The Condor 95:330–342

BEHAVIORAL ECOLOGY OF BLACK-LEGGED KITTIWAKES DURING CHICK REARING IN A FAILING COLONY[1]

BAY D. ROBERTS[2] AND SCOTT A. HATCH[3]
Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service,
1011 East Tudor Road, Anchorage, AK 99503

Abstract. Compared with their Atlantic counterparts, Black-legged Kittiwakes (*Rissa tridactyla*) in North Pacific colonies are notably unproductive. A large colony on Middleton Island, Alaska, has in most years since 1981 seen complete breeding failure and the population has declined by half. We compared parent-offspring behaviors in this colony during two years that differed in overall breeding success. Potential indicators of food stress included parental attendance at the nest, foraging trip lengths, chick feeding and begging rates, and sibling aggression. Whereas chick feeding and begging rates were strongly correlated with overall breeding performance, patterns of time allocation by adults (nest attendance and foraging trips) were not. Contrasts between years and comparisons with data from other colonies in and outside Alaska point to food shortage as the likely cause of recurrent breeding failure on Middleton.

Key words: Black-legged Kittiwake; Rissa tridactyla; *behavior; breeding failure; food shortage; Alaska.*

INTRODUCTION

The Black-legged Kittiwake (*Rissa tridactyla*) is an abundant seabird in temperate to arctic regions of the North Pacific and North Atlantic oceans. It breeds colonially in groups comprising a few birds to tens of thousands of birds on island or mainland cliffs. Because their colonies and nests are conspicuous and easy to observe, kittiwakes have been studied extensively in both northern ocean systems (e.g., Barrett 1978, Coulson and Thomas 1985, Hatch and Hatch 1988, Harris and Wanless 1990, Murphy et al. 1991).

Pacific kittiwakes have low breeding productivity compared with populations in certain regions of the northeastern Atlantic. In Alaskan colonies, the number of young fledged per breeding pair averages 0.31 annually, and a recent five-year mean (1985–1989) was only 0.19 chicks pair^{-1} (Hatch et al., in press). By contrast, annual productivity averages more than one chick pair^{-1} at many colonies in Britain (Coulson and Thomas 1985, Harris and Wanless 1990). The reasons for low productivity in the Pacific are poorly understood. Much indirect evidence points to an inadequate or inaccessible food supply as a basic cause, but severe predation is a contributing factor in many colonies.

Here we report on behavioral studies conducted at a large kittiwake colony in the Gulf of Alaska that exhibits the poor productivity characteristic of many Pacific colonies. We observed individually marked kittiwakes in two years, quantifying means and variation in parental attendance at the nest, foraging trip lengths, chick feeding, sibling aggression, and begging behavior. We offer this description of chick-rearing behavior in a failing colony as a basis for comparison with other, more productive colonies of kittiwakes.

METHODS

FIELD TECHNIQUES

The study was conducted on Middleton Island (58°25′N, 146°19′W), which has one of the largest colonies of Black-legged Kittiwakes in Alaska. The nesting population varied in recent years from about 80,000 to 40,000 pairs (Sowls et al. 1978; Hatch et al., in press). A downward trend is evident in spite of considerable annual variation in kittiwake numbers (Hatch et al., unpubl. manuscript).

We made observations in two years that differed in overall breeding success (as measured on 5–12 study plots around the island, totaling 300–700 nests). At 0.76 chicks nest^{-1}, 1984 was the most successful year for kittiwakes in 13 years

---

[1] Received 21 October 1992. Accepted 28 January 1993.

[2] Present address: 2400 East Valley, Seattle, WA 98112.

[3] Corresponding author.

monitored since 1978 (Hatch et al., in press, unpubl. data). Productivity in 1988 (0.21 chicks nest^{-1}) was about average (13-year mean 0.16 chicks nest^{-1}). Total or near-total breeding failures (<0.05 chicks nest^{-1}) have occurred in eight of the last 10 years on Middleton (1983–1992). During years with poorer productivity than in 1988, too few young have survived to allow meaningful observations of parental behavior in the chick stage.

We used two study plots on the east side of Middleton Island, where kittiwakes nested on low bluffs and vegetated slopes. Plot B (208 pairs) and Plot C (274 pairs) were situated about 150 m apart on the same bluff. Twenty-nine individuals were captured with mistnets before egg-laying and with noose mats during late chick rearing on Plot B in 1984 (Roberts 1988). On Plot C in 1988, 300 birds were caught before egg-laying with three successive firings of a rocket net. Each bird was given a unique combination of metal and colored plastic bands. Sexes were determined by observation of copulation or courtship feeding.

Egg and chick survival on the behavior plots was monitored in 19 (1984) and 116 (1988) nests in which one or both members of the pair were banded. A chick was considered to have fledged when it was first observed to fly from its nest.

Fifteen pairs on Plot B were included in behavioral studies in 1984. Data were collected from 22 June to 14 August by two observers using a 15–60× spotting scope from a blind on the beach below the plot. Total observation time was 2,697 nest-hours (Table 1). All 15 nests were watched simultaneously during daylight hours, beginning between 06:00 and 08:00 in the morning and ending between 20:00 and 22:00 at night. Breaks of 30–60 min occurred occasionally between observation shifts of 2–3 hr. The longest period of continuous observation was 10 hr. Each pair in the study was watched from the day its first egg hatched until its chick(s) fledged or died.

Thirty-four of the 116 pairs monitored for breeding success on Plot C were observed during chick rearing in 1988. Observations totaling 4,797 nest-hours were made with binoculars by four observers from 28 June to 16 August. Ten to 12 pairs were observed simultaneously from 06:00–08:00 hr to 20:00–22:00 hr each day. Watches were continuous throughout the day, with no breaks between the different observers' shifts of 2–3 hr. Pairs in the first group of 12 nests were observed from the day their first egg hatched to the day the chick(s) fledged or died. As pairs failed, other banded pairs that still had chicks were added to the focal group to ensure an adequate sample size during the mid to late chick-rearing period.

TABLE 1. Sampling effort for quantifying kittiwake adult and chick behaviors in two years on Middleton Island.

Chick age (days)	Sampling effort[a]		
	1984		1988
	Attendance	Feeding[b]	All behavior
0–10	15 (936)	11 (665)	20 (1,217)
11–20	13 (827)	9 (550)	15 (1,293)
21–30	7 (613)	4 (371)	15 (1,186)
31+	5 (321)	3 (234)	8 (1,101)
Overall	15 (2,697)	11 (1,820)	34 (4,797)

[a] Number of nests observed at each chick stage; total nest-hours observed in parentheses.

[b] Feeding behavior was difficult to see in a few nests studied in 1984; sample sizes were reduced accordingly (see Methods).

Adult and chick behaviors were monitored continuously using all-occurrences sampling (Altmann 1974). Activities assessed for each nest included a complete record of presence and absence of the adults. Arrival times and departures of the male and female were recorded to the nearest minute, as was the occurrence of food begging by the chick(s) and feeding—the transfer of any amount of food between an adult and chick. We also noted the total number of food items (boluses) transferred. Sibling aggression was quantified by counting the number of pecks, or jabs with the bill, delivered from one member of a brood (invariably the larger, first-hatched chick) to its sibling. In 1984, the interiors of four of the 15 nests observed were difficult to see. We were unable to observe all occurrences of feeding, begging, and pecking, and therefore excluded such nests from the analysis of those behaviors.

We computed the following attributes for successive 10-day intervals and for the chick-rearing period as a whole: (1) Number of departures per hour (total occurrences divided by total observation time) for the male and female. Departures (and associated absences) were classified according to whether the departing bird's mate was present upon departure (Type 1) or absent (Type 2). (2) Durations of all daytime absences and some overnight absences for which starting and return times were observed (1988 only; breaks in observation precluded comparable analyses of trip durations in 1984). An overnight absence

TABLE 2. Determination of independent sampling units: tests for correlation between members of a pair.

Behavior	Year	Partial correlation[a]	n (pairs)	P[b]
Type 1 absences				
Occurrence	1988	0.43	33	0.008
Duration	1988	0.17	32	0.179
% Feeding on return	1988	0.41	17	0.065
Type 2 absences				
Occurrence	1988	0.23	33	0.108
Duration	1988	0.33	21	0.082
% Feeding on return	1988	0.01	13	0.488
Food provisioning				
Occurrence	1984	0.55	11	0.061
	1988	0.33	33	0.036
Items hr^{-1}	1984	0.07	11	0.428
	1988	0.28	33	0.067

[a] Partial correlation (controlling for chick age and brood size) of male deviation from grand mean paired with female deviation from grand mean. Analysis performed on rank values.

[b] One-tailed probability.

was deemed to have occurred if a lone adult was present when observations ended (after 20:00 in the evening) and the same adult was alone when observations resumed before 08:00 the following morning. This assumes that multiple changeovers at a given nest did not occur during the night (cf. Coulson and Wooller 1984 for supporting evidence). (3) Percentage of absences greater than 15 min duration that were followed by chick feeding on return of the traveling bird. Absences shorter than 15 min were excluded to reflect more accurately the success of actual foraging trips (as opposed to brief absences for loafing, bathing, or other nonforaging activities). (4) Begging rate, expressed as the number of 1-min intervals per hour with at least one adult present during which any amount of begging occurred. Begging was considered successful if the chick received food within 2 min after the behavior. (5) Feeding rates, expressed as occurrence (number of 1-min intervals per hour during which any amount of feeding occurred) and items (boluses) transferred per hour. (6) Pecking rates, expressed as total number of bill jabs per hour of observation with two chicks in a nest. There was no seasonal component to variation in sibling aggression because few two-chick broods persisted beyond the first 10-day interval (see below).

ANALYSIS

This study involved many hours of continuous sampling in two years (Table 1), which resulted in large numbers of observations of specific behavioral events. Analyses of variance, however, revealed significant components of variation among individuals. For instance, individual variation in trip lengths was highly significant for Type 1 absences ($F_{65,1026} = 5.25, P < 0.001$) and Type 2 absences ($F_{65,1550} = 7.92, P < 0.001$) in 1988. Thus, our sample of independent observations was no greater than the number of individuals included in the study. Similarly, it was inappropriate to use as independent observations our measures of rates, such as departures per unit time or percent feeding on return, calculated over any interval less than the total observation time for an individual.

We also checked whether individuals could be safely treated as independent sampling units. Similarity of response between members of a pair might occur if mated kittiwakes tended to be of similar age, breeding experience, or individual quality (Coulson 1966, Coulson and Thomas 1985). Interdependence could also arise if one bird's behavior directly influenced that of its mate. We computed partial correlations between the deviations of each paired male and female from their population grand means. Some attributes of behavior were significantly correlated within pairs, and those correlations that were nonsignificant were uniformly positive (Table 2). From this we concluded that only pairs were able to meet the assumption of independence, and our unit of observation for significance testing was the mean value of a given behavioral attribute in a given pair. A yearly response was the mean of means for pairs. Standard errors of rates and proportions were calculated using Cochran's (1977) method for cluster sampling (clusters = pairs). Pairs observed less than 25 hr during one of the four stages of chick rearing were excluded from the analysis.

We used nonparametric statistical tests because many of the variables we analyzed did not meet the assumptions of normality or homogeneity of variances. For between-year comparisons, we used an analysis of variance on ranked values of the response variable (Conover and Iman 1981). The effects of chick age and brood size were controlled by entering as covariates the mean age (days since hatching) of the oldest or only chick in a nest and mean brood size (a value between 1 and 2 if brood reduction occurred during a given interval of observations). We used Wilcoxon's signed-ranks matched-pairs tests for differences within years (between sexes or stages of chick rearing).

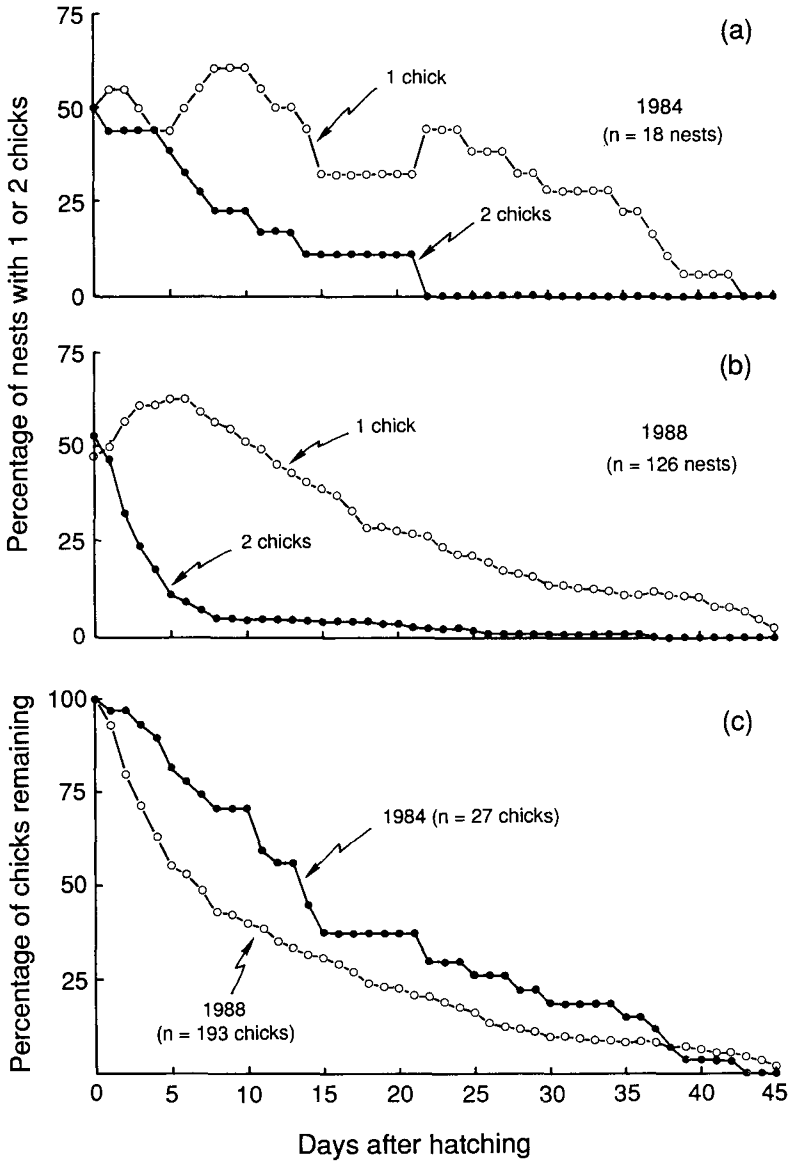


FIGURE 1. Percentage of nests containing broods of one or two chicks in relation to time since hatching in (a) 1984 and (b) 1988. Day 0 is the hatching date of the second egg in nests initially containing two chicks. (c) Combined survivorship of first- and second-hatched chicks in 1984 and 1988.

RESULTS

CHICK SURVIVAL

Half the nests selected for behavioral observations started out with two chicks, but the second-hatched chick in broods of two usually disappeared within two weeks (Fig. 1). Five days after hatching, 40% of nests contained two chicks on Plot B in 1984 (Fig. 1a), whereas only 10% still contained two chicks at the same stage on Plot C in 1988 (Fig. 1b). Thus, mortality was higher during the early chick period in the latter year, although few chicks on the study plots survived to fledge (at about 40 days of age) in either year.

Fledging success was poor on Plot B in 1984 compared with the whole-island mean. This was due to a combination of sampling error (none of the focal pairs fledged young, although other nests on Plot B were successful) and the depredations

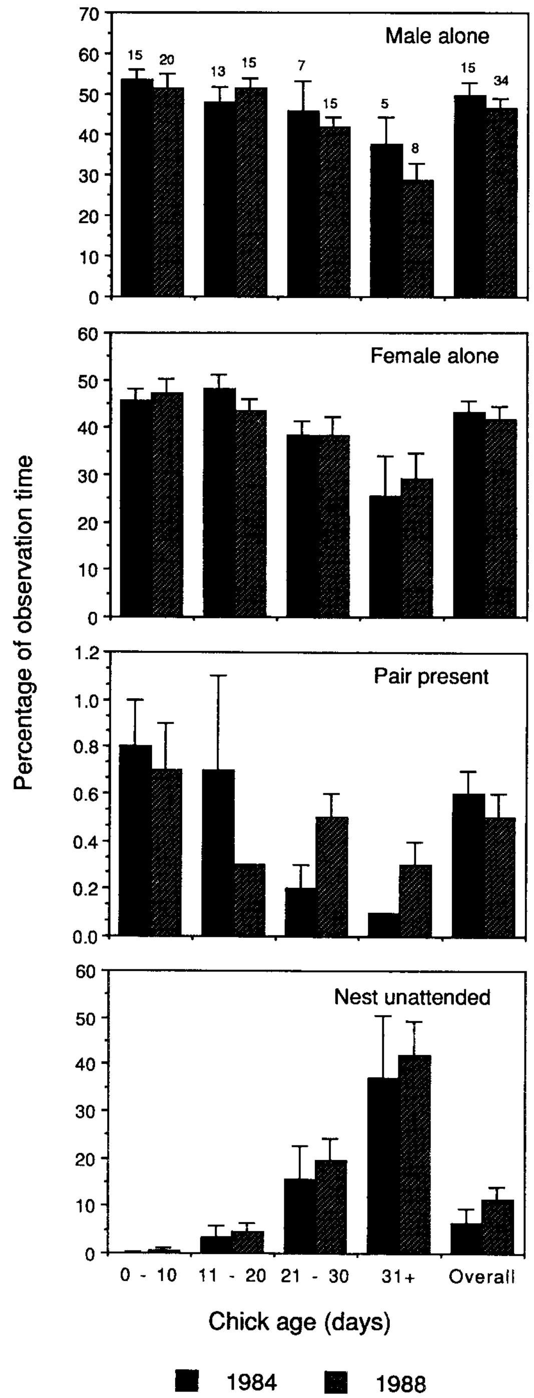


FIGURE 2. Parental attendance at the nest by Black-legged Kittiwakes during chick-rearing in two years on Middleton Island. Number of nests observed (top panel) and standard errors are shown.

of a Glaucous-winged Gull (*Larus glaucescens*) who defended the plot as a feeding territory.

PARENTAL ATTENDANCE

Overall, parental attendance did not differ substantially between 1984 and 1988 (Fig. 2). Pairs spent an average of just 0.05% of their time together at the nest, or 8 min day^{-1}. Sample nests were attended by a single adult or pair about 94% of the time in 1984 and 89% of the time in 1988. Males tended to spend more time alone at the nest than females (47% vs. 42%); that difference was significant in 1988 ($P < 0.05$, Wilcoxon test). Individual pairs, however, departed sharply from the mean patterns of male-female roles. In 1984, the ratio of lone male to lone female attendance ranged from 2.4 (mostly male attendance) to 0.6 (mostly female attendance).

Attendance decreased steadily as chicks aged, ranging from nearly 100% attendance for chicks aged 1–10 days to a low of 58% attendance (1988) for chicks older than 31 days (Fig. 2). A stepwise multiple regression of the effects of chick age and calendar date on parental attendance in 1988 showed that chick age accounted for 56% of the variability in attendance ($r = 0.75$; df = 1, 511; $P < 0.001$), whereas calendar date had no significant effect. In an analysis of covariance, chick age accounted for 9% of the variation in attendance in 1988 after the effect of pairs was removed ($r = 0.30$, df = 1,472, $P = 0.068$), and calendar date had no effect. Both analyses suggest that chick age per se, not calendar date, was responsible for changes in parental attendance during chick rearing.

ADULT ABSENCES FROM THE NEST

The mean duration of a Type 1 absence (mate attending the nest upon departure) was about 2 hr in 1988 (Table 3). There were no consistent trends in the characteristics of Type 1 absences over the chick-rearing period, nor did trip lengths vary significantly between males and females ($P > 0.05$).

The frequency and mean duration of Type 2 absences increased steadily during chick rearing in 1988 (Fig. 3). Males had a higher frequency of Type 2 absences than females, but their trips were of shorter duration (Table 3).

Type 1 absences averaged about four times longer than Type 2 absences, although the ranges of trip lengths were similar (Fig. 4). Overnight

TABLE 3. Characteristics of Type 1 departures (mate present at nest) and Type 2 departures (mate absent from nest) by adult kittiwakes in 1988.[a]

Chick age (days)	Attribute[b]	Type 1 departures			Type 2 departures		
		Males	Females	Total	Males	Females	Total
0–10	Rate of occurrence	0.11 ± 0.03 (18)	0.07 ± 0.01 (18)	0.17 ± 0.03 (18)	0.02 ± 0.01 (20)	0.03 ± 0.01 (20)	0.05 ± 0.02 (20)
	Duration of absence (hr)	1.99 ± 0.35 (18)	1.58 ± 0.30 (16)	1.89 ± 0.34 (18)	0.08 ± 0.06 (9)	0.05 ± 0.02 (8)	0.07 ± 0.04 (14)
	% Feeding on return	33.5 ± 14.9 (5)	23.7 ± 7.1 (5)	36.0 ± 6.3 (12)	—	—	—
11–20	Rate of occurrence	0.07 ± 0.02 (14)	0.06 ± 0.01 (14)	0.13 ± 0.02 (14)	0.15 ± 0.03 (15)	0.05 ± 0.02 (15)	0.19 ± 0.04 (15)
	Duration of absence (hr)	2.21 ± 0.51 (13)	3.18 ± 0.53 (12)	2.53 ± 0.43 (14)	0.14 ± 0.07 (13)	0.10 ± 0.04 (13)	0.13 ± 0.05 (15)
	% Feeding on return	46.7 ± 10.2 (3)	40.6 ± 9.8 (3)	53.9 ± 6.7 (9)	10.0 ± 10.0 (2)	—	16.7 ± 16.7 (2)
21–30	Rate of occurrence	0.16 ± 0.04 (13)	0.08 ± 0.01 (13)	0.23 ± 0.04 (13)	0.36 ± 0.06 (14)	0.13 ± 0.03 (14)	0.49 ± 0.08 (14)
	Duration of absence (hr)	2.6 ± 0.72 (13)	2.90 ± 0.51 (13)	2.48 ± 0.53 (13)	0.21 ± 0.05 (14)	0.40 ± 0.12 (14)	0.29 ± 0.06 (14)
	% Feeding on return	37.1 ± 9.8 (7)	42.1 ± 13.4 (6)	41.6 ± 6.1 (11)	10.8 ± 4.2 (5)	49.1 ± 36.6 (2)	29.2 ± 10.8 (6)
31+	Rate of occurrence	0.11 ± 0.03 (7)	0.10 ± 0.02 (7)	0.20 ± 0.05 (7)	0.53 ± 0.08 (7)	0.16 ± 0.04 (7)	0.69 ± 0.09 (7)
	Duration of absence (hr)	1.62 ± 0.33 (7)	1.64 ± 0.29 (7)	1.60 ± 0.27 (7)	0.53 ± 0.18 (7)	0.85 ± 0.24 (7)	0.62 ± 0.17 (7)
	% Feeding on return	56.5 ± 16.1 (3)	23.7 ± 4.0 (4)	37.8 ± 6.9 (7)	16.2 ± 6.2 (6)	21.1 ± 5.8 (5)	19.1 ± 4.5 (7)
Overall	Rate of occurrence[c]	0.10 ± 0.02 (31)	0.07 ± 0.01 (31)	0.17 ± 0.02 (31)	0.19 ± 0.04 (33)	0.06 ± 0.01 (33)	0.26 ± 0.05 (33)
	Duration of absence (hr)[d]	1.91 ± 0.27 (31)	2.12 ± 0.24 (29)	2.04 ± 0.24 (31)	0.19 ± 0.05 (26)	0.33 ± 0.09 (25)	0.21 ± 0.05 (30)
	% Feeding on return[e]	40.1 ± 5.7 (19)	38.6 ± 4.8 (17)	41.2 ± 3.7 (25)	20.2 ± 4.7 (10)	25.7 ± 9.0 (5)	22.3 ± 3.6 (11)

[a] Analysis limited to trips with departure and return observed on the same day (daytime absences). All values are mean ± SE; sample sizes (no. of individuals or pairs) in parentheses.

[b] Rate of occurrence is mean departures $\text{nest}^{-1}\ \text{hr}^{-1}$; % feeding on return computed for individuals and pairs with ≥5 departures, excluding absences of ≤15 min duration.

[c] Wilcoxon matched-pairs signed-ranks tests comparing overall means for males and females: Type 1, ns; Type 2, $P < 0.001$.

[d] Significance tests as in footnote c: Type 1, ns; Type 2, $P < 0.05$.

[e] Significance tests as in footnote c: Type 1, ns; Type 2, ns.

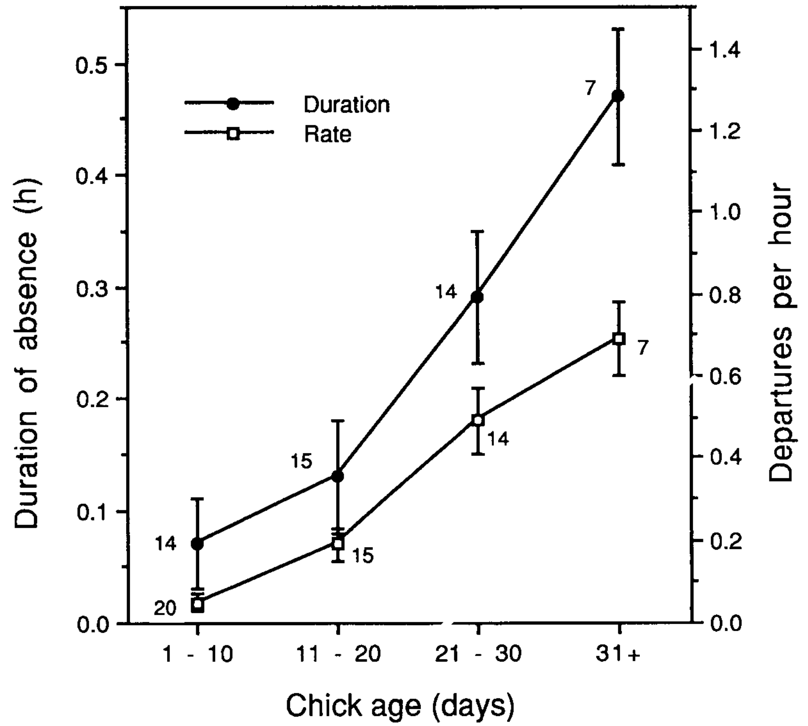


FIGURE 3. Rate of occurrence and mean duration of Type 2 daytime absences (mate absent on departure) in relation to chick age in 1988. Means, sample sizes (nests), and standard errors are shown.

absences (range 8–28 hr) averaged much longer than either type of daytime trip.

Type 1 absences that were followed by chick feeding on return were significantly longer than those not followed by chick feeding ($P < 0.001$, Wilcoxon test, $n = 24$ pairs) (Fig. 5). The durations of Type 2 absences showed a similar effect ($P < 0.01$, Wilcoxon test, $n = 11$ pairs), whereas overnight absences were of about the same duration whether or not they resulted in chick feeding ($P = 0.095$, Wilcoxon test for 22 pairs).

Data from 1988 indicate the importance of night-time foraging, as 62% of overnight trips resulted in chick feeding on return of the adult (Fig. 5). By contrast, only 41% of Type 1 absences longer than 15 min and 22% of Type 2 absences longer than 15 min in daytime were associated with chick feeding (Table 3).

CHICK FEEDING

Both the occurrence of feeding bouts (min hr^{-1}) and the rate of food transfers (items hr^{-1}) were significantly greater in 1984 than in 1988 (Table 4). The rate of food transfer was significantly greater at all stages of chick development, while feeding occurrence was greater only in the first 10-day interval. There appeared to be no change across intervals in either measure of the feeding rate. Males fed chicks less often than their mates on Plot B in 1984 ($P = 0.051$); however, the reverse was true on Plot C in 1988 ($P = 0.073$). The number of items delivered per hour was less for males than for females in 1984 ($P < 0.05$).

Diurnal variation in feeding rates was relatively strong in 1984, with feeding occurring most often in the early morning and tapering off during the day (Wilcoxon matched-pairs signed-ranks tests comparing mean occurrence of feeding in different periods of the day: 06:00–09:59 vs. 14:00–17:59, $n = 14$ nests, $P = 0.016$; 06:00–09:59 vs. 18:00–22:00, $n = 8$ nests, $P = 0.012$). Morning feeding activity was less pronounced in 1988, but still slightly elevated compared with the rest of the day (06:00–09:59 vs. 14:00–17:59, $n = 25$ nests, $P = 0.032$).

SIBLING AGGRESSION AND FOOD BEGGING

Sibling aggression was common in nests containing two chicks. Mean pecking rates were 1.80

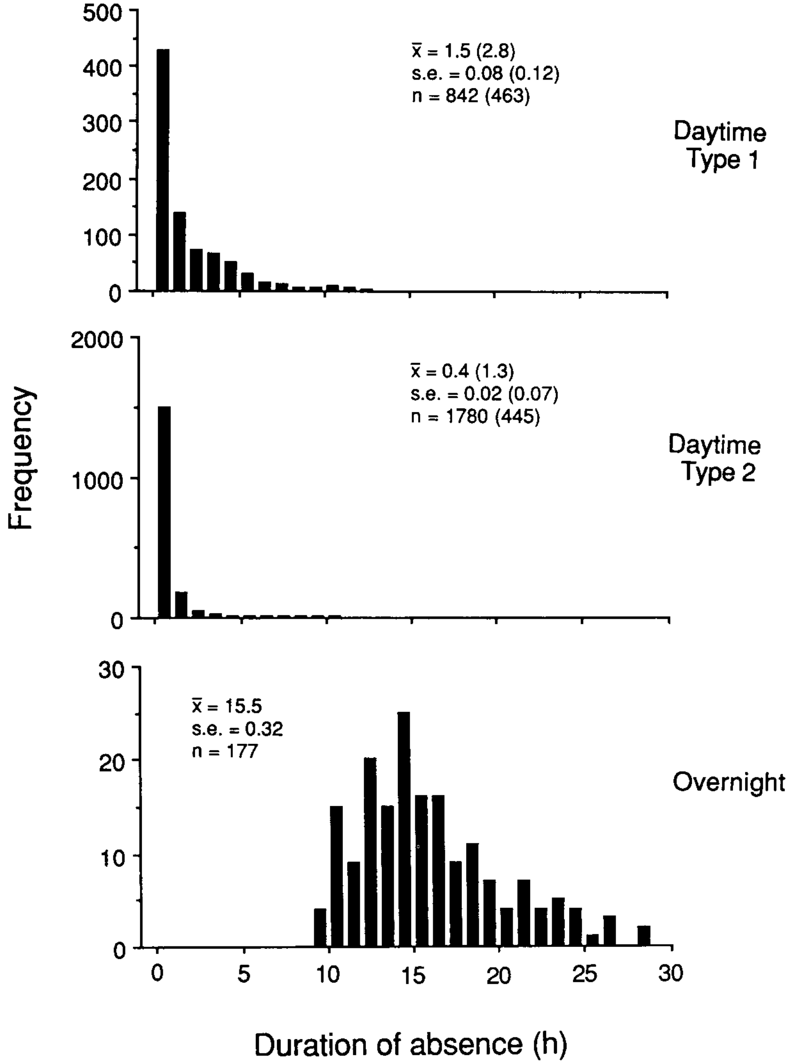
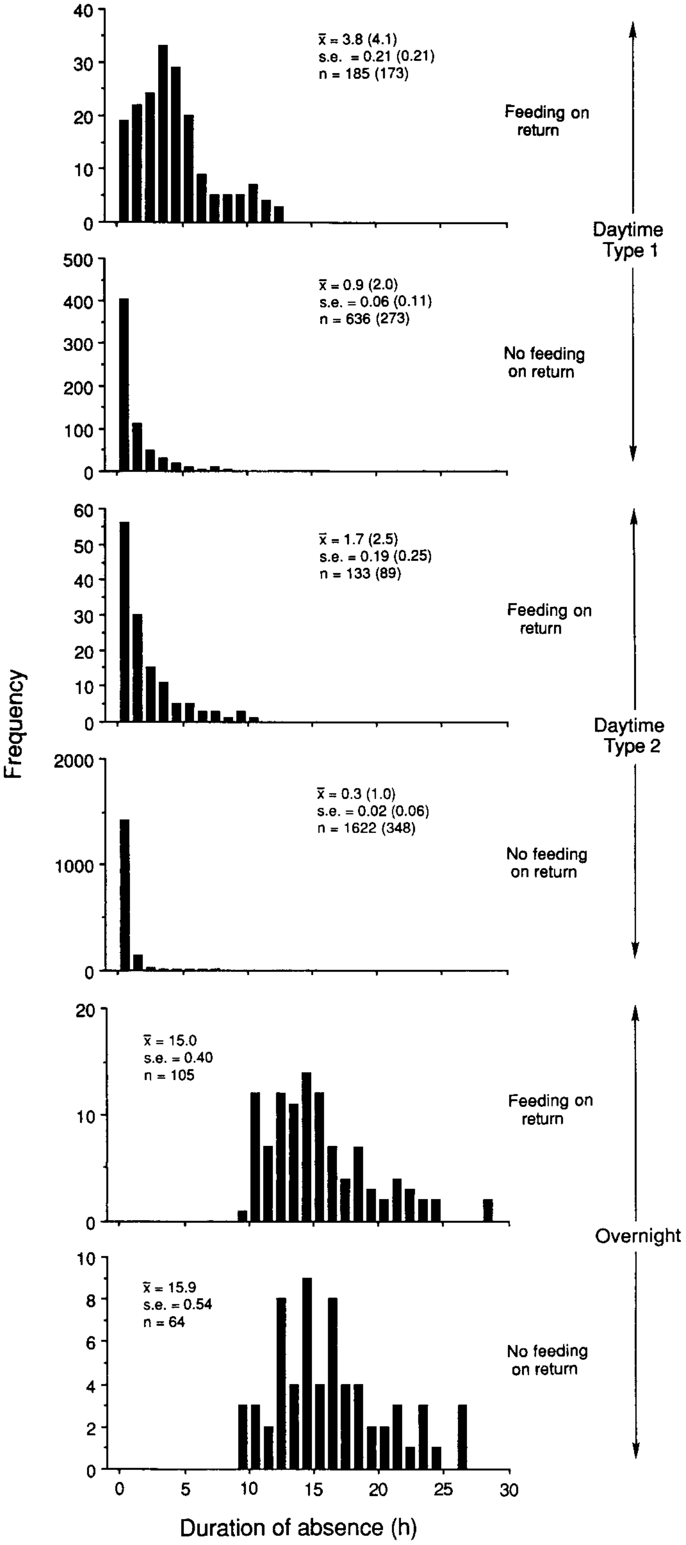


FIGURE 4. Frequency distributions of trip lengths for two types of daytime absences (Type 1, mate present on departure; Type 2, mate absent on departure) and for overnight absences of Black-legged Kittiwakes on Middleton Island in 1988. Means differ from Table 3 because sample sizes are foraging trips, not pairs. Values in parentheses exclude absences of ≤15 min duration.

pecks hr^{-1} in 1984 ($n = 9$ nests) and 3.16 pecks hr^{-1} in 1988 ($n = 14$ nests). The difference between years was not significant ($P = 0.225$).

Overall begging rates were significantly lower and resulted in feeding more often in 1984 than in 1988 (Table 5). Begging rates remained relatively stable as chicks aged in 1984, but increased steadily in 1988. A minor proportion of the begging bouts observed resulted in chicks receiving food (35% in 1984 and 22% in 1988).

Observations suggested that persistent begging by a chick induced a higher frequency of Type 2 departures in the attending adult. Parents unable to feed hungry, begging chicks often deserted their nests for short intervals. Although the correlation between frequency of unsuccessful begging and the frequency of Type 2 departures was not significant in 1988 ($r = 0.14$, $n = 43$ nests, $P = 0.173$), unsuccessful begging and the frequency of Type 2 absences that resulted in chick feeding were positively correlated ($r = 0.47$, $n = 43$ nests, $P = 0.001$).


x̄ = 3.8 (4.1)
s.e. = 0.21 (0.21)
n = 185 (173)
Feeding on return
x̄ = 0.9 (2.0)
s.e. = 0.06 (0.11)
n = 636 (273)
No feeding on return
Daytime Type 1
x̄ = 1.7 (2.5)
s.e. = 0.19 (0.25)
n = 133 (89)
Feeding on return
x̄ = 0.3 (1.0)
s.e. = 0.02 (0.06)
n = 1622 (348)
No feeding on return
Daytime Type 2
x̄ = 15.0
s.e. = 0.40
n = 105
Feeding on return
x̄ = 15.9
s.e. = 0.54
n = 64
No feeding on return
Overnight
Frequency
0
10
20
30
40
0
100
200
300
400
500
0
10
20
30
40
50
60
0
1000
2000
0
10
20
0
2
4
6
8
10
0
5
10
15
20
25
30
Duration of absence (h)

DISCUSSION

Reduced chick feeding and increased begging rates pointed to food stress as a likely cause of breeding failure in 1988. It is puzzling that parental attendance was not better correlated with chick-rearing success, but the activity budgets of off-duty birds were not monitored. It is conceivable that in 1988 kittiwakes were obliged to spend a larger proportion of their time away from the nest either foraging or flying to and from distant feeding areas. Also, our sampling scheme itself may have partly obscured the differences between years. Chick losses resulted in small numbers of active nests remaining in our fixed sample at later stages in 1984. In 1988, we tried to overcome the problem by adding active nests to the focal group as required to maintain the sample size. A danger in doing that, however, is that the sample may have been progressively composed of better quality birds—those able to cope with poor conditions and persist long enough to be included in the study. Such a bias would reduce our ability to detect annual differences in parameters measured over the whole chick period.

The relative lengths of Type 1 and Type 2 absences suggested that kittiwakes strived to maintain continuous attendance with their chicks. A bird that departed while its mate was present at the nest tended to spend more time away, whether or not it returned with food, than a bird that left its nest completely unattended. Presumably, the opportunity to rendezvous and communicate frequently at the nest would assist pairs in coordinating their turns at guarding chicks and foraging at sea. Thus, Type 1 departures may prove to be typical of kittiwakes in a thriving colony. Type 2 absences often gave the impression of a harried response by an on-duty adult to the incessant begging of hungry chicks. Most were of short duration and did not result in chick feeding. As begging rates increased, however, some on-duty adults deserted the nest to search for food, as indicated by the positive correlation between begging rates and Type 2 absences that resulted in chick feeding.

In both 1984 and 1988, kittiwake attendance was high while chicks were young (1–10 days)

←

FIGURE 5. Frequency distributions of trip lengths for absences that did or did not result in chick-feeding on return (1988 only). Values in parentheses exclude absences of ≤15 min duration.

TABLE 4. Rates of food-provisioning by adult kittiwakes during chick-rearing in two years on Middleton Island.[a]

Chick age (days)	Measurement[b]	1984 Males	1984 Females	1984 Total	1984 n	1988 Males	1988 Females	1988 Total	1988 n	P[c]
0–10	Occurrence	0.28 ± 0.05	0.42 ± 0.04	0.70 ± 0.06	11	0.22 ± 0.04	0.15 ± 0.02	0.37 ± 0.06	20	0.001
	Items hr^{-1}	0.44 ± 0.10	0.69 ± 0.06	1.13 ± 0.12	11	0.26 ± 0.05	0.18 ± 0.03	0.44 ± 0.08	20	0.000
11-20	Occurrence	0.14 ± 0.04	0.24 ± 0.04	0.38 ± 0.06	9	0.16 ± 0.02	0.13 ± 0.02	0.29 ± 0.03	15	0.697
	Items hr^{-1}	0.38 ± 0.08	0.79 ± 0.12	1.18 ± 0.13	9	0.19 ± 0.03	0.17 ± 0.02	0.36 ± 0.03	15	0.000
21–30	Occurrence	0.16 ± 0.03	0.15 ± 0.04	0.31 ± 0.06	4	0.19 ± 0.02	0.19 ± 0.04	0.38 ± 0.05	15	0.487
	Items hr^{-1}	0.50 ± 0.06	0.54 ± 0.10	1.04 ± 0.04	4	0.24 ± 0.03	0.27 ± 0.05	0.51 ± 0.07	15	0.006
31+	Occurrence	0.15 ± 0.01	0.14 ± 0.02	0.29 ± 0.02	3	0.17 ± 0.04	0.12 ± 0.03	0.28 ± 0.05	8	0.795
	Items hr^{-1}	0.53 ± 0.05	0.52 ± 0.07	1.05 ± 0.09	3	0.21 ± 0.05	0.16 ± 0.04	0.37 ± 0.07	8	0.012
Overall	Occurrence[d]	0.22 ± 0.04	0.29 ± 0.02	0.51 ± 0.05	11	0.20 ± 0.03	0.14 ± 0.01	0.34 ± 0.04	34	0.001
	Items hr^{-1}[e]	0.44 ± 0.07	0.67 ± 0.05	1.11 ± 0.10	11	0.23 ± 0.03	0.19 ± 0.02	0.43 ± 0.05	34	0.000

[a] All values are mean ± SE; sample sizes are numbers of pairs observed.

[b] Occurrence is number of 1-min intervals hr^{-1} in which feeding occurred; items hr^{-1} is mean number of boluses seen transferred between adult and chicks in 1 hr.

[c] Significance of F-ratio for the comparison of totals (sexes combined) in 1984 and 1988. ANOVA on ranked values of dependent variable (behavior), controlling for mean brood size (all tests) or mean brood size and mean chick age (tests for overall effect).

[d] Wilcoxon matched-pairs signed-ranks tests comparing overall means for males and females: 1984, $P = 0.051$; 1988, $P = 0.073$.

[e] Significance tests as in footnote d: 1984, $P < 0.05$; 1988, ns.

TABLE 5. Occurrence and success of food-begging behavior in kittiwake chicks during two years on Middleton Island.[a]

Chick age (days)	Occurrence[b] 1984	Occurrence[b] 1988	P[c]	Success (%) 1984	Success (%) 1988	P[c]
0–10	1.03 ± 0.17 (11)	1.66 ± 0.21 (20)	0.000	41.7 ± 3.7 (11)	20.9 ± 1.8 (20)	0.000
11–20	1.59 ± 0.53 (9)	1.99 ± 0.21 (15)	0.118	35.1 ± 6.7 (9)	22.9 ± 2.6 (15)	0.135
21–30	1.89 ± 0.86 (4)	3.72 ± 0.97 (15)	0.031	28.4 ± 9.3 (4)	26.3 ± 2.3 (15)	0.981
31+	1.16 ± 0.39 (3)	5.70 ± 1.75 (8)	0.026	30.1 ± 4.8 (3)	17.5 ± 2.3 (8)	0.073
Overall	1.20 ± 0.24 (11)	2.62 ± 0.47 (34)	0.002	35.1 ± 3.9 (11)	22.0 ± 1.5 (34)	0.003

[a] All values are mean ± SE; sample sizes (no. of pairs) in parentheses.

[b] Occurrence is number of 1-min intervals hr^{-1} with adult present during which begging occurred. A begging bout was successful if food was received within 2 min after its occurrence.

[c] Significance of F-ratio for the comparison of annual means. ANOVA on ranked values of dependent variable (behavior), controlling for mean brood size (all tests) or mean brood size and mean chick age (tests for overall effect).

and steadily decreased as chicks aged. About 20% of the nests were unattended at any time once the chicks were three weeks old. In another Alaskan colony (St. Paul Island, Bering Sea), Braun (1981) reported that chicks were first left unattended at 34 days old during two years in which kittiwakes had, by Alaskan standards, good breeding success (ca. 0.6 chicks nest^{-1}). Mean time to complete a foraging trip was 3.5 hr on St. Paul, roughly similar to our mean of 4.1 hr for successful trips at Middleton (excluding absences lasting ≤15 min in both instances). Braun (loc. cit.) reported a rate of 2.91 ± 0.45 feedings hr^{-1} in 1979 (productivity 0.75 chicks nest^{-1}), while we recorded 1.11 and 0.43 items hr^{-1} delivered in 1984 and 1988 (Table 4). A sizeable difference in feeding rates between St. Paul Island and Middleton is evident in spite of possible differences in the units of measure.

The tendency of kittiwakes on Middleton to leave their chicks alone in the nest is different from the norm in some Atlantic colonies, where adults maintain a continuous watch until the chicks can fly (Pearson 1968, Barrett 1978, Barrett and Runde 1980, Galbraith 1983, Harris and Wanless 1990). Departures from this pattern are generally associated with poor breeding success. For instance, Wanless and Harris (1989) observed up to 50% of broods unattended in a year with low productivity on the Isle of May, northeastern Scotland. Barrett and Runde (1980) made a similar observation on Runde, West Norway. However, in follow-up studies on the Isle of May (Wanless and Harris 1992), annual differences in attendance were not so pronounced, in spite of wide variation in breeding success (1.1 chicks nest^{-1} in 1989 vs. 0.17 chicks nest^{-1} in 1990). Some 25–26 days after hatching, about 20% of one-chick broods were unattended at midday (when attendance was highest), and 25–30% of single chicks aged 30–35 days were unattended both years. Those values are not very different from our findings on Middleton (18% of chicks unattended at any time between the ages of 21 and 30 days and 40% of chicks unattended after 31 days).

Data from Atlantic colonies are available for limited comparisons of two other parameters we studied, the duration of foraging trips and chick-feeding rates. At North Shields, England, Coulson and Wooller (1984) recorded about 6.5 changeovers per day in kittiwake pairs tending chicks aged 1–14 days. Given no overnight changes and 16 hr of daylight, their rate of turnover corresponds to a mean absence of 2.5 hr per foraging trip. Similarly, Pearson (1968) estimated 2.6 hr per foraging trip in nearby colonies on the Farne Islands. Thus, kittiwakes required roughly 40% longer to complete a successful foraging trip at Middleton. The pattern is complicated, however, by recent data from the Isle of May (Wanless and Harris 1992) indicating mean trips of 5.2 hr in a good year (1.1 chicks nest^{-1}) and 9.6 hr in a poor year (0.17 chicks nest^{-1}). Foraging trips at Middleton in 1988 (0.21 chicks nest^{-1}) were shorter than either year studied at the Isle of May.

Pearson (1968) recorded five feeds per day to one-chick broods on the Farne Islands. On the Isle of May, one-chick broods received 1.8–2.3 feeds per 10-hr observation period from hatching to fledging (Galbraith 1983). Our measures of feeding rates are not directly comparable to either study. Feeding bouts on Middleton were interrupted frequently by absences of varying length, and we could not be sure whether food transferred on a given visit to the nest was gathered during the most recent absence or an earlier one. Nevertheless, the data suggest a higher feeding frequency in the Atlantic colonies. Specifically, the number of 1-min intervals per hour in which feeding occurred on Middleton was 0.34 in 1988 (Table 4). That is, feeding occurred during just 5.4 min over a 16-hr period of daylight, which would equal Pearson's (1968) result if a typical feeding bout in his study lasted 1 min or less. In fact, complete feeding bouts almost certainly lasted longer than that on the Farne Islands, just as they did on Middleton.

A general conclusion from these contrasts is that behaviors pertaining to parental time allocation (nest attendance and foraging trip durations) are relatively flexible in kittiwakes and difficult to predict on the basis of presumed differences in food availability. Behaviors more closely associated with actual food handling (chick feeding and solicitation) are better suited to serve as food stress indicators. The data from Middleton provide a bench mark of kittiwake behavior in a stressed colony. More data from Atlantic colonies are desirable because at present there are no colonies in Alaska that approach the high levels of breeding productivity routinely observed there. Comparative work in the northeastern Atlantic is also timely because some colonies in that area have recently experienced total breeding failures, while other colonies continue to be highly productive (Harris and Wanless 1990, Danchin 1992).

ACKNOWLEDGMENTS

This paper is based partially on a thesis submitted by Roberts to the University of California, Santa Barbara, in partial fulfillment of the requirements for the Master of Arts degree in biology. We thank Edward Murphy (University of Alaska, Fairbanks) for guidance and criticism during the 1984 field season, and Stephen Rothstein for direction and advice during data analysis and write-up of Roberts' thesis. This study would not have been possible without the volunteer efforts of our observers, Susan Bonfield, Catherine Fowler, Kathy Omura, Holly Hogan, Lisa Haggblom, and Mark Simpson, and we thank them all. John Dunlap contributed an original computer program that greatly facilitated data entry. We are grateful for logistical help and other support provided by personnel of the Federal Aviation Administration while we lived on the island. David Irons, John Piatt, Brian Fadely, and Julie Porter kindly reviewed and improved the manuscript. This research was supported in part by the Department of Biology, Fisheries and Wildlife, University of Alaska, Fairbanks, and a Sigma Xi grant to Roberts.

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Barrett, R. T. 1978. The breeding biology of the kittiwake, Rissa tridactyla (L.), in Troms, North Norway. Ph.D.diss., Tromso Museum, Univ. of Tromso, Norway.

Barrett, R. T., and O. Runde. 1980. Growth and survival of nestling kittiwakes *Rissa tridactyla* in Norway. Ornis Scand. 11:228–235.

Braun, B. M. 1981. Siblicide, the mechanism of brood reduction in the Black-legged Kittiwake, *Rissa tridactyla.* Unpubl. M.Sc.thesis, Univ. of California, Irvine, CA.

Cochran, W. G. 1977. Sampling techniques. John Wiley & Sons, New York.

Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am. Stat. 35:124–129.

Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla.* J. Anim. Ecol. 35:269–279.

Coulson, J. C., and C. S. Thomas. 1985. Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla* (L.). Proc. Brit. Ecol. Soc. Behav. Ecol. Symp. 25:489–503.

Coulson, J. C., and R. D. Wooller. 1984. Incubation under natural conditions in the kittiwake gull, *Rissa tridactyla.* Anim. Behav. 32:1204–1215.

Danchin, E. 1992. Food shortage as a factor in the 1988 kittiwake *Rissa tridactyla* breeding failure in Shetland. Ardea 80:93–98.

Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes *Rissa tridactyla.* Bird Study 30:109–120.

Harris, M. P., and S. Wanless. 1990. Breeding success of British kittiwakes *Rissa tridactyla* in 1986–1988: evidence for changing conditions in the Northern North Sea. J. Appl. Ecol. 27:172–187.

Hatch, S. A., and M. A. Hatch. 1988. Colony attendance and population monitoring of Black-legged Kittiwakes on the Semidi Islands, Alaska. Condor 90:613–620.

Hatch, S. A., G. V. Byrd, D. B. Irons, and G. L. Hunt, Jr. In press. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. *In* K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey [eds.], The status, ecology and conservation of marine birds of the North Pacific. Can. Wildl. Serv. Spec. Pub., Ottawa, Canada.

Murphy, E. C., A. M. Springer, and D. G. Roseneau. 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla* L.) at a colony in western Alaska. J. Anim. Ecol. 60:515–534.

Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521–552.

Roberts, B. D. 1988. The behavioral ecology of breeding Black-legged Kittiwakes (*Rissa tridactyla*) on Middleton Island, Alaska. M.Sc.thesis, Univ. of California, Santa Barbara, CA.

Sowls, A. L., S. A. Hatch, and C. J. Lensink. 1978. Catalog of Alaskan seabird colonies. U.S. Dept. Interior, U.S. Fish and Wildlife Service, FWS/OBS-78/78.

Wanless, S., and M. P. Harris. 1989. Kittiwake attendance patterns during chick rearing on the Isle of May. Scot. Birds 15:156–161.

Wanless, S., and M. P. Harris. 1992. Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145–154.