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The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland

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We measured the breeding performance, body condition, time budgets and foraging ranges of Kittiwakes *Rissa tridactyla* at Sumburgh Head, Shetland, in two years of contrasting food availability. Kittiwakes in Shetland generally feed their young almost entirely on sandeels, and fisheries data indicated that stocks of sandeels in Shetland waters were at least ten times higher in 1991 than in 1990. Fledging success of Kittiwakes was nil in 1990 and 68% of eggs laid in 1991, although clutch-size and hatching success were no different between years. Post-hatching foraging trips in 1991 were of comparable duration to those recorded at other colonies in conditions of good food supply (2–3 h), while trips recorded during incubation or post-hatching in 1990 were approximately three times longer on average than at corresponding stages of the breeding season in 1991. Radio-tracking data indicated that adults generally stayed within 5 km of the colony in 1991 but flew more than 40 km from the colony on each trip in 1990. Eggs were apparently not left unattended in either year, despite the fact that this required adults to incubate for periods in excess of 44 h in 1990. The extent to which adults were able to increase trip durations, foraging ranges and incubation shift lengths between years, while maintaining hatching success, indicates the degree to which Kittiwakes are normally buffered against adverse feeding conditions during incubation. Reduced nest attendance and lower body-condition of adults post-hatching in 1990, in conjunction with complete post-hatching breeding failure, indicate that adults were beyond the limits of their buffering capacity during chick-rearing in 1990.

The responses of seabirds to changes in prey availability have attracted much attention in recent years, particularly with respect to life history theory (e.g. Martin 1987, Hamer *et al.* 1991) and to monitoring of marine fish stocks (e.g. Baird 1990, Burger & Piatt 1990). Cairns (1987) emphasized that the extent to which different parameters of breeding ecology are affected by changes in available food supply depends upon both the magnitude of the change and the actual levels of food supply which birds experience. Effects are also likely to vary between species, with features such as surface feeding, specialized and inflexible feeding habits, limited foraging ranges, limited ability to increase time spent foraging and energetically expensive food-searching techniques all making some species more susceptible than others to perturbations in their food supply (Furness & Ainley 1984).

Sandeels *Ammodytes marinus* were the main component in the diets of most seabird species breeding in Shetland during the 1970s and early 1980s (over 90% in most cases; Martin 1989, Monaghan *et al.* 1989, Hamer *et al.* 1991). The availability of sandeels to seabirds in Shetland declined markedly during the 1980s, due to a three- to four-fold reduction in sandeel stock biomass and recruitment (Kunzlik 1989, Bailey *et al.* 1991). The effects of this decline in prey availability upon breeding success varied greatly between species, possibly due to differences in ability to forage at depth or to utilize alternative prey (Heubeck 1989, Bailey *et al.* 1991).

Kittiwakes *Rissa tridactyla* in Shetland generally feed their young almost entirely on sandeels, which they catch at or just below the surface of the sea (Harris & Wanless 1990). Breeding success of Kittiwakes in Shetland fell markedly during the late 1980s in conjunction with the decline in stocks of sandeels in Shetland waters (in most colonies to zero; Walsh *et al.* 1991, Danchin 1992).

Previous studies of the responses of Kittiwakes to reductions in food supply have described changes in diets (Barrett & Furness 1990) and breeding success (Springer *et al.* 1986) that have been linked to changes in the marine food chain (Aebischer *et al.* 1990). These studies have suggested that patterns of nest attendance by breeding adults change in years of poor food supply (Galbraith 1983, Barrett & Runde 1980), but they were not able to assess the extent of changes in nest attendance because of a lack of knowledge concerning the typical situation in periods of abundant food supply. Coulson & Wooller (1984) and Coulson & Johnson (in press)

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described the nest attendance patterns of Kittiwakes at a colony in northeast England during a period of high breeding success (1.23 young fledged per pair that laid eggs). However, variations between colonies in patterns of nest attendance have not been investigated, and to date no studies have examined variation at one colony in relation to food supply. One effect of low food availability may be that an increase in foraging effort results in a decline in adult body-condition (body-mass corrected for body-size), as has occurred in Arctic Terns *Sterna paradisaea* (Monaghan *et al.* 1989). Such effects have not been examined in Kittiwakes.

Studies of responses to changes in food supply are often restricted by a lack of simultaneous data on prey abundance (Burger & Piatt 1990). In Shetland, research-vessel surveys using small-mesh midwater trawls in conjunction with echolocation (see Bailey *et al.* 1991 for details of methods) indicated that in 1991 stocks of 0-group sandeels (those most commonly taken by seabirds) were at least ten times higher than in 1990 (P. Monaghan *et al.*, unpubl. data). This allows the responses of seabirds to a quantifiable change in prey abundance to be examined by comparing between 1990 and 1991.

This paper examines the breeding success, adult body condition, diets and colony attendance patterns of Kittiwakes breeding in Shetland in 1990 and 1991. In addition, we use radio-tracking data to assess whether or not changes in periods of absence from the colony are representative of changes in distances travelled by adults.

METHODS

Breeding data for Kittiwakes at Sumburgh Head on the southern tip of mainland Shetland were collected in 1990 and 1991. Actively occupied nests (Heubeck *et al.* 1987) at a plot of approximately 50 nests on the western side of Sumburgh Head were mapped and numbered in late April, and the numbers and fates of eggs laid at them were determined by regular (usually daily) observations, throughout the breeding season, from a wooden hide placed approximately 200 m from the plot.

A random sample of adults breeding in the plot or at nearby sites within the colony was caught at their nests during incubation or chick-rearing, using a nylon noose attached to the end of a roach pole. Adults were weighed using a Pesola spring balance, and the following measurements were taken: maximum wing chord (ensuring the outermost primary feather was fully grown), tarsus-length and length of head-plus-bill. Independent duplicate measurements, taken in accordance with the procedure recommended by Barrett *et al.* (1989), differed by no more than 1.7% between measurers. Sexes of trapped birds were determined from their head-plus-bill lengths (Coulson *et al.* 1983) and checked where possible by behavioural observations (position during copulation for colour-ringed birds; see below). The two methods were in agreement in every case.

Most adults caught within the study plot were given a unique combination of either three or four colour-rings in combination with a monel ring. In addition, all were marked with picric acid. The first adult caught at each nest was marked on the breast and tail; at nests where both adults were caught, the second was marked on the crown of the head. During incubation in 1990, adults were marked with a swab soaked in picric acid and attached to the end of a roach pole.

Measurements and weights of adults were used to calculate an index of body-condition, in terms of body-mass corrected for body-size (Reid 1988, Hamer & Furness 1991). An index of body-size was calculated from body measurements using principal components analysis (Norusis 1991; the index produced by the analysis is the sum of variables standardized to have means of nought and standard deviations of one). Body-mass was regressed upon the factor score representing body-size, and the residuals, each expressed as a proportion of the predicted mass, were used as a measure of body-condition. This measure was used in two analyses of variance to determine whether body-condition varied between years and sexes or, in 1991, with stage of the breeding season.

The diet of birds at the colony was determined from samples of food regurgitated by adults during handling. These were collected in polythene bags and stored at −5°C for subsequent identification in the laboratory.

Attendance of marked adults and their partners at the colony was assessed by continuous observation of birds leaving or returning to their nests. Birds were observed continuously during daylight hours (between 0300h and 2300h B.S.T.) on 14 days between 6 June and 16 July 1990 (280 h of observation—160 h before the median hatching date, 120 h after it—of which 240 h were in six separate periods, each of two consecutive days) and on 13 days between 15 June and 20 July in 1991 (260 h—140 h before the median hatching date, 120 h after it). A team of observers, all of whom were familiar with the plot, worked in relay for periods of 4 h and noted any arrivals or departures to the nearest minute. In addition, the identity (marked or unmarked) of each bird at a nest was checked at half-hourly intervals throughout the observation period to determine whether any arrivals or departures had been missed. Any such cases (less than 10% of the total) were assumed to have left or arrived mid-way through the preceding half-hour, producing an error of up to 15 min in the estimated time of arrival or departure, with an average error of 7.5 min. Data were recorded only from nests with eggs or live chicks.

Attendance data were used to calculate the time in minutes between an adult leaving its nest and returning to the nest (trip duration) and the number of times that partners changed over at the nest (changeover frequency). In calculating trip duration, we excluded trips started after 1800h each day in 1991 and after 1800h on the second of two consecutive days of observation in 1990, because these were likely to overrun the observation period. We also excluded trips of less than 30-min duration, because these were likely to include a large proportion of non-feeding trips (see Coul-

Table 1. *Breeding data for Kittiwakes at Sumburgh Head, Shetland, in 1990 and 1991*

Year studied	No. nests studied	Clutch size		Hatching success[1] (%)	Fledging success[2] (%)	Breeding success[3] (%)	Mean no. chicks fledged per nest
		Mean	s.d.				
1990	47	1.60	0.50	81.3	0.0	0.0	0.00
1991	52	1.45	0.50	79.7	84.8	67.6	0.98

[1] Number of eggs hatched, expressed as a percentage of the number laid.
[2] Number of chicks fledged, expressed as a percentage of the number hatched.
[3] Number of chicks fledged, expressed as a percentage of the number of eggs laid.

son & Johnson in press). Comparisons of trip durations and changeover frequencies between years were made on the basis of nest means obtained during incubation and chick-rearing.

Attendance data were recorded only during hours of daylight (0300h–2300h B.S.T.) and, in 1990, birds that were absent at the end of one day's recording and the beginning of the next were assumed not to have returned and departed again in the intervening 4 h. This was unlikely to overestimate trip length, since Kittiwakes generally roost offshore rather than return to the colony during darkness (Coulson & Wooller 1984), and any bird which arrived at night would be very unlikely to depart again before dawn.

In addition to the above, we also calculated the proportion of each observation period for which eggs or chicks were left unattended by both parents simultaneously (calculated separately for each nest, then combined to produce mean values across all nests for incubation and chick-rearing periods in both years).

Distances travelled by breeding adults were determined in both years by attaching radio-transmitters to adults incubating eggs or rearing chicks (n = 13 birds in 1990; n = 9 birds in 1991) and tracking them throughout periods of absence from the nest. Each transmitter weighed 5 g and was approximately 1 cm wide, 1 cm high and 3 cm long, with a 25-cm horizontal whip antenna which protruded *c.* 20 cm beyond the tail. Transmitters were attached, by means of adhesive tape and two small plastic cable ties, to the central tail feathers of birds caught at their nests. These transmitters have been shown to have little effect upon behaviour in Kittiwakes (see Wanless *et al.* in press) and did not affect trip durations in this study (Kruskal–Wallis one-way analysis of variance, $P > 0.1$).

Signals were detected from a static receiving station using two scanning receivers, one connected to a three-element Yagi antenna (used for monitoring birds at the colony), the other to two eight-element Yagi antennae arranged in parallel (used for tracking birds when they were away from the colony). Both were situated on a tracking hut at Sumburgh Head (90 m a.s.l.), and a null-peak system was used to determine the direction, corrected to true north, in which the signal was strongest. Trials using identical transmitters held at a height of 2 m above the ground or mounted on a fishing boat at a height of 5 m above the sea indicated that this system could detect signals up to 40 km from the receiving station with an accuracy of ±3° (Wanless *et al.* in press).

Signals were also detected with an eight-element Yagi antenna mounted on a vehicle and placed between 2 and 10 km from the static receiving station. This allowed the location of birds wearing transmitters to be determined by triangulation. The accuracy of this method was assessed by using a light aircraft fitted with two three-element Yagi antennae to search for tagged birds at locations indicated by triangulation. This was successful in every case.

Individual birds were followed continuously (or searched for, if out of range) for periods of up to 44 h in 1990 and 20 h (between 0300h and 2300h) in 1991. The amount of information collected for each bird varied due to differences in the life of individual radio-tags, but most birds were followed for 5–10 days.

RESULTS

Breeding success, body-condition and diet

Adults laid eggs at 47 nests within the study plot in 1990 and at 52 (of which 49 were clearly visible from the hide) in 1991. Among these birds, there was no difference between years in clutch-size or hatching success (Table 1; for clutch-size, $\chi^2_1 = 1.51$, $n = 99$, $P = 0.22$; for hatching success, $\chi^2_2 = 0.78$, $n = 99$, $P = 0.68$). However, fledging success differed markedly between years (zero in 1990 and 85% of chicks hatched in 1991; Table 1; $\chi^2_2 = 59.7$, $n = 99$, $P < 0.001$). Chicks died on average 14 days after hatching (range = 2–38 days) in 1990 and 28 days after hatching (range = 23–28 days) in 1991.

A total of 19 adults was caught at 18 nests (all in the study plot) during chick-rearing in 1990. A further 64 were caught at 54 nests (25 in the study plot, 29 at neighbouring sites within the colony) during incubation (n = 21) or post-hatching (n = 43) in 1991. Post-hatching body-mass was related to body-size index by the equation: *mass* (g) = 13.8*size* + 380 (Fig. 1; linear regression; $F_{51,1} = 18.5$, $P < 0.001$). Based

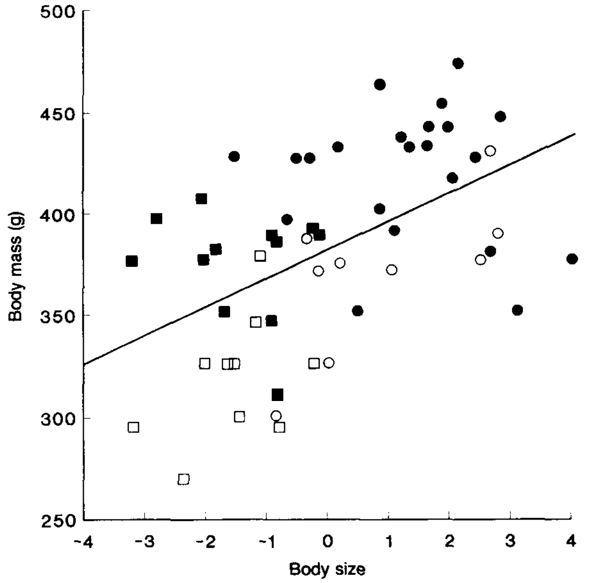

Figure 1. Post-hatching body-mass against body-size for male and female Kittiwakes breeding at Sumburgh Head, Shetland, in 1990 and 1991. Open figures are data for 1990; solid figures are data for 1991. Squares are females; circles are males.

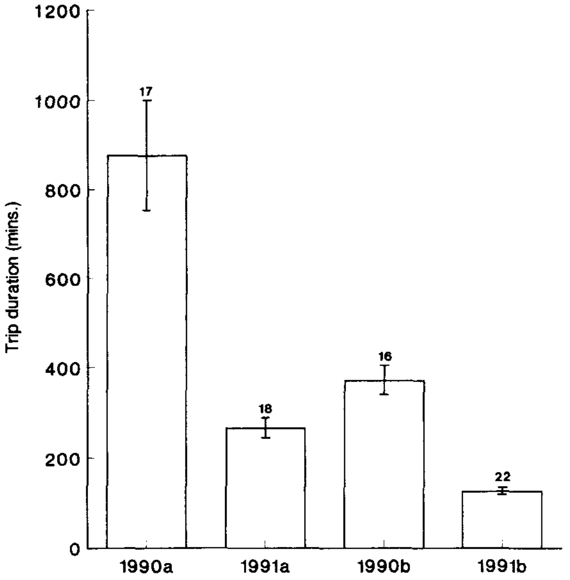

Figure 2. Average trip lengths per nest for Kittiwakes in 1990 and 1991, according to stage of season: a = incubation; b = post-hatching. Error bars are ±1 s.d. Figures above bars are numbers of nests.

upon residuals from this regression, adults of similar size were 15% heavier on average post-hatching in 1991 than in 1990 (Fig. 1). This difference was highly significant (two-way analysis of variance of body-condition, with normally distributed homoscedastic data; $F_{52,1} = 27.2$, $P < 0.001$; sample sizes are less than the number of adults caught because not all variables used to calculate body-condition were measured for all adults). There was no significant difference between post-hatching body-condition of males and females in the two years ($F_{52,1} = 2.8$, $P = 0.1$). Body-condition in 1991 (calculated from a separate regression for birds caught during incubation or post-hatching in this year) did not differ significantly between sexes (two-way ANOVA; $F_{54,1} = 2.0$, $P = 0.2$) or stages of the season ($F_{54,1} = 1.2$, $P = 0.3$).

In total, 27 adults produced regurgitates in 1991, while only seven did so in 1990. All regurgitates in both years were composed entirely of sandeels.

Trip durations and ranges

Trip durations were recorded on 142 occasions from 21 nests in 1990 (43% from 17 nests during incubation, 57% from 16 nests during chick-rearing; four of the latter were not marked during incubation). In 1991, trip durations were recorded on 966 occasions from 25 nests (30% from 18 nests during incubation, 70% from 22 nests during chick-rearing; seven of the latter were not marked during incubation). The proportions of trip durations not recorded—because the observation period either started after adults had left their nests or finished before adults returned to their nests—were 33.2% and 25.1%, respectively, in 1990, and 17.7% and 9.3%, respectively, in 1991. In addition, seven trip durations (2.0%) were not recorded in 1990 because birds were absent from the colony for an entire 44-h observation period; 35 trip durations recorded in 1990 (24.6%) included absences overnight.

Average trip durations per nest were approximately twice as long during incubation as during chick-rearing in both years, and trips at corresponding stages of the season were approximately three times as long in 1990 as in 1991 (Fig. 2; two-way ANOVA; for effect of stage of season, $F_{72,1} = 25.7$, $P < 0.001$; for effect of year, $F_{72,1} = 48.5$, $P < 0.001$). Birds fitted with radio-tags generally travelled out of range of the receivers in 1990 (a round-trip of at least 80 km; Wanless *et al.* in press), whereas only four of 117 trips (3.4%) were of this length in 1991, all others staying within 5 km of the colony.

Changeover frequencies

Changeovers were recorded on 251 occasions (49.8% during incubation, 50.2% during chick-rearing) in 1990 and 1607 occasions (30.8% during incubation, 69.2% during chick-rearing) in 1991. The number of changeovers recorded in 1991 exceeded the total number of trips (complete plus incomplete trips) recorded because trips that commenced after 1800h were excluded from the latter analysis.

Figure 3 shows the number of changeovers occurring at different times of day in both years (excluding changeovers resulting from trips of less than 30 min duration) during incubation and chick-rearing. Data for 1990 are the result of approximately 50% fewer nest-hours of observation post-

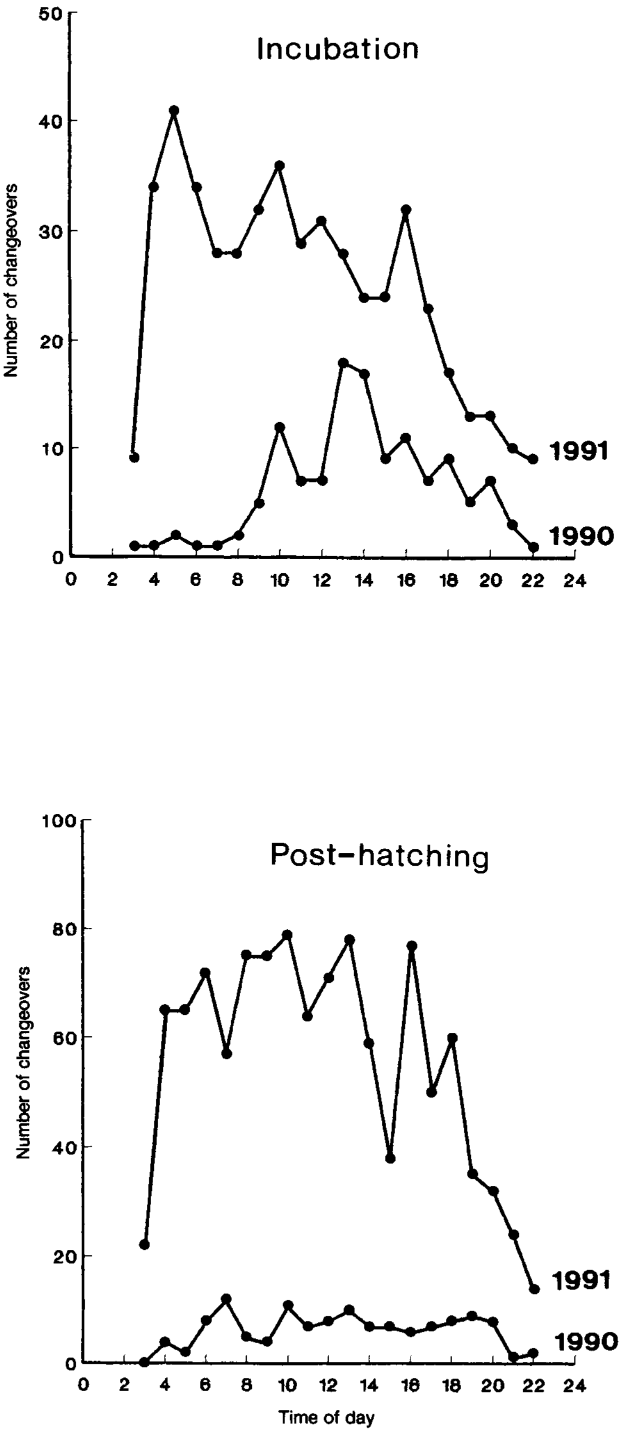

Figure 3. Number of changeovers of nesting Kittiwakes with time of day in 1990 and 1991 during incubation and post-hatching. Note the different scales on the *y*-axes.

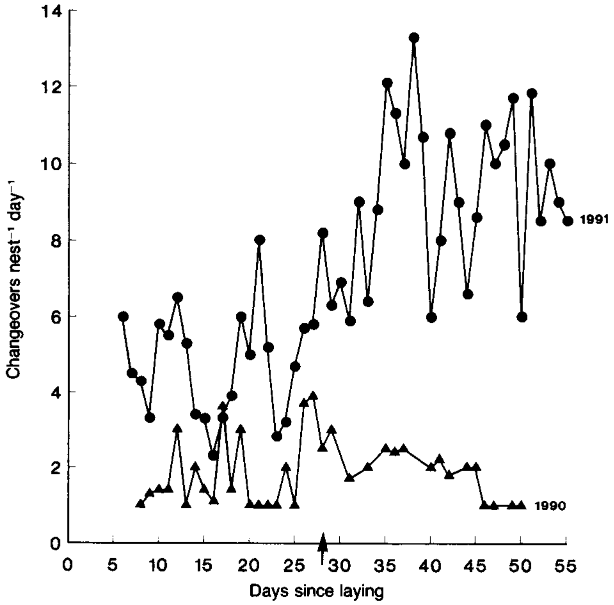

Figure 4. Mean number of changeovers of Kittiwakes per nest per day relative to laying date in 1990 and 1991. The arrow denotes approximate time of hatching.

hatching, the difference between years being due mainly to nest failure. Data for the two years are therefore not directly comparable in terms of absolute numbers of changeovers, although diurnal patterns are comparable. At both stages of the season in 1991, the number of changeovers per hour rose sharply between 0300h and 0400h and declined rapidly after 1600h. In 1990, the frequency of changeovers during incubation rose gradually to a peak during the early afternoon before declining throughout the rest of the day, whereas changeovers post-hatching showed no pronounced pattern. In both years and at both stages of the season, changeovers occurred at their lowest frequencies before 0400h and after 2000h.

Figure 4 shows the mean number of changeovers per nest per day, relative to laying date, during daylight hours in 1990 and 1991. In 1991, the frequency of changeovers rose markedly after hatching (median, accounting for differences in the numbers of nests producing each daily changeover rate, = 4.5/day during incubation, 8.8/day post-hatching). In 1990, changeovers occurred at low frequency throughout the season (median = 1.4/day during incubation, 2.4/day post-hatching). Median changeover rate varied significantly between years (non-parametric two-way ANOVA, Zar 1984; $H_{360,1} = 176.2$, $P < 0.01$) and stages of the season ($H_{360,1} = 70.2$, $P < 0.01$).

Frequency and timing of nest desertion

Observations of attendance were made at half-hour intervals at nests with eggs or live young on 8512 occasions in 1990 (67% during incubation, 33% during chick-rearing) and on

Table 2. *Percentage of observations for which neither adult of a Kittiwake pair was present at the nest during incubation and chick-rearing in 1990 and 1991*

Year studied	Incubation			Chick-rearing		
	n	Mean	s.d.	*n*	Mean	s.d.
1990	21	0.01	0.02	20	16.7	15.6
1991	18	0.00	0.00	22	0.04	0.11

n = number of nests. s.d. = standard deviation of each mean. Sample sizes in 1990 are greater than those for trip durations because complete trips were not recorded from four nests.

10,578 occasions (58% during incubation, 42% during chick-rearing) in 1991. Table 2 shows the proportion of observations for which neither adult was in attendance, expressed as a mean across all nests, for incubation and chick-rearing periods in both years. Nests were almost never left unattended in 1991 or during incubation in 1990, whereas they were unattended on 17% of observations during chick-rearing in 1990. Statistically, there was no difference between years during incubation (Mann–Whitney *U*-test; $Z = -1.0$, $n = 39$ nests, $P = 0.34$), whereas there was a highly significant difference between years for nests with live chicks ($Z = -4.0$, $n = 42$ nests, $P < 0.01$). In 1990 all but two chicks were first deserted within ten days of hatching and all were deserted within 15 days of hatching.

DISCUSSION

Relationship with changes in sandeel stocks

Fisheries data indicate that changes in the breeding ecology of Kittiwakes in Shetland between 1990 and 1991 were related to changes in stocks of sandeels in surrounding waters. However, although in northern Britain sandeels are a major source of food for Kittiwakes in the breeding season, they may be unimportant in winter and spring (Coulson & Thomas 1985, Aebischer *et al.* 1990), presumably because they shoal less frequently at the surface at these times (Pearson 1968). Clutch-size and hatching success of Kittiwakes at a colony in northeast England declined during the 1960s and 1970s in conjunction with spring food supply (herring *Clupea harengus*), despite the presence of apparently normal stocks of sandeels during the summer (Coulson & Thomas 1985). This was attributed to 'carry-over' effects of food shortage from the spring period, persumably affecting adult body-condition and egg production capacity.

This raises the possibility that recent changes in the breeding success of Kittiwakes in Shetland are related to food supply during the pre-breeding period rather than during the breeding season itself. However, in our study, clutch-size and hatching success showed little variation between years, whereas fledging success was greatly affected (Table 1). This could indicate that food supply pre-hatching did not differ between years, if hatching success and fledging success are indices of food availability during periods within the breeding season (Cairns 1987). However, trip durations and changeover frequencies differed between years by a factor of three during incubation (Figs 2 and 4), and the delayed onset of breeding failure in 1990 probably reflects the extent to which adults were able to buffer themselves against reduced food supply by increasing the durations of foraging trips and incubation shifts. Although we have no data concerning chick growth (chicks were not accessible at the study plot), the main cause of chick mortality in 1990 appeared to be starvation. Changes in breeding ecology between years were thus attributable to events during the summer rather than prior to the start of the breeding season. These changes were almost certainly related to changes in the availability of sandeels, although our sample of years was small, and there were parallel trends between variation in sandeel stocks and other environmental factors (Aebischer *et al.* 1990).

Several studies have recorded changes in the diets of seabirds following reductions in the availability of main prey items (e.g. Montevecchi *et al.* 1988, Martin 1989). The diets of Kittiwakes in northern Norway changed considerably following a decline in stocks of capelin *Mallotus villosus* in the Barents Sea (Barrett & Furness 1990). By contrast, food items regurgitated by Kittiwakes at Sumburgh Head consisted entirely of sandeels even when stocks of sandeels in surrounding waters were very low. Although data for 1990 are based on a small sample size, they are consistent with data from at least one other colony in Shetland (R.W. Furness, pers. comm.). The lack of any dietary switching is due in part to a lack of availability of alternative food items. Sprats *Sprattus sprattus* have been absent from Shetland waters since the late 1970s (Corten 1986), and young herring do not occur in the area (Kunzlik 1989). Furthermore, Kittiwakes in Shetland are unable to make efficient use of discards from trawlers as an alternative food supply (Hudson & Furness 1988). This lack of dietary switching may also reflect, to some extent, the nutritional requirements of chicks, since other species of fish which may have been available (e.g. saithe *Pollachius virens* and whiting *Merlangius merlangus*; see Uttley *et al.* 1990) have lower calorific density than sandeels (Harris & Hislop 1978). Chick growth and post-fledging survival of Great Skuas *Catharacta skua* are related to the proportion of sandeels in the diet (Hamer *et al.* 1991) and, if the same is true for Kittiwakes in Shetland, this may place a constraint upon the use of alternative food resources to feed chicks.

Changes in activity patterns and comparison with other studies

While diet showed little variation between years, presumed foraging trips were approximately three times longer on average in 1990 than at corresponding stages of the season in 1991 (Fig. 2). The maximum trip durations that could be recorded were 20 h in 1991 and 44 h in 1990. However, this difference in methodology did not contribute significantly towards the difference between years in recorded trip duration because less than 1% of trips recorded in 1991 were longer than 10 h and the longest recorded was 16.7 h (3.3 h short of the maximum that could have been recorded). In 1990, by contrast, 22% of recorded trips were longer than 10 h, the longest recorded trip duration was 44 h and a further 2% were definitely in excess of 44 h.

Trips that included a period spent roosting offshore overnight were generally longer than those that did not, the average difference being roughly equal to the number of hours of darkness (Coulson & Wooller 1984)—4 h in this study. In 1990, 25% of the trips recorded included an overnight period, which could account for a difference in trip duration between years of around an hour on average. However, the recorded difference between years was much longer than this (over 10 h during incubation and over 4 h during chick-rearing; Fig. 2).

Trip durations were determined for only 42% of trips in 1990 and 73% of trips in 1991. However, evidence from changeover rates (Fig. 4) suggests that recorded trips were not substantially different in duration to trips with the beginning or end missed. Changeover rates can be used to calculate expected trip durations, because nests were not left unguarded (except post-hatching in 1990) and changeover intervals were generally less than a minute (in keeping with other studies; Galbraith 1983, Coulson & Wooller 1984). The rates recorded during incubation and post-hatching in 1991 (4.5/20 h and 8.8/20 h, respectively) produce estimated trip durations of 4.4 h and 2.3 h, respectively. These are close to the observed values of 4.5 h during incubation and 2.1 h post-hatching. Similarly, the changeover rate during incubation in 1990 (1.4/20 h) produces an estimated trip duration of 14.3 h, which is close to the observed value of 14.6 h. While the average trip duration expected from changeover frequency post-hatching in 1990 (8.3 h) is 34% higher than the observed value of 6.2 h, this difference is probably due to adults leaving chicks unguarded in 1990, which would decrease the rate of changeovers at the nest. Since changeover frequency is a good estimator of trip duration when chicks are not left unattended, it may be used in such circumstances as a convenient index of trip duration, without the need to monitor birds during entire periods of absence from the nest.

The durations of such periods are an indication of foraging effort, although individuals may carry out other activities whilst away from the colony; Gabrielson & Mehlum (1988) suggested that adult Kittiwakes spend around half the time away from the nest foraging. In our study, periods of absence from the colony reflected distances travelled by adults, since radio-tagged birds habitually flew more than 40 km from the colony in 1990 but stayed within 5 km of Sumburgh in 1991.

The average duration of post-hatching daytime trips in Shetland in 1991 (2.1 h) is close to figures of 2.6 h and 2.8 h for similar trips recorded at colonies in northeast England during periods of abundant food supply and high breeding success (Pearson 1968, Coulson & Johnson in press). This suggests that average trip durations of 2–3 h may be the norm for Kittiwakes rearing chicks in conditions of good food supply.

In our study, changeovers occurred at their lowest frequencies between 2000h and 0400h in both years (Fig. 3). This is in keeping with a similar pattern recorded in northeast England (Coulson & Johnson in press). In 1991, changeover frequency at Sumburgh Head increased rapidly after 0400h (Fig. 3). This was probably due to birds returning from overnight roosting sites (Coulson & Wooller 1984), although Kittiwakes have been recorded feeding at night (Coulson & Johnson in press). In 1990, changeover rates did not increase until 0600—0900h, which suggests that adults were probably spending the night further from the colony in 1990, an impression supported by radio-tracking data (Wanless *et al.* in press).

Eggs were virtually never left unattended during recording periods in either year (Table 2). Although desertions for short periods are easy to miss if observations are not made sufficiently frequently, we recorded attendance continuously, with additional checks on each nest at 30-min intervals. In 1990, adults were apparently willing to remain on the nest for continuous periods in excess of 44 h, which is considerably longer than the longest period recorded in 1991 (16.7 h). Some adults may have deserted their eggs overnight in 1990, although radio-tagged birds did not, and adult Kittiwakes are capable of remaining at the nest without access to water for periods of up to 67 h (Coulson & Wooller 1984). Nocturnal desertion of eggs has been recorded in several species of gull but serves primarily as a mechanism for avoiding nocturnal predation (Drent 1970, Chardine & Morris 1983), which does not affect Kittiwakes at Sumburgh Head.

Chicks were virtually never left unguarded during the day in 1991, whilst in 1990 they were deserted for 17% of the daytime on average (Table 2). This agrees with a similar pattern found at colonies on the Barents Sea coast (Barrett & Runde 1980). At a colony in northeast England, in a year with good food supply, chicks were not left unguarded until they were about 20 days old (Coulson & Johnson in press), whereas in our study virtually all chicks were first left unguarded within 10 days of hatching in 1990. While these two comparisons indicate that the frequency and timing of desertion vary with food supply, daytime desertion rates recorded by Coulson & Johnson (in press) following the first desertion at each nest were similar to those found in 1990 in Shetland. Furthermore, Galbraith (1983) found that chicks at a colony on the Isle of May were never left unguarded during the daytime in a year with moderately poor food supply.

Kittiwakes at Sumburgh Head experience substantial breeding failure due to predation by Great Skuas, and differences among colonies in the willingness of adults to leave chicks unguarded probably result from differences in the likelihood of unguarded chicks suffering predation (Galbraith 1983). Caution should therefore be exercised in interpreting changes in nest desertion patterns in relation to food supply, as different pressures may operate in different environments.

Buffering against adverse environmental conditions

The extent to which adults were able to increase trip durations, foraging ranges and shift lengths between years (Fig. 2), while maintaining hatching success (Table 1), indicates the degree to which birds breeding in 1991 were buffered against adverse feeding conditions during incubation. Reduced nest attendance and lower body-condition of adults post-hatching in 1990 (Table 2, Fig. 1), in conjunction with complete post-hatching breeding failure (Table 1), indicate that adults were beyond the limits of their buffering capacity during chick-rearing. The willingness of adults to leave chicks unguarded in 1990, even though average trip durations were only half as long post-hatching as during incubation (Fig. 2), suggests an additional constraint upon shift length during chick-rearing. This may have been the result of poor adult body-condition (Fig. 1) or of a need to maintain chick provisioning rates (Barrett & Runde 1980, Galbraith 1983).

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