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The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland

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(With 4 figures in the text)

Great skuas on Foula, Shetland have responded to a decline in the availability of sandeels since the late 1970s by increasing the proportion of other items in their diets. This change is correlated with the annual recruitment of sandeels in Shetland waters. Since 1983 there has been a 10-fold increase in predation by great skuas upon other seabirds, as Furness & Hislop (1981) suggested might occur in response to a low availability of sandeels. Changes in diet have been accompanied by a 50% reduction in adult territorial attendance as adults increased their foraging effort, such that between 1987 and 1989 breeding adults were probably working as hard as they were able to. Despite this, breeding success was less than 40% in 1987 and less than 15% in 1988 and 1989. The major cause of breeding failure was predation of unguarded chicks by adults from neighbouring territories. The willingness of adults to expose their chicks to high predation risk is probably maintained because of a positive correlation between chick pre-fledging growth and post-fledging survival, which is expressed up to the age of two years and which will place a strong pressure upon adults to feed their chicks as well as possible. The high expenditure of effort by adults in 1987 and 1988 did not affect the weights of those birds incubating eggs in 1988 and 1989, but there was a slight (3%) decrease in egg size between the late 1970s and the late 1980s. Changes in the age structure of the breeding population and the absence in 1989 of 28% of adults colour-ringed during incubation in 1988 suggest an increase in the rate of egress since the 1970s. These changes probably represent an increase in the long-term costs of reproduction to adults at this colony.

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Introduction

Life-history theory envisages reproduction as a costly process, in which breeding individuals need to balance the demand for allocating resources to rearing young against the demands of maintaining body condition (Williams, 1966; Gadgil & Bossert, 1970). Optimal reproductive tactics should serve to maximize each individual's life-time reproductive success (Pianka, 1976), and there should be an inverse relationship between reproductive effort in any one year and the expectation of future offspring, if reproduction subjects breeding individuals to risk (Goodman, 1974). Several empirical studies (reviewed by Reznick, 1985) support the notion of costs to high levels of reproductive effort, although Tuomi, Hakala & Haukioja (1983) suggested that adults can often buffer themselves against the demands of reproduction, for instance by storing food reserves for use during breeding. Manipulation of brood sizes in birds (Nur, 1984; Reid, 1987) has produced evidence of increased costs to adults in terms of lower survival after increased reproductive effort. However, Pettifor, Perrins & McCleery (1988) shed doubt upon Nur's results, and other manipulative experiments (Browne, 1982; Feifarek, Wyngaard & Allan, 1983) have suggested that reproduction may be costly only when adults are subjected to extra stress, or when food availability is limited.

Great skuas *Catharacta skua* in Shetland enjoyed high breeding success and steady population growth in the 1970s (Furness, 1987), due mainly to an abundance of sandeels *Ammodytes marinus* (Furness & Hislop, 1981; Furness, 1987). During this period, adults spent a small proportion of the available time foraging (Furness & Hislop, 1981). Since the 1970s there has been a marked decline in the availability of sandeels around Shetland (Gauld, McKay & Bailey, 1986; Hudson & Furness, 1988; Monaghan, Uttley & Burns, 1988; Harris & Wanless, 1990) and great skuas may be expected to respond to this decline in resource availability by increasing the foraging component of their reproductive effort. However, they are a long-lived iteroparous species, and so should not increase their effort in one season beyond their ability to buffer themselves against reduced survival or lower future breeding success.

This paper presents up to 16 years of data on various aspects of the breeding ecology of great skuas in Shetland. It examines the ways in which adults have responded to changes in sandeel availability, and the repercussions of these changes upon annual breeding statistics and long-term reproductive potential.

Methods

Data were collected from the largest British colony of great skuas, at Foula, Shetland. Data for 1987 were collected mainly by RC, for 1988–89 by KH and for all other years mainly by RWF. Information regarding the diets of both chicks and non-breeders were obtained for every year except one between 1973 and 1989, while data regarding the diets of breeding adults were obtained in 1989. Samples were obtained from food regurgitated by chicks while they were being ringed and from pellets of non-digestible material deposited at sites frequented by non-breeders and in breeding territories, using methods described by Furness & Hislop (1981). The relationship between chick diet and sandeel availability was examined using data from The Department of Agriculture and Fisheries for Scotland concerning sandeel recruitment in Shetland waters (Kunzlik, 1989).

Most of the time which great skuas spend away from their territories is used for foraging (Furness, 1987). The attendance of adults at their territories can therefore be used as an index of the ease of obtaining food (Furness & Hislop, 1981). Territorial attendance of adults was determined at 3 stages of the breeding season in 1987, 1988 and 1989 and at one stage in 1976. These were during incubation, the first 2 weeks post-hatching and the rest of the pre-fledging period. Attendance was determined by walking round marked study territories and counting the number of adults at each one. This was used to produce a mean value for the number of adults attending territories with live chicks, and the proportion of occasions when both adults were absent from a territory simultaneously.

Breeding success of great skuas was determined in 1975, 1976, 1987, 1988 and 1989, using methods described by Furness (1983, 1984). In all cases, samples of nests were marked in early May, the eggs laid at them were measured and the fates of these eggs were determined by visiting territories containing marked nests at regular intervals until surviving chicks fledged, in late July or early August.

Variations between years were examined in terms of chick growth and post-fledging survival as well as chick production and survival to fledging. In excess of 10,000 great skua chicks were weighed and measured on Foula between 1975 and 1989, in the manner described by Furness (1983). The ages of these chicks were calculated from their wing lengths (Furness, 1983), and only chicks between 13 and 34 days old (i.e. on the linear part of their growth curve; Furness, 1983) were used to compare weights of chicks of similar ages in different years.

Poor growth as a chick may have repercussions after fledging. To assess the relationship between chick growth and post-fledging survival, ring recovery data supplied by the British Trust for Ornithology were used to determine the age-specific recovery rates for cohorts of great skuas ringed as chicks on Foula each year between 1963 and 1987 (the latest year for which all required recovery data were available) after correcting for differences between years in fledging success. These were then compared with each year's data for chick growth.

Possible changes in the body condition of adults at the start of the breeding season were examined by determining the weights of incubating adults during May and June in 1979, 1980, 1988 and 1989. Adults were caught in a clap net (Spencer, 1984) placed at the nest, and were weighed and measured. The measurements were then used in a discriminant analysis (Norusis, 1984) to determine sex by comparison with 40 birds (18 females plus 22 males) found dead on Foula and sexed by internal examination. This allowed the weights of males and females to be determined separately to a high degree of accuracy (approximately 90% of the birds of known sex were classified correctly by the analysis).

Approximately half the great skuas breeding on Foula were ringed as chicks, and so can be aged accurately from their ring numbers. Ringed adults trapped in 1988 and 1989 were used to assess the age structure of the breeding population, after accounting for differences in the numbers and proportions of chicks ringed in different years. In addition, all adults trapped in 1988 were given a combination of 4 coloured rings to allow identification of individuals. These were located in 1989 by searching the study area on consecutive days during May. This was continued until no new birds were recovered. Territories where birds marked in 1988 were not seen in 1989 were then visited on 2 occasions specifically to search for these birds. Finally, the whole island was searched during June, to check whether any marked birds had moved their territories out of the study area.

Results

Diets

During the 1970s and early 1980s great skuas on Foula fed their chicks mainly on sandeels, which have a higher calorific value and contain a smaller proportion of indigestible material than other items in their diet (Table I; Furness & Hislop, 1981). From 1983 to 1984, the proportion of sandeel in chicks' regurgitates fell from 95% to 61%, with nearly all of the difference being compensated for by an increase in whitefish regurgitates. The situation remained more or less unchanged between 1984 and 1987, with birdmeat comprising between 3% and 6% of the diet. From 1987 to 1988, the proportion of regurgitates comprising sandeel fell from 56% to 5%, while the proportions comprising whitefish and birdmeat regurgitates rose from 42% to 77% and from 3% to 18%, respectively (Table I). These changes are closely associated with changes in sandeel

TABLE I

The percentages of different items in food regurgitated by great skua chicks on Foula between 1 and 15 July, for every year from 1974 to 1989

Year	*n*	Sandeel (%)	Whitefish (%)	Birdmeat (%)
1974	90	91	9	0
1975	90	70	28	2
1976	95	86	14	0
1977	56	86	14	0
1978	45	71	24	4
1979	49	73	24	2
1980	69	68	28	4
1981	64	88	6	6
1982	21	95	5	0
1983	41	95	2	2
1984	36	61	33	6
1985	58	62	33	5
1986	61	66	30	5
1987	36	56	42	3
1988	22	5	77	18
1989	21	14	76	10

For every year, *n* is the number of regurgitates and the number of chicks producing them, since every chick produced a single regurgitate. The percentages refer to the proportions of regurgitates containing each food item. Deviations of the summed values from 100% are due to rounding errors

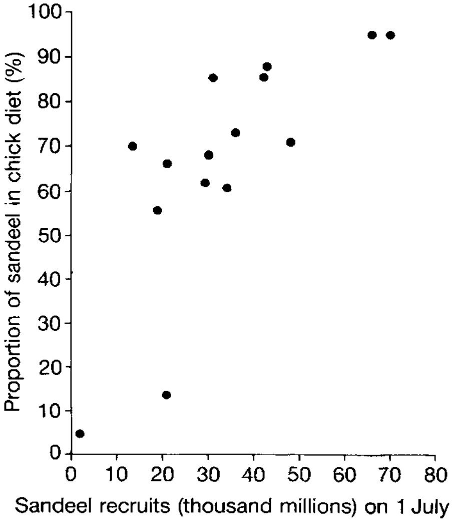

FIG. 1. The percentage of sandeel in regurgitates produced by great skua chicks on Foula between 1 and 15 July of every year from 1975 to 1989 against the number of sandeels, in thousand-millions, recruited in Shetland waters in the previous year. Data for sandeel recruitment are from Kunzlik (1989).

TABLE II

Food items in pellets produced by non-breeding great skuas on Foula between 1 and 15 July, for every year from 1973 to 1989 except 1985, and by breeding adults in 1989

Year	*n*	Sandeel (%)	Whitefish (%)	Bird (%)	Other (%)
1973	100	71	27	2	0
1974	100	24	71	5	0
1975	100	21	69	6	4
1976	100	72	26	2	0
1977	100	59	35	4	2
1978	100	64	35	1	0
1979	100	41	54	3	2
1980	100	17	74	6	3
1981	100	18	77	4	1
1982	100	13	80	3	4
1983	305	9	70	17	4
1984	100	0	74	23	3
1986	200	0	82	14	5
1987	98	9	77	10	4
1988	200	0	73	24	4
1989	247	4	62	30	4
1989 (B)	549	1	69	29	2

For every year, *n* is the number of pellets analysed. The number of birds producing these pellets is similar to the number of pellets in the case of non-breeders, while the sample for breeding birds was collected from 50 territories. The percentages refer to the proportions of pellets containing each item. 'Other' items were invertebrates, rabbits, mice, fulmar *Fulmarus glacialis* eggs or great skua eggs. 1989 (B) refers to breeding adults

abundance, since there is a positive Pearson correlation between the proportion of sandeel in chicks' diet and the number of sandeels recruited to the Shetland population in the previous year ($r = 0{\cdot}75$, $n = 15$, $P = 0{\cdot}001$; Fig. 1: this parametric test was used because the data for both diet and recruitment conform to normal distributions, as determined by Kolmogorov-Smirnov one-sample tests. Similar tests were performed on all data before using parametric analyses). Recruitment in the previous year was used because most of the sandeels fed to great skua chicks are one year old (Furness, 1987).

The diet of non-breeders on Foula shows a similar change to that of chicks, with a gradual decline in the representation of sandeel being balanced by an increase in the proportion of whitefish, and latterly of birdmeat, in the diet. The increase in the representation of birdmeat in the diet of non-breeders was equally marked but occurred five years earlier than that in the diet of chicks (Table II). In 1989, the proportions of sandeel and birdmeat in the diet of breeding adults were very similar to those in the diet of non-breeders but not to those in the diet of chicks (Tables I and II).

Adult territorial attendance

The changes in the diets of chicks between 1976 and 1989 were accompanied by marked changes in the territorial attendance of adults. In 1987, 1988 and 1989, the mean attendance was 1·5 adults

TABLE III

Territorial attendances of adult great skuas with live chicks on Foula in 1976, 1987, 1988 and 1989

Year	*n*	Stage of season	Mean no. of birds present	% nests with both birds absent
1976	160	3	1·47	0·00
1987	60	1	1·54	0·10
1987	60	2	1·54	0·00
1987	58	3	1·07	10·34
1988	156	1	1·55	1·28
1988	150	2	1·52	1·28
1988	32	3	1·03	12·50
1989	194	1	1·51	1·55
1989	185	2	1·45	1·08
1989	90	3	1·17	11·11

For stages of season: 1 = incubation; 2 = the first two weeks after hatching; 3 = the rest of the pre-fledging period. *n* is the number of observations producing each mean

per territory during incubation and the first two weeks post-hatching, and 1–1·2 adults per territory during the rest of the pre-fledging period (Table III). Comparison with the same stage of the breeding season in 1976 reveals a 50% reduction in territorial attendance between this year and 1987 (Table III). Over the same period of time, the proportion of territories with no adults in attendance following the first two weeks post-hatching increased from nought to 10% (Table III). In a test for a difference in the numbers of territories with nought, one and two adults in attendance in 1976 and 1987–89, $\chi^2 = 35{\cdot}57$, $P < 0{\cdot}0001$ with two degrees of freedom.

Breeding statistics

During this period there was a small (3%) but significant decrease in egg size (Table IV: in a *t*-test comparing clutches in 1975 with pooled data for 1987–89, $t = 7{\cdot}88$, $P < 0{\cdot}001$ with 1493 degrees of freedom). Clutch size and hatching success were unchanged (Table V), while fledging success declined from 91·1% in 1976 to 7·8% in 1988 and 16·5% in 1989, with the value for 1987 intermediate (Table V). Visits to the colony in July of every year from 1977 to 1986 indicated, from

TABLE IV

Sizes of eggs laid by great skuas on Foula in 1975, 1987, 1988 and 1989

Year	*n*	Mean length (mm)	Mean width (mm)	Mean internal volume (mm^3)	Standard deviation
1975	749	71·07	50·04	85·42	5·77
1987	52	70·67	49·54	83·25	4·96
1988	307	70·62	49·86	84·34	5·12
1989	387	70·32	49·32	82·18	5·68

n is the sample size. Internal egg volumes were calculated from the equation given by Coulson (1963)

TABLE V

Breeding data for great skuas on Foula, between 1975 and 1989

Year studied	No. nests studied	Mean clutch size	Hatching success (%)	Fledging success (%)	Breeding success (%)
1975	447	1·87	66·1	95·3	63·0
1976	434	1·93	73·3	91·1	67·5
1987	23	1·95	77·7	61·1	35·6
1988	160	1·93	72·3	7·8	5·7
1989	198	1·95	75·2	16·5	12·4

the number of pairs with chicks, that breeding success in these years was much closer to the values for 1975 and 1976 than to those for later years. The differences in breeding success between years are not caused by biases in sampling with respect to laying date or location within the colony, since none of the years differed in its median hatching date (as determined by a Kruskal–Wallace one-way analysis of variance) and the same part of the colony was studied each year. The proximate cause of the low breeding success between 1987 and 1989 was high chick mortality due to predation by adults at neighbouring territories. Of 192 ringed chicks found dead in 1988 and 1989, 35 had previously been found alive with injuries, often severe, resulting from attacks by neighbouring adults, and many more chicks, both ringed and unringed, were found injured than starved. Nearly all dead chicks, including 185 of the 192 with rings, were partially eaten when found. This predation was possible because both parents foraged simultaneously, unlike in previous years, when females stayed on their territories and guarded their chicks (Furness, 1987).

TABLE VI

Mean differences in grams between the observed and expected weights of great skua chicks between 13 and 34 days old on Foula in different years

Year	*n*	Mean	S.D.
1975	1049	+30·4	65·6
1976	1171	0·0	99·9
1977	2123	−15·8	78·8
1978	929	+28·4	82·2
1979	366	+26·8	68·0
1980	643	+6·6	87·5
1981	1032	−45·0	105·7
1982	629	+4·5	51·6
1983	1224	+16·7	74·4
1984	846	+4·0	54·8
1985	898	+7·2	72·9
1986	777	+4·9	60·8
1987	293	−46·0	84·6
1988	466	−134·6	96·8
1989	200	−60·9	84·6

S.D. is the standard deviation of each mean; *n* is the number of chicks measured each year

Chick growth and post-fledging survival

During the 1970s the growth of great skua chicks on Foula followed a logistic curve (Furness, 1987). Table VI shows the weights of chicks between 13 and 34 days old for every year between 1975 and 1989, expressed in terms of the mean difference between the weights of individual chicks and the expected weight derived from this curve. This method is not biased by differences in the mean ages of samples, and no sample differed significantly in its median hatching date. Chick growth was significantly better in the period 1975–86 than during 1987–89 (in a *t*-test on pooled data, $t=35{\cdot}32$, $P<0{\cdot}001$ with 12,644 degrees of freedom). Differences between years in chick growth are strongly associated with differences in sandeel availability, since the growth of chicks is positively correlated with the percentage of sandeel in their diets ($r=0{\cdot}72$, $n=15$, $P=0{\cdot}002$; Fig. 2).

Poor growth of chicks before fledging appears to result in high post-fledging mortality. For cohorts of chicks ringed on Foula between 1975 and 1987, there is a negative Pearson correlation between the mean difference from expected weight for similarly-aged chicks and the proportion of ringed chicks recovered dead away from Foula (i.e. after fledging) in their first year of life (Fig. 3; Pearson correlation, $r=-0{\cdot}60$, $n=13$, $P=0{\cdot}03$). Furthermore, a cohort which suffers high first-year mortality also suffers high mortality in its second and third years (in Pearson correlations between recovery rates at age 0 and at ages 1 and 2 for birds hatched between 1963 and 1987, $r=0{\cdot}69$, $n=25$, $P=0{\cdot}001$ and $r=0{\cdot}73$, $n=25$, $P=0{\cdot}0001$, respectively).

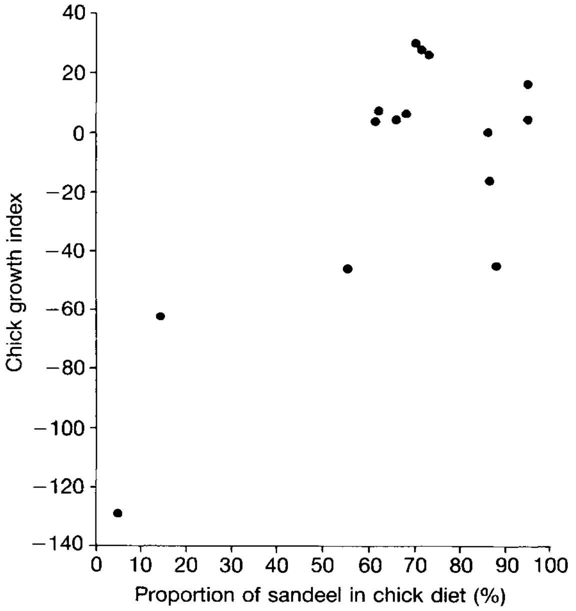

FIG. 2. Chick growth index against percentage of sandeels in the diet of great skua chicks between 1975 and 1989. The index is the mean difference between observed and expected weights of chicks (Table VI).

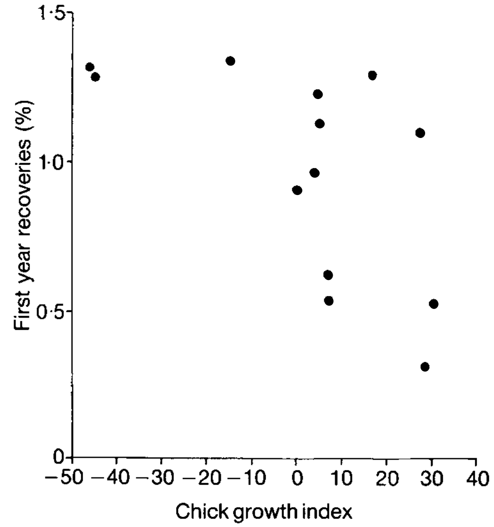

FIG. 3. First year recovery rates of great skua chicks ringed on Foula between 1975 and 1987 against chick growth index. The index is the mean difference between observed and expected weights of chicks (Table VI).

Ages and weights of breeding adults

The high foraging effort exerted by adults in 1987 and 1988 did not reduce the body condition, as determined from weight, of those birds breeding the following season. The weights of random samples of incubating adults of both sexes in 1988 and 1989 were no different to those obtained in 1979 and 1980 (Table VII: in t-tests comparing pooled data for 1979–80 with those for 1988–89, $t = 1{\cdot}24$, $P > 0{\cdot}2$ with 114 degrees of freedom for females and $t = 0{\cdot}78$, $P > 0{\cdot}4$ with 136 degrees of freedom for males).

While there was no change in the weights of incubating birds, this increase in foraging effort may have resulted in a higher proportion of adults being unable to recover from the exertions of the previous season and so failing to breed in consecutive years. Evidence in support of this hypothesis

TABLE VII

Weights of incubating female and male great skuas on Foula in 1979, 1980, 1988 and 1989

Year	*n*	Female mean weight (g)	S.D.	*n*	Male mean weight (g)	S.D.
1979	8	1444	65·2	9	1343	97·2
1980	26	1491	68·8	36	1359	81·4
1988	70	1451	87·7	50	1365	96·7
1989	31	1475	86·7	24	1379	98·3

S.D. is the standard deviation of each mean; *n* is the sample size

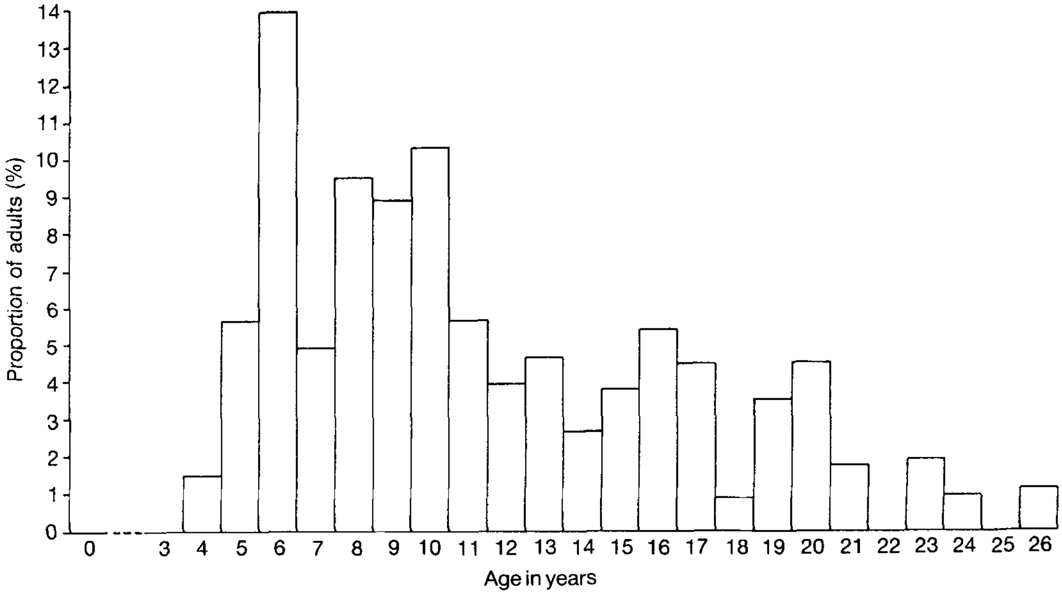

FIG. 4. Percentage of birds of different ages in a sample of 91 great skuas breeding on Foula in 1988 or 1989. All these birds had been ringed as chicks. Percentages are corrected for differences in annual ringing effort and population size.

was obtained from changes in the ages of breeding birds and in the proportion of adults breeding in consecutive years. Figure 4 shows the age structure of the breeding population between 1988 and 1989, as determined from the ages of nest-trapped adults which had been ringed as chicks. The number of adults of each age has been corrected for absolute and relative ringing effort, by dividing by the proportion of chicks ringed each year, and this corrected number has been converted to a percentage of the total over all ages. In 1988–89, 35% of the breeding population were apparently aged eight or less (Fig. 4).

Of 120 adults colour-ringed in 1988, 99 were seen on Foula in 1989 and 87 were seen to breed (i.e. incubated or defended eggs). No adults moved their nests by more than 80 metres between years, and no marked birds which did not breed were seen on the island after mid-June.

Discussion

Diet and reproductive effort

Changes in the mean territorial attendance values of great skuas since 1976 (Table III) indicate that between this year and 1987 they greatly increased the time, and presumably the effort, they spent foraging for food. Before 1988 breeding birds were continuing to provide easily-digestible food of high calorific value (sandeels) for their chicks in years when non-breeders had switched to alternative food sources (Tables I and II). Furthermore, at least in 1989, adults were feeding themselves differently to chicks but in a similar way to non-breeders (Tables I and II). These data suggest that much of this extra effort was being allocated to reproduction, and not simply to maintaining adult body condition. The importance of maintaining a high proportion of sandeel in the diets of chicks is demonstrated by the positive correlation between dietary representation and chick growth (Fig. 2), while the positive correlation between sandeel recruitment and dietary representation (Fig. 1) indicates that these changes are directly related to changes in sandeel abundance. A similar link between breeding success and sandeel abundance in Shetland has been demonstrated for Arctic terns *Sterna paradisaea* by Monaghan, Uttley & Okill (1989) and by Monaghan, Uttley, Burns, Thaine & Blackwood (1989).

Between 1987 and 1988 there was a marked change in chick diets, but this was not accompanied by any further increase in adult foraging effort. Caldow (1988) calculated from time budget data and allometric energetics equations that in 1987 the daily energy expenditure of breeding great skuas on Foula averaged five times basal metabolic rate. The equivalent figure for 1974–76 was about 3·5 BMR. Five times BMR is slightly higher than the putative ceiling (about 4 BMR) suggested by Drent & Daan (1980). Recent labelled water studies with gannets *Sula bassana* have indicated that daily energy expenditure may equal six times BMR during chick rearing in Newfoundland (Birt-Friesen, Montevecchi, Cairns & Macko, 1989) but this figure is much higher than found in most seabird studies to date (Birt-Friesen *et al.*, 1989). The fact that great skuas had reached 5 BMR in 1987 suggests that in 1988 breeding adults may not have been able to increase their foraging effort further because they were not physically able to do so. Direct measurements of metabolism under the present conditions of food shortage would be interesting in this regard.

This high energy expenditure would not necessarily represent abnormally high parental investment if it simply reflected the fact that adults were devoting their time to energetically expensive foraging rather than energetically inexpensive activities such as chick-guarding (Bryant, Hails & Tatner, 1984; Finch, 1984). However, since the main cost to adults of an increase in their foraging effort is probably a reduction in the time available to care for themselves, so that they have to use their endogenous reserves (Martin, 1987), then an increase in the time spent foraging to feed young probably does represent an increase in parental investment.

The reason why great skuas chose to spend so much time and effort foraging in 1987, 1988 and 1989 probably lies in the inverse relationship between chick growth and post-fledging mortality up to the age of two (Fig. 3 and see **Results**). This will greatly lower the value to adults of chicks which grow poorly, even if they do fledge, and so will place a strong pressure upon adults to feed their chicks as well as possible. This agrees with the suggestion by Martin (1987) that the consequences of compromises made by adults during previous stages of the breeding season may be clearly expressed by their young after fledging.

The importance of maintaining chick growth rates is indicated by the fact that between 1987 and 1989 adults were prepared to leave their chicks unguarded while both parents foraged (Table III), even though this resulted in many chicks being killed and eaten by adults from neighbouring territories. There is a trade-off between increased foraging effort and an increased probability of chick predation, as suggested by Martin (1987). This may further explain the lack of an increase in foraging effort between 1987 and 1988. The large difference in predation upon chicks between these two years presumably reflects an increase in the willingness of adults to risk attack from neighbouring adults returning from foraging trips.

Long-term costs of reproduction

The high parental investment by adults between 1987 and 1989, in terms of both high energy expenditure and likely increased exposure to risks associated with foraging, is difficult to reconcile with the idea that long-lived iteroparous individuals should adopt reproductive tactics which favour adult survival and maintenance of reproductive potential in preference to the success of any one reproductive attempt. Of course, increased energy expenditure does not necessarily mean an increased cost to adults in terms of survival or resources for future breeding attempts. It is possible that even the high energy expenditure of adults in these years did not exceed their ability to buffer themselves against these costs, and this is supported by the data for weights of adults of both sexes during incubation, which were as high in 1988 and 1989 as in previous years (Table VII). However, mean egg size decreased significantly between 1975 and 1987 (Table IV and see **Results**) and this may indicate that although adults were able to maintain body weight over this period they were not able to maintain protein reserves, which are much more important than fat reserves as determinants of egg size and quality (Houston, Jones & Sibly, 1983). Several studies have demonstrated an affect of adult age upon egg size (Coulson, 1963; Coulson, Potts & Horobin, 1969; Davis, 1975; Coulson & Horobin, 1976; Becker & Erdelen, 1986), but since this is not the case with great skuas (Furness, 1983) then a decrease in egg size is unlikely to result from changes in the age structure of the breeding population. Egg size affects breeding success through its influence upon chick growth and mortality (Parsons, 1970; Nisbet, 1973; Galbraith, 1988), but since the decrease in egg size between 1975 and 1987 was too slight to have any discernible effects upon breeding success it cannot be taken as evidence of a reduction in the reproductive potential of adults at this colony. However, two lines of evidence indicate that some individuals have suffered such a reduction.

In 1988–89 35% of the breeding population were apparently aged eight or less (Fig. 4), whereas in the 1970s the mean age of first breeding at this colony was 7–8 (Furness, 1987). While this is not a direct comparison, it none the less strongly suggests a lowering in the age of first breeding, indicative of an increase in adult mortality or emigration (Porter & Coulson, 1987), since it is highly unlikely that a third of the birds incubating eggs in 1988–89 were breeding for the first time. The data may be biased by differences in the numbers of chicks fledged each year, but a decrease in annual breeding success would result in greater representation of older birds, not younger ones. The fact that this lowering in the age of first breeding is associated with a decrease in the ease of finding food suggests that young great skuas on Foula were previously constrained by social pressures or lack of space (Monaghan, 1980; Furness & Monaghan, 1987) rather than the need to develop foraging skills (Burger, 1980; Greig, Coulson & Monaghan, 1983).

Ten percent of adults colour-ringed in 1988 were present on Foula in 1989 but did not breed, while a further 18% were not seen at all in 1989. It is very unlikely that any of the birds absent in 1989 were breeding elsewhere, since great skuas are highly site-faithful (Furness, 1987 and see **Results**) and no marked birds were reported from any other great skua colonies in 1989. These data strongly suggest that adult egress (absence from the colony, though not necessarily due to mortality) has increased since the 1970s, and that at least some of this increase is the result of birds failing to breed in some years. It is likely that the birds which breed in a particular season are those which were able to recover sufficiently from the efforts of the previous season, whereas those birds unable to recover are not represented in the breeding population. The decrease in egg size since the 1970s suggests that, even among breeding birds, this recovery may not be complete.

The increase in adult egress may be related to winter conditions rather than food supply during the breeding season. However, there is no evidence to suggest that this is so, and it seems unlikely given that the winter dispersal of great skuas extends from Greenland to Brazil (Furness, 1978). The increase in egress since 1980, the absence in 1989 of 28% of marked adults breeding in 1988 and the decrease in egg size since 1975, in conjunction with the high reproductive effort of adults between 1987 and 1989, strongly suggest that adults at this colony are now suffering greater long-term costs of reproduction. The described changes in diet and their relationship to changes in sandeel recruitment indicate that this has occurred as a result of a decline in food availability during the breeding season.

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