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The Effects of Fluctuating Food Availability on Breeding Arctic Terns (*Sterna paradisaea*)

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Reproduction is a costly process that involves an investment of effort that can decrease parental condition and survival (Partridge 1989, Stearns 1992). In long-lived iteroparous species such as seabirds, reproductive costs produce a tradeoff in energy allocation between current and future breeding attempts (Clutton-Brock 1984), and the breeding effort should be adjusted to maximize lifetime reproductive success. Food availability can have substantial effects on the relative costs of reproduction and thus may be an important factor in determining reproductive strategies in seabirds (Boekelheide and Ainley 1989, Sydeman et al. 1991, Pons and Migot 1995).

Cairns (1987) hypothesized that during periods of reduced food supply, seabirds should increase foraging effort in order to buffer the effects of food scarcity on breeding performance. Further reductions in food may result in parents being unable to increase foraging effort without incurring excessive costs, resulting in a decline in reproductive success (Monaghan et al. 1989, 1992). Finally, during periods of extreme food shortage, condition and survival of adults may be adversely affected (Hamer et al. 1991). Food supply is expected to affect breeding parameters within a specific range of prey availability, outside of which it will have little effect (Cairns 1987, Phillips et al. 1996).

The abundance of sandeels (*Ammodytes marinus*) was severely reduced in Shetland waters between 1985 and 1990 due to successive years of poor recruitment of the group-0 cohort (i.e. fish spawned in the current year) and a subsequent decline in spawning-stock biomass (Wright and Bailey 1993). Seabirds responded by increasing their foraging effort (Uttley 1992, Hamer et al. 1993, Monaghan et al. 1994) and exploiting alternative prey species (Martin 1989, Hamer et al. 1991). Despite these changes in behavior, the breeding success of surface-feeding species was adversely affected (Monaghan et al. 1989; Hamer et al. 1991, 1993; Phillips et al. 1996).

Arctic Terns (*Sterna paradisaea*) suffered six consecutive years of almost complete breeding failure on Shetland (Walsh et al. 1990) due to adults abandoning clutches and chicks starving shortly after hatching (Monaghan et al. 1989, 1992). The number

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of breeding Arctic Terns at Shetland declined by 55% between 1981 and 1989 due to lack of recruitment and possibly to increased rates of nonbreeding, emigration, and mortality (Avery et al. 1993). Arctic Terns are more vulnerable to reductions in food supply than most other seabirds at Shetland owing to their low degree of behavioral plasticity (Monaghan et al. 1992). This results from small body size (Craik and Becker 1992), specialization toward surface feeding at short ranges from the colony (Pearson 1968), and lack of alternative prey species (Uttley et al. 1989).

In 1991, a dramatic increase in the availability of sandeels at Shetland resulted from large numbers of group-0 fish being swept north from Orkney by currents (Wright and Bailey 1993). Recruitment of these fish into the Shetland stock resulted in an abundance of group-1 fish in 1992 and an increased spawning-stock biomass in subsequent years (Anonymous 1995). This increase in sandeel abundance was associated with improved breeding performance for other species of surface-feeding seabirds, including Black-legged Kittiwakes (*Rissa tridactyla*; Hamer et al. 1993), Parasitic Jaegers (*Stercorarius parasiticus*; Phillips et al. 1996), and Great Skuas (*Catharacta skua*; Ratcliffe 1993). Despite the extreme sensitivity of Arctic Terns to changes in food availability, no published information exists on their breeding performance since the recovery of the sandeel population at Shetland. Here, we examine the responses of Arctic Terns to variations in sandeel abundance at Shetland from 1990 to 1994.

Methods.—The availability of prey to Arctic Terns was inferred from the SOAFD (Scottish Office Agriculture and Fisheries Department) estimates of sandeel abundance in Shetland waters (Anonymous 1995). The data provided a meaningful index of prey availability to terns because the locations of the sandeel fishing grounds and tern colonies were closely juxtaposed (Monaghan 1992), and the sea-surface availability of sandeels is directly related to their abundance (Wright and Bailey 1993). Estimates of sandeel abundance were made from Virtual Population Analysis (VPA) of catch-at-age data from research trawls and commercial catches at fishing grounds around Shetland (Cook and Reeves 1993). Abundance was estimated separately for the first (up to 30 June) and second halves of the year (after 30 June). The biomass of group-0 and group-1 sandeels (in metric tons) in each half of the year was estimated by multiplying the estimated group abundance by the average mass of an individual (Anonymous 1995). VPA suffers from inaccuracies due to the difficulty in sampling cohorts randomly and the assumptions concerning natural mortality rates and terminal mortality (Cook and Reeves 1993). However, it is the best estimate of trends in sandeel abundance available for Shetland waters, and it provides a coarse independent index of tern food supply.

Arctic Terns were monitored annually at 15 to 22 colonies throughout Shetland from 1990 to 1994. Colonies were visited every 7 to 10 days, from mid-May until early August in each year. Randomly sampled nests were selected in each colony and their clutch size was determined. The largest egg in a clutch (hereafter the "A" egg, because the largest egg in a clutch always hatched first) was weighed to the nearest 0.1 g using a Pesola balance, and maximum length (L) and breadth (B) were measured to the nearest 0.1 mm using Vernier calipers. Internal egg volume (V) was estimated from the equation of Davis (1975):

$$V = 0.00048\ LB^2 .\qquad(1)$$

Egg density (D) was estimated by dividing egg mass by egg volume. The laying date of the A egg in each clutch was predicted using the relationship between egg density and days to hatching:

$$\text{days to hatching} = 111.9\ D - 102.2.\qquad(2)$$

The relationship was highly significant ($r^2 = 0.62$, $F = 425.1$, df = 1 and 256, $P < 0.0001$) and predicted the hatching date to within 3 days for 95% of the eggs. The laying date was calculated by subtracting the incubation period of 21 days (Cramp 1985) from the hatching date, and the data were expressed in days after 30 April.

We used analysis of variance (ANOVA) to analyze data on laying dates and egg volume and G-tests to analyze data on clutch size. We used logistic regression to test whether clutch size was independent of laying date, with the proportion of one-egg clutches being the dependent variable. The effects of year, clutch size, and laying date on A-egg volume were tested with analysis of covariance (ANCOVA).

To estimate adult body condition, we captured terns on nests using walk-in traps during the last 10 days of incubation from 1990 to 1993. We measured the maximum flattened wing chord ($\pm$ 1 mm) and body mass ($\pm$ 1 g) for all birds. Chick growth was estimated by measuring wing length ($\pm$ 1 mm) and body mass ($\pm$ 0.1 g) of chicks encountered in the study colonies. The age of chicks with unknown hatching dates was estimated by modeling wing length against age for chicks with known hatching dates. Wing length (WL) increased with age (a) according to a logistic equation ($r^2 = 0.96$) that predicted the age of 95% of chicks to within one day:

$$WL = \frac{177.19}{1 + e^{2.55 - 0.23(a)}}\qquad(3)$$

The mean growth rate of chicks in each year was analyzed during the linear stage of development (4 to 14 days old, Nisbet et al. 1995). Only one measurement from each individual was included in the analysis. The growth rate was analyzed using ANCOVA, with year defined as a categorical variable and chick age as the covariate. Mean growth incre-

TABLE 1. Annual variation in biomass (thousands of metric tons) of group-1 sandeels during the first half of the year and group-0 and group-1 sandeels during the second half of the year. Data are from Anonymous (1995).

Year	Group-1 (1st half)	Group-1 (2nd half)	Group-0 (2nd half)
1987	24.8	14.1	3.0
1988	2.0	1.1	9.3
1990	6.8	1.4	7.5
1991	3.2	1.9	112.9
1992	97.0	58.3	13.4
1993	11.5	6.9	50.1
1994	43.0	25.8	6.2

ments (g per day) were calculated as the slope of the regression between age and mass within each year.

Productivity estimates were based on peak counts of fledged chicks for the whole colony and the number of Arctic Tern pairs at each colony as estimated from flush counts (Walsh et al. 1995). Productivity was expressed as the overall proportion of pairs that fledged chicks; data were analyzed using logistic regression.

Results.—The abundance of group-0 and group-1 sandeels was very low in 1990 (Table 1), as it had been since 1987 (Anonymous 1995). Sandeel recruitment was extremely high in 1991, low in 1992, moderate in 1993, and very poor in 1994. The abundance of group-1 sandeels in the first half of the year was a function of group-0 recruitment in the previous year (Table 1).

Laying date of Arctic Terns on Shetland differed significantly among years (ANOVA, $F = 405.2$, df = 4 and 1,345, $P < 0.0001$; Table 2), being latest in 1990, intermediate in 1991, and uniformly early in subsequent years. Clutch size differed significantly among years ($G^2 = 499.7$, df = 8, $P < 0.001$; Table 2). The percentage of one-egg clutches was very high (52%) in 1990 compared with other years but declined in subsequent years. The average clutch size increased from 1990 until 1993 and declined slightly in 1994.

There was a strong tendency for the proportion of one-egg clutches to increase with later laying dates (logistic regression, $G^2 = 23.5$, df = 1, $P < 0.001$). This could result in annual variations of clutch size being an artifact of differences in laying date in those years. However, the effect of year was still significant independent of laying date, with 1990 having a significantly higher percentage of one-egg clutches than other years (logistic regression, $G^2 = 83.2$, df = 4, $P < 0.001$). This suggests that one-egg clutches were more likely in years of low food availability than would be expected from the laying date of the clutch.

The volume of the A egg varied significantly between years (ANOVA, $F = 42.8$, df = 4 and 1,345, $P < 0.001$; Table 2), being significantly lower in 1990 than in all other years and lower in 1991 than in 1993. The effect of year remained significant independent of laying date (ANCOVA; laying date, $F = 22.6$, df = 1 and 1,345, $P < 0.001$; year, $F = 2.46$, df = 5 and 1,345, $P < 0.05$). There was no effect of clutch size on A-egg volume independent of laying date (ANCOVA; laying date, $F = 35.14$, df = 1 and 1,345, $P < 0.001$; clutch size, $F = 2.83$, df = 2 and 1,345, $P > 0.05$).

Body mass of incubating adults at Shetland from 1990 to 1993 averaged 112.9 ± SE of 0.63 g ($n = 166$). The stage of incubation (number of days until hatching) had no effect on the incubation mass of adults ($F = 0.29$, df = 1 and 166, $P > 0.5$). Because wing length (used as an index of body size) was positively related to mass ($r^2 = 0.02$, $F = 4.13$, df = 1 and 166, $P < 0.05$) we used ANCOVA to examine annual variations in mass independent of body size. Adult masses were 15% lower in 1990 than in other years ($F = 26.9$, df = 3 and 166, $P < 0.0001$; Table 2) but did not vary significantly from 1991 to 1993.

We did not obtain growth data in 1990 because all of the chicks starved before the age of 4 days. Chick growth varied significantly from 1991 to 1994. Year had a significant effect on the slope of the regression lines between age and chick mass (ANCOVA, age × year; $F = 8.50$, df = 4 and 1,088, $P < 0.001$; Table 2).

TABLE 2. Annual variation in breeding parameters of Arctic Terns on Shetland, 1990 to 1994. Values are $\bar{x}$ ± SE (n in parentheses) with the exception of productivity (see footnote).

	1990	1991	1992	1993	1994
Laying date[a]	39.8 ± 0.3 (392)	32.9 ± 0.3 (315)	27.4 ± 0.3 (357)	23.7 ± 0.4 (157)	26.8 ± 0.4 (129)
Clutch size	1.5 ± 0.03 (392)	1.9 ± 0.03 (315)	2.2 ± 0.03 (357)	2.5 ± 0.04 (157)	2.3 ± 0.05 (129)
A-egg volume (ml)	16.2 ± 0.1 (392)	16.9 ± 0.1 (315)	17.1 ± 0.1 (357)	17.3 ± 0.1 (157)	17.2 ± 0.1 (129)
Chick growth (g/day)	No data	7.8 ± 0.1 (380)	7.8 ± 0.1 (330)	6.9 ± 0.2 (313)	7.2 ± 0.3 (73)
Productivity[b]	0.00 (588)	0.70 (594)	0.72 (1,215)	0.38 (1,074)	0.21 (707)
Adult mass (g)	97.8 ± 2.3 (14)	113.9 ± 0.7 (78)	115.9 ± 1.0 (34)	113.7 ± 1.1 (40)	No data

[a] Days after 30 April.
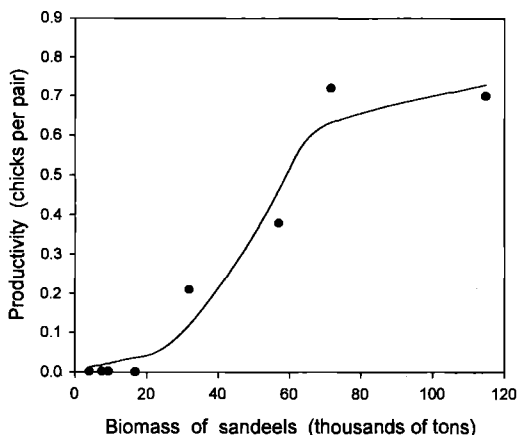[b] Number of chicks raised per pair.

FIG. 1. Relationship between biomass of sandeels and productivity of Arctic Terns. Data on sandeel biomass taken from Anonymous (1995). Data on tern productivity from 1987 to 1989 were from Walsh et al. (1990).

Growth rates in 1991 and 1992 were 0.7 g per day higher than in 1993 and 1994.

Productivity varied significantly among years (logistic regression, $G^2 = 1,186.4$, df $= 4, P < 0.001$). No chicks fledged from any of the study colonies in 1990, but productivity improved dramatically to approximately 0.7 chicks per pair in 1991 and 1992. Productivity decreased significantly to 0.38 per pair in 1993 and further decreased to 0.21 chicks per pair in 1994. There was a significant relationship between tern productivity and the combined biomass of group-0 and group-1 sandeels between 1987 and 1994 (data for 1987 to 1989 from Walsh et al. 1990) that conformed to a logistic curve ($F = 50.9$, df $= 5, P < 0.005$; Fig. 1):

$$P = \frac{0.73}{1 + e^{4.28(0.08M)}},\qquad(4)$$

where P is tern productivity and M is sandeel biomass (thousands of tons). Variation in sandeel biomass explained 96% of the variance in Arctic Tern productivity. Productivity was uniformly low when sandeel biomass was below 25,0000 tons and increased linearly to an asymptote of 0.73 chicks per pair when sandeel abundance exceeded 70,000 tons (Fig. 1).

Discussion.—From 1988 to 1990, the distribution of sandeels around Shetland was patchy and their availability was very low (Wright and Bailey 1993). In 1991, acoustic transects detected an influx of group-1 and older sandeels into Shetland waters that resulted in increased abundance early in that year (Wright and Bailey 1993). These sandeels were not sampled by the VPA surveys and so are not represented in Table 1. The recruitment of group-0 fish was exception-

ally high during the second half of 1991 owing to large numbers of fish being swept into Shetland waters by currents from northeastern Orkney. This resulted in a further increase in abundance and a wider distribution of sandeels (Wright and Bailey 1993). Recruitment was poor in 1992 and 1994 and moderate in 1993 (Anonymous 1995), resulting in group-1 fish being scarce in 1993 and moderately abundant in 1994. These data clearly indicate that the food supply of Arctic Terns fluctuated considerably during our study period.

Studies of larids have shown that food supply is an important determinant of laying date (Safina et al. 1988), clutch size (Sydeman et al. 1991, Pons and Migot 1995), and egg volume (Hiom et al. 1991, Bolton et al. 1992, Oro et al. 1995). Egg production is costly for Arctic Terns, with each egg representing 16% of adult body mass (Cramp 1985). The group-1 fish that normally are fed to female Arctic Terns were very scarce from 1988 to 1990, and a large proportion of the diet in 1988 was made up of post-larval group-0 fish (Monaghan et al. 1992) that have very low calorific value (Hislop et al. 1991). The quality of courtship feeding can affect egg laying (Nisbet 1973, 1977), and the lack of group-1 sandeels from 1988 to 1990 was associated with decreased egg production. The increased availability of group-1 sandeels from 1991 to 1994 coincided with earlier laying dates, larger clutch sizes, and larger A eggs in Arctic Terns.

When food supply fluctuates unpredictably throughout the breeding season, females should lay as many eggs as prelaying nutrient reserves allow and opt for a brood-reduction strategy later in the season should conditions not improve (Bolton et al. 1992). Because Arctic Terns feed mainly on group-1 fish during prelaying, but provision chicks with group-0 fish that appear after the laying period, the availability of sandeels early in the season probably is not a good indicator of their abundance later on (Wright and Bailey 1993). It is probable that clutch size in Arctic Terns is maximized within the limitations of nutrient reserves and that regulation of breeding effort occurs later in the season by brood reduction or clutch desertion (Monaghan et al. 1992). The very low body masses of Arctic Terns during 1987, 1988, and 1990 (Avery et al. 1992; Monaghan et al. 1989, 1992; this study) indicate that somatic reserves may indeed have limited egg production during those years.

Monaghan et al. (1992) proposed a threshold level of adult body mass in Arctic Terns below which terns should abandon breeding attempts in order to conserve residual reproductive value. The fact that Arctic Terns continued to incubate below the "threshold" body mass in 1990 (Avery et al. 1992) suggests that birds incurred serious reproductive costs that year. The decline in the tern population size on Shetland has been greater than would be predicted from low productivity alone (Avery et al. 1993), suggest-

ing that the low masses were associated with increased mortality. Adult body mass increased in 1991 and has remained at a similar level in subsequent years, suggesting that the increased availability of sandeels has allowed Arctic Terns to maintain an improved body condition. The body masses observed between 1991 and 1993 were higher than those reported for West Scotland (Craik and Becker 1992) and Orkney (Sim et al. 1993) and similar to those for the Coquet Island (Monaghan et al. 1989). These masses were well above the threshold levels for clutch desertion proposed by Monaghan et al. (1992), and no clutches were deserted between 1991 and 1994.

Variations in growth rates of chicks have been associated with changes in sandeel availability in many studies of Shetland seabirds (Hamer et al. 1991, Danchin 1992, Uttley et al. 1994, Phillips et al. 1996). Similarly, growth rates of Arctic Tern chicks were associated with the abundance of group-0 and group-1 sandeels. During 1991 and 1992, when sandeel availability was high, growth rates at Shetland were higher than those recorded in 1983 and 1984 (Ewins 1985) and also were higher than those documented for Arctic Terns nesting north of the Arctic Circle (Lemmetyinen 1972, Klaassen et al. 1989). In 1993 and 1994, growth rates at Shetland were lower, coinciding with reductions in sandeel abundance. Monaghan et al. (1992) suggested that group-0 sandeels were used primarily to feed chicks, but during the years of their study all of the tern chicks died before the age of 5 days. Older chicks can ingest larger group-1 sandeels (Ewins 1985) that have a higher total energy content (Hislop et al. 1991). Thus, the availability of both group-0 and group-1 fish can affect chick growth.

Arctic Terns failed to raise any chicks to fledging age in 1990, a result similar to that from 1985 to 1989 (Walsh et al. 1990). Prolonged breeding failures associated with poor food supply also have been documented in Atlantic Puffins (*Fratercula arctica*) on Røst in Norway (Barrett et al. 1987, Anker-Nilssen 1995) and in Black-Legged Kittiwakes in the Bering Sea (Springer et al. 1986). The group-0 fish are especially important for small Arctic Tern chicks (0 to 4 days old) that would have difficulty ingesting larger prey. The low availability of group-0 fish in the late 1980s and 1990 was responsible for mass posthatching starvation of tern chicks at most Shetland colonies (Monaghan et al. 1992).

Predation by gulls (*Larus* spp.) and Great Skuas occurred at many Shetland tern colonies (Ewins 1985, Monaghan et al. 1989, pers. obs.), and this also could be indirectly related to sandeel availability. Decreases in marine food supplies can result in obligate piscivores having to spend more time foraging at the expense of nest defense, whereas polyphagous gulls and skuas could switch from a diet of fish to seabird chicks (Hamer et al. 1991, Spear 1993, Bukacinska et

al. 1996, Phillips et al. 1996). Further research is required to understand how the interaction between sandeel abundance and avian predation affects tern productivity.

Cairns (1987) suggested that relationships between breeding performance and food supply should be nonlinear, being responsive only within a narrow range of prey availability and being relatively constant above and below certain threshold values. The relationship between Arctic Tern productivity and the combined biomass of group-0 and group-1 sandeels conformed to a logistic curve (Fig. 1), which provides some support for Cairns' (1987) model. Similar logistic relationships between productivity and food supply have been demonstrated for Parasitic Jaegers at Shetland (Phillips et al. 1996).

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