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The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*

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Territorial attendance, chick growth rate and breeding success of Arctic Skuas *Stercorarius parasiticus* in Shetland were lowest in the late 1980s when recruitment of Sandeels *Ammodytes marinus* in the surrounding waters was poor. The relationships between both fisheries-based and avian indices of food availability and annual variation in Arctic Skua chick growth and breeding success between 1976 and 1994 were better described by a threshold effect rather than linear functions. Arctic Skuas conform to the model proposed by Cairns, which predicts the responses of seabirds to changes in prey availability. Skua clutch size, egg volume, hatching success and hatching date were not reliable indices of Sandeel availability. However, annual fluctuations in Arctic Skua breeding numbers may be a useful indicator of changes in prey abundance.

Seabirds exhibit deferred maturity, high adult survival and low reproductive rates and consequently have moderately stable population sizes (Furness & Monaghan 1987). Large-scale mortality of adult seabirds is rare (Cairns 1987) and generally is associated only with dramatic reductions in food availability such as the periodic El Niño Southern Oscillation events (Schreiber & Schreiber 1984). Life-history theory predicts that individuals will try to trade off current against future reproductive potential in order to maximize their contribution to succeeding generations (Stearns 1992). One important factor influencing this trade-off is food supply. Adults should increase their present breeding effort in response to a reduction in prey availability only if it does not jeopardize their residual reproductive value by decreasing their probability of survival or of breeding successfully in later years (Drent & Daan 1980, Reznick 1985).

Increases in breeding effort, for example in the time devoted to foraging, can act to buffer seabirds from environmental perturbation. Such behavioural plasticity may mask the effects of food shortage on chick growth or breeding success (Birkhead & Nettleship 1987, Burger & Piatt 1990, Uttley *et al.* 1994). Cairns (1987) predicted that a reduction in prey availability at a seabird colony would, depending on its severity, sequentially affect several distinct parameters of breeding performance, the most sensitive of which would be behavioural. With a slight limitation of food supply, changes in colony attendance patterns (i.e. total numbers of non-breeding and off-duty birds present) and adult activity budgets would be apparent. Under more restricting conditions, chick growth rates would be reduced and breeding success would be affected. However, only when food is extremely scarce would any increase in breeder mortality be anticipated. Each of these variables should show a nonlinear relationship with the level of food abundance, responsive only within a specific range of prey availabilities and tending to vary gradually, or not at all, when conditions are good (Cairns 1987, 1992). Many studies that document annual variation in one or more aspects of seabird breeding performance in relation to fish abundance do so for a very limited number of years. To date, none at a single colony has tested rigorously over a broad spectrum of food availabilities whether these proposed nonlinear relationships exist.

Arctic Skuas *Stercorarius parasiticus* breeding in Shetland feed predominantly by kleptoparasitism of Sandeels *Ammodytes marinus* taken from Arctic Terns *Sterna paradisaea*, Puffins *Fratercula arctica*, Guillemots *Uria aalge*, Razorbills *Alca torda* and Kittiwakes *Rissa tridactyla* (Furness 1987). During the 1980s there was a considerable reduction in Sandeel recruitment in Shetland waters (Bailey *et al.* 1991), and this was implicated in the widespread breeding failure of a number of these seabird species (Martin 1989, Monaghan *et al.* 1989, Harris & Wanless 1990, Bailey *et al.* 1991). Most attempts to relate such changes in seabird ecology to prey abundance have been hindered by the lack of fish stock assessment data at a local scale. In the case of the Arctic Skua, there is the potential, in addition to fisheries data, to quantify annual variation in the availability of fish-carrying hosts and to use this information to create separate and independent indices of food availability.

This paper examines the relationships between food supply and the foraging effort, breeding success and size of a population of Arctic Skuas at a colony in Shetland using a long-term data series collected from 1974 to 1994. The validity of the hierarchical set of responses to reduced food supply proposed by Cairns (1987) is assessed. In addition,

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we test the potential to use annual fluctuations in the size of a breeding population as an indicator of changes in food availability.

METHODS

The study was carried out on Foula, Shetland (60°08'N, 2°05'W). Breeding data were recorded between 1974 and 1994 and related to independent indices of food availability based on avian or fisheries data, primarily (1) the number of chicks fledged by one of the Arctic Skua's principal kleptoparasitic hosts, the Arctic Tern, and (2) the estimated number of recruiting (0-group) plus 1-year-old (1-group) Sandeels in Shetland waters on 1 July in each year (data until 1983 from Bailey *et al.* [1991] and from 1984 to 1994 from Anonymous [1994]). This latter index was chosen although Arctic Terns provisioned their chicks on 0-group Sandeels. During the late 1980s, however, virtually all skua chases were of Puffins and Guillemots, both of which were feeding predominantly on larger, mostly 1-group fish (Furness 1990, Phillips *et al.* 1995). The total number of pairs of Arctic Terns breeding on Foula in each year was also recorded by direct counts of incubating birds in June. The number of Arctic Tern chicks fledged (estimated by counts at the colony in mid- to late July) was preferred as the index of host availability for most analyses because, in the absence of more precise data (e.g. on tern hatching success), it was thought to most accurately reflect the numbers of adult Arctic Terns likely to be provisioning chicks during the period when the Arctic Skua chicks were being reared.

The Arctic Skua colony was counted by R.W.F. in most years by recording apparently occupied territories and in 1979, 1992, 1993 and 1994 by marking nests. The former method may slightly underestimate numbers (Furness 1982). Data for the years 1974–1982 were taken from Furness (1983). Additional counts were made in 1985 and 1989–1991 by S. Gear (unpubl. reports to Nature Conservancy Council/Scottish Natural Heritage) and in 1986 by a team of observers (Ewins *et al.* 1988). For these years and also for 1974 and 1975, the numbers were taken as the mean of two independent counts. The size of the Arctic Skua colony in each year was compared with each of the independent indices of food availability.

The changes in Arctic Skua numbers in successive years were examined in terms of annual net recruitment to the breeding population. Annual net recruitment was calculated, following the approach of Ollason and Dunnet (1983), as the difference between the observed numbers in a given year and the expected number of breeders surviving from the previous year corrected for an estimate of the annual mortality rate. Colour-ringing of Arctic skuas from 1992 to 1994 indicated a mean annual return rate of 86.4%, with no bird absent in 1993 returning in 1994. There are no mortality rate estimates available for Arctic Skuas on Foula prior to the 1990s, and so a mortality rate of 13.6% (derived from the colour-ringing data) was used in the model (Phillips *et al.* 1995). Net recruitment is a complex parameter involving not only the recruitment of new breeders to the breeding population but also intermittent breeding and potential emigration (although this is not recorded in skuas; Furness 1987) of established adults (Ollason & Dunnet 1983). A negative value for net recruitment can therefore be interpreted as a consequence of higher mortality rate or of established birds being absent from the colony or potential first-time breeders refraining from recruiting in a given year. The net recruitment index, expressed as a proportion of the population in each year, was compared with the indices of food availability.

Arctic Skuas regurgitate freshly obtained fish to their mate and chicks after returning from almost all absences from the territory (Furness 1987). Time spent away can therefore be used as an index of foraging effort (Cairns 1987, Monaghan *et al.* 1989, Hamer *et al.* 1991). Comparison among years was made by recording the number of adults present at each visit to marked territories (Hamer *et al.* 1991). The frequency of observer visits was never more than twice daily in 1987 or once daily in other years. Neighbouring adults did not cause confusion in determining attendance as they were chased out by the territory owners. Spot attendances were converted to a mean for each individual territory at four different stages of the season: incubation and 0–9 days, 10–19 days and 20–30 days after the first chick in each brood had hatched. The mean of these values was then determined for different clutch and brood sizes in each year. In 1979, territories were not visited after the chicks were 20 days old and therefore comparison between 1979 and the other years was limited to the first three of these stages.

In 6 years, eggs were measured (length and breadth to the nearest 0.1 mm using callipers) and volumes calculated as $0.00048 \times \text{length} \times \text{breadth}^2$ (Coulson 1963). Clutch size (either one or two eggs) was recorded. Hatching success and date were monitored in 5 years by visiting marked nests at intervals from the onset of incubation until the chicks hatched. Chick survival to 1 week of age was estimated from visits to territories between 6 and 8 days post-hatching. If any hatched chick was not recorded at that time, the territory was checked at least twice subsequently. Counts were made of the number of chicks seen fledged at all territories on the island in 1986 and from 1988 to 1994, and from a sample of 28 nests in the north of Foula in 1987. Although unfledged Arctic Skua chicks are difficult to locate, once they can fly chicks are conspicuously present either on or near their natal territories for at least a week post-fledging. These counts were completed before the end of July, by which time virtually all pairs had fledged their chicks.

For all years between 1976 and 1994, except 1990, the wing-lengths (maximum flattened chord excluding down) and weights of chicks were measured during chick ringing. In years when chicks were measured only once, this occurred when most chicks were approximately halfway through the fledging period. Logistic growth curves were fitted to changes in wing-length and weight with age using

Table 1. *Variation in the indices of food availability for Arctic Skuas on Foula*

	Sandeel data[a]		Arctic Tern data	
Year	0-group numbers[b]	1-group numbers[b]	Breeding population size (pairs)	Number of chicks fledged
1976	41,765	3459	5650	4000
1979	30,605	3528	4400	3000
1986	16,600	1235	200	0
1987	1288	2013	300	0
1988	1422	157	250	0
1989	3740	204	300	0
1990	1577	554	115	0
1991	54,000	261	1010	300
1992	4691	8926	1500	600
1993	18,079	775	1500	1100
1994	no data	no data	1000	250

[a] Data provided by the International Council for the Exploration of the Sea.

[b] Total numbers of Sandeels (in millions) in Shetland waters on 1 July each year.

all chick measurements from 1992. In each year, all chick ages were predicted from their wing-length (Hamer *et al.* 1991) and their hatching dates were estimated by subtracting the predicted age of each chick from the date of measurement. Possible differences among years in wing growth were investigated using measurements from chicks of known hatching date in 1976, 1979, 1980, 1992, 1993 and 1994. This made it possible to assess error in the use of wing-length to estimate age and hatching date. The deviation for each chick from its expected weight predicted from the 1992 curve was calculated, and individual chick growth indices were expressed as a proportion of the expected value. The annual means of these values were standardized relative to a value of one in the baseline year, 1992. Annual differences in chick growth and hatching date were compared with the avian and fisheries-based food indices.

All data were tested for normality using Kolmogorov-Smirnov one-sample tests and for homoscedasticity using Bartlett's test. Most analyses, including the fitting of logistic curves, were carried out using the statistical package SPSS/PC+. Nonparametric ranges tests were performed according to Zar (1984). Unless stated otherwise, means are given ± 1 s.e., with sample sizes given in parentheses.

RESULTS

Data for avian and fisheries-based indices of food availability in selected years are given in Table 1.

Number of occupied territories

The number of occupied Arctic Skua territories on Foula was at a peak in the late 1970s, then fell sharply by 6.6% per year for 6 years and continued to decline until 1990 (Fig. 1). There was a slight recovery in 1992, after which numbers again declined. The numbers of territories correlated with total Arctic Tern numbers ($r_{17} = 0.81$, $P < 0.001$), the number of tern chicks fledged ($r_{17} = 0.68$, $P < 0.002$), and the number of 0-group plus 1-group Sandeels in Shetland waters on 1 July in each year ($r_{16} = 0.62$, $P < 0.01$). Changes in the net recruitment index also correlated with total Arctic Tern numbers ($r_{18} = 0.55$, $P < 0.02$) and the number of tern chicks fledged ($r_{18} = 0.54$, $P < 0.02$) but not with Sandeel numbers ($r_{17} = 0.10$, n.s.).

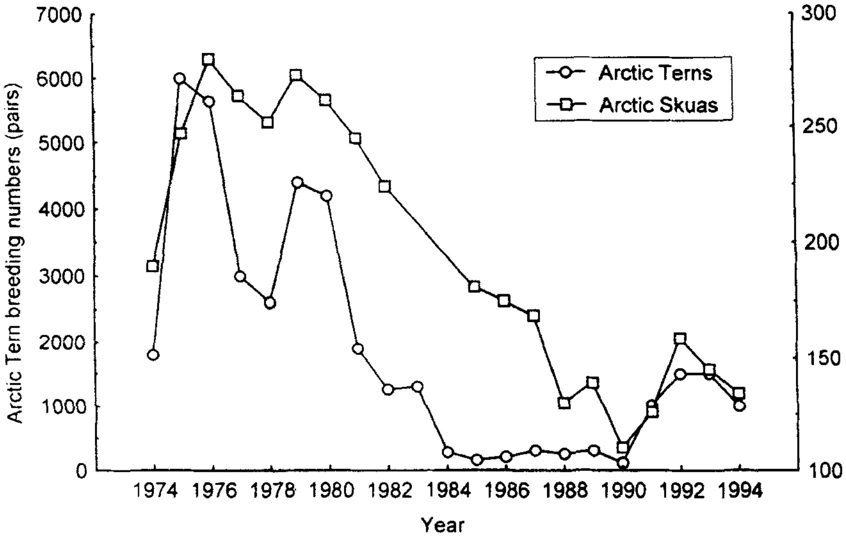

Figure 1. Arctic Skua and Arctic Tern numbers on Foula, 1974–1994.

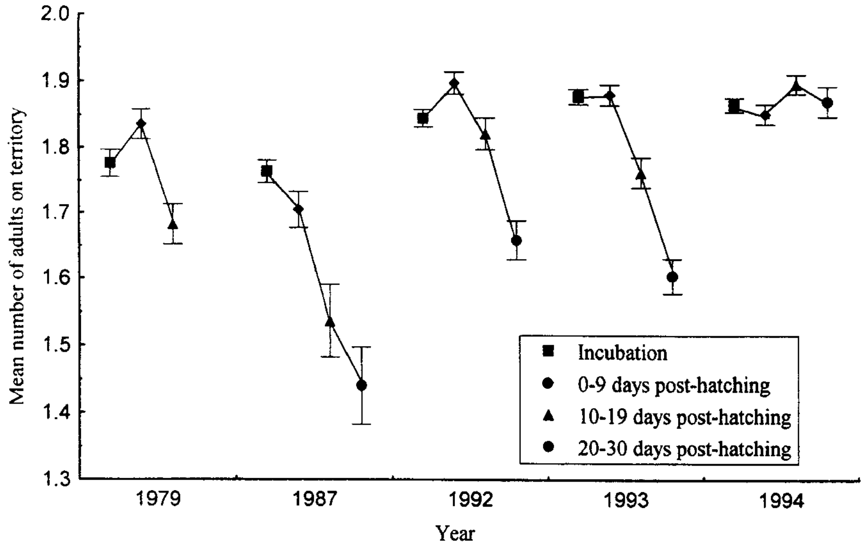

Figure 2. Territorial attendance of Arctic Skuas on Foula in 1979, 1987, 1992, 1993 and 1994. Error bars are ±1 s.e.

Adult attendance

Variation in foraging effort of adults with different brood sizes might confound the detection of annual trends in attendance patterns. There was a single significant effect of brood size on attendance, in 1979 during days 10–19 of chick-rearing, where the attendance of pairs with a single chick was higher (Mann-Whitney *U*, $z = -2.4$, $n = 80$, $P < 0.02$). However, there was no difference among years in the relative number of pairs with broods of one rather than two chicks at this stage ($\chi^2_4 = 2.4$, n.s.), and so the data on attendance in each year were pooled with respect to brood size.

There were significant differences in the mean number of adults present on marked territories between 1979, 1987, 1992, 1993 and 1994 at all stages in the season (Fig. 2): incubation (Kruskal-Wallis ANOVA, $\chi^2_4 = 17.4$, $n = 588$ territories, $P < 0.002$), 0–9 days chick-rearing (Kruskal-Wallis ANOVA, $\chi^2_4 = 38.4$, $n = 453$ territories, $P < 0.0001$), 10–19 days chick-rearing (Kruskal-Wallis ANOVA, $\chi^2_4 = 35.7$, $n = 387$ territories, $P < 0.0001$) and 20–30 days chick-rearing (Kruskal-Wallis ANOVA, $\chi^2_3 = 44.4$, $n = 285$ territories, $P < 0.0001$). Nonparametric ranges tests indicated that during incubation, 0–9 days and 10–19 days post-hatching, attendance was significantly lower in 1987 than in all other years. Attendance during the middle stage (10–19 days) of chick-rearing was also significantly higher in 1994 than in 1979, 1987 or 1993 but not 1992. During 20–30 days post-hatching, attendance in 1987 was lower than in 1992 or 1994 but not significantly different from 1993, and during this stage attendance was also significantly higher in 1994 than in the other years.

Breeding data

The data on egg measurements indicated a very slight but significant increase in egg breadth (ANOVA, $F_{5,1196} = 4.7$, $P < 0.001$) and volume (ANOVA, $F_{5,1196} = 3.2$, $P < 0.01$) but not length (ANOVA, $F_{5,1196} = 0.7$, n.s.) since the 1970s (Table 2). A ranges test (Newman-Keuls) showed a significant difference in volume, with eggs approximately 2% larger in 1992 and 1994 than in 1979.

There was a significant difference among years in the mean clutch size ($\chi^2_4 = 12.3$, $P < 0.02$; Table 2), with fewer eggs per nest in 1979. However, there was no difference in hatching success ($\chi^2_4 = 8.4$, n.s.) nor was there a significant difference in chick survival to 1 week post-hatching ($\chi^2_3 = 6.0$, n.s.), but the comparison could be made only between 1979, 1992, 1993 and 1994.

Productivity varied greatly between 1986 and 1994 (Table 2). Fewer chicks survived to fledging in the late 1980s than in 1986 and far fewer than in the 1991–1994 seasons. Logistic curves were fitted to the relationships between the number of Arctic Skua chicks fledged per pair and the number of Arctic Tern chicks fledged ($F_{2,6} = 15.1$, $P < 0.005$, $r^2 = 0.83$; Fig. 3) and between Arctic Skua chicks fledged per pair and the estimated number of 0-group plus 1-group Sandeels in each year ($F_{2,5} = 29.4$, $P < 0.002$, $r^2 = 0.92$; Fig. 4). In the former case, the logistic curve was a significantly better fit ($F_{1,6} = 9.8$, $P < 0.05$) than was a linear equation (Zar 1984). There was no significant linear relationship between Arctic Skua productivity and Sandeel numbers.

Comparing chicks of known age in 1976, 1979, 1980, 1992, 1993 and 1994 (Table 3) indicated that Arctic Skua chicks measured in 1979 had wing-lengths significantly shorter (by 3–4 mm on average) than those of similar-aged chicks in the other years (Kruskal-Wallis ANOVA, $\chi^2_5 = 28.2$, $n = 650$ chicks, $P < 0.001$). However, only in 1979 was there a significant difference between the predicted and the observed hatching dates (paired *t*-test, $t_{104} = 5.4$, $P < 0.001$; Table 3). The deviation in 1979 is slight and less than half a day.

Table 2. *Breeding statistics for Arctic Skuas on Foula, 1976–1994 (sample sizes in parentheses)*

Year	Mean clutch size	Mean egg length (mm)	Mean egg breadth (mm)	Mean egg volume (cm^3)	Hatching success (%)	Chick survival to 1 week (%)	Chicks fledged per pair
1976	—	58.8 ± 0.35 (54)	40.5 ± 0.13 (54)	46.3 ± 0.43 (54)	—	—	—
1979	1.81 (186)	58.3 ± 0.12 (323)	40.5 ± 0.06 (323)	45.9 ± 0.18 (323)	71.4 (322)	93.0 (230)	—
1986	—	—	—	—	—	—	0.63
1987	1.93 (28)	58.7 ± 0.28 (52)	40.7 ± 0.15 (52)	46.7 ± 0.44 (52)	74.1 (54)	—	0.21
1988	—	—	—	—	—	—	0.15
1989	—	—	—	—	—	—	0.13
1990	—	—	—	—	—	—	0.09
1991	—	—	—	—	—	—	0.87
1992	1.86 (151)	58.4 ± 0.16 (267)	40.9 ± 0.07 (267)	46.9 ± 0.21 (267)	81.2 (277)	88.4 (225)	0.91
1993	1.91 (140)	58.4 ± 0.14 (260)	40.8 ± 0.08 (260)	46.6 ± 0.21 (260)	76.3 (266)	92.1 (203)	0.97
1994	1.93 (130)	58.3 ± 0.15 (246)	40.9 ± 0.08 (246)	46.8 ± 0.22 (246)	77.7 (251)	87.0 (192)	0.90

Comparing the mean estimated chick hatching date in each year indicated there were annual differences (Kruskal-Wallis ANOVA, $\chi^2_5 = 362$, $n = 1942$ chicks, $P < 0.001$; Table 4). In general, hatching tended to be later in the late 1970s and 1991. Hatching dates in 1988 and 1994 were significantly earlier (see Table 4). The mean in each year was positively correlated with both the number of pairs of breeding Arctic Terns ($r_{16} = 0.56$, $P < 0.02$) and the number of tern chicks fledged ($r_{16} = 0.48$, $P < 0.05$) but not with the index of Sandeel abundance ($r_{15} = 0.19$, n.s.). The mean hatching date also correlated with the net recruitment index ($r_{16} = 0.66$, $P < 0.005$).

Differences in chick growth showed significant linear correlations with 0-group plus 1-group Sandeel numbers in each year (in regression analysis, $F_{1,15} = 5.6$, $P < 0.05$, $r^2 = 0.27$; Fig. 5) but not with the number of Arctic Tern chicks fledged (in regression analysis, $F_{1,16} = 0.8$, n.s., $r^2 = 0.05$). Logistic curves were fitted to chick growth *v* Sandeel numbers ($F_{2,14} = 4.5$, $P < 0.05$, $r^2 = 0.39$) and chick growth *v* the number of tern chicks fledged ($F_{2,15} = 4.6$, $P < 0.05$, $r^2 = 0.38$; Fig. 6). In the former case, the logistic curve was not a significantly better fit than the linear equation ($F_{1,14} = 2.6$, n.s.).

DISCUSSION

Fluctuations in the size of the breeding population

As prey abundance declines, adults would be expected to abandon a breeding attempt once they reach the maximum extent of their buffering capabilities and before their survival is likely to be affected (Drent & Daan 1980). If this is the case, population size, of which adult mortality rate is a crucial determinant (Croxall & Rothery 1991), might be considered insensitive to annual changes in food availability. However, established birds may refrain from breeding in some years (Coulson 1984, Boekelheide & Ainley 1989, Murphy *et al.* 1991). Similarly, potential new recruits may choose not to establish territories if conditions are unfavourable (Boekelheide & Ainley 1989, Coulson 1991). If food availability influences either of these factors, fluctuations in the size of the breeding population might have some value as an indicator of environmental conditions.

Most authors consider population size to be an inappropriate indicator of environmental change because the time scale involved is usually long term (Morrison 1986, Temple & Wiens 1989, Furness & Greenwood 1993). However, both the number of Arctic Skuas breeding and net recruitment to the breeding group on Foula over the last 20 years showed a close correspondence with each index of food availability. Annual variation in net recruitment, and consequently in numbers breeding, may produce a sensitive response in Arctic Skuas and possibly in other seabird species.

Cairns's (1987) model and Arctic Skua breeding on Foula

Because of the uncertainties involved in measuring marine productivity directly, a number of parameters of seabird reproductive performance have been advocated as useful monitors of changes in fish abundance (Cairns 1987, 1992, Montevecchi 1993). One complicating factor in the utilization of seabird breeding variables for the monitoring of a

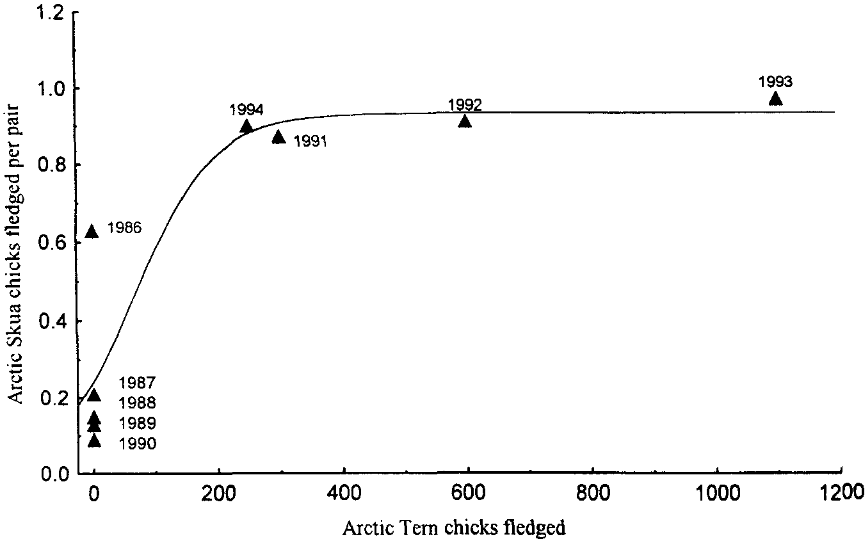

Figure 3. Logistic curve fitted to changes in Arctic Skua breeding success in relation to the number of Arctic Tern chicks fledged on Foula, 1986–1994.

particular fish stock is the ability of polyphagous species to switch to alternative prey items (Cairns 1987, 1992, Martin 1989, Hamer *et al.* 1991, Montevecchi 1993). An analagous situation existed for the Arctic Skua during the course of this study. Although the food (Sandeels) remained the same, the species of kleptoparasitic host changed (Phillips *et al.* 1995). Arctic Terns tended to be the principal host in the mid- to late-1970s, Puffins predominated during the mid- to late-1980s, Guillemots were the most important in 1989 and only from 1991 onwards did Arctic Terns reappear as a major host species. This variation in host selection might go some way in uncoupling Arctic Skua breeding from Arctic Tern reproductive success. However, the assessment of fish numbers is fraught with technical difficulties (Bailey *et al.* 1991). Often the temporal and spatial overlap between the areas monitored by fisheries scientists and those adjacent to seabird colonies is relatively broadscale (e.g. Martin 1989, Aebischer *et al.* 1990, Bailey *et al.* 1991, this study). Rarely, as in this study, is there the opportunity to use independent measures of food abundance.

Cairns (1987) considered that the sensitivity of seabird reproductive parameters to fluctuations in food availability would vary, so that their relationship with food abundance would be a threshold rather than a linear function. Breeding success was likely to improve rapidly as food supply rose from poor to moderate and change only slowly when conditions were favourable. Chick growth rate should follow a similar pattern but remain constant as soon as prey became relatively abundant. Activity budgets would trend in the opposite direction, with time spent foraging exhibiting relative constancy in poor to moderate conditions as adults worked near maximally but showing more sensitivity to relatively minor fluctuations when food supply was good. The concurrent reductions in Sandeel recruitment in Shetland wa-

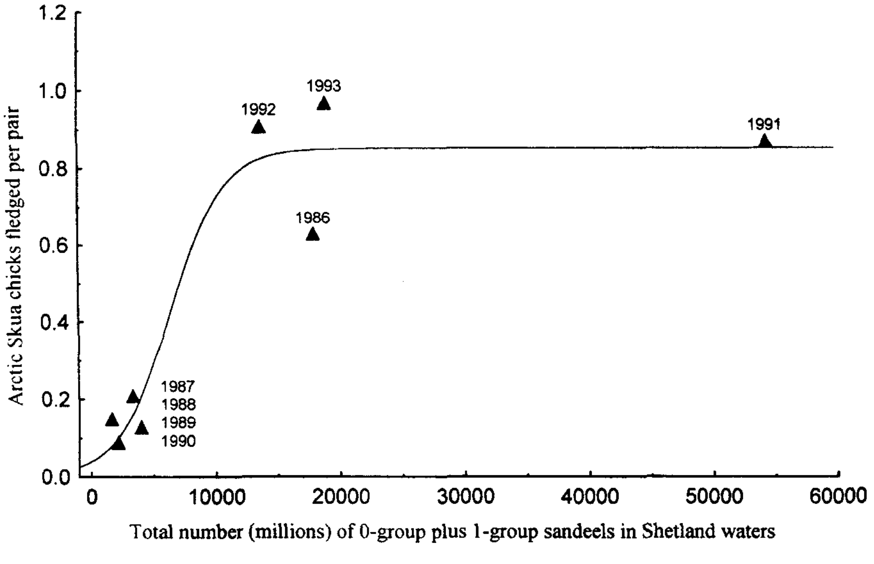

Figure 4. Logistic curve fitted to changes in Arctic Skua breeding success in relation to the numbers of 0-group and 1-group Sandeels in Shetland waters on 1 July, 1986–1994.

Table 3. *Comparison between actual and predicted hatching dates and actual and predicted wing-lengths of Arctic Skua chicks on Foula*

Year	Number of hicks	Mean hatching date[a]		Wing-length residual[c] (mm)
		Actual	Predicted[b]	
1976	9	59.2 ± 2.1	59.2 ± 2.3	−2.2 ± 4.1
1979	105	55.2 ± 0.5	55.5 ± 0.5	−3.4 ± 0.6
1980	10	56.0 ± 1.5	56.5 ± 1.9	−3.2 ± 4.2
1992	179	51.3 ± 0.4	51.2 ± 0.5	0.1 ± 0.5
1993	181	51.9 ± 0.6	51.8 ± 0.6	−0.0 ± 0.9
1994	166	48.1 ± 0.4	48.0 ± 0.4	0.3 ± 0.8

[a] Days from 1 May.

[b] Obtained for each chick by subtracting its estimated age (calculated from chick wing-length using the 1992 curve of wing-length *v* age) from the date of measurement.

[c] Calculated by subtracting the predicted wing-length of chicks (predicted from their age using the 1992 curve) from the measured value.

Table 4. *Mean estimated hatching dates (days from 1 May) for all Arctic Skua chicks measured on Foula, 1976–1994, using the 1992 curve of wing-length v age to estimate chick age*

Year	Hatching date	Number of chicks
1976	53.5 ± 0.55	134
1977	52.5 ± 0.61	82
1978	53.0 ± 0.41	142
1979	56.1 ± 0.33	227
1980	50.9 ± 0.40	120
1981	50.5 ± 0.45	99
1982	50.6 ± 0.39	102
1983	50.0 ± 0.51	73
1984	49.4 ± 0.65	40
1985	50.5 ± 0.75	48
1986	51.8 ± 0.77	57
1987	51.0 ± 0.83	61
1988	47.3 ± 0.66	96
1989	49.9 ± 0.59	55
1990	—	—
1991	55.7 ± 0.67	46
1992	51.4 ± 0.44	202
1993	51.7 ± 0.62	192
1994	48.0 ± 0.44	166

Note: Nonparametric ranges tests (the data were heteroscedastic) indicated that mean hatching dates in (1) 1988 and 1994 were significantly earlier than 1976–1982, 1986 and 1991–1993; (2) 1983–1984, 1989, 1993 were significantly earlier than 1976–1979 and 1991; (3) 1980–1982, 1985–1987 and 1992 were significantly earlier than 1979 and 1991 and (4) 1976–1978 were significantly earlier than 1991.

ters during the 1980s, and consequently in the size and productivity of the Arctic Terns breeding on Foula (Table 1), provided an opportunity to test whether Arctic Skuas responded to this decrease in resource availability by modifying their reproductive strategy in the way Cairns's model suggests.

Recent reviewers have suggested that the seabird reproductive parameters most likely to be sensitive to fluctuations in food availability are behavioural (Cairns 1987, 1992, Montevecchi 1993). Seabirds have considerable scope to adjust activity budgets in order to increase the amount of time they spend foraging (Monaghan *et al.* 1989, Hamer *et al.* 1991, 1993, Uttley *et al.* 1994). In accordance with Cairns's model, when Sandeel recruitment was poor in 1987 (Table

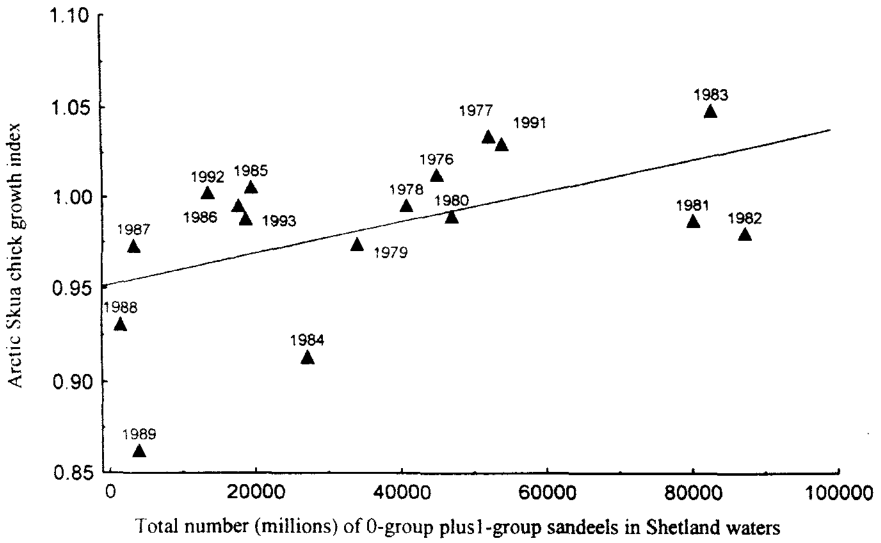

Figure 5. Arctic Skua chick growth index on Foula in relation to the numbers of 0-group and 1-group Sandeels in Shetland waters on 1 July, 1976–1993.

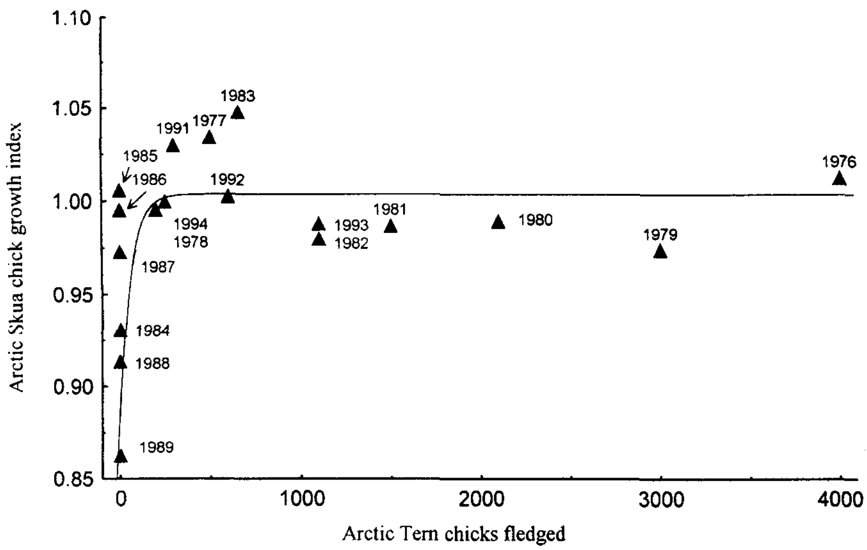

Figure 6. Logistic curve fitted to changes in Arctic Skua chick growth on Foula in relation to the number of Arctic Tern chicks fledged, 1974–1994.

1), breeding Arctic Skuas reduced the amount of time they spent on territory. This higher foraging effort (assuming that individuals prefer to spend discretionary time on territory) was apparent throughout the breeding season, including incubation.

Adult attendance was exceptionally high in 1994. Because activity budgets are likely to show most responsiveness to short-term, intraseasonal fluctuations in food supply, it may be that relatively low foraging effort late in the 1994 season reflected greater Sandeel availability during that particular stage. Unfortunately, there are no fisheries data available for the waters around Foula to test this hypothesis. If Sandeels were more available to Arctic Skuas provisioning older chicks in 1994, the attendance data would corroborate Cairns's suggestion that activity budgets are the most accurate and sensitive indicator of fluctuations in prey abundance when conditions are good.

In 1987, the number of adults present did not drop below a mean of 1.4 per territory, and chicks were virtually never left unattended during daylight even though chick growth was relatively poor. By comparison, Great Skua *Catharacta skua* chicks on Foula were frequently left alone during the late 1980s while both parents foraged simultaneously, and the chicks experienced heavy cannibalism as a consequence (Hamer *et al.* 1991). Possibly Arctic Skua adults make a compromise between time spent off territory collecting food for chicks and that spent on- territory defending them from predation, in this case by Great Skuas, a major source of chick mortality (Furness 1987). While the risk of predation is certainly one factor, an alternative hypothesis for the continued presence of adults on territory in 1987 when chicks were not achieving maximal growth rates is one of energetic constraint. Adults might have reached the limit of their potential buffering abilities, and no further increase in foraging effort may have been physiologically possible without incurring a cost in terms of body condition (Drent & Daan 1980, Monaghan *et al.* 1989, Hamer *et al.* 1993).

Despite the buffer of increased foraging effort apparent in years with low food availability, there were clear relationships between the indices of food availability and Arctic Skua chick growth. Variations in chick growth have been used successfully as indices of marine productivity in a number of other studies (Ricklefs *et al.* 1984, Safina *et al.* 1988, Monaghan *et al.* 1989, Hamer *et al.* 1991) despite at least two possible confounding influences. Unless chicks are starving, chick wing-length growth is usually considered to be relatively independent of fluctuations in food availability (Gaston 1985, Barrett *et al.* 1987), although this is not always the case (Safina *et al.* 1988, Cruz & Cruz 1990). The results presented here indicate a slight retardation of chick wing-length growth in some years. If food availability is poor, using wing-length would then underestimate actual chick age and hence, if chicks are lighter than predicted, also underestimate the discrepancy between a chick's observed weight and the weight it would be expected to have reached by that time (which should in fact be that of an older chick). Since the error in estimating the mean hatching date of chicks in 1979, the year in which wing-length growth was poorest, was less than half a day (Table 3), this is unlikely to be a problem here. However, there is also the factor that lighter chicks in years of poor food availability may experience a lower survival rate, possibly through brood reduction (Williams & Croxall 1991). This has implications for the calculation of annual chick growth indices if differential survival occurs before the chicks are measured. Data on early season chick mortality indicated no difference between 1979, 1992, 1993 and 1994, but in comparison with the late 1980s, Sandeel recruitment in Shetland waters in each of those years was high. The data presented in this paper could therefore include overestimations of the mean chick growth rate in the very poor years if more chicks had starved to death before they could be measured.

Regardless of this possibility, the annual variation in chick growth correlated with the estimated number of 0-group plus 1-group Sandeels in Shetland waters on 1 July each year. There was no significant linear correlation with the number of Arctic Tern chicks fledged; this relationship was described better by a logistic curve. From Figures 10 and 11 it is apparent that in 1985 and 1986, when Arctic Tern productivity was nil, mean chick growth was only marginally poorer than that in the baseline year (1992), presumably because Arctic Skuas were chasing Puffins as an alternative host (Phillips *et al.* 1995). The shape of the curve in Figure 6 implies little improvement in chick growth once food abundance attained a certain threshold level. This is to be expected given that most studies suggest chick growth is constrained by intrinsic factors once food is abundant (e.g. Shea & Ricklefs 1985).

Poor growth of chicks between 1987 and 1990 was associated with depressed breeding success. Relating this to the independent indices of food availability provided evidence for the suggested curvilinear trends (Figs 3 and 4). Breeding success was at the asymptote in 1991–1994. That relatively fewer chicks fledged in 1986, and very few in 1987 (when chicks weighed on average 3% less than predicted), might suggest that minor variation in chick body condition has serious implications. An alternative explanation is that another factor constraining fledging success was also dependent to some extent on food supply. The amount of Sandeel in the diet of breeding Great Skuas fell during the 1980s and was replaced initially by gadid fish discarded by fisheries and then by birdmeat (Hamer *et al.* 1991), and it is possible that the incidence of predation of Arctic Skua chicks and fledglings may have increased during that period. In that case, the situation in 1986–1987 for Arctic Skuas on Foula would be analagous to that described for Arctic and Common Terns *Sterna hirundo* breeding sympatrically on Mousa, Shetland, in 1988 (Uttley *et al.* 1989). In that study, Common Tern breeding success was nil despite "normal" chick growth, apparently because specialist predators of terns were unable to feed on Arctic Tern chicks (this species had already suffered reproductive failure) and so turned to Common Tern chicks as an alternative food source.

The positive correlation between the mean hatching date in Arctic Skuas and the Arctic Tern indices of food availability in each year was unexpected. Other studies show the opposite and more intuitive result that laying (and presumably hatching) is normally delayed when fish stocks decline (Safina *et al.* 1988, Monaghan *et al.* 1989, Aebischer *et al.* 1990). Using hatching date as an alternative indicator of potential changes in the timing of breeding related to food availability might be confounded by differential survival of early or late-hatched chicks in different years. There is little evidence, however, that this differential survival was a major factor here. In 1988 for example (the earliest year recorded; Table 4), the sample size was sufficiently large that it must have included more than the earliest hatched chicks, and in addition, during the 1991–1994 breeding seasons (despite little variation in Arctic Skua productivity; Table 2), there were marked differences in mean hatching date. Annual fluctuations in mean hatching date was likely to have another source. There was a strong relationship between hatching date and the net recruitment index, implying some consequence of changes in the demography of the Arctic Skua population on Foula. In the years when food availability was poor and net recruitment low, few new recruits (and possibly also established breeders that deferred the previous year) were present in the breeding population. The tendency of laying date to advance with age in skuas (Davis 1976, Hamer & Furness 1991) would tend to ensure earlier mean laying and hatching dates. Increases in clutch size and egg volume with age (also recorded for skuas; Hamer & Furness 1991) would also explain the lower values recorded for these two variables in 1979. In 1979, the population was at the peak of a recent expansion and was likely to have contained a greater proportion of new recruits or younger birds than in later years. Whatever the explanation, neither clutch size, hatching date nor clutch volume appear to be reliable indicators of any annual changes in prey availability for Arctic Skuas on Foula.

By contrast, variations in chick growth and breeding success provided considerable empirical evidence for the existence of threshold relationships between breeding variables and food abundance.

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