Wilson Bull., 106(2), 1994, pp. 289–298

CHICK MOVEMENTS AND ADOPTION IN A COLONY OF BLACK-LEGGED KITTIWAKES

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ABSTRACT.—We studied Black-legged Kittiwakes (*Rissa tridactyla*) in an Alaskan colony where movement of young among nests was possible because of moderate terrain and close nest spacing. Thirty-three percent of chicks in a focal group departed their nests prior to fledging, and seven of the vagrant chicks (58%) were adopted by foster parents. The overall frequency of adoption in three years was 8% of 88 chicks from 57 focal nests. Premature nest-departure occurred at different stages among first- and second-hatched chicks. Departing second-hatched chicks were usually expelled by their nest mates within a few days after hatching. First-hatched chicks left at all stages and usually were the sole nest occupant when they departed. The evidence for parent-offspring recognition was equivocal. Adults accepted alien chicks that appeared in the nest and also occasionally attacked their own young outside the nest. However, asymmetry in the response of parents and nonparents to vagrant chicks seeking access to a nest suggested that adults were often able to discriminate appropriately. Vagrant chicks appeared to have little control over their fate—most entered nests where they were smaller than the resident young and suffered nest-mate aggression. Reproductive error seems the likely explanation for the acceptance and foster caregiving observed in adult kittiwakes. *Received 26 Jan. 1993, accepted 18 Sept. 1993.*

Foster parenting appears to be a fairly common phenomenon in colonial ground-nesting gulls and terns (e.g., Holley 1981, Carter and Spear 1986, Pierotti and Murphy 1987, Morris et al. 1991). The young of these species leave their nests within a few days after hatching and wander freely over their own and occasionally over neighboring territories. Such predisposing factors result in reported adoption rates of 2–15% per nest among *Larus* gulls, depending on the species and habitat (Hébert 1988). In contrast to their ground-nesting relatives, Black-legged (*Rissa tridactyla*) and Red-legged (*R. brevirostris*) kittiwakes typically nest on narrow cliff ledges. Chicks ordinarily remain within the immediate confines of the nest until they are able to fly, which minimizes the possibility of brood mixing and adoption. Nest area confinement may also account for a reported absence of parent-offspring recognition before fledging (Cullen 1957). There is, however, one account of naturally occurring adoptions in Black-legged Kittiwakes (Pierotti and Murphy 1987), and in food-stressed colonies it is not uncommon for young to leave the nest prematurely because of sibling rivalry (Braun and Hunt 1983).

We studied Black-legged Kittiwakes in a colony where chick mobility outside the nest was not restricted greatly. We observed considerable

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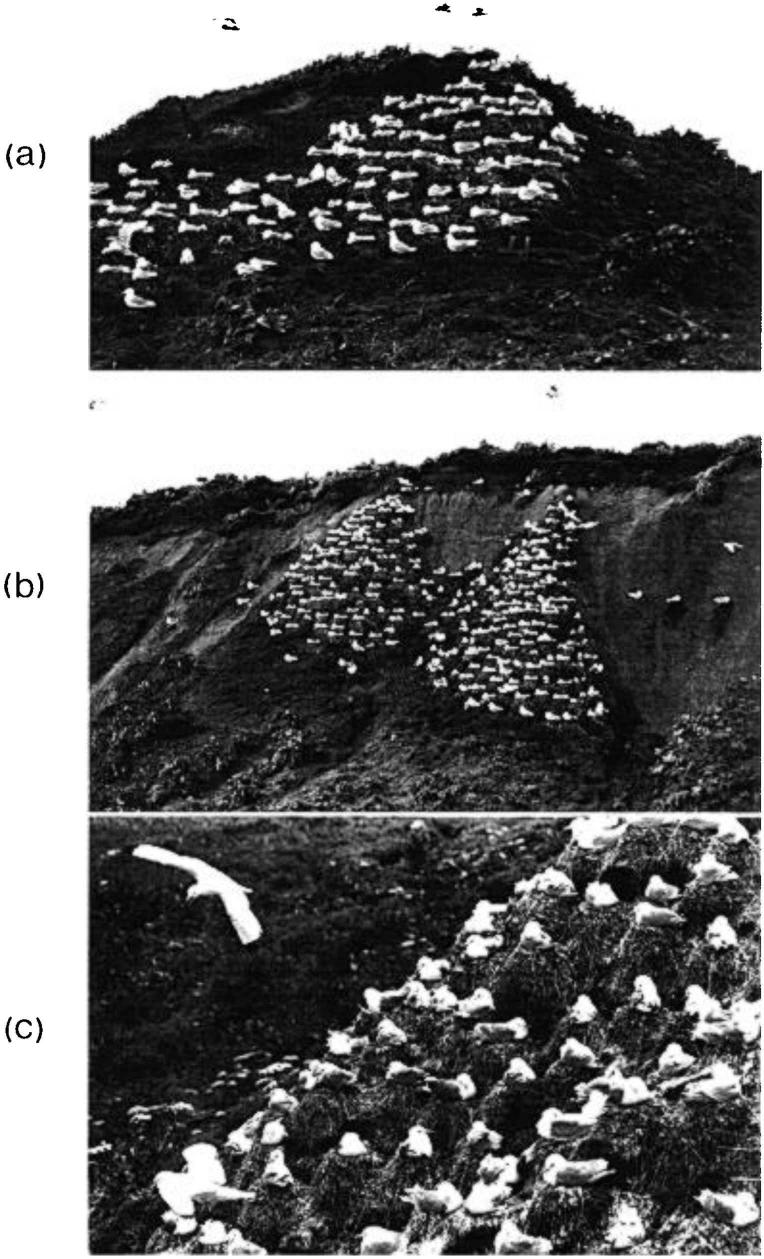
(a)
(b)
(c)

chick movement among nests, involving young of widely varying age and size. Our aim in this paper is to document the frequency and circumstances of premature nest-leaving in kittiwakes and to revisit the issue of parent-offspring recognition in this species.

METHODS

Middleton Island (north-central Gulf of Alaska, 58°25′N, 146°19′W) supports a large but declining colony of Black-legged Kittiwakes (ca 39,000 pairs in 1991; Hatch et al. 1993a). We used two study plots there for observations in three years (Plot B [1984 and 1985] and Plot C [1988]). The plots were situated about 150 m apart on a low bluff on the northeast side of the island. Whereas kittiwakes commonly nest on the narrow ledges of sheer cliffs, our plots were characterized by moderately sloping terrain and close, relatively uniform nest spacing (Fig. 1).

Productivity was generally low on Middleton (0.76, 0.04, and 0.21 chicks per nest, islandwide, in 1984, 1985, and 1988, respectively; Hatch et. al. 1993b) and most of the nests observed on the behavior plots failed each year. Because of the similar outcomes and small samples in some instances, data from all three years are combined for describing patterns of chick movement and adoption in this colony.

Plots were observed throughout chick-rearing (about 25 June to mid-August) using a 15–60× spotting scope from below Plot B (1984–1985) or binoculars from the bluff above Plot C (1988). Samples of focal nests (15 nests each in 1984 and 1988, eight nests in 1985) in which one or both of the adults were individually color-banded were watched simultaneously, beginning between 06:00 and 08:00 ADT in the morning and ending between 20:00 and 22:00 at night. In 1984, breaks of 30–60 min occurred occasionally between observation shifts of 2–3 h. Observations were continuous in 1985 and 1988.

Chick losses reduced our sample of focal nests in 1984 and 1985. In 1988, we added new nests to the focal group, as required, to maintain an active sample of 15 nests under observation. In all, 34 different nests were closely observed during all or a portion of the chick-rearing period in 1988. Data from the focal nests were supplemented with less intensive observations on nonfocal nests in 1985 (46 additional nests on Plot B) and 1988 (125 additional nests on Plot C). The contents of nonfocal nests were checked a minimum of once daily, which allowed us to detect some chick movements when the event itself was not actually observed. For instance, if a nonfocal nest that previously contained two chicks had three chicks, we assumed that a chick movement into that nest had occurred and made further observations on the behavior and fates of the individuals involved. Usually the alien chick could be distinguished from its nest mates by its markings, degree of feather growth, injuries, coloration, or obvious size differences in comparison to the resident chicks. We sometimes deduced the nest from which a chick had come by noting which nest in the vicinity had most recently lost a chick.

Mean clutch sizes were 1.9–2.0 eggs in the focal nests. In 1984, first and second-hatched chicks were distinguished by marking the head of the first chick hatched with picric acid. In later years, we assumed that the larger chick had hatched first (Braun and Hunt 1983), because eggs hatched asynchronously, usually 1–2 days apart.

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FIG. 1. Characteristic nesting habitat of Black-legged Kittiwakes on the northeast side of Middleton Island: (a) Plot B, (b) Plot C, (c) detail of Plot C from the bluff top showing close nest spacing and moderate slope.

We defined a chick movement as any instance of a chick residing outside its nest cup for any period of time. Chicks that departed either re-entered their natal nest, entered a foster nest, or died outside of any nest. A chick that left a nest and unsuccessfully attempted to enter one or more other nests was considered to have made one movement. We considered a chick adopted if we observed it being fed on one or more occasions by a foster parent at a non-natal nest.

When a chick moved out of a nest, we recorded the date and time, the chick's age, nest type (natal or non-natal), nest contents, relative age (natal nests) or size (non-natal) of any chicks left behind, and categorized the cause of departure. Our categories included (1) nest-mate aggression—chick was observed being pecked by nest mate(s) immediately before leaving, was known to be a frequent victim of aggression, or showed tell-tale injuries on the head, (2) adult non-attendance—a chick not in the above category left its nest while both adults were away, (3) accidents—chick fell or was inadvertently knocked out of a nest by adult, (4) gull disturbance—chick evaded a foraging Glaucous-winged Gull (*Larus glaucescens*) by leaving its nest, (5) parent-following—parent walked out of the natal nest and chick followed, and (6) prefledging activity—non-flying movements by chicks ≥40 days old. If a chick departed and re-entered its natal nest repeatedly (up to 23 departures were recorded in the extreme case), we assigned a single, predominant (most frequently observed) category for the purpose of tabulating the causes of nest-leaving at natal nests.

When a vagrant chick attempted to enter a nest, we recorded the date and time, nest type (natal or non-natal), presence or absence of adult(s), and adult response (attack or passive) to the entering chick. If the chick gained access to the nest, we noted its size relative to other chicks present, the occurrence of nest-mate aggression, whether the vagrant chick was fed by adult(s), and the duration of its stay. We recorded the final fate of vagrant chicks and their foster nest mates, along with age and cause of the deaths observed.

In summarizing data on chick movements and adult-chick interactions, we computed frequencies based on either the number of chicks sampled or, where appropriate, on the total number of behavioral events observed. We employ statistical tests of association (*G*-tests; Sokal and Rohlf 1981) only in the former case, because observations of the latter type were not independent (i.e., some of the same chicks were involved in multiple events).

RESULTS

Frequency of premature nest-leaving.—Twenty-nine (33%) of 88 chicks in focal nests departed their natal nests prematurely (Table 1). Having left its natal nest, a chick typically continued to wander, making an average of 4.5 movements in and out of nests before its fate was determined (Table 1). The frequency with which chicks departed their natal nests depended on the interacting effects of chick age and status within the brood. Most second-hatched chicks either departed their natal nest or died within three weeks after hatching. Those that departed were rarely (8.3%) the sole occupant of the nest when they left (Table 1). In contrast, first-hatched chicks were likely to leave at any stage during chick-rearing (58% moved after 31 days of age), and they were usually (88.2%) the sole nest occupant when they departed.

Causes of premature nest-leaving.—The majority of wandering chicks less than three weeks old were judged to have left their natal or acquired nests because of aggression from nest mates (Table 2). Accidents (chicks

TABLE 1

FREQUENCY OF PREFLEDGING KITTIWAKE CHICKS LEAVING THEIR NATAL NESTS AND NUMBER OF MOVES PER VAGRANT CHICK[a]

	First-hatched chicks			Second-hatched chicks			
Chick age (days)	No. chicks observed	No. leaving (%)	Sole occupants (%)	No. chicks observed	No. leaving (%)	Sole occupants (%)	Movements per chick[b]
1–10	48	6 (12.5)	4 (66.7)	25	9 (36.0)	1 (4.0)	1.7 ± 0.14 (45)
11–20	23	5 (21.7)	5 (100.0)	6	2 (33.3)	0 (0.0)	4.5 ± 1.44 (15)
21–30	20	2 (10.0)	1 (50.0)	4	2 (50.0)	0 (0.0)	4.2 ± 1.02 (10)
31+	12	7 (58.3)	7 (100.0)	1	0 (0.0)	—	8.6 ± 2.31 (18)
Overall[c,d]	56	17 (30.4)	15 (88.2)	32	12 (37.5)	1 (8.3)	4.5 ± 0.80 (76)

[a] Frequencies calculated for chicks in focal nests only; movements per chick include information from non-focal nests.

[b] Mean ± SE; number of chicks in parentheses. Movements from natal and acquired nests included.

[c] Sample sizes do not sum to overall totals because not all chicks were observed through all stages of chick rearing. Overall estimates of nest-leaving frequency are minimum values for the same reason.

[d] G-tests of overall difference between first- and second-hatched chicks; % leaving, $G = 0.46$ (1 df, ns); % sole occupants, $G = 19.62$ (1 df, $P < 0.001$).

falling from nests) were also an important risk among the youngest chicks (<10 days old). As chicks aged, premature nest-leaving was more frequently ascribed to parental non-attendance. Again, hatching order was an important determining factor, as the majority of second-hatched chicks departed because of nest-mate aggression, whereas most first-hatched chicks departed because of parental non-attendance, accidents, or other factors (e.g., gull disturbance or parent-following).

TABLE 2

APPARENT REASONS FOR PREFLEDGING KITTIWAKE CHICKS LEAVING THEIR NATAL NESTS[a]

	Number (%) of chicks leaving and cause				
Chick attribute	Nest mate aggression	Nest unattended	Accidents	Other[b]	Total chicks
Age (days)					
1–10	17 (53.1)	1 (3.1)	9 (28.1)	5 (15.6)	32
11–20	2 (18.2)	6 (54.5)	1 (9.1)	2 (18.2)	11
21–30	1 (12.5)	4 (50.0)	1 (12.5)	2 (25.0)	8
31+	0 (0.0)	9 (60.0)	1 (6.7)	5 (33.3)	15
Hatching order[c]					
First	3 (8.8)	14 (41.2)	7 (20.6)	10 (29.4)	34
Second	16 (72.7)	1 (4.5)	3 (13.6)	2 (9.1)	22

[a] Data from focal nests and non-focal nests included.

[b] Includes gull disturbance, parent-following, and pre-fledging activity.

[c] Distribution of causes differs significantly between first- and second-hatched chicks ($G = 26.7$, 3 df, $P < 0.001$).

TABLE 3
ADULT RESPONSES TO VAGRANT KITTIWAKE CHICKS ATTEMPTING TO ENTER NESTS

Chick age (days)	Percent adult-chick encounters in which adult attacked[a]			
	Non-parent			
	Empty nests	Active nests[b]	Overall	Parent
1–10	66.7 (15)	32.2 (31)	46.9 (49)	0.0 (4)
11–20	33.3 (3)	21.4 (14)	23.5 (17)	5.3 (19)
21–30	100.0 (7)	28.6 (7)	66.7 (15)	0.0 (5)
31+	25.0 (12)	12.9 (31)	16.3 (43)	8.3 (36)

[a] Sample sizes (no. of encounters) in parentheses.
[b] Nests containing eggs or chicks.

Consequences of premature nest-leaving.—Fourteen (48.3%) of the 29 focal chicks that prematurely left their nests re-entered their natal nests after a mean absence of 1.9 ± 0.86 h (range 0.02–8.1 h). Six chicks (42.9%) that re-entered natal nests eventually fledged, while the remainder died. Chicks that departed, returned, and survived at their natal nests were all relatively advanced in age (five were >30 days old and the sixth was 26 days old) when they made their excursion.

Among vagrant chicks that did not return to their natal nests, 12 (80.0%) gained access to a non-natal nest, whereas three (20.0%) never entered any nest and died. Seven chicks that entered non-natal nests were fed by resident adults. Thus, the overall rate of adoption was 8.0% (seven of 88 focal chicks). None of the adopted chicks from focal nests fledged. Including records from nonfocal nests, we observed 13 adopted chicks, of which one (7.7%) fledged, 10 (76.9%) died, and the fates of two chicks (15.4%) were unknown.

Whereas seven (58.3%) of 12 focal chicks that gained access to a non-natal nest were fed, in our inclusive sample of focal and nonfocal nests, only 13 (10.5%) of 124 chick movements into non-natal nests resulted in adoption. Often when a chick entered a non-natal nest, it was attacked by the resident adult. That response bore little relation to the age of the alien chick but was more prevalent when the prospective foster parent had no nest contents of its own (Table 3).

Chicks gaining access to active non-natal nests were usually smaller than the resident chicks. They frequently suffered aggression from their acquired nest mates, especially when they changed nests at a young age (Table 4). When a chick gained access to a nest where the resident chicks were smaller than itself, it usually escaped any aggressive response from its acquired nest mates.

We saw a few instances of aggression by a parent toward its own

TABLE 4

PERCENTAGE OF MOVES INTO NON-NATAL NESTS RESULTING IN VAGRANT CHICKS SUFFERING NEST MATE AGGRESSION[a]

Chick age (days)[b]	Size of vagrant chick relative to resident chick(s)	
	Larger	Smaller
1–10	0.0 (2)	91.7 (24)
11–20	0.0 (1)	13.0 (23)
21–30	— (0)	42.9 (7)
31+	14.3 (14)	41.2 (17)

[a] Sample sizes (no. movements) in parentheses.

[b] Age of vagrant chick.

wandering chick when the latter attempted to re-enter its natal nest (Table 3). However, of 64 attempts by wandering chicks to re-enter their natal nests when a parent was present, 63 (98.4%) were successful. In all (focal and nonfocal nests combined), we saw 131 attempts by vagrant chicks to enter non-natal nests while adults were present. Ninety-nine such attempts (75.6%) were successful. The age of the vagrant chick had little influence—34 (63.0%) of 54 attempts were successful among chicks aged 1–10 days, as were 15 (88.2%) of 17 attempts from 11–20 days old, eight (53.3%) of 15 attempts from 21–30 days old, and 42 (93.3%) of 45 attempts among chicks older than 30 days. A vagrant chick attempting to enter a non-natal nest with no adult present invariably gained access (N = 54 movements observed).

The mean residence time of an adopted chick in its non-natal nest was 12.7 ± 2.8 days (N = 13). Residence times were shorter for chicks that did not receive care, averaging 5.2 ± 0.9 h (N = 172 visits observed). We saw one instance of an adopted chick attacking and ejecting a resident chick. The victim was smaller than the adopted chick, which itself later fell from its foster nest and died. An adopted chick ejected two other alien chicks at one nest, and the fate of a resident chick was unknown at one nest where the resident and adopted chicks were similar in size and, therefore, indistinguishable. In remaining cases of adoption, the resident chick eventually fledged (one nest), the resident chick failed but the alien chick died first (one nest), or the alien chick was the sole occupant when it was adopted (eight nests).

DISCUSSION

The incidence of adoption in kittiwakes (8% of chicks from 57 nests) was comparable to rates reported for other larids (Hébert 1988). The assumptions that adoption is rare and its associated selection pressures are minimal in kittiwakes (Cullen 1957) should be reconsidered accordingly. To be sure, the habitat we observed on Middleton Island was unusual in the relative absence of physical barriers to chick movement. In a typical colony, many nests are isolated on small ledges, which precludes any excursions of young outside the nest. Often there are places where nests are grouped on larger ledges, however, and in that situation, the close nest spacing of kittiwakes may actually promote exchanges of vagrant chicks among nests. Pierotti and Murphy (1987) reported six adoptions among kittiwakes nesting in a typical cliff colony.

Although both members of a brood were inclined to wander from the nest, the circumstances in which that occurred clearly differed between first- and second-hatched chicks. In competition for limited food, disadvantaged younger chicks typically departed (or were ejected) as a result of sibling aggression (see also Braun and Hunt 1983, Roberts and Hatch 1993). First-hatched chicks departed at an older mean age. Many of their excursions were possibly only an expression of prefledging restlessness, although they tended to be linked with persistent absence of the adults. Almost invariably, a first-hatched chick leaving its nest had already exercised the option of driving off its younger and smaller sibling.

The evidence was equivocal regarding individual recognition of young by adult kittiwakes. Adults were seen to attack their own young outside the nest, but chicks that entered a foster nest while the adults were away were accepted. This suggests that kittiwakes "recognize" their brood primarily by location (Cullen 1957) and that selection has favored the decision rule, "always accept young you find in the nest" (Beecher 1988). There was, however, a large disparity between parents and non-parents in the occurrence of aggression toward wandering chicks and in the likelihood of a chick's gaining access to a nest with an adult present. If kittiwakes identify their young only by location, it is difficult to explain the generally passive response of parents toward chicks attempting to reenter their natal nests.

Not surprisingly, non-parents were more likely to attack in cases where the adult had no nest contents when a foreign chick arrived. In that case, the adult had a reasonably firm basis to "know" the chick was not its own. Nevertheless, most adoptions occurred in situations where the foreign chick was the sole dependent when it became established. The main problem a chick faced once it had gained access to a foster nest was not acceptance by the adults but attacks administered by its acquired nest mates. Thus, most wandering chicks made several moves before succumbing or finding a permanent home.

As an apparently altruistic behavior, adoption in gulls has been explained hypothetically on the basis of reciprocal altruism (Pierotti 1980, 1982), kin selection (Waltz 1981), or the possibility that foster parents gain valuable experience or future assurance of a breeding territory (Carter and Spear 1986). Alternatively, adoption can be viewed simply as a reproductive error that selection has been unable to eliminate (Riedman 1982, Holley 1984, Plissner and Gowaty 1988). Because an adopted chick clearly benefits from the behavior, it may be that strong selection for survival tactics among disadvantaged chicks primarily drives the system (Pierotti and Murphy 1987, Hébert 1988, Morris et al. 1991). In the colony we studied, there was little, if any, measurable cost to host young or foster parents associated with adoption, because food shortage and gull predation ensured that few chicks fledged in any case.

Among second-hatched chicks at least, we saw little evidence that disadvantaged young ''elected'' to leave their natal nest (Pierotti and Murphy 1987, Morris et al. 1991). Kittiwakes may differ from flat ground nesters in that respect. Most movements occurred when young chicks were effectively expelled by siblings or acquired nest mates. Nor did vagrant chicks appear to exercise any choice of potential foster nests or the relative size or their prospective nest mates (Pierotti and Murphy 1987, Hébert 1988). Being easier to reach, downslope nests were the usual targets. Otherwise, a chick's attempt to enter a foster nest seemed more or less directed at random (Holley 1988). Most vagrants ended up in sites where they were smaller than the resident chicks and thus were no better off than they had been at home. That outcome was likely because soliciting chicks were usually small, and potential foster nests with small chicks were well-guarded by adults. A chick had a better chance of entering an empty nest or a nest where the resident young was older, larger, and sometimes unattended (Roberts and Hatch 1993).

We view the possibility of simple reproductive error as the most parsimonious explanation of alloparental behavior in kittiwakes. The reluctance of adults to admit foreign chicks who approached while they were present argues against the idea that foster parents stood to benefit by adopting. We suggest that recently failed kittiwakes adopted chicks that appeared in their nests because they were hormonally conditioned for care giving (Emlen 1976, Plissner and Gowaty 1988) and because, on balance, selection has favored an inhibition against rejecting chicks that reside in the nest.

ACKNOWLEDGMENTS

This paper is based partially on a thesis submitted by Roberts to the Univ. of California, Santa Barbara, in partial fulfillment of the requirements for the M.A. degree in biology. We thank Edward Murphy for guidance and criticism during the 1984 field season, and Stephen Rothstein for direction and advice during data analysis and write-up of the thesis. We are especially grateful to Susan Bonfield, Catherine Fowler, Kathy Omura, Holly Hogan, Lisa Haggblom, and Mark Simpson for assistance with the field work. Personnel of the Federal Aviation Administration were helpful during our stays on Middleton Island. We thank Craig Ely and Margaret Petersen for comments on the manuscript. This research was supported in part by the Dept. of Biology, Fisheries and Wildlife, Univ. of Alaska, Fairbanks, and a Sigma Xi grant to Roberts.

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