

Vegetation Cover, Kleptoparasitism by Diurnal Gulls, and Timing of Arrival of Nocturnal Rhinoceros Auklets

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Habitat selection has consequences in determining the reproductive success of colonial seabirds, given that they breed in large numbers within small areas, where a relatively small number of environmental factors are influential. Habitat selection in seabirds has received considerable attention in relation to the parents' reproductive performance (Spaans 1971, Nettleship 1972, Hunt and Hunt 1976, Hudson 1982, Pugsek 1983, Coulson and Porter 1985). Ground-nesting seabirds are vulnerable to predation of their eggs and chicks (Buckley and Buckley 1980); hence, protection from predators is an important aspect of habitat selection. The physical structure of nesting habitat can provide shelter from predators (Richardson 1961, Brown 1967, Pierotti 1982). Vegetation cover, for example, has been reported to increase reproductive success of gulls, possibly because it provides offspring with a refuge or shelter from avian predators (Brown 1967, Davis and Dunn 1976). Reproductive success also appears to be determined by parental age and experience, which are correlated with position in the nesting colony (Jones 1994).

Rhinoceros Auklets (*Cerorhinca monocerata*) are medium-sized alcids that nest in burrows. Adults hold fish crosswise in their bills when bringing food to their nestlings (Richardson 1961, Vermeer and Devito 1986). On Teuri Island, Rhinoceros Auklets enter the colony about 30 min after sunset and leave before sunrise (Watanuki 1990). Young are fed in the evening and at night. Nocturnal food deliveries may be an adaptation for avoiding predation and kleptoparasitism by gulls (Vermeer and Cullen 1979, Watanuki 1990).

Large numbers of Rhinoceros Auklets construct nest burrows in areas with dense vegetation cover at Teuri Island. Black-tailed Gulls (*Larus crassirostris*) on the island frequently steal fish from auklets that are returning to feed their young (Thoresen 1983, Watanuki 1990). To evaluate the importance of vegetation cover at auklet nesting colonies relative to kleptoparasitism by gulls, I compared kleptoparasitic behavior, timing of arrival of auklets, and auklet chick growth for different habitat types (one was habitat where vegetation cover was artificially removed).

Methods.—My study was conducted from late April to July in 1993 and 1994 on Teuri Island (44°25'N,

141°19'E) located 28 km from the western shore of Haboro, Hokkaido, Japan. The island supported 172,000 to 180,000 breeding pairs of Rhinoceros Auklets, 29,000 pairs of Black-tailed Gulls, and smaller numbers of five other seabird species (Watanuki et al. 1986). Four major habitat types were available for breeding auklets: (1) areas dominated by *Calamagrostis langsdorffii*; (2) areas covered primarily with *Polygonum sachalinense*; (3) areas covered with *Artemisia montana*; and (4) areas with no vegetation.

In 1993, two study sites (each 160 m²) were established to examine the effects of vegetation cover within the *Calamagrostis* habitat. Vegetation was completely removed from one site ("removal" site) after the auklets laid eggs in late May; the other site was unmodified ("*Calamagrostis*" site). In 1994, I established a third 160-m² site where little vegetation grew naturally ("sparse-vegetation" site). The same *Calamagrostis* and removal sites were used in both years; vegetation at the removal site recovered before the breeding season began in 1994.

To gain access to chicks, I made a small hole at the distal end of each nest burrow under observation. The excavations were covered with stones or small rubber mats, which could be readily removed. Observation holes were dug in early May; the location of each burrow was marked by a wooden stake. Nest contents were checked every five days. Because incubating auklets are sensitive to disturbance (Vermeer and Cullen 1979, Watanuki 1987), I did not handle adults during incubation. Egg-laying dates were estimated by backdating from known hatching dates using a mean incubation period of 45 days (Leschner 1976). The appearance of eggshells near burrow entrances indicated hatching. Freshly hatched chicks were placed in a cloth bag of known mass and weighed with a 100-g Pesola scale. Subsequently, chicks were weighed every five days with a 500-g Pesola scale. Chicks reaching 45 days of age were considered to have fledged (Watanuki 1987). Chicks not located for 10 days in succession were classified as having died. Chick growth patterns approximated a linear function against development time (Watanuki 1987) between masses of 50 and 300 g. Individual growth rates were estimated using linear regression. Differences in parameters related to reproductive success between sites and years were tested using one-way ANOVA and the Scheffé multiple comparisons test.

Observations of kleptoparasitic interactions between gulls and auklets were carried out at the *Calamagrostis* (15 days) and removal sites (15 days) in

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1993. In 1994, observations were made at the *Calamagrostis* site (9 days), the removal site (9 days), and the sparse-vegetation site (8 days). Observations periods lasted 5 min and were conducted every 15 min, starting 0.5 h before sunset and ending 1.5 h after sunset. The number of arriving auklets, the number of auklets attacked by gulls, and the density of gulls were recorded at each site. Starting 45 min after sunset, I used a Night Viewer C-1525 (Hamamatsu Photonics, Inc.) to facilitate observations. Differences in the proportion of auklets attacked by gulls in different habitats were examined with polynomial regression.

Results.—Auklet nesting densities (nests/m²) did not differ significantly between the *Calamagrostis* and removal sites in 1993 or in 1994 (*Calamagrostis*, 0.7 in 1993, 0.8 in 1994; removal, 0.9 in 1993 and 1994). In 1993, the mean hatching date at the *Calamagrostis* site was similar to that at the removal site. Auklet chicks at the *Calamagrostis* site grew faster than those at the removal site (Table 1). In 1993, the mean fledging mass at the *Calamagrostis* site was greater than at the removal site, although fledging age did not differ significantly between sites (Table 1). The variance in adult body mass was significantly greater at the removal site than at the *Calamagrostis* site (Hartley test, $F = 3.47$, $df = 2$ and 11 , $P < 0.05$) in 1993, although mean body mass of adults did not differ significantly between sites.

In 1994, the mean hatching date at the *Calamagrostis* site was significantly earlier than at the sparse-vegetation site (Table 1). The mean hatching date at the removal site was not significantly different from those at the other two sites (Table 1). In 1994, chicks at the *Calamagrostis* site grew faster than those at the removal and sparse-vegetation sites; growth rates at the latter sites did not differ significantly (Table 1). The mean fledging mass at the sparse-vegetation site was lower than at the *Calamagrostis* and removal sites, although the latter two sites did not differ significantly (Table 1). The mean fledging age did not differ significantly among sites in 1994 (Table 1).

The density of gulls waiting on the ground, the percentage of arriving auklets kleptoparasitized by the gulls, and the number of auklets arriving at the colony are shown in Figure 1. In 1993, the density of waiting gulls at the removal site was greater than that at the *Calamagrostis* site ($F = 19.2$, $df = 1$ and 14 , $P < 0.0001$; Fig. 1A). A higher proportion of auklets was attacked by gulls at the removal site (38.4%) than at the *Calamagrostis* site (8.6%; $F = 7.52$, $df = 2$ and 13 , $P < 0.05$; Fig. 1C). The frequency of kleptoparasitism decreased as evening approached at the *Calamagrostis* site ($r^2 = 0.183$, $P < 0.001$) but not at the removal site ($r^2 = 0.101$, $0.05 < P < 0.1$). Moreover, the peak time for arriving auklets was significantly later at the removal site than at the *Calamagrostis* site ($F = 52.9$, $df = 1$ and 28 , $P < 0.001$; Fig. 1E).

In 1994, the density of waiting gulls at the sparse-vegetation site was substantially greater than gull

TABLE 1. Parameters related to reproductive success of Rhinoceros Auklets in 1993 and 1994 ($\bar{x} \pm SD$ with n in parentheses).*

	Calamagrostis			Sparse-vegetation		
	1993	1994	1994	1993	1994	1994
No. nests	19	14	15	17	15	13
No. hatched	19	14	15	17	15	13
No. disappeared	2	0	0	5	0	4
No. fledged	17	14	15	12	15	9
Hatching date ^b	16.8 ± 3.7 (19) ^{**}	20.5 ± 5.2 (14) ^{AB**}	25.2 ± 6.9 (15) ^C	19.0 ± 4.2 (17) ^{C**}	25.2 ± 6.9 (15) ^C	30.1 ± 7.2 (13) ^B
Growth rate (g/5 days)	41.4 ± 8.1 (17) ^{DE**}	61.6 ± 14.8 (13) ^{DEF**}	45.0 ± 10.5 (12) ^{FH}	31.8 ± 12.3 (12) ^{EH**}	45.0 ± 10.5 (12) ^{FH}	38.2 ± 12.3 (9) ^C
Fledging mass (g)	410.9 ± 43.0 (17) ^{**}	396.4 ± 48.6 (14) ^{**}	375.0 ± 69.4 (15) ^{JK}	346.3 ± 71.4 (12) ^I	375.0 ± 69.4 (15) ^{JK}	295.6 ± 75.8 (9) ^{JK}
Fledging age (days)	48.4 ± 2.0 (17)	47.1 ± 5.7 (14)	49.2 ± 3.1 (15)	50.0 ± 2.6 (12)	49.2 ± 3.1 (15)	50.3 ± 3.6 (9)

* Values with same letter in superscript significantly different (ANOVA; *, $P < 0.05$; **, $P < 0.01$).

^b Number of days after 1 May.

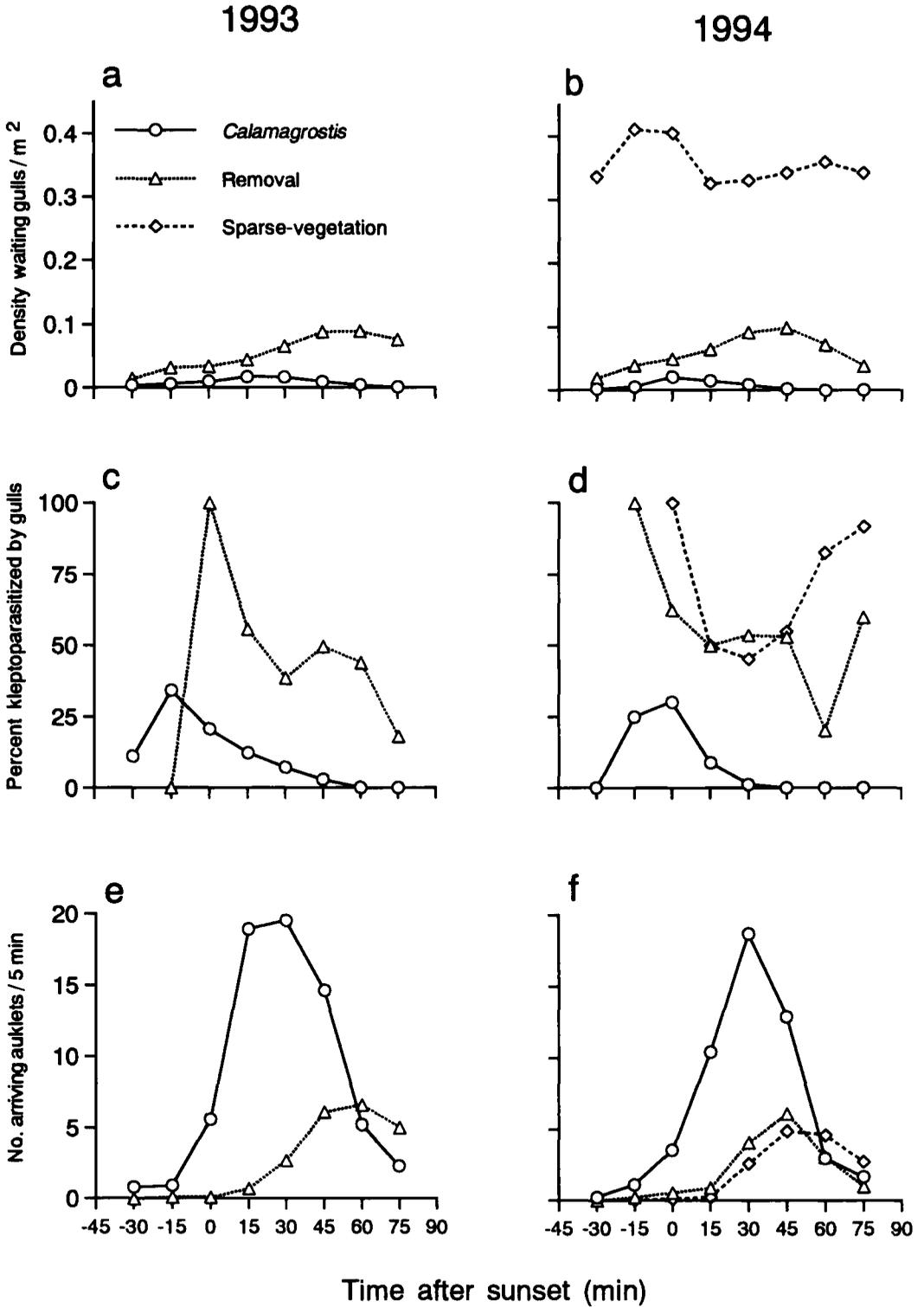


Fig. 1. Density of waiting Black-tailed Gulls, percentage of arriving Rhinoceros Auklets kleptoparasitized by gulls, and timing of arrival of auklets at colonies in three vegetation types, 1993 and 1994.

densities at the *Calamagrostis* and removal sites ($F = 508$, $df = 2$ and 21 , $P < 0.001$; Fig. 1B). Gulls attacked a higher proportion of auklets at the removal (49.7%) and sparse-vegetation sites (67.3%) than at the *Calamagrostis* site (8.7%; $F = 19.7$, $df = 2$ and 18 , $P < 0.001$; Fig. 1D). The proportion of auklets attacked was smaller toward nightfall at the *Calamagrostis* site ($r^2 = 0.131$, $P < 0.05$) but not at the removal site ($r^2 = 0.109$, $P > 0.05$). In contrast, at the sparse-vegetation site, the later in the evening it was, the larger the percentage of auklets attacked ($r^2 = 0.254$, $P < 0.05$). The peak times of arriving auklets at the removal and sparse-vegetation sites were later than at the *Calamagrostis* site ($F = 8.15$, $df = 2$ and 23 , $P < 0.005$; Fig. 1F).

Discussion.—Parental age, egg quality, timing of breeding, and nesting density can influence seabird reproductive success (Nettleship 1972, Lloyd 1979, Vermeer 1980, Bolton 1991, Harris et al. 1992). In order to eliminate the effects of timing of breeding and nest density, I selected study sites where these two variables did not differ significantly.

The density of waiting gulls at the removal site was greater than at the *Calamagrostis* site in both 1993 and 1994. The percentage of auklets attacked by gulls was also higher at the removal site than at the *Calamagrostis* site in both years, presumably because of the higher numbers of gulls at the removal site. The removal of vegetation provided open spaces for gulls to land, which may have made the removal site more attractive to the gulls.

At the *Calamagrostis* site, the percentage of auklets attacked by gulls declined later in the evening. Under low light intensities, Black-tailed Gulls have difficulty locating and attacking auklets that are carrying fish (Watanuki 1990). Auklets nesting at the removal site arrived at their colony later in the evening than did auklets nesting at the *Calamagrostis* site, possibly to avoid attacks by gulls. The percentage of auklets attacked by gulls at the removal site did not decline significantly as evening approached, however. Many gulls occurred on the ground at the removal site, and auklets probably were unable to avoid kleptoparasitism because they lacked effective physiological adaptations (e.g. good vision under poor light conditions; Watanuki 1990).

Auklets on Teuri Island fed their chicks once per day (Watanuki et al. 1986). Because Rhinoceros Auklets do not forage at sea during darkness (Watanuki 1990), adults that were robbed by gulls would not have been able to feed their chicks until the following evening. As a result, chicks at the removal site grew more slowly than those at the *Calamagrostis* site in both 1993 and 1994. Thus, areas with vegetation cover were probably more suitable for auklet nesting because the increased cover provided shelter from gull kleptoparasitism. In recent years, the coverage of *Calamagrostis* has increased on Teuri Island, with a concomitant increase in nesting Rhinoceros Auklets.

However, part of the *Calamagrostis* habitat has been destroyed by soil erosion, which may have resulted in decreased reproductive success at that part of the island.

Annual variation in chick growth of Rhinoceros Auklets appears to be related to food supply, and information gathered on food supply has focused on the size of food loads brought by parents to their young (Vermeer and Cullen 1979, Watanuki 1987, Bertram et al. 1991, Burger et al. 1993). On Teuri Island, the diet of Rhinoceros Auklet chicks consisted mostly of the fishes *Ammodytes personatus* and *Engraulis japonica*. The mean body size of *E. japonica* is larger than that of *A. personatus*. The proportion of *E. japonica* in the chick diet was 60% in 1993 and 90% in 1994. Therefore, the average food size was significantly larger in 1994 than in 1993 (A. Kato, Y. Watanuki, and E. Hayashi pers comm.). This appeared to explain why chick growth rates were higher in 1994 than in 1993 at both the *Calamagrostis* and the removal sites. An abundant food supply in 1994 might have been responsible for a decrease in the effect of kleptoparasitism by gulls on chick fledging mass at the *Calamagrostis* and the removal sites.

Although the sparse-vegetation site seemed to be similar to habitat at the removal site, there were some differences. First, the percentage of kleptoparasitism at the sparse-vegetation site increased toward midnight, whereas it decreased at the removal site. Because there were large numbers of gulls at the sparse-vegetation site, arriving auklets almost always landed near a gull. Second, the mean fledging mass at the sparse-vegetation site was significantly lower than at the other sites. Auklet chicks at the sparse-vegetation site hatched later than at the *Calamagrostis* site. Later-hatched chicks grew significantly slower than those hatched earlier (Nettleship 1972, Bertram et al. 1991). This difference became evident after chicks reached a mass of 300 g. The difference in mean body mass among breeders could be attributed to differences in the physiological condition of arriving birds (Nettleship 1972, Jones 1994). Therefore, the variation in body mass of parents and the earlier hatching date at the *Calamagrostis* site relative to the sparse-vegetation site suggested that the quality of nesting parents differed between sites.

In conclusion, removal of vegetation cover from the nesting colony may have increased the rate of kleptoparasitism by Black-tailed Gulls and reduced auklet reproductive success. This suggests that habitats that provide vegetation cover are higher-quality nesting sites for Rhinoceros Auklets because these sites offer shelter from kleptoparasitism by Black-tailed Gulls.

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