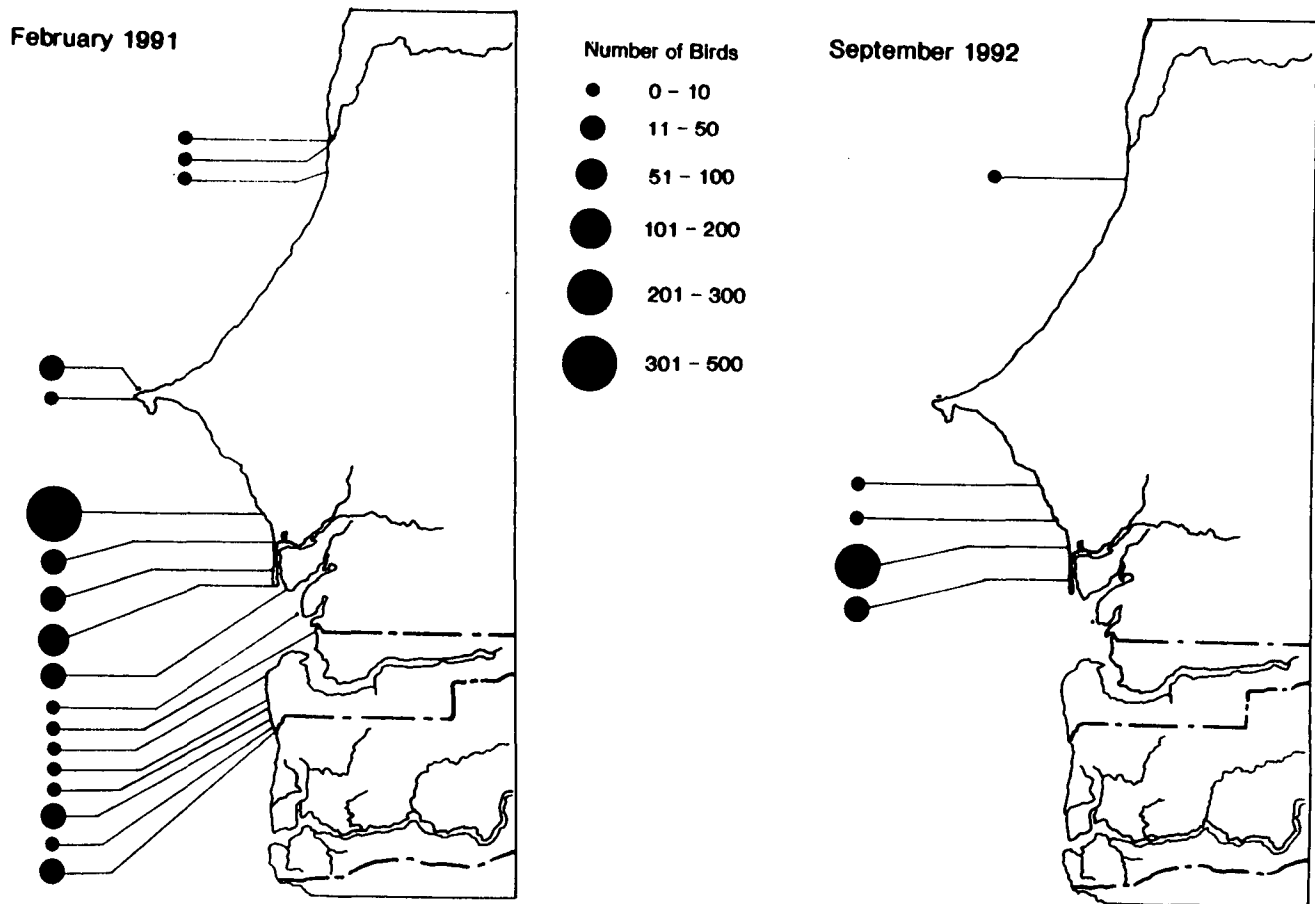


Figure 2. The distribution of Audouin's Gulls in Senegambia in February 1991 and September 1992.

TABLE I. AGE COMPOSITION AND NUMBERS OF AUDOUGIN'S GULLS RECORDED IN SENEGAMBIA DURING FEBRUARY 1991 AND SEPTEMBER 1992.

Age class	FEBRUARY 1991		SEPTEMBER 1992	
	individuals	%	individuals	%
Adult	319	60.1	237	85.9
Third Winter	2	0.4	1	0.4
Second Winter	39	7.3	14	5.1
First Winter	171	32.2	24	8.6
Totals	531	100.0	276	100.0

Repeat counts at the Allahein River mouth, at the same time of day, suggested a rapid turnover of birds. On 15 February 1991, 11 adults and 21 immatures were recorded but on 18 February all 39 birds were adult. In 1992, 54 adults and 6 first year birds were recorded near Sangomar on 25 September and two days later there were 179 adults, 9 second winter and 12 first year birds. Individually identifiable birds seen at Sangomar on 25 September 1992 were still present on 1 November (J. Willsher pers.comm.).

### DISCUSSION

Observations of Audouin's Gulls during 1992 in Senegambia suggested a build up of numbers from late August/mid-September. There are few records of Audouin's Gulls between September and February but few observers have visited the area during this period. Birds could winter further south and return north during January/February or remain with large numbers of wintering Lesser Black-Backed Gulls *Larus fuscus* in Senegambia. Many of these Audouin's Gulls were ringed. For example, on 30 September 1992, 24 (14%) of 167 birds were ringed: 18 had a darvic and 6 had a metal ring only. Three of the darvic-ringed birds had been marked at the Ebro Delta colony in NE Spain. Ringing details of the other 15 birds are as yet unknown, but it is likely that they were also ringed in Spain (D.Oro pers.comm.).

Our observations, taken with those of others, identify Senegambia as an important area for wintering Audouin's Gulls, holding at least 2.4% and 1.3% of the world population (ca.11,000 pairs, D.Oro pers.comm.) in February 1991 and September 1992 respectively. Presumably some also winter in, and pass along the coast of, Mauritania although there are only a few records from there (Urban *et al.* 1986). It seems possible that some winter further south along the west African coast. We did not record any hunting or other activity likely to adversely affect Audouin's Gulls or other palearctic gulls and terns.

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### SUMMARY

Senegambia is an important wintering area for the globally threatened Audouin's Gull *Larus audouinii*. 531 and 276 Audouin's Gull were recorded in Senegambia during February 1991 and September 1992 respectively. A relatively high proportion of birds had been ringed in Spanish breeding colonies.

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## BOOK REVIEWS

SEALY, SPENCER G. (Ed) 1990. Auks at Sea. Studies in Avian Biology No. 14. 180pp. \$16.00. Cooper Ornithological Society, Los Angeles. ISBN: 0-935868-49-6.

This is a series of 17 papers - the Proceedings of an International Symposium of the Pacific Seabird Group held in December 1987. The passage of time has not diminished the importance of the publication. Unlike many similar proceedings this is well produced and makes stimulating reading.

The papers (all but one by North American workers) are grouped into five sections - food patch use by feeding seabirds, allocation of time and energy, chick rearing at sea, diet in relation to prey resources, and auks in peril. The latter includes the decline of Guillemots in California, mortality due to the Apex Houston spill and Barents Sea auks. The last paper is the only one directly relevant to our geographic area, being a description of the differential responses of Common and Brunnich's Guillemots (the former decreased by 70-90% over three years, the latter only slightly) to a crash in the capelin stocks of the southern Barents Sea. However, most of the contributions have direct relevance to "local" species, e.g. time budgets and energy expenditure, feeding habitat selection and parent-young interactions in Guillemots, aggregative feeding by Puffins and Guillemots. Most of those which do not, are plain intriguing - e.g. Ancient Murrelet chicks (which are not fed on land) travelling 48 km during their first day at sea, the gelatinous diet (jelly-fish and ctenophores) of Parakeet Auklets. There can be no Seabird Group member who will not gain from reading this publication.

It can be obtained from the Cooper Ornithological Society, 439 Calle San Pablo, Camarillo, California 93012-8506, USA. Price includes postage. Unfortunately all orders must be paid in advance by cheque or money order in U.S. funds only. Credit cards are no use - I have checked. An American friend might be able to help.

M.P. Harris

BIRKHEAD, TIM. 1993. Great Auk Islands. A field biologist in the Arctic. 275pp. £22.00. T. & A.D. Poyser, London. ISBN 0-85661-077-1.

I read Great Auk Islands during the week that the British Association for the Advancement of Science agonised over how to increase the number of students taking science subjects at school and university. In his opening chapter Tim Birkhead makes it clear that his aim in writing this book was to try and convey something about both the excitement and frustration of conducting research. Hence Great Auk Islands is a great deal more than a rehash of scientific papers on auk ecology and behaviour in a popular form. It is a highly personal account not only of the trials and tribulations of fieldwork but also the thought processes involved in carrying out the research. Provided that modern youth does not mind getting cold, wet, hungry, seasick or being attacked by polar bears or Herring Gulls this book should inspire some of today's students to take up the challenge of research in Arctic ecosystems.

Unlike many other volumes in the Poyser series the book is not organised into chapters dealing with various aspects of breeding biology and behaviour of the study species, rather it chronicles the author's experiences over seven summers spent in the Canadian Arctic at field camps at Cape Hay, Coburg Island, Great Island, Funk Island and Gannet Clusters. This autobiographical approach makes for enjoyable reading but it does have one major drawback in that it is not easy to know where to find information about a particular aspect of a species' biology. This problem is exacerbated by a highly idiosyncratic index. Hence I can find a reference to 'bed-settee' but not Brunnich's Guillemot, 'pancakes' but not Puffin.

As well as describing the results of a wealth of recent research on Common and Brunnich's Guillemots by Tim Birkhead and his many Canadian co-workers the book also contains information about Arctic exploration and exploitation. This interweaving of ancient and modern is used to particular advantage in the section on the Great Auk where the tragic history of this splendid bird is combined with speculation about how its chick developed and what it ate.

The book maintains the high standard of production we have come to expect from the Poyser series and is superbly illustrated with numerous drawings by David Quinn and photographs in both black and white and colour. I can thoroughly recommend it.

Sarah Wanless

## THE SEABIRD GROUP 1994

*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 K.C. Hamer, M.P. Harris, J.D. Okill and J. Sears.

*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, 13, 14 and 15 are



available at £5 + 50p postage 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.

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## 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.

*Seabird* is indexed in the Aquatic Sciences and Fisheries abstracts, Ecology Abstracts and Animal Behaviour Abstracts of Cambridge Scientific Abstracts databases and journals.

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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 authoritative 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.