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THE RELATIONSHIP BETWEEN FOOD SUPPLY, REPRODUCTIVE EFFORT AND BREEDING SUCCESS IN ARCTIC TERNS *STERNA PARADISAEA*

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SUMMARY

(1) This study compares the foraging performance, adult body condition and breeding success of arctic terns (*Sterna paradisaea* Pontoppidan) in a successful (Coquet Island) and an unsuccessful (Shetland) breeding colony.

(2) During courtship feeding, males in Shetland brought larger fish to their mates than did the birds on Coquet. However, the latter brought more energy-rich fish, made more foraging trips per hour and their rate of energy transfer to their mates was higher.

(3) There was no difference between the two colonies in clutch or egg size, or in hatching success.

(4) During chick-rearing, birds in both areas concentrated on sandeels as prey. In contrast to Coquet, the Shetland birds brought their young a very high proportion of small fish, and lost a high proportion of their large prey to conspecific kleptoparasites; they also foraged at a higher rate and brought less energy per chick per hour.

(5) The chicks in the Shetland colony grew at a slower rate than those on Coquet and the majority died in the first week of life. Breeding success on Coquet was good.

(6) In both areas, adults lost weight during the breeding period. The birds on Shetland were lighter than those on Coquet, but their subsequent rate of weight loss was less. During the chick-rearing period on Coquet, birds fledging two young remained heavier than those where one young died of starvation in the first week after hatching.

(7) The data suggest that the birds in Shetland had difficulty in finding sandeels of the 4–8 cm size-class to feed their young, and that the adults themselves were in poor condition prior to the chicks hatching. Adult arctic terns appear to adjust their breeding effort in response to body condition. These findings are discussed in relation to the life-history strategy of arctic terns and factors influencing their food availability.

INTRODUCTION

In comparison with other types of bird, seabirds are long-lived, lay small clutches and show deferred maturity, delaying breeding until at least the second year of life and often considerably longer (see Furness & Monaghan 1987 for references). The strain of breeding on the adult birds can be considerable, and the time of maximum adult mortality coincides with the end of the breeding season in some species (Coulson *et al.* 1983; Monaghan & Metcalfe 1986). Life-history theory leads us to expect such animals to trade-off current against future reproductive potential such that, when food is in short supply during the breeding season, the adults will abandon a breeding attempt if the perceived risks to their survival are too great (e.g. Drent & Daan 1980; Reznick 1985; Pugesek 1987).

Food availability may also affect whether or not birds attempt to breed at all (Drent & Daan 1980).

Small seabirds such as terns have less leeway in their annual energy budgets than do larger species, and spend a very high proportion of the available time foraging when they have young (Pearson 1968). This, coupled with their small foraging ranges (Pearson 1968), makes them very vulnerable to food shortages near the breeding colonies, such as may arise from a change in prey availability or an increase in competition (Ashmole 1963), and we should expect them to be especially prone to nest desertion. While the overall numbers of breeding common (*Sterna hirundo*) and arctic terns (*S. paradisaea*) in Britain appear to have been comparatively stable in the 1970s (Thomas 1982), there have recently been some dramatic colony shifts and local fluctuations in numbers, particularly in the Northern Isles. In Shetland, which holds over 40% of the British population of the arctic tern (Bullock & Gomersall 1981), these birds have had consistently poor annual breeding success since 1984 (Heubeck & Ellis 1986). The reasons for this breeding failure have been unclear. An interaction between local environmental conditions and the state of the adults will determine the outcome of a breeding attempt. Therefore, we have examined the relationship between food supply, reproductive effort and breeding success in arctic terns by comparing the breeding and foraging performance and the adult body condition of arctic terns breeding in Shetland with those breeding on Coquet Island, Northumberland, where such consistent breeding failure has not occurred.

METHODS

The locations of the two study sites are shown in Fig. 1. Sample plots were set up early in the 1987 breeding season in the central area of arctic tern colonies at Garthness in the South Mainland of Shetland (124 nests) and on Coquet Island (38 nests). All nests were marked with tagged canes, and adults were marked during incubation using dye-soaked sponges placed on the nest. Data on laying dates and breeding success were collected by checking nests at approximately 2-day intervals. Egg length and breadth were measured to the nearest 0·1 mm using vernier calipers. Egg volume was calculated as $0{\cdot}48 \times \text{breadth}^2 \times \text{length}$ (Dunn 1972). Additional data on laying dates, egg and clutch sizes were collected from outside of the sample plots in both study areas. Due to the progressive growth of the vegetation on Coquet Island making obervations difficult, accurate data on hatching success and fledging success were obtained from only twenty-six of the thirty-eight study nests.

Soon after birds arrived at the colonies, hides were positioned close to the study plots. On average, two 3–4-h watches were undertaken daily throughout the breeding period; to avoid bias towards any particular time of day, the timing of watches was randomized over the daylight hours. Adult terns carry single prey items in their bills. Thus, the rate at which food was brought to females during courtship, and to chicks after hatching, was monitored by direct observation. Prey items were identified as sandeel (predominantly *Ammodytes marinus*), saithe (*Pollachius virens*), clupeids (predominantly herring *Clupea harengus* and sprat *Sprattus sprattus*) and others (predominantly three-spined sticklebacks *Gasterosteus aculeatus* and small prawns). Fish size was estimated (with reference to the adult's bill) as falling into one of four categories, i.e. 0–4 cm, >4–8 cm, >8–12 cm and >12 cm. The energy content of fish was estimated using the conversion factors for the appropriate species and size-class published by Harris & Hislop (1978). The rate at which food brought to the young was stolen by other arctic terns was also recorded.

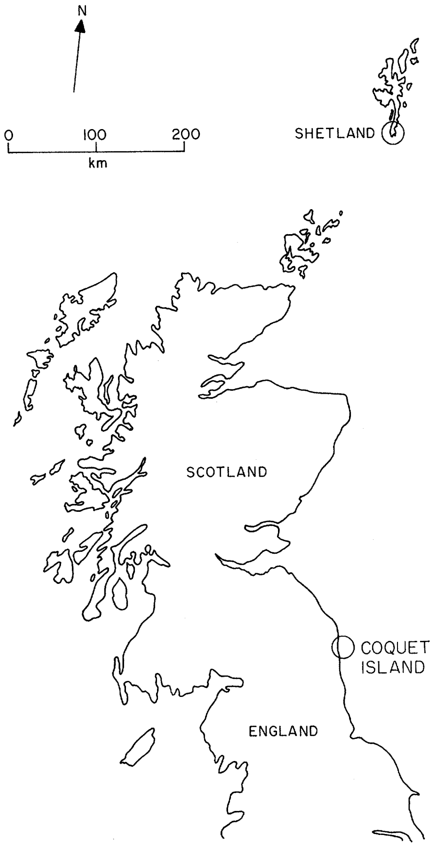

FIG. 1. The location of the two main study areas, Shetland and Coquet Island.

To minimize disturbance and to facilitate the location of chicks, small wire fences *c*. 30 cm high were erected around groups of nests similar to those used in other studies (e.g. Pearson 1968; Langham 1972a; Nisbet & Drury 1982). Chicks were individually marked at hatching and chick growth was monitored by taking weights (to the nearest 1 g using a spring balance) and wing lengths (to the nearest 1 mm) approximately every 3 days. All chicks found dead were collected and, where age at death was not known, this was estimated from the wing length.

Adult body weight was monitored using load cells concealed in fibreglass rocks. These were connected to an Ohaus C501 electronic balance and Epson HX-20 micro-computer operated by the observer in the hide. Full details of this method will be published elsewhere. When placed in breeding territories, the artificial rocks were regularly used by adult terns as perches. When a bird landed on a balance, readings were taken at 1·3-s intervals and a mean computed over several minutes. The weight readings obtained were very stable and standard deviations were low (<1 g); on the few occasions when larger variances were recorded, the records were discarded. When more than one weight was obtained per day for the same bird, a mean value was calculated. Five balances were in operation in each study area, and these could be moved between nest sites. Weight changes over the breeding period were examined by calculating the average weight of birds over a 10-day period and plotting this against the mean weighing date of each bird.

TABLE 1. The average breeding performance of arctic terns in Shetland and on Coquet in 1987

	Shetland			Coquet		
	Mean	S.E.	*n*	Mean	S.E.	*n*
Clutch size	1·90	0·03	279	1·80	0·04	80
Chicks hatched per egg laid	0·71	0·03	124	0·80	0·06	38
Chicks fledged per chick hatched	0·00	0·00	124	0·56	0·80	26
Chicks fledged per pair	0·00	0·00	124	0·92	0·13	26

This minimized biases due to the amount of food in the stomach and due to some birds having been weighed more frequently than others.

RESULTS

Breeding success

Laying dates differed significantly between Shetland and Coquet, with laying date being later in the former. The median laying date in Shetland was 2 June and on Coquet 28 May (Mann–Whitney U-test, $U=927{\cdot}5$, Shetland $n=153$, Coquet $n=68$). Table 1 gives the basic breeding success of arctic terns in the two areas in 1987. The figures for Coquet are very similar to those recorded by Langham (1972b) in 1965–67 (mean clutch size 1·80–1·86, mean chicks fledged per pair 0·91–0·96). No significant difference was found between clutch sizes on Coquet and Shetland ($t=1{\cdot}52$, d.f. 356, Table 1). While there was a significant difference in the length of the A (first laid) eggs, (with those on Coquet being slightly longer, Table 2, $t=-2{\cdot}50$, d.f. 273, $P<0{\cdot}02$), no significant difference was found between Shetland and Coquet in the other egg dimensions (Table 2), nor was there any significant difference in egg volume. The difference in the length of the A egg is very small and unlikely to be of any biological significance. No significant difference in hatching success was found between Shetland and Coquet ($t=-1{\cdot}40$, d.f. 160, Table 1). However, very few chicks fledged on Shetland; in contrast fledging success on Coquet was good (Table 1).

Foraging performance

Courtship

Figure 2 shows the composition of food brought by males during the courtship phase in Shetland and Coquet (i.e. the latter half of May), in relation to both numbers of fish and

TABLE 2. The mean (S.E.) lengths and breadths of arctic tern eggs laid on Shetland and Coquet in 1987. (No C eggs were laid in the study area on Coquet)

	Mean length (mm)	Mean breadth (mm)	*n*
Shetland A egg	39·9 (0·1)	29·3 (0·9)	201
Coquet A egg	40·5 (0·2)	29·3 (1·0)	74
Shetland B egg	39·5 (0·2)	29·2 (0·1)	151
Coquet B egg	39·7 (0·2)	29·0 (0·2)	58
Shetland C egg	38·5 (0·5)	29·2 (0·6)	11

TABLE 3. The relative frequency with which arctic terns were seen to bring in different size-classes of fish during (a) courtship and (b) the first week of chick life on Shetland and Coquet in 1987

	Size-class (cm)			
	0–4	>4–8	>8–12	>12
(a) Courtship				
Shetland	5 (4%)	1 (1%)	32 (26%)	84 (69%)
Coquet	70 (42%)	48 (29%)	41 (25%)	7 (4%)
(b) Chicks				
Shetland	1332 (89%)	65 (4%)	53 (4%)	48 (3%)
Coquet	121 (43%)	124 (44%)	30 (10%)	8 (3%)

energy content. A much greater proportion of the fish on Shetland was sandeels, and the difference between the two areas is significant ($\chi^2 = 86{\cdot}9$, d.f. 1, $P < 0{\cdot}001$). The bulk of the diet on Coquet was sprats, which have a higher calorific content than sandeels per unit body length (Harris & Hislop 1978). In energy terms, sandeels contributed comparatively little to courtship feeding on Coquet (15%). There was a significant difference between the two areas in relation to the proportions in which the different size-classes of fish were brought in by males (Table 3; $\chi^2 = 164{\cdot}8$, d.f. 3, $P < 0{\cdot}001$). With respect to sandeels alone, the arctic terns in Shetland brought in a much greater proportion of large fish than did the birds on Coquet (Fig. 3; $\chi^2 = 120{\cdot}8$, d.f. 3, $P < 0{\cdot}001$); no intermediate sized fish (> 4–8 cm) were observed in Shetland.

However, when the rate at which energy was brought to females was examined, there was a significant difference between the two areas in the frequency distributions of energy per foraging trip, with the Coquet birds more often bringing in large amounts of energy,

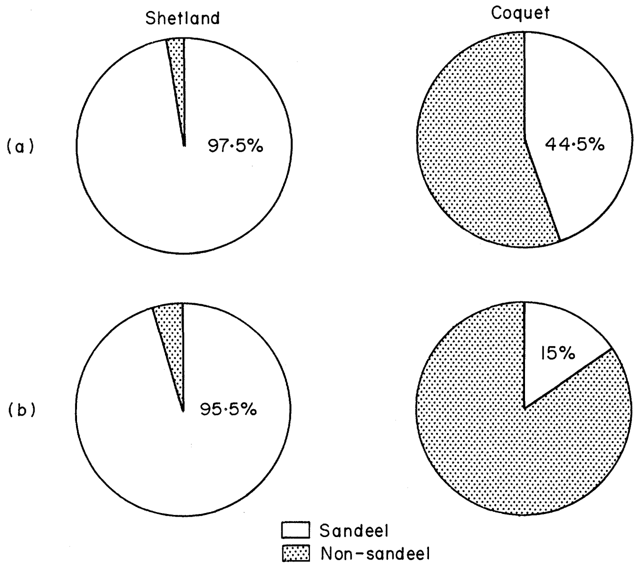

FIG. 2. The composition of courtship food brought by male arctic terns in Shetland and on Coquet in 1987, in terms of (a) number of fish and (b) energy content (kJ). Shetland $n = 132$, Coquet $n = 166$.

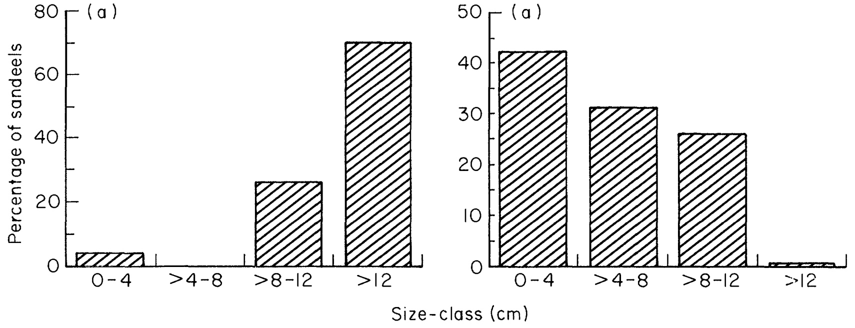

FIG. 3. The size-classes of sandeels brought by male arctic terns during courtship in 1987 on (a) Shetland and (b) Coquet.

i.e. >20 kJ per trip (Fig. 4a; Kolmogorov–Smirnov $Z = 2{\cdot}37$, $n = 45$ Shetland, 144 Coquet; $P < 0{\cdot}001$). This is due to the predominance of sprats in the courtship food on Coquet. In addition, the Coquet birds tended to make more foraging trips per hour than did the birds on Shetland (Fig. 4b; Kolmogorov–Smirnov $Z = 8{\cdot}21$, $n = 330$ Shetland, 185 Coquet, $P < 0{\cdot}001$), resulting in a higher overall rate of energy transfer (Fig. 4c; Kolmogorov–Smirnov $Z = 7{\cdot}39$, $P < 0{\cdot}001$).

Chick-rearing

Comparative data are available only for the early part of chick-rearing period, since in Shetland very few chicks survived beyond their first week. There was no significant difference between Shetland and Coquet in the proportion of the diet comprised of sandeels during the early chick period (Fig. 5). The non-sandeel component of the diet in Shetland was primarily saithe which have a comparatively low calorific value (Harris Hislop 1978), whereas on Coquet it was largely sprats.

There was a significant difference between Shetland and Coquet in the size distribution of fish taken during the early chick period (Table 3, $\chi^2 = 437{\cdot}3$, d.f. 3, $P < 0{\cdot}001$). Figure 6 shows the proportion of sandeels of different sizes fed to young chicks in Shetland and Coquet in 1987, which differed significantly ($\chi^2 = 280{\cdot}2$, d.f. 3, $P < 0{\cdot}001$). There was a very marked increase in the proportion of small sandeels fed to Shetland chicks in 1987 compared with 1983 ($\chi^2 = 615{\cdot}7$, d.f. 3, $P < 0{\cdot}001$), and the modal size class in 1983 (4–8 cm) was almost completely absent in 1987 (Fig. 6).

During the first week after hatching, arctic terns in Shetland tended to make more foraging trips per hour than the birds on Coquet (Fig. 7a; Kolmogorov–Smirnov $Z = 2{\cdot}72$, $n = 382$ Shetland, 170 Coquet, $P < 0{\cdot}001$), but were more likely to bring back less energy per foraging trip (Fig. 7b; Kolmogorov–Smirnov $Z = 3{\cdot}89$, $P < 0{\cdot}001$). This resulted in a difference in the frequency distributions of the rate of energy transfer to the chicks (Fig. 7c; Kolmogorov–Smirnov $Z = 2{\cdot}3$, $P < 0{\cdot}001$); the birds on Coquet being more likely to deliver large amounts of energy per chick per hour than the birds on Shetland.

Due to intraspecific kleptoparasitism, not all of the food which adults brought to their chicks was actually consumed by them. During the first week after hatching, the frequency with which birds lost their fish to other arctic terns differed significantly between Shetland and Coquet with respect to the larger fish (Table 4). At both sites, the probability of kleptoparasitism was highest for larger fish (Table 4).

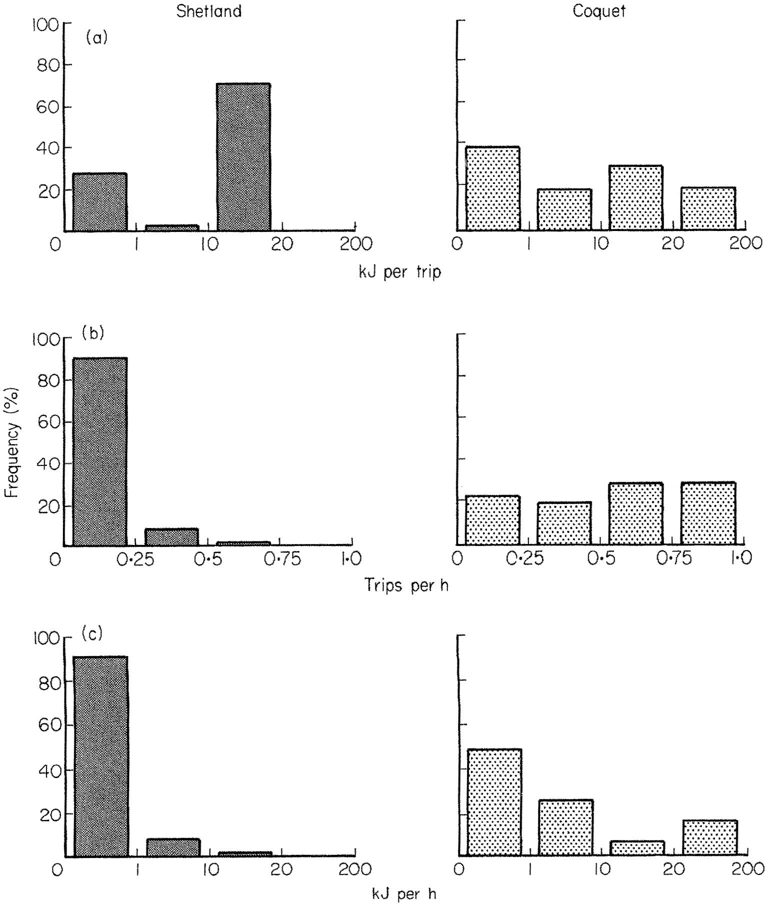

Fig. 4. (a) The amount of energy brought per foraging trip; (b) the number of foraging trips per hour and (c) the amount of energy brought per hour by male arctic terns during courtship on Shetland and Coquet in 1987. Note the unequal size categories on the x-axis, necessary to accommodate the very skewed distributions.

Chick growth

During the period when growth can be taken to be approximately linear and for which sufficient information was available for both study sites (i.e. the first 2 weeks of chick life), the growth rate of chicks was significantly faster on Coquet in 1987 than on Shetland (Fig. 8). Chicks of a given size (as indicated by wing length) were lighter in Shetland than on Coquet.

Adult weight

In both Shetland and Coquet, adults lost weight during the breeding season (Fig. 9). On Coquet, adults that fledged two chicks were heavier at a given stage in the breeding period than those that fledged only one (Fig. 10). In both these groups the clutch size and hatching success were the same (two eggs laid and both young hatched), but in the latter group the B chick died within the first week of life. This was not due to predation but appears to have been due to starvation and/or neglect. Adults on Shetland were lighter than either of the two groups on Coquet prior to the chicks hatching. The subsequent rate

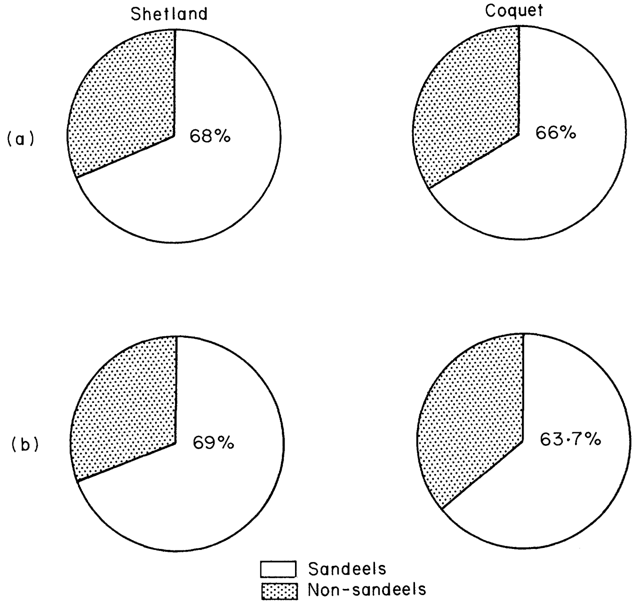

FIG. 5. The composition of the food brought to arctic tern chicks in Shetland and Coquet in 1987 in terms of (a) numbers and (b) energy content. Shetland $n = 1489$, Coquet $n = 290$.

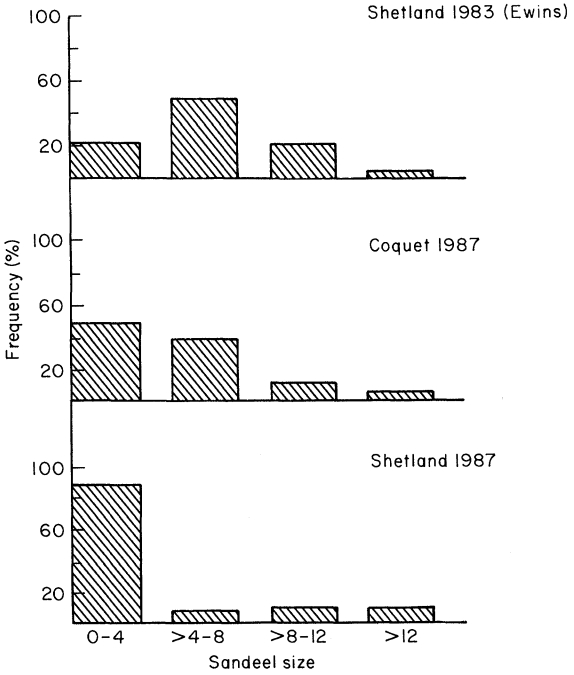

FIG. 6. The proportion of different size-classes of sandeels fed to arctic tern chicks on Shetland and Coquet in 1987, and Shetland in the last successful breeding season in 1983. Data for 1983 are from Ewins (1985).

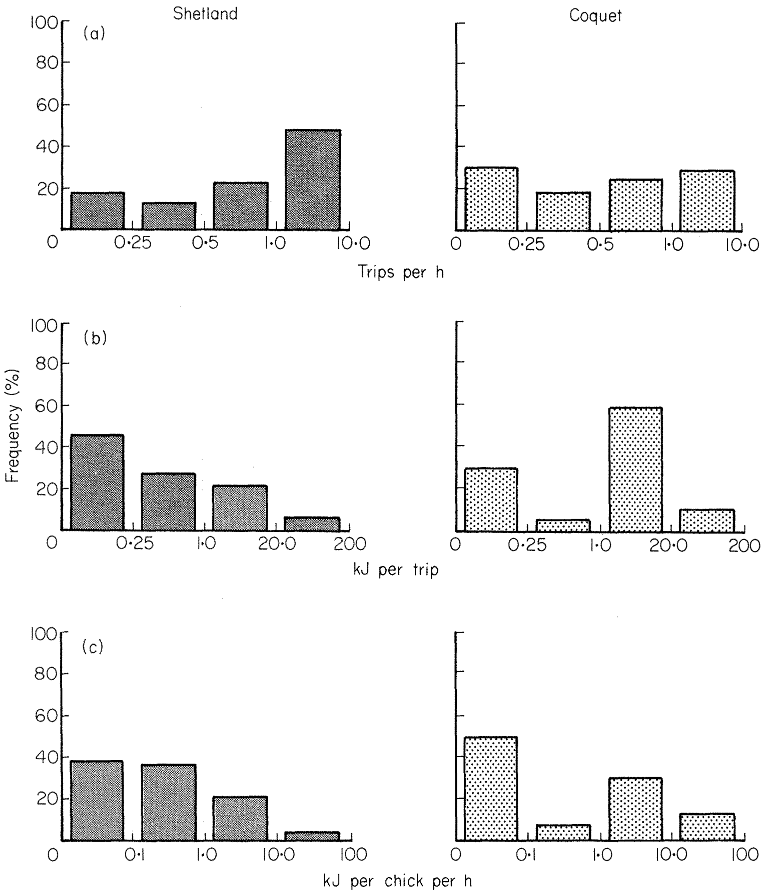

FIG. 7. (a) The number of foraging trips per hour made by arctic tern pairs during the first week of chick life on Shetland and Coquet in 1987; (b) the number of kJ per trip and (c) the number of kJ per chick per hour. Note the unequal size categories on the horizontal axis necessary to accommodate the very skewed distributions.

TABLE 4. The proportion of fish of different sizes lost by arctic terns to conspecifics during the first week after hatching. Sample sizes are given in parentheses. There were no significant differences between Shetland and Coquet in the proportion of fish lost in either of the two categories below 8 cm long. Categories above 8 cm were lumped for analysis due to small sample on Coquet; $\chi^2 = 7{\cdot}72$, 1 d.f. $P < 0{\cdot}01$

	Size-class (cm)			
	0–4	>4–8	>8–12	12+
Shetland	0·2% (1332)	12% (65)	47% (53)	48% (48)
Coquet	0·8% (121)	5% (124)	17% (30)	12·5% (8)

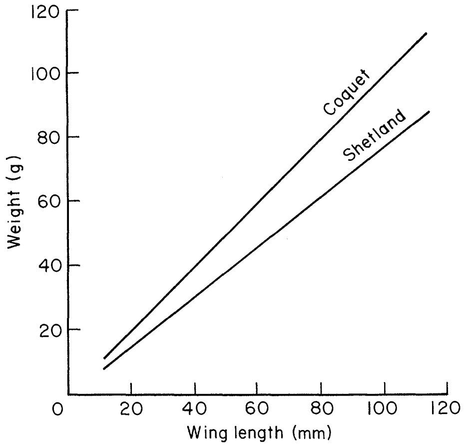

FIG. 8. The growth rates of arctic tern chicks on Shetland and Coquet in 1987. The difference between the two slopes is highly significant ($F_{1,534}=47{\cdot}36$, $P<0{\cdot}001$). Shetland $n=445$, $r=0{\cdot}89$, $P<0{\cdot}001$, $y=0{\cdot}78x+0{\cdot}16$; Coquet $n=93$, $r=0{\cdot}93$, $P<0{\cdot}001$, $y=1{\cdot}02x+0{\cdot}70$.

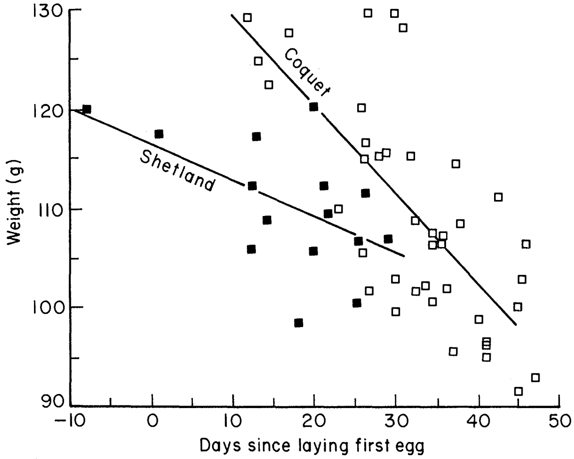

FIG. 9. Changes in the body weight of breeding adult arctic terns on Shetland (■) and Coquet (□) in 1987. The difference between the two slopes is significant ($F_{1,51}=4{\cdot}90$, $P<0{\cdot}05$). Shetland $n=15$, $r=-0{\cdot}55$, $P<0{\cdot}05$, $y=-0{\cdot}36x+116{\cdot}41$; Coquet $n=40$, $r=-0{\cdot}72$, $P<0{\cdot}001$, $y=-0{\cdot}89x+137{\cdot}92$.

of weight loss of Shetland birds was less than that of Coquet birds overall (Fig. 9) and that of the Coquet birds rearing only one chick (Fig. 10).

Predation

Very little predation was observed on Coquet, and breeding success was good (Table 1). Predation on chicks by common gulls (*Larus canus* L.) became frequent on Shetland only after a large number of arctic terns had already failed, and this appears to have been due to a combination of prolonged parental absence, breakdown of colonial defence as pairs deserted and high chick activity. However, these factors remain to be quantified.

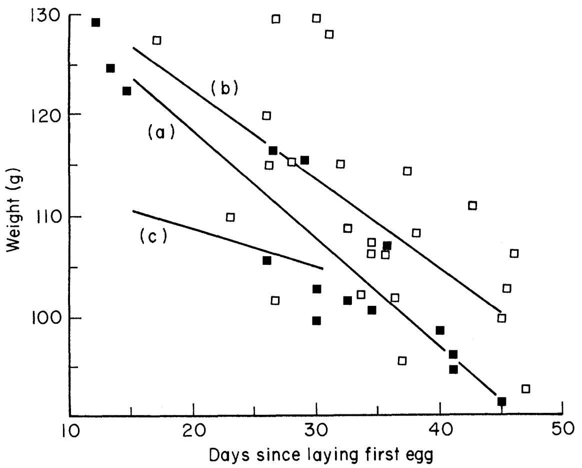

FIG. 10. Changes in the body weight of arctic tern adults on Coquet that hatched two chicks and fledged (a) one chick (■) and (b) two chicks (□). There was no significant difference between the slopes of these lines; the difference between the elevations was significant ($F_{1,37}=9{\cdot}9$, $P<0{\cdot}003$). (a) $n=16$, $r=-0{\cdot}93$, $P<0{\cdot}01$, $y=-1{\cdot}04x+138{\cdot}76$; (b) $n=24$, $r=0{\cdot}63$, $P<0{\cdot}01$, $y=0{\cdot}85x+139{\cdot}3$. Also shown for comparison is the regression line for Shetland adults (c), taken from Fig. 9. There was a significant difference between the slopes of the Shetland birds (c) and those on Coquet rearing one chick (a) ($F_{1,27}-13{\cdot}71$, $P<0{\cdot}001$). There was no significant difference in the slopes of the Shetland birds (c) and the Coquet birds rearing two chicks (b); the difference between the elevations was significant ($F_{1,36}=9{\cdot}4$, $P<0{\cdot}004$).

DISCUSSION

In 1987, arctic terns in Shetland laid a clutch size similar to that recorded on Coquet Island (Table 1). However, while hatching success was also similar, more than half the young hatched on Coquet were successfully fledged; in contrast, on Shetland virtually no young were successfully reared. The results of this study demonstrate considerable differences in the foraging performance of birds in the two areas from as early as the courtship period. Males in Shetland brought larger fish during courtship than did the birds on Coquet, intermediate sized sandeels (>4–8 cm) being completely absent in Shetland. However, this size-class may not generally be important during courtship in Shetland, since Ewins (1985) found that it formed only around 10% of the courtship food in a year when arctic tern breeding success on Shetland was good. Male terns tend to bring in the largest prey available during courtship (Taylor 1979); therefore, the observed size distribution of courtship prey may reflect males maximizing foraging efficiency by bringing in large fish. Despite the larger prey, the rate of food delivery and of energy transfer to females was lower in Shetland than on Coquet. Nonetheless, although male provisioning of females during courtship makes an important contribution to egg production in terns (Nisbet 1973, 1977), we found no difference in clutch size or egg volume in the two areas. However, we have found differences in egg composition (P. Monaghan *et al.* unpublished). Moreover, the observed lower mass of adults in Shetland after laying suggests that the cost incurred in egg production in terms of adult body condition was higher in Shetland than on Coquet.

Differences in foraging performance persisted during the chick-rearing period. Although the diet composition in the two areas was similar, with sandeels forming almost 70% of the diet of young chicks, there were considerable differences in the size of prey fed to the young. The Shetland chicks were fed largely on very small sandeels and, as in courtship, there appeared to be a shortage of sandeels of intermediate size. This size-class appears to be a very important part of the food of chicks, forming over 40% of the sandeels fed to young chicks on Coquet and almost 50% of the diet in Shetland when breeding success was good (Fig. 6, Ewins 1985). Based on the median Coquet figures for the rate of food delivery and energy brought per chick per foraging trip from the distributions in Fig. 7, and the prey calorific values of Harris & Hislop (1978), arctic terns in Shetland would have to bring one small sandeel to a chick every 2 min to match the rate of energy provisioning of chicks recorded on Coquet. This is considerably greater than the observed rate (Fig. 7a). Despite tending to make more foraging trips per hour than the Coquet birds, the Shetland adults brought in less energy per unit time; for larger fish, they suffered a much higher rate of conspecific kleptoparasitism, with almost half of the fish greater than 8 cm long being lost (Table 4). The chicks grew less well than those on Coquet, and virtually none survived the first week of life.

Loss of mass during the breeding period has been documented in many bird species (e.g. Bryant 1979; Coulson *et al.* 1983; Nur 1984, Jones 1987a, b), and Langham (1968) found breeding arctic terns weighed in July to be significantly lighter than birds weighed in June. This has been interpreted as a consequence of physiological stress or as an adaptive response to increase foraging efficiency by reducing flight costs (Freed 1981; Norberg 1981; Reznick 1985; Monaghan & Metcalfe 1986). Adult arctic terns lost weight during the breeding period in both areas. The birds on Shetland were lighter than adults on Coquet throughout the period for which comparable data are available (Fig. 9), though their rate of weight loss was less. We do not have data on the body size of birds in the two areas. However, the arctic tern breeds over a very large area and there is little geographical variation in body size and little sexual dimorphism (Cramp 1985); any differences in size which may occur are likely to be minor and such that the birds on Coquet would be smaller than those on Shetland in accordance with Bergman's rule. On Coquet Island, birds that succeeded in fledging only one of two chicks hatched were consistently lighter than birds that fledged both young (Fig. 10). A similar effect has been reported earlier in the breeding period in long-tailed skuas (*Stercorarius longicaudus*) in which birds that lost the least weight laid the largest clutches (De Korte 1985). In the arctic terns, those birds

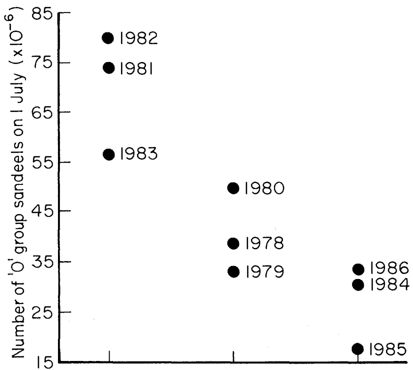

FIG. 11. The breeding success of arctic terns in Shetland between 1978 and 1986 in relation to the number of 0-group sandeels estimated to be in the area on 1 July. Tern data from Ewins (1985) and Heubeck & Ellis 1986. Sandeel data from Anon. (1987).

that fledged only one chick apparently did not provide the second chick of the brood with sufficient food. The consequent brood reduction may represent adults adjusting their breeding effort to suit their foraging capacity as has been suggested in other studies (Nur 1984; Ricklefs & Hussell 1984; Lifjeld 1988). This may differ in relation to parental age or quality. The existence of an 'optimal working capacity' (Drent & Daan 1980) or threshold below which parents will not permit their body condition to fall due to the increased mortality risk would explain the lower rate of weight loss of the birds in Shetland, their body weight having approached the threshold earlier in the breeding season.

The poor breeding success of the arctic tern in Shetland in 1987 thus appears to have been primarily a consequence of food shortage. The size of sandeels fed to tern chicks in both study areas fall within the 0-group age class (Warburton 1983). Currently available fishery assessments indicate that the relative abundance of 0-group sandeels in Shetland as estimated on 1 July each year has been low in some years of poor arctic tern breeding success (Fig. 11). However, several factors independent of sandeel abundance could influence the availability of suitable sized sandeels to the terns. For example, changes in sandeel shoaling behaviour, movement patterns, timing of breeding or hatching could be involved. Alternatively, changes in sandeel breeding success or the size of the breeding stock may have occurred. A sandeel fishery began in Shetland early in the 1970s with the highest landings of fish in the early 1980s (Warburton 1983). However, while sandeel landings in Shetland have recently decreased, this appears largely to be due to changes in fishing effort in response to economic factors, rather than a change in sandeel abundance. The factors influencing fish abundance and availability to seabirds are clearly complex, and at present we do not have data on the sandeel which would allow us to distinguish between the potential explanations of their current low availability to arctic terns in Shetland.

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