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The role of food supply in the breeding performance of terns

Final Report to the Nature Conservancy
Council and the Royal Society for the
Protection of Birds

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Notes:

In 1984, it became evident to the Shetland Ringing Group and others monitoring seabirds in Shetland that arctic terns had had a very poor breeding season. This situation continued in 1985, and a study carried out in 1986 suggested that predation by gulls was an important factor. However, it was felt by many others that the cause of the breeding failure was starvation of the chicks. Since the internationally-important population of arctic terns in Shetland was known to feed on sandeels, and there was a locally important sandeel fishery around Shetland, it was felt that the situation demanded further investigation. Therefore the Nature Conservancy Council (NCC) and the Royal Society for the Protection of Birds (RSPB) agreed to fund a study by Glasgow University of the role of food supply in the breeding performance of terns. This is the report of that study, carried out between 1987 and 1989.

The study confirmed that tern chicks were starving to death in Shetland and that other more subtle changes were occurring in adult tern body condition. Both of these effects were caused by a lack of suitable-sized sandeels (or alternative prey) at specific stages in the breeding cycle. This lack of high quality alternative prey is an important difference between Shetland and other sites where arctic terns were studied. The study also highlighted the lack of understanding of the role of sandeels in the marine ecosystem. This lack of understanding led to the initiation of a large-scale collaborative project examining the biology of sandeels around Shetland (part-funded both by NCC [now NCCS] and RSPB) and the feeding biology of seabirds (carried out by Glasgow University under NERC funding). These projects are still in progress, but preliminary reports may be available from us.

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1. INTRODUCTION

1.1 Overall Aim of this Study

The primary aim of this project was to quantify the influence of low food supplies on breeding arctic terns *Sterna paradisaea*, through comparative studies of key aspects of their breeding performance in situations of differing food availability. This thereby provides scientific information important in the design of effective tern conservation policies in relation to fisheries practice.

1.2 Background and Specific Objectives

A variety of factors are known to influence the breeding success of terns, and until relatively recently habitat disruption and competition from large gulls were considered to be the main causes of breeding failure (Thomas 197x). Studies of the effects of variation in food supplies, while shown to relate to breeding numbers of terns in some areas (e.g. Monaghan & Zonfrillo 1986) have been hampered by a lack of quantitative information on changes in relevant fish stocks within the foraging areas.

This study, which was carried out during the three year period 1987 - 89, was initiated at a time of increasing concern over a dramatic decline in the breeding success of the arctic tern in Shetland. This breeding failure began in 1984, and since then virtually no young have been produced in an area which formerly held over 32,000 breeding pairs, some 40% of the breeding population of arctic terns in the British Isles (Bullock & Gomersall 1981, Thomas 1982).

The cause of this breeding failure was unclear, and in a preliminary study in 1986 predation from gulls had again been suggested as an important factor (Coulson & Megson 1987). In contrast with many other situations, detailed information was available on changes in a relevant fish stock in around Shetland, that of the sandeel *Ammodytes marinus*, the main seabird prey in the area. This is because a sandeel fishery commenced in Shetland inshore waters in 1974, and since then fisheries scientists at the Scottish Office Agriculture and Fisheries Department have produced annual estimates of the size, age structure and production of the stock. This study therefore aimed to :

1) Examine in detail the timing of breeding failure of arctic terns in Shetland.

2) Quantify the diet and foraging performance of breeding birds during the courtship and chick rearing periods.

3) Examine the changes in key breeding parameters such as the timing of laying, egg quality, clutch size, hatching success, foraging rates and chick growth.

4) Examine adult body condition in relation to breeding performance.

5) Relate these Shetland data to changes in relevant prey stocks.

6) Compare the breeding and foraging performance and adult body condition of arctic terns in Shetland with those breeding successfully elsewhere.

1.3. Content of this Report

This report summarises the main findings of the study. Several scientific publications and a PhD thesis have arisen from this work; details and abstracts of these are given in Appendix 1.

2. METHODS

A brief summary of the methods is given here. Full details can be found in the publications listed in Appendix 1.

2.1. Study Areas

Data on arctic terns attempting breeding in Shetland were collected in the breeding seasons of 1987, 1988 and 1989; the study areas in 1987 and 1988 were in the South Mainland area (Garth's Ness and Mousa respectively) and in 1989 at Bridge of Walls, West Mainland. Arctic terns were also studied at the RSPB reserve at North Hill, Papa Westray, Orkney in 1988 and 1989. Successfully breeding arctic terns on the RSPB reserve on Coquet Island, Northumberland were studied in all three seasons. Additional field assistance at these sites was provided by Jane Blackwood, Sue White and Gina Scanlon in Shetland, Chris Thain, Neil Gartshore and John Osborne on Coquet and Chris Thain in Orkney.

2.2 Data Collection

It was important that breeding birds were disturbed as little as possible. Some disturbance was however inevitable, and methods were designed to reduce this as far as possible.

Courtship feeding of females by males, feeding of chicks and attendance of eggs and young were quantified by observation from hides erected close to or within breeding colonies. Typically, watches were of four hours duration and spread across all daylight hours to minimise diurnal effects. Birds were marked using nest sponges soaked in picric acid dye.

Laying dates, clutch sizes, egg sizes, hatching success and chick growth, survival and fledging were recorded by repeatedly checking a sample of nests throughout the season. Low barriers were erected around nests in order to prevent disturbed chicks from wandering during necessary intrusions into the colony.

Egg quality (protein and lipid content) was measured in small samples (10 clutches) collected under licence from the NCC. The possibility of Shetland terns laying eggs which were not viable due to low quality or pollutant burden was tested by transporting eggs laid on Shetland to Orkney, where they were swapped for native Orkney eggs. Their hatching success and the growth and survival of the resulting chicks was monitored.

Adult body mass (as an index of adult body condition) was monitored by concealed electronic balances placed in breeding territories, and operated from the hide. Weights of known individuals were monitored throughout all or part of the breeding season.

Data were stored and analysed on Glasgow University's ICL 3890 mainframe computer, using the SPSS-X package.

3. RESULTS

3.1 Breeding parameters

3.1.1 Timing of breeding

The median dates of clutch initiation are shown in Table 1. In each year a latitudinal effect was apparent, clutch initiation being slightly later at the more northerly site (Table 1). Using non-parametric analysis of variance, no significant within-site differences in laying date were found between the three years.

Table 1. The median (modal) dates of clutch initiation

	1987	n	1988	n	1989	n
Shetland	2 June (2)	115	31 May (30)	100	-	
Coquet Is.	28 May (27)	62	24 May (23)	91	24 May (24)	97
Orkney	-		30 May (31)	42	28 May (28)	42

3.1.2 Clutch size

The frequency distributions and mean clutch sizes recorded at the study sites are given in Table 2. Mean clutch size declined in Shetland over the three years, but increased in Coquet. The frequency distribution of clutch sizes differed between the years in both areas ($X^2 = 21.07$ Shetland, 12.87 Coquet; 4d.f. and $P<0.05$ in each case), the proportion of 1 egg clutches increasing in Shetland but decreasing in Coquet (Table 2). The frequency distribution of clutch sizes did not differ between Shetland and Coquet in 1987 or in 1988, but did in 1989 ($X^2 = 13.76$, 2 d.f. $P<0.01$), the Shetland birds having a much greater proportion of single egg clutches. The average clutch size recorded in Orkney was high, and in 1989 30% of the birds had three egg clutches (Table 2).

Table 2. The distributions (percentages) and means of clutch sizes of arctic terns at the study sites in each year

		Clutch size			
		1	2	3	Mean (n)
Shetland	1987	56 (20)	194 (70)	28 (10)	1.90 (279)
	1988	30 (26)	82 (71)	3 (3)	1.76 (115)
	1989	18 (35)	32 (61)	2 (4)	1.70 (52)
Coquet	1987	18 (23)	61 (76)	1 (1)	1.80 (80)
	1988	16 (18)	69 (75)	6 (7)	1.89 (64)
	1989	11 (11)	72 (75)	14 (14)	2.03 (97)
Orkney	1988	11 (17)	46 (72)	7 (11)	1.94 (64)
	1989	4 (7)	37 (63)	18 (30)	2.27 (59)

2.1.3. Egg quality

To illustrate the differences found in egg size, the mean size of eggs laid by arctic terns in the three study sites in 1988 are shown below (Table 3). The volume of a- and b-eggs varied significantly between Shetland, Orkney and Coquet (Table 3. 2-way ANOVA by location and clutch size. Location effect: a-eggs - $F_{2,468} = 3.20$, $p < .05$; b-eggs - $F_{2,360} = 4.03$, $p < .05$). One way ANOVA showed that the volume of a-eggs varied with location in single-egg clutches only (Table 3. $F_{2,95} = 5.75$, $p < .01$), whilst the volume of b-eggs varied with location in two-egg clutches only (Table 3. $F_{2,325} = 4.25$, $p < .05$). In both cases, eggs from Coquet were larger than those from Shetland (Scheffe's MCP). However, total clutch volume did not vary between the sites. Egg composition was examined using standard methods. Tables 4 and 5 shows the data on the composition of eggs in two egg clutches collected at the three sites in 1988.

Differences between sites were examined by 1-way ANOVA. Average egg dry weight (a & b combined) differed significantly between eggs from the different sites (Table 4. $F_{2,49} = 4.17$, $p < 0.05$) (Coquet eggs heavier than Orkney, Scheffe's MCP, $p < 0.05$). This difference was due to eggs from Orkney having less albumen (Table 4. $F_{2,49} = 22.35$, $p < 0.001$) than those from Shetland or Coquet (Scheffe's MCP, $p < 0.05$). Dry yolk lipid mass also varied between sites (Table 4. $F_{2,49} = 3.54$, $p < 0.05$) eggs from Orkney containing less than those from Coquet or Shetland, but insignificantly so (Scheffe's MCP). As a result, the yolk lipid index was lower for Orkney eggs (Scheffe's MCP, $p < 0.05$) in both first- ($F_{2,23} = 6.70$, $p < 0.05$) and second-laid eggs ($F_{2,23} = 7.72$, $p < 0.05$ Table 5).

The mass of each egg component was significantly correlated with egg volume, suggesting that the lower albumen and yolk lipid content of eggs in the sample from Orkney may have been a consequence of the smaller volume of those eggs. The volume of the eggs in the sample from Orkney was indeed smaller than those from Shetland or Coquet ($F_{2,49} = 4.53$, $p < 0.05$; Scheffe's MCP). Albumen dry weight did not increase with egg volume on the Coquet sample alone, but this relationship was significant for each of the other two sites. Analysis of co-variance revealed that the elevations of the relationship between egg volume and albumen dry weight varied between the three sites (site effect: $F_{2,48} = 17.5$, $p < .001$; site x volume interaction effect: ns). Examination of the regression lines shows that the Orkney relationship was at a lower elevation than that for Shetland, showing that, for any given egg volume, the Orkney eggs contained less albumen than did the Shetland eggs. (Regressions of albumen (A) versus egg volume (V): Shetland: $A = 0.06V + 0.445$, $n = 20$, $r = 0.593$, $p < 0.01$; Coquet: $A = 0.03V + 1.009$, $n = 16$, $r = 0.242$, n.s.; Orkney: $A = 0.08v - 0.044$, $n = 16$, $r = 0.630$, $p < 0.01$). Analysis of co-variance of the yolk lipid / egg volume relationships yielded no significant differences between the sites.

The data on egg composition suggest that, while there were some differences between sites, those arctic terns which laid a clutch in Shetland were not producing eggs of very low quality. This was confirmed in the egg transfer experiment detailed in 3.1.5 below.

2.1.4. Breeding success

Hatching success is shown in Table 6 and fledging success (defined as chicks which reached 18 days old) is shown in Table 7.

Table 3. The estimated volume of eggs laid by arctic terns on Shetland, Orkney and Coquet Island in 1988

	Volume (ml)							
Site	a-egg			b-egg		c-egg	total clutch	
	1-egg	2-egg	3-egg	2-egg	3-egg	3-egg	2-egg	3-egg
SHETLAND	16.23(.28)	16.78(.12)	17.54(.20)	16.24(.18)	16.51(.64)	16.41(.46)	33.09(.29)	50.47(-)
n	20	49	2	38	2	2	31	1
COQUET	17.74(.82)	16.92(.16)	15.43(.85)	16.58(.17)	16.42(.68)	15.16(.59)	33.50(.31)	47.02(1.60)
n	16	69	6	68	6	6	68	6
ORKNEY	17.14(.42)	16.87(.24)	16.21(.21)	16.39(.20)	16.25(.32)	14.94(.42)	33.30(.41)	47.39(.85)
n	11	31	4	30	4	4	30	4

Table 4. The mean (s.e.) dry composition by weight (g) of eggs from two egg clutches on Shetland, Orkney and Coquet Island in 1988

		SITE		
		SHETLAND	ORKNEY	COQUET
n of clutches		10	8	8
PARAMETER	EGG			
WHOLE EGG				
TOTAL	a	5.02 (.07)	4.84 (.14)	5.15 (.12)
	b	4.89 (.07)	4.67 (.13)	4.99 (.11)
NON-LIPID	a	3.38 (.06)	3.26 (.10)	3.47 (.08)
	b	3.27 (.05)	3.15 (.10)	3.34 (.06)
LIPID	a	1.67 (.04)	1.58 (.05)	1.68 (.05)
	b	1.63 (.04)	1.53 (.05)	1.65 (.06)
SHELL				
TOTAL	a	1.02 (.02)	1.08 (.05)	1.05 (.04)
	b	1.02 (.02)	1.04 (.03)	1.02 (.03)
ALBUMEN				
TOTAL	a	1.42 (.02)	1.24 (.04)	1.48 (.03)
	b	1.39 (.03)	1.21 (.07)	1.47 (.03)
YOLK				
TOTAL	a	2.58 (.05)	2.51 (.09)	2.61 (.09)
	b	2.48 (.05)	2.42 (.07)	2.50 (.08)
NON-LIPID	a	0.91 (.02)	0.94 (.04)	0.93 (.04)
	b	0.85 (.82)	0.89 (.03)	0.85 (.03)
LIPID	a	1.67 (.04)	1.58 (.05)	1.68 (.05)
	b	1.63 (.04)	1.53 (.05)	1.65 (.06)

Table 5. The mean (s.e.) lipid indices and percentage composition by yolk of eggs from two-egg clutches on Shetland, Orkney and Coquet Island in 1988

PARAMETER	EGG	SHETLAND	ORKNEY	COQUET
n of clutches		10	8	8
PERCENT YOLK	(a)	51.36 (.49)	51.86 (.80)	50.66 (.80)
	(b)	50.66 (.60)	51.76 (.90)	50.06 (.90)
YOLK LIPID INDEX	(a)	.648 (.004)	.628 (.004)	.645 (.005)
	(b)	.656 (.007)	.632 (.005)	.660 (.003)
TOTAL LIPID INDEX	(a)	.333 (.004)	.325 (.005)	.326 (.005)
	(b)	.333 (.005)	.326 (.006)	.330 (.007)

Table 6. Mean hatching success per nest (s.e.) of arctic terns at the study colonies in each year. - indicates data not available.

	1987	n	1988	n	1989	n
Shetland	0.71 (.03)	124	0.32 (.04)	93	-	
Coquet Is.	0.80 (.06)	38	0.62 (.04)	91	0.77 (.07)	92
Orkney	-		0.69 (.12)	13	0.75 (.04)	32

Table 7. Mean (per nest) fledging success (s.e.) of arctic terns at the study colonies in each year

	1987	n	1988	n	1989	n
Shetland	0.00 (.00)	124	0.00 (.00)	93	0.04 (.02)	53
Coquet Is	0.56 (.08)	26	0.00 (.00)	23	0.77 (.04)	84
Orkney	-		0.33 (.11)	12	0.15 (.05)	32

Hatching success was generally similar between sites, except in 1988, when there was a significant difference, hatching success on Shetland being extremely low (Table 6. 1-way ANOVA, $F_{2,194} = 11.07$, $p < 0.001$). Low hatching success on Shetland in that year was caused by a high incidence of nest desertion during incubation. Figure 1 shows the difference in the failure rate of nests in Shetland in 1987 and 1988. Desertion during incubation was very rare at the other sites.

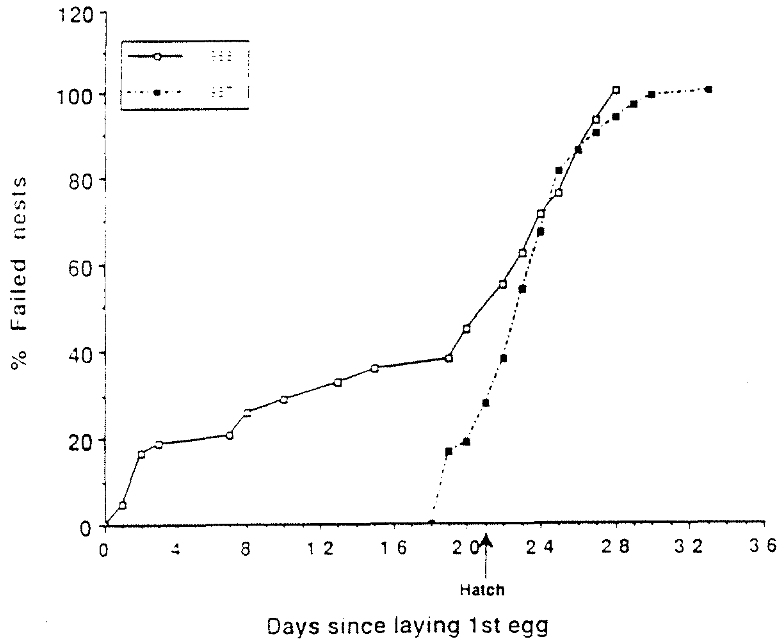

Figure 1. The rate of nest failure of arctic terns during incubation in Shetland in 1987 and 1988. The difference between years is highly significant Kolmogorov-Smirnov D = 0.36; n (nests) 1987 = 95, 1988 = 36, P<0.005).

In Shetland, the majority of chicks died in the first week of life, as shown for 1987 in Figure 2. While some corpses were scavenged by gulls, chicks were largely found dead at the nest. Reduced adult attendance left the young more exposed, but gull predation was clearly not the primary cause of breeding failure. The low fledging success on Coquet in 1988 (Table 7) was apparently due to a lack of adequate cover in the study area, which allowed predation of chicks by black-headed gulls. Many pairs re-laid and 60 second clutches produced an average of 0.83 young per nest. Vegetation cover was greater for birds raising second clutches. In 1989, for the first time in the study, a small number of young were fledged from the study site in Shetland (Table 7). This corresponded with anecdotal information collected in 1988 which suggested that tern colonies in the north-west of Shetland were slightly more successful than those on the South Mainland where the 1987 and 1988 study sites were located. However, fledging success and a maximum estimate of number of young fledged per pair in the north west site in 1989 (mean = 0.075 chicks/pair, s.e. = 0.04, n = 53; *n.b.* some pairs may have failed before the study plot was established) were still low in comparison to both Coquet Is., where breeding success (mean = 0.956 chicks/pair, s.e. = 0.09, n = 92) was very high, and Orkney, where breeding success as measured in terms of number of young reaching 18 days was also lower than Coquet Is. (mean = 0.281 chicks/pair, s.e. = 0.08, n = 32). However, this measure of fledging is known to be an inflated estimate for Orkney for 1989. In this year all but one chick surviving beyond 18 days is thought to have succumbed to predation, possibly by gulls.

Figure 2. The age of arctic tern chick mortality in Shetland in 1987

23.1.5. Experimental manipulation of hatching location

In 1988, in a further test of the hypothesis that arctic terns in Shetland were producing viable eggs *i.e.* eggs which did not possess any inherent defects, such as small size, poor quality, high pollutant burden or genetic abnormality, which may have hindered normal development, nine clutches of two eggs were transported from Mousa, Shetland, to Papa Westray, Orkney, where they replaced clutches taken for composition analysis. Clutches collected from Papa Westray were temporarily replaced with dummy eggs made from modelling clay. These dummies ensured that adults continued to incubate until donor clutches arrived from Shetland. The collected donor clutches were packed in cotton-wool in a large cut-out polystyrene block. They were then sent by boat, car and plane to Papa Westray, where they were exchanged for the dummy clutches approximately 12 hours after collection on Mousa. Donor and recipient nests were selected and matched in order that there was no more than one days' difference between clutch initiation dates. Incubation spans were therefore as normal as possible, preventing effects on adult behaviour from extended or shortened incubation periods.

Hatching success

Of the 18 eggs transferred from Shetland to Orkney, 16 hatched (89%). This was not significantly different from the observed hatching success of native Orkney eggs of which 19 out of 27 hatched (n = 13 nests) ($X^2 = 2.65$, d.f. = 1, $p > .05$).

Fledging success

The donor nests were outside the main study plot on Papa Westray and the fate of the young was hard to determine, since regular visits were not possible and some broods disappeared without known cause and may simply have wandered away from the 'natal' area. However, of those 12 chicks whose progress it was possible to monitor, three fledged (25%), which was not significantly different from the overall fledging success of 33% in the main study plot, and much higher than the fledging success of eggs which were laid and hatched on Shetland.

Growth rate

The rate of wing growth and weight gain with age of the chicks which hatched from transported eggs is shown in Table 8, along with data from untransported chicks from Orkney and Shetland. Transported Shetland chicks gained weight (Analysis of covariance. Difference in slopes: $F_{1,32} = 56.8$, $p < .001$) and grew their wings (Analysis of covariance. Difference in slopes: $F_{1,32} = 22.1$, $p < .001$) faster than untransported Shetland chicks. Furthermore, those transported chicks did not differ from native Orkney chicks in their rate of growth or weight gain (Analysis of covariance. No slope or intercept differences).

Table 8. The growth rates of chicks up to 14 days old from transported and untransported eggs in 1988

GROUP	n[1]	n[2]	r	b	s.e. b
A. WING WITH AGE					
SHETLAND	77	23	0.90	2.01	0.11
ORKNEY	31	14	0.88	5.74	0.57
TRANSPORTED	36	13	0.75	4.99	0.37
B. WEIGHT WITH AGE					
SHETLAND	77	23	0.81	3.14	0.26
ORKNEY	35	14	0.87	5.67	0.56
TRANSPORTED	37	13	0.77	4.52	0.49

1 - no. measurements; 2 - no. chicks

2.2. Adult colony attendance

Nest attendance by adult birds is likely to vary in relation to food availability, and will also give an indication of the degree of exposure of the young to predators. Figure 3 shows the proportion of time in Shetland and Orkney in 1988 for which eggs and chicks were incubated and brooded on each day relative to the hatching of the first chick. The data plotted include all of the nests which were active on each day, regardless of their ultimate success or failure. Inactive nests i.e. nests which had already failed by the day in question are not included. There is no significant difference in the consistency of incubation between Shetland (99.3%, s.e. = 0.22, n = 167 nest-days) and Orkney (99.9%, s.e. = 0.02, n = 298).

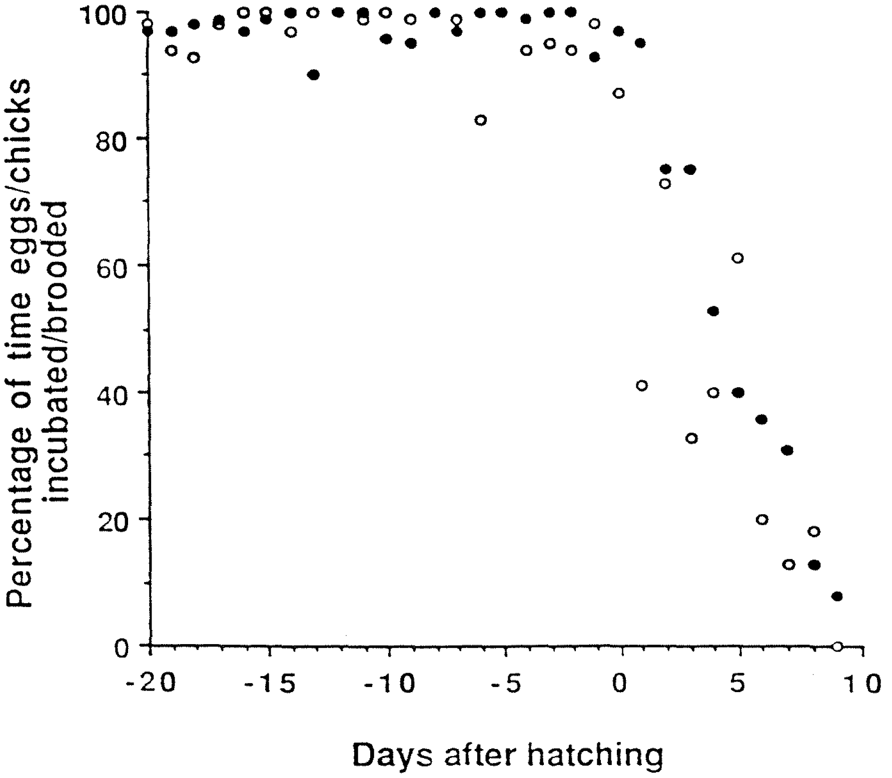

Figure 3. The proportion of time in Shetland and Orkney for which eggs and chicks of arctic terns were incubated/brooded in 1988.

The mean proportion of time for which chicks were brooded in 1988 declined with chick age at both sites (Fig. 3) although this was only significant on Orkney (Pooled data for all nests over first ten days, sexed and unsexed. Shetland: $r_s = -0.46$, $p > 0.05$, $n = 10$; Orkney: $r_s = -1.00$, $p < 0.001$, $n = 10$) but chicks on Shetland were, on average, brooded consistently less than chicks on Orkney from the day of hatching to day 9 inclusive (Figure 3 Wilcoxon matched-pairs signed ranks test: $T_s = -2.0$, $p < 0.01$, d.f. = 8).

An alternative way of examining nest attendance is to consider the extent to which nests were unattended. The percentages of nests in 1989 which were unattended for part of an observation spell are shown in Table 9.

Table 9. The percentages of nests not continuously attended during observation periods in 1989

	% of nests	n (nest-days)
a) incubation		
Shetland	7.7	65
Coquet Is.	10.6	357
Orkney	7.2	305
b) 1st seven days of chick life		
Shetland	49.4	81
Coquet Is.	43.0	142
Orkney	63.1	149

As in 1988 there was no significant difference between birds at the three sites in the consistency of incubation (Table 9. $X^2 = 2.1$, d.f. = 2, ns), but attendance of young chicks did differ between locations. However, direct comparison is not meaningful here, since the average age of chicks differs between groups (chicks in Shetland being much younger), and attendance varies with chick age. Pairwise comparisons (by age of brood), using Wilcoxon's matched-pairs-signed-ranks test, showed that attendance at Shetland and Orkney was similar, whilst at both it was less than at Coquet Is. ($p < 0.05$).

These data demonstrate that, while those adults which persisted with the breeding attempt in Shetland were generally able to maintain incubation, chicks were less well attended than at a successful colony. This is likely to be a consequence of foraging difficulties experienced by the parent birds.

2.3. Foraging

Since there was considerably more variation in foraging parameters between days than between nests on the same day, data on diet and feeding rates were examined by calculating mean figures per day, from which overall means with confidence limits could be derived. Data on courtship feeding rates were not collected in 1989. All data on the chick rearing period are from the first week of life only, since most broods in Shetland failed to develop beyond this age.

2.3.1. Courtship feeding

Detailed data on courtship feeding were collected in 1987 and 1988. The importance of sandeels in the courtship items fed to females by males in 1987 and 1988 is shown in Table 10.

Table 10. The mean percentage (s.e.) of observed arctic tern courtship prey which were sandeels in the study areas in 1987 and 1988

		% sandeels	n(days)	n (fish)
Shetland	1987	98 (1)	19	122
	1988	79 (5)	22	378
Coquet	1987	58 (7)	26	166
Orkney	1988	96 (2)	15	63

The proportion of the courtship food which consisted of sandeels was reduced in Shetland in 1988 in comparison to 1987 in terms of fish numbers (Table 10. Mann-Whitney U = 86.0, $p < 0.001$) and also in terms of energy (Mann-Whitney U = 89.0, $p < 0.001$). No data on diet composition during courtship were available for Coquet in 1988. In 1987, there was a significant difference between Shetland and Coquet, sandeels being relatively unimportant in the courtship diet of terns on Coquet (Table 10. Mann-Whitney U = 140.0, $p < 0.001$); in energetic terms, sandeels contributed only 15% of energy transferred to the female from the male. In 1988, a greater proportion of the courtship prey observed in Orkney was sandeels than observed in Shetland (Table 10. Mann-Whitney U = 81.5, $p < 0.001$). The contributions of sandeels to courtship prey were similar in Orkney in 1988 and in Shetland in 1987. In 1988, the alternative courtship prey utilised by arctic terns in Shetland were largely saithe *Pollachius virens*, whereas on Coquet in 1987 they were mainly sprat *Sprattus sprattus*.

Table 11. The percentage of each size class of sandeels fed to females during courtship in each of the study areas

		0-4cm	>4-8cm	>8-12cm	>12cm	n (fish)
Shetland	1987	4	1	26	69	122
	1988	40	18	24	18	291
Coquet	1987	42	31	25	2	166
Orkney	1988	11	69	20	0	61

The size of sandeels utilised by males feeding females in 1987 and 1988 is shown in Table 11. There was a significant difference between the size of courtship sandeels on Shetland in 1987 and in 1988 (Table 11. $X^2 = 130.5$, d.f. = 3, $p < 0.001$), those in 1988 being much smaller. Courtship sandeels on Shetland in 1987 were also much larger than those on Coquet (Table 11. $X^2 = 164.8$, d.f. = 3, $p < 0.001$). However, as noted above, sandeels were a small component of the courtship diet of terns on Coquet in 1987. In 1988, courtship sandeels on Orkney were on average larger than those on Shetland (Table 11. $X^2 = 74.9$, d.f. = 3, $p < 0.001$).

Table 12. Foraging rates of arctic terns at the study sites during courtship in 1987 and 1988

	mean	s.e.	n (days)
a) Trips / Hour			
Shetland 1987	0.04	0.01	20
Shetland 1988	1.03	0.17	22
Coquet 1987	0.68	0.08	26
Orkney 1988	0.46	0.06	15
b) kJ / Trip			
Shetland 1987	19.77	1.93	20
Shetland 1988	8.46	1.64	22
Coquet 1987	18.45	4.24	26
Orkney 1988	5.50	0.73	15
c) kJ / Hour			
Shetland 1987	0.94	0.27	20
Shetland 1988	6.74	1.28	22
Coquet 1987	13.27	3.67	26
Orkney 1988	2.49	0.36	15

Using energy equivalents for the prey species given in Harris and Hislop (1978), it was calculated that, in energetic terms, male terns on Coquet in 1987 provisioned their mates with significantly more energy per feed than those in Shetland (Table 12b. Kolmogorov Smirnov $Z = 2.37$, $n = 45$ Shetland, $n = 144$ Coquet, $p < 0.001$); this is largely because sprats have a higher energetic value than sandeels. In addition, Coquet males fed their mates more frequently (Table 12a. K-S $Z = 8.21$, $n = 330$, $n = 185$, $p < 0.001$). As a result, Coquet females received energy at a much faster rate (Table 12c. K-S $Z = 7.39$, $p < 0.001$).

In 1988, males in Shetland made many more feeding trips per hour than in 1987 (Table 12a. Mann-Whitney $U = 00.0$, $p < 0.05$), but provisioned their mates with less energy per trip (Table 12b. Mann-Whitney $U = 44.0$, $p < 0.001$). However, the increased feeding rate more than compensated for the poor quality of the prey and females in 1988 received energy at a faster rate than in 1987 (Table 12c. Mann-Whitney $U = 61.0$, $p < 0.001$). Shetland females in 1988 also received energy at a faster rate than those on Orkney (Table 12c. Mann-Whitney $U = 92.0$, $p < 0.001$), as a consequence of their higher feeding rate (Table 12a. Mann-Whitney $U = 84.0$, $p < 0.001$).

2.3.2. Chick-rearing

The diet composition of young tern chicks (up to one week old) at the three study sites is shown in Table 13 (based on daily means).

Table 13. The mean proportion of observed arctic tern prey which were sandeels in the study areas during the first week of the chick-rearing period

	mean	s.e.	n (days)	n (fish)
Shetland 1987	0.67	0.06	17	1489
Shetland 1988	0.68	0.03	8	148
Shetland 1989	0.32	0.18	20	408
Coquet 1987	0.70	0.05	13	290
Coquet 1988	0.21	0.12	9	70
Coquet 1989	0.86	0.18	15	81
Orkney 1988	0.99	0.00	14	188
Orkney 1989	0.61	0.08	17	745

In general, sandeels comprised an important component of the diet of young arctic terns at all three sites (Table 13). However, the alternative prey to sandeels differed between sites, and in some cases differed between years. On Coquet terns are able to feed on clupeids, sprat and young herring, which are, like sandeels, oily, energy dense fish. In 1987 these fish became more frequent in the diet as chicks grew ($X^2 = 20.3$, d.f. = 2, $p < 0.001$), but it is not clear whether this change occurred in response to the changing needs of the chicks or as a consequence of a seasonal change in the availability of prey. In Orkney in 1989, young rockling were the alternative prey to sandeels. These are also energy rich, but are rather small (approximately 4cm long); these became less frequent in the diet of older chicks. On Shetland the non-sandeel food source was variable, possibly influenced by the locations of the study colonies in each year. In 1987 at Garths Ness, silver-winged ghost moths were a frequent prey, as well as saithe. In 1988 on Mousa, saithe were almost the sole non-sandeel prey, but in 1989, at Bridge of Walls, saithe were rare in the diet, and insects represented 87% of non-sandeels, and 64% of all chick prey; these were moths and caterpillars. Rockling do occur in Shetland waters and it is not clear why these were not utilised more by arctic terns in Shetland. Detailed information on their distribution is not available.

The proportion of young chicks' diet which was sandeel in Shetland in 1989 was less than in 1987 or 1988 (Table 13. 1-way anova: $F_{2,42} = 139.4$, $p < 0.001$; Scheffe's MCP). Sandeels were also less frequent on Orkney in 1989 than in 1988 (Table 13. $z = 15.6$, $p < 0.001$), but here, as already mentioned, a good quality alternative (rockling) was utilised.

Table 14. The percentage of various size classes of sandeels fed to chicks in the first week after hatching in each of the study areas

	0-4cm	>4-8cm	>8-12cm	>12cm	n (fish)
Shetland 1987	87%	3%	5%	5%	1008
Shetland 1988	49%	51%	0%	0%	103
Shetland 1989	27%	71%	2%	0%	101
Coquet 1987	51%	40%	7%	2%	203
Coquet 1988	-	-	-	-	4
Coquet 1989	21%	69%	10%	0%	67
Orkney 1988	55%	44%	1%	0%	186
Orkney 1989	11%	66%	17%	6%	409

Table 14 shows the size distribution of sandeels fed to young chicks at the study sites. Non-sandeels prey items were of a comparatively uniform (of course) length on Orkney and Shetland: all insects fed to young in Shetland were under 4cm long, whilst saithe were between 4-8cm; rockling fed to chicks in Orkney were predominantly (85%) under 4cm long.

Chicks in Shetland in 1987 were predominantly fed on the smallest size class of sandeels, but the size of sandeels fed to chicks tended to be larger in 1988 than in 1987 (Table 14, $X^2 = 295.3$, d.f. = 3, $p < 0.001$) and and larger again in 1989 (Table 14. $X^2 = 9.95$, d.f. = 1, $p < 0.01$). In 1987 and 1989, chicks on Shetland received smaller sandeels than those at the other sites (Table 14. 1987: $X^2 = 310.9$, d.f. = 3, $p < 0.001$; 1989; $X^2 = 39.7$, d.f. = 6, $p < 0.001$). On Coquet in 1988, clupeids fed to chicks were smaller than in 1987 ($X^2 = 21.8$, d.f. = 3, $p < 0.001$). The size of fish fed to chicks increased with increasing chick age.

Table 15 shows the rate at which chicks were provisioned in terms of feeds per hour, the energy provided to the chick per feed and the rate of energy of chicks. Due to a lack of appropriate calorific values, we have not yet calculated rates of energy gain for chicks on Shetland in 1989, because of the high proportion of their diet which was insect.

The highest chick feeding frequency was recorded in Shetland in 1987. This appeared to compensate to some extent for the apparently poor quality of prey in that year (see above) since energy gain rates in 1987 and 1988 were similar (Mann-Whitney U-test, $p > 0.05$). In 1987, despite feeding their chicks more frequently (K-S z = 2.72, n = 382, n = 170) terns on Shetland provisioned their young with energy at a slower rate than those on Coquet. In 1988, there were no inter-site differences between any measures of feeding rate. In 1989 the number of trips made per hour per chick differed significantly between the three sites (K-W anova. H = 21.2, d.f. = 2, $p < 0.001$) being less on Coquet Is. than on Shetland or Orkney (multiple comparison test).

Table 15. Foraging rates of arctic terns at the study sites during chick-rearing in 1987 and 1988

	mean	s.e.	n (days)
a) Trips / Chick / Hour			
Shetland 1987	1.08	0.13	17
Shetland 1988	0.63	0.12	8
Shetland 1989	0.86	0.61	20
Coquet 1987	0.51	0.09	14
Coquet 1988	0.80	0.30	10
Coquet 1989	0.37	0.25	16
Orkney 1988	1.03	0.13	14
Orkney 1989	1.11	0.33	17
b) kJ / Trip			
Shetland 1987	3.90	1.25	17
Shetland 1988	2.40	0.22	8
Shetland 1989	-	-	
Coquet 1987	6.67	1.35	13
Coquet 1988	4.47	1.69	9
Coquet 1989	2.91	2.31	16
Orkney 1988	1.60	0.22	14
Orkney 1989	4.87	2.90	17
c) kJ / Chick / Hour			
Shetland 1987	1.66	0.29	17
Shetland 1988	1.34	0.29	8
Shetland 1989	-	-	
Coquet 1987	4.09	0.94	14
Coquet 1988	3.58	1.49	10
Coquet 1989	0.93	0.77	16
Orkney 1988	1.92	0.42	14
Orkney 1989	4.83	3.52	17

2.4 Adult weights

Changes in the body weights of breeding adult arctic terns were examined by calculating mean weights of known individuals over 10-day periods (using daily mean weights where a bird was weighed more than once in a day). Insufficient data were collected on Shetland in 1989, and the data for Coquet in 1988 will have been affected by the failure of the first breeding attempt. The relationships for each study site, in each year, between adult body mass and the number of days elapsed since laying are shown in Table 16. Measurements of adult birds trapped at the three study sites confirmed that there were no body size differences between them.

Table 16. The relationships defining the dependence of adult body mass (y) on the number of days elapsed since laying (x) ($y = a + b.x$) based on 10-day mean masses

		b	a	r	n
Shetland	1987	-0.36	116.41	-0.55 ***	15
	1988	-0.80	111.46	-0.69 ***	20
	1989	-	-	-	-
Coquet	1987	-0.89	137.92	-0.72 ***	40
	1988	-0.13	105.04	-0.12 ns	17
	1989	-0.15	112.32	-0.12 ns	13
Orkney	1988	-0.40	121.62	-0.49 *	27
	1989	-0.27	121.69	-0.54 *	31

* $p < 0.05$
** $p < 0.001$

In 1987, adult terns in Shetland were lighter than those on Coquet, but lost weight at a slower rate (Table 16, analysis of covariance. $F_{1,52} = 4.9$, $p < 0.05$). Shetland terns lost weight faster in 1988 than in 1987 (ANOVA. $F_{1,28} = 20.3$, $p < 0.001$). The relationships between adult body weight and stage of the breeding season in 1989 were the same as those observed in 1988 for terns at both Orkney and Coquet (Table 16. Analysis of covariance. ns). It is interesting that terns on Coquet have not shown significant weight loss over the season in two out of three years.

It was also interesting to note that on Coquet arctic terns rearing two young remained heavier than those rearing only one, demonstrating that weight loss is not simply an adaptive response to increase foraging efficiency. In addition the more successful birds brought in larger fish in the second week after hatching than in the first ($X^2 = 30.5$, d.f. = 3, $p < 0.001$) whereas the less successful birds did not. Consequently, birds raising two chicks brought in larger prey in the second week than those raising one ($X^2 = 29.9$, d.f. = 3, $p < 0.001$).

3. CONCLUSIONS

It is clear from this study that:

1) Arctic terns in Shetland were dependent on 1-group sandeels during the courtship and egg formation period, and on 0-group when feeding young. Over the period of this study, arctic terns in Shetland failed to obtain sufficient sandeels of the appropriate age/size-classes when they are required. This, rather than predation by gulls, was the primary cause of breeding failure.

2) There was no alternative prey of sufficient quality and profitability available in the Shetland area to compensate for the low availability of sandeels. On Orkney and Coquet, terns had access to other high quality prey such as rockling or clupeids. Terns on Shetland utilised

saithe and insects to provision their young. The restricted spectrum of high quality prey in Shetland made the birds very vulnerable to changes in sandeel stocks.

3) Adults compensated for poor food supply early in the breeding season by working harder; those birds which did breed produce a clutch of near normal size and eggs of normal quality. However, this resulted in adult arctic terns being in poor condition from early on in the breeding season. This was accompanied by desertion of eggs and young, and probably reduced their ability to compensate for poor food supply when feeding young.

4) The size of sandeels utilised in courtship feeding and chick-rearing reflects the abundance of 0-group and 1-group sandeels in the area. Furthermore, there is a very close relationship between the productivity of 0-group sandeels in the area and the breeding success of arctic terns (see Figure 4 below). These birds thus provide a good indication of changes in the population of 0-group fish in the vicinity of their breeding colonies.

5) This study had provided important data on the relationships between seabirds and sandeels and highlighted our lack of understanding of the role of sandeels in the marine ecosystem in northern Britain. It has led to a large-scale collaborative project between ourselves and an Aberdeen University group, investigating the distribution, abundance and behaviour of sandeels in relation to seabird foraging behaviour and breeding performance.

6) Irrespective of the cause of the decline of sandeel productivity and spawning stocks around Shetland, it is clearly important that conservation policies for marine birds address the requirement to protect food supplies. This is especially important in an area such as Shetland where a large community of seabirds is dependent on a single prey species.

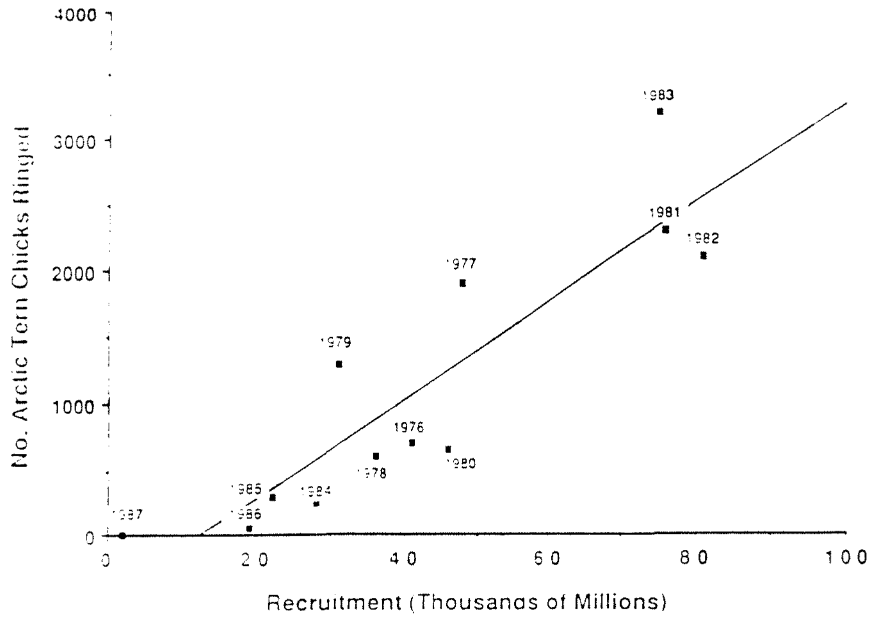

Figure 4. The relationship between the production of 0 group sandeels and the breeding success of arctic terns in Shetland

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4. REFERENCES

Bullock, I.D. & Gomersall, C.H. 1981. The breeding populations of terns in Orkney and Shetland in 1980. Bird Study 28: 187-200.

Coulson, J.C. & Megson, G. 1987. Unpublished report to the Nature Conservancy Council, CSD, Peterborough.

Harris, M.P. & Hislop, J.R.G. 1978. The food of young puffins *Fratercula arctica*. J. Zool. 185: 213-236.

Monaghan, P. & Zonfrillo, B. 1986. Population dynamics of seabirds in the Firth of Clyde. Proc. R. Soc. Edin. 90B: 363-275.

Thomas, G.J. 1972. A review of gull damage and management methods at nature reserves. Biol. Conserv. 4: 117-127.

Thomas, G.J. 1982. Breeding terns in Britain and Ireland, 1975-79. Seabird 6: 59-69.

APPENDIX 1. PUBLICATIONS ARISING FROM THIS STUDY

1. Monaghan, P., Uttley, J.D., Burns, M.D., Thain, C. & Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns *Sterna paradisaea*. J. Anim. Ecol. 58: 261-274.

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 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) Their 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 within 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 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.

2. Uttley, J., Monaghan, P. & White, S. 1989. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. Ornis Scand. 20: 273-277.

Abstract: Changes in the availability of sandeels *Ammodytes* have been shown to be the cause of recent widespread breeding failure of some surface feeding seabirds in Shetland. In this paper we compare the breeding performance and chick diet of common and arctic terns in Shetland in 1988 with a previous study of these species in north-east England, when prey availability and breeding success were good. In Shetland young Saithe *Pollachius virens* comprised 80% of the diet of common tern *Sterna hirundo* chicks in the first week of life. Chicks on this diet grew as well as those in north-east England. However, heavy predation of common tern young by avian predators appears to have occurred, and possible reasons for this are discussed. Arctic terns *S. paradisaea* concentrated on sandeels; growth of their young was poor, and the majority died in the first week after hatching. We discuss potential explanations for the apparent inability of arctic terns to exploit saithe, which may relate to the energetics of chick growth and foraging economics.

3. Monaghan, P., Uttley, J.D. & Okill, J.D. 1989. Terns and sandeels: seabirds as indicators of changes in marine fish populations. J. Fish Biol. (suppl. A) 35: 339-340.

Abstract: In Shetland, arctic terns feed mainly on sandeels, and feed 0-group fish to their young. Since 1974, sandeels have been fished in local waters and 0-group fish form a major component of the catch. Changes in the age of fish fed to females during courtship and to chicks later in the season reflected changes in the sandeel population which were indicated by Virtual Population Analysis of fisheries data. A highly significant relationship was found between an index of tern productivity from ringing data and recruitment of sandeels over a twelve year period.

4. Uttley, J., Monaghan, P. & Blackwood, J. 1989. Hedgehog *Erinaceous europaeus* predation on arctic tern *Sterna paradisaea* eggs: the impact on breeding success. Seabird 12: 3-6.

Abstract: There have been few direct observations of hedgehog predation at seabird colonies. This paper reports such an observation and documents the impact of hedgehog predation on the breeding success of a colony of arctic terns in Shetland. During incubation nocturnal nest predation and desertion were found to be very high (less than 10% of eggs hatched) at one colony where hedgehogs were present and taking eggs. The nest failure rate at another where hedgehogs were absent, was virtually zero during incubation.

5. Uttley, J. 1990. The effect of variation in food supply on the allocation of parental effort in arctic terns. Ardea in press.

Summary

1) The time budgets, and contribution to chick-rearing of male and female arctic terns, were compared at a site of poor food availability (Shetland) and a site of better food availability (Orkney).

2) On Shetland, incubation was as constant as on Orkney, but young chicks were brooded for less time when food was short.

3) When food supply was good, males and females divided the incubation duties equally during laying. However, when food supply was poor, males incubated less than females, who incubated for a greater proportion of their time than they did when food supply was good.

4) When food supply was good, females undertook a high proportion of the brooding of young chicks, whereas males fed the chicks more often and fed them larger prey than the females did. When food supply was poor, males brooded the young for the same proportion of time as they did when food supply was good, but females reduced the time for which they brooded the young. Furthermore, females fed the young as much as males did, and fed the chicks similarly sized prey to the males.

5) The results are discussed in the light of other data on courtship feeding rates, clutch size, egg size and quality and adult body condition. The paper concludes that arctic terns can make adjustments during the laying period in order to compensate for poor food availability when eggs are being formed by the female.

6. Monaghan, P., J.D. Uttley & M.D. Burns. 1990. Effect of changes in food availability on reproductive effort in arctic terns. Ardea in press.

Abstract: The breeding effort of arctic terns in two conditions of low food availability in Shetland (A - poor food supply during courtship and very poor during chick-rearing; B - very poor during courtship and poor during chick-rearing) was compared to that of arctic terns breeding in two areas of good food supply. In Shetland situation B courtship prey were very small, and males provisioned females at a relatively high rate. Neither the onset of laying nor egg size appeared to be affected; clutch size was slightly reduced in Shetland B, and a significantly higher proportion of birds deserted during incubation. Sandeels were the main chick prey and feeding rates were highest when prey were small. No young fledged in the Shetland situations. Adults at the good food supply sites were heavier than those in Shetland and there was a significant positive relationship between adult weight at the time of hatching and the time to nest failure. These data are discussed in relation to the proximate role of food supply in influencing reproductive decisions and a model is proposed suggesting that individual arctic terns have a critical threshold body weight below which they abandon breeding.

7. Uttley, J. 1991. The influence of food supply on the parental investment of arctic terns *Sterna paradisaea*. Unpubl. Ph.D. Thesis, Univ. of Glasgow.

Summary: The aims of this project were to examine the effects of food shortage on the breeding biology of the arctic tern *Sterna paradisaea*, a small, surface-feeding seabird with a short foraging range in the breeding season. A comparative approach was adopted, and various aspects of arctic tern breeding biology were studied both on Shetland, where the main prey of arctic terns, lesser sandeels *Ammodytes marinus* are less available than they have been previously, and other suitable prey are absent, and on Orkney, where food supply for arctic terns appears to be better. Further data from Coquet Island, Northumberland, collected during a broader study, of which this study is a part, were also utilised.

Investment in egg production was investigated through measurements of courtship feeding rates and clutch size, egg size and quality. This was followed by analyses of the time budgets of male and female arctic terns during laying, incubation, hatching, early chick life and later chick life. The results showed that egg production was little affected, if at all, by food shortage, and evidence was presented to show that adjustments in male and female investment patterns enabled the maintenance of clutch quality. This is discussed in relation to arctic terns' breeding strategy.

The performance of adult arctic terns feeding chicks was assessed in detail, in relation to food supply, brood age and weather conditions. Differences in the diet of chicks and the rate at which they were provisioned were discussed and the profitability of feeding sandeels to chicks was shown to be lower on Shetland than on Orkney. Potential reasons why arctic terns did not exploit alternative prey to a greater extent were discussed. The behaviour of arctic terns in a situation of food shortage was also shown to influence the rate at which young were provisioned. Conspecific kleptoparasitism had a very large impact on chicks' food intake rates at the poor food supply site, and the occurrence of kleptoparasitism and its frequency for different prey categories was shown to concur with predictions from the literature. A model showed that the risk of kleptoparasitism could not explain the lack of large prey items in the diet of chicks in terms of energetics, and other explanations were discussed. Diversion of food from chicks to females was also more frequent where food supply was poor, and the implications of this were also discussed.

Finally the results of a pilot study into the free-ranging energetics of arctic terns, as measured by the doubly-labelled water method, were presented. Although inconclusive, the results suggested that arctic terns raising young in conditions of food shortage may incur high levels of energy expenditure. The usefulness of the doubly-labelled water technique is discussed in the light of its potential behavioural consequences.

8. Monaghan, P., Uttley, J.D. & Burns, M.D. 1991. The influences of changes in prey availability on the breeding ecology of terns. In: Proceedings of the XX International Ornithological Congress, Christchurch, New Zealand.

Abstract: Small surface feeding seabirds such as terns have restricted foraging ranges and less lee-way in the annual budgets than larger species. They are particularly sensitive to changes in prey availability. There is a good relationship between tern breeding success in both west and northern Scotland and fisheries estimates of prey abundance. Arctic terns in Shetland are dependent on 0-group sandeels to feed their young, but on older age classes during courtship feeding. Recent dramatic changes in the availability of different age classes of sandeels have been found to affect the breeding ecology of terns in different ways. Studies of reproductive effort and the adult body condition of arctic terns in Shetland in comparison with birds breeding successfully elsewhere have shown that adult condition is an important determinant of the outcome of the breeding attempt. In Shetland, the performance of the terns at different stages in the breeding cycle, and comparisons with other seabird species, provide a good indicator of changes in the size and structure of sandeel populations in the vicinity of their breeding colonies.

9. Uttley, J., Tatner, P. & Monaghan, P. in prep. The free-living energetics of arctic terns *Sterna paradisaea*. (provisionally for submission to Auk)

10. Uttley, J. in prep. Food supply and prey quality as determinants of the incidence of kleptoparasitism in arctic terns *Sterna paradisaea*. (provisionally for submission to Animal Behaviour)

11. Uttley, J. in prep. No reduction of arctic tern egg quality when food supply is poor. (provisionally for submission to Ornis Scand.)

12. Dodman, T. & Uttley, J. in prep. Factors affecting the breeding success of arctic terns on Papa Westray, Orkney. (provisionally for submission to Bird Study/Scottish Birds/Seabird)

13. Uttley, J. in prep. The potential effect of low barriers to restrict the movement of tern chicks on predation rate. (provisionally for Seabird/J. Field Ornithol.)

Further analyses of adult body weight data from 1988 and 1989 are being performed, the emphasis being on individual weight changes and how this relates to patterns of investment and breeding success.