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BREEDING BIOLOGY OF CRESTED, LEAST, AND WHISKERED AUKLETS ON BULDIR ISLAND, ALASKA

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ABSTRACT.—Nest site characteristics, breeding phenology, productivity, and mortality factors were evaluated from 1974 to 1976 for the Crested Auklet (*Aethia cristatella*), the Least Auklet (*A. pusilla*), and the Whiskered Auklet (*A. pygmaea*), which nested together in a colony at Buldir Island in subarctic Alaska. These species were compared and data from Buldir were compared with those from previous studies at an arctic colony.

The auklets actively competed for nest sites and differed in their choice of site substrates. Crested Auklets, the largest of the three, used the largest nest crevices. Breeding activities occurred on Buldir from mid-May to mid-August. Crested Auklets had a slightly longer nesting period than the other species. Reproductive success (fledglings/eggs) was approximately 50% for Crested and Least auklets, and apparently higher for Whiskered Auklets. Little predation on eggs or chicks was recorded, but avian predators were the major cause of adult auklet mortality.

The three species of the genus *Aethia* nest primarily on islands in or near the Bering Sea and the Sea of Okhotsk (Fig. 1). Crested (*A. cristatella*) and Least (*A. pusilla*) auklets nest together in mixed colonies throughout most of their ranges (A.O.U. 1957). The Whiskered Auklet (*A. pygmaea*) has a more restricted range, but it occurs with the other two species at some colonies in the Aleutian Islands (Murie 1959). The biology of these three species of auklets is poorly known, except at St. Lawrence Island, Alaska, where Crested and Least auklets have been studied intensively (Fay and Cade 1959; Bedard 1967, 1969a, b; Sealy 1968, 1973, 1975; Searing 1977). Stejneger (1885) and Kozlova (1957) presented limited data on all three species of auklets from the Commander Islands. Murie (1959), Gabrielson and Lincoln (1959), Sekora et al. (1979), and Byrd and Gibson (1980) have provided information on the distribution of auklets in the Aleutian Islands, but few data are available from this region on breeding biology.

During avifaunal investigations on Buldir Island from 1974 to 1976, certain aspects of the biology of Crested, Least, and Whiskered auklets were studied in a mixed colony including over 250,000 birds (Byrd et al., in press). In this paper, we summarize data on nest site characteristics, breeding phenology, productivity, and mortality of the three species and compare these data with those from previous studies at St. Lawrence Island in arctic Alaska. We compared breeding schedules at Buldir and St. Lawrence islands in order to test the hypothesis that climate dictates the timing and duration of the breeding cycle at high latitudes. We also tested the premise, developed at St. Lawrence, that Crested and Least auklets are segregated in the talus habitat by the sizes of boulders (hence, crevices).

STUDY AREA AND METHODS

Buldir Island (52°21′N, 175°56′E) is the westernmost island in the Rat Island group, Aleutian Islands, Alaska (Fig. 1). It is the most isolated island in the Aleutians, being 113 km west of the nearest island. Buldir (6.4 km long, 3.2 km wide) has an area of about 2,000 ha. Volcanic in origin, the island has three dominant peaks, the tallest being 655 m.

The main island of Buldir has about 8 ha of talus slopes, and Middle and Outer Rocks, 2 km offshore, have a combined area of 1 ha of talus. All talus areas on the island are inhabited by auklets. The island has 20 km of coastline including 7.8 km (39%) of large-diameter boulders. This boulder habitat was used by auklets, but to a lesser extent than talus. The Main Talus colony, our primary study area, is located on the north-central side of Buldir Island (Fig. 1). This talus slope encompasses 4.3 ha and ranges from 0.5 to 4.0 m deep.

Buldir is one of the few Aleutian Islands where no land mammals have been introduced. Twenty species of seabirds nest there, including 12 species of alcids (G. V. Byrd, unpubl. data). The most common birds nesting in the talus slopes with the three species of *Aethia* are Parakeet Auklets (*Cyclorrhynchus*

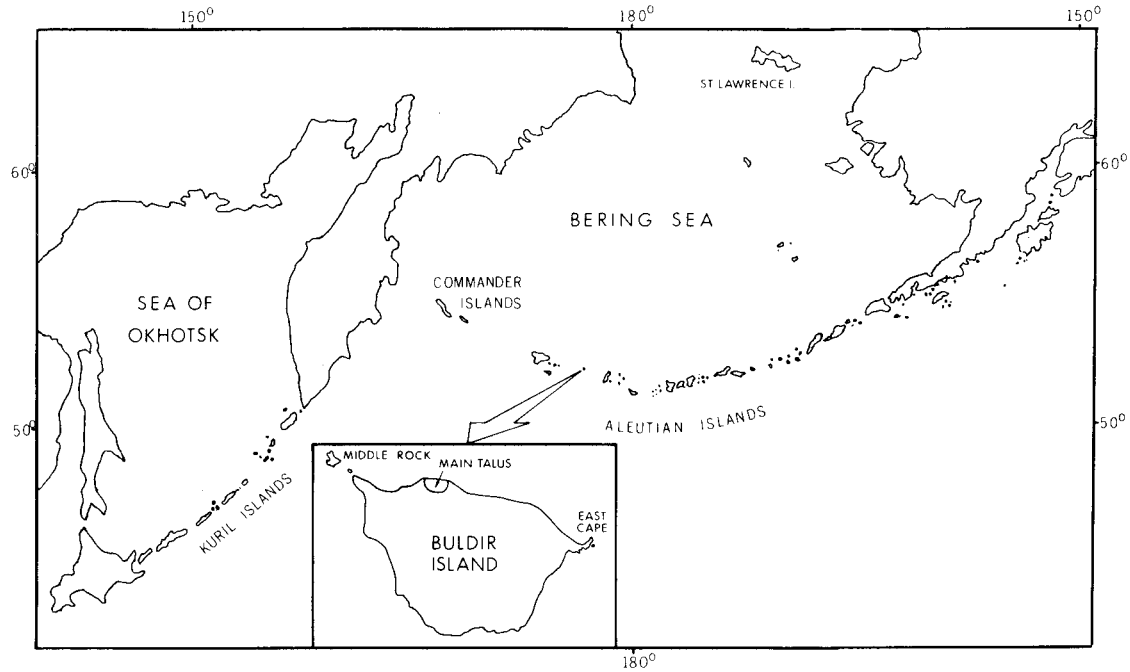

FIGURE 1. Location of Buldir Island and the Main Talus study area.

psittacula) and Horned Puffins (*Fratercula corniculata*).

Investigations were conducted at Buldir from mid-May through late August in 1974 and 1975, and mid-May through late September 1976. In 1974 and 1975 observations of auklets were incidental to more intensive studies of other species, but in 1976 biologists visited the study area at least weekly. During the laying period, crevices in a specified area of the study area were searched approximately every three days to determine the distribution of egg-laying dates. Egg fates and hatching dates were determined by checking eggs in marked crevices weekly during incubation and every three days during the hatching period. To calculate the sizes of nest site, three measurements, perpendicular to each other, were made in 107 nest crevices.

RESULTS AND DISCUSSION

HABITAT USE

Crested, Least, and Whiskered auklets nest in rock crevices throughout their ranges (Murie 1959, Bedard 1969a). At Buldir, Crested and Least auklets nested mostly in talus slopes. Whiskered Auklets used the talus and also nested under beach boulders above the high-tide line.

Lack (1968) suggested that alcids may compete intensely for nest sites and that nesting habitat may limit breeding populations. Rowan (1965) proposed a similar idea for burrow-nesting petrels in a colony where abortive laying on the surface occurred, presumably by mature birds unable to obtain suitable nest sites. At Buldir, we found suggestive evidence that auklets were limited by a shortage of nest sites. In February 1975 an earthquake caused a small rockslide near the east side of the Main Talus. In June 1975 we found auklets nesting in the new area in addition to the previously inhabited areas. This suggests that an excess of adults was present, who had previously been unable to obtain nest sites. In addition, we found eggs on the surface of talus slopes each year of the study.

Bedard (1969a) examined the segregation between Crested and Least auklets at St. Lawrence. He noted that the density of Crested Auklets was positively correlated with boulder size, and that the density of Least Auklets decreased in areas with large-diameter surface boulders. Assuming that the size of surface boulders was related to the size of rock crevices, Bedard (1969a) suggested that Crested and Least auklets selected different nest sites because of the large differences in their body size.

We measured the volume of nest spaces, and determined that Crested Auklets had significantly ($P < 0.01$) larger nest sites than Least and Whiskered auklets (Table 1). Whiskered Auklets used sites that did not differ significantly from those of Least Auklets ($P > 0.01$). Evidence of displacement was noted at Buldir. On 29 May 1976 a Crested Auklet was found incubating an egg in a crevice that had been

TABLE 1. Comparison of volumes of nest crevices for three auklet species on Buldir Island.

Species	Mean adult weight (g)	Nest crevice volume (cm^3)	
		Mean	SD
Crested Auklet	264*	1,567.7 (55)**	342.1
Least Auklet	84	117.6 (40)	65.5
Whiskered Auklet	121	162.5 (12)	70.3

* G. V. Byrd, unpubl. data.
** Number of nests in parentheses.

used by a pair of Horned Puffins the previous season. Five days later (2 June) a Horned Puffin was found incubating at the same site, and no evidence of the Crested Auklet or its egg was seen. Another time, a Least Auklet was incubating an egg on 28 May 1976, and on 2 June it had been replaced by a Crested Auklet incubating its egg. As before, we saw no indication that the Least Auklet had been there. Active displacement according to body size and the size of the nest entrance may be a fairly common means by which birds compete for nest sites. Miller (1968) found that in hole-nesting passerines, a larger species prevented a smaller one from using holes suitable for either, while the smaller species nested in holes that were only large enough for it.

On Buldir and St. Lawrence islands (Bedard 1969a) social dominance among species of auklets seems to depend on the differences in body size. On Buldir, Crested Auklets always displaced Least and Whiskered auklets in encounters ($n = 38$). The outcome of encounters between the two smaller auklets was less predictable, but Whiskered Auklets displaced Least Auklets in 70% of the encounters we observed ($n = 25$). This suggests that Crested Auklets should be able to use the nest sites they prefer.

We examined the relative use of nesting substrate by each species to further evaluate interspecific preferences for nest sites. All three species of auklets used rock and soil substrates (Table 2). Whiskered Auklets showed a significant preference (χ^2, $P < 0.01$) for rock substrates, while the other species showed no significant preferences for either substrate. Crested Auklets preferred depressions for nest sites, but Least and Whiskered auklets most frequently chose flat surfaces on which to deposit eggs (Table 2). The depressions used by Crested Auklets apparently were dug by the birds. Crested Auklets are larger and therefore probably better able to dig depressions than the smaller auklets. Their eggs are relatively large, so a depression may lessen the chance that they will be dislodged from precarious sites. Crested Auklets nested below contact points between boulders much less frequently than the other two species, probably because these sites tended to be too small for them.

We found Crested Auklets nesting in two 10-m^3 "talus caves" or chambers, up to 4 m deep in the Main Talus. Each chamber contained 10–20 Crested Auklet nests, but no Least or Whiskered auklet nests. A single communal entrance led into each cave. For nests in sight of each other, nearest-neighbor distances were 1 m or more, but where visual barriers occurred, eggs were found within 15 cm of each other.

NESTING PHENOLOGY

On 30 April 1974 we saw thousands of auklets resting on the sea within 5 km of Buldir, but none were seen on the Main Talus. All three species were present on the Main Talus study area by 15 May (1974–1976), when the talus was mostly snow-free. In contrast, at St. Lawrence Island, approximately 1,200 km farther north (63°46′N), auklets first arrive on the nesting slopes by 20–29 May, when snow usually still covers most of the rock crevices (Sealy 1968, 1975; Searing 1977).

Egg-laying for all three species of auklets was highly synchronous; most individuals laid within a period of 10 to 12 days (Table 3). Although sample sizes are small, our data suggest that the peak of laying for Crested Auklets may have been slightly later than for the other two species. The peak of hatching for Crested Auklets was clearly later because the species had a longer incubation period than the two smaller species. Laying and hatching dates at Buldir are approximately two weeks earlier

TABLE 2. Relative use of various substrates by nesting auklets at Buldir Island.

Species	Rock substrate			Soil substrate		
	Unmodifed rocks	Depression in pebbles	Total rock	Unmodified soil	Depression in soil	Total soil
Crested Auklet (52)*	14**	35	49	21	30	51
Least Auklet (26)	35	4	39	46	15	61
Whiskered Auklet (11)	73	9	82	18	0	18

* Sample size in parentheses.
** Values represent percent of total for each species.

TABLE 3. Distribution of laying and hatching dates for auklets on Buldir Island in 1976.

Species	Date laid						Date hatched					
	n	24–26 May	27–29 May	30 May–1 June	2–5 June	5–7 June	*n*	24–30 June	1–4 July	5–8 July	9–12 July	13–16 July
Crested Auklet	30	5*	7	6	11	1	36	0	6	13	16	1
Least Auklet	11	2	5	2	1	1	15	3	8	3	1	0
Whiskered Auklet	6	2	2	1	1	0	6	4	0	2	0	0

* Number of eggs.

than those recorded by Sealy (1968) and Searing (1977) at St. Lawrence. Sealy (1975) concluded that snow cover was the proximate factor influencing the timing of egg laying of at least some pairs at St. Lawrence. At Buldir our study area was snow-free by mid-May each year of the study, but snow in late springs might delay nesting.

Since we did not know the exact dates of laying or hatching (our data were ± 3 days), we were able to determine only minimum incubation periods. Crested Auklets incubated at least 40–41 days ($n = 7$), and Least and Whiskered auklets incubated approximately 35–36 days ($n = 5$ and 3, respectively). It appears that incubation was more protracted at Buldir than at St. Lawrence, where Sealy (1968) found average periods of 35.6 days (range 34–47) for Crested Auklets and 31.2 days (range 28–36) for Least Auklets.

The first fledglings of each species were seen on the sea at the end of July each year, but most chicks fledged during the first 10 days of August. As might be expected, Whiskered and Least auklet chicks fledged slightly earlier than Crested Auklets. Sealy (1968) found the same situation on St. Lawrence, where Crested Auklets fledged from mid-August to early September. Stejneger (1899) found Whiskered Auklets still present in the central Kuril Islands 22–25 August. At Buldir most auklets had departed by mid-August, but a few individuals of each species were seen as late as 22 August.

PRODUCTION

We recorded an overall reproductive success of 51% for Crested and Least auklets and 86% for a small sample of Whiskered Auklets at Buldir (Table 4). Since most of the eggs we monitored were found after incubation was underway, our estimate of hatching success may be excessive. Fledging success estimates are based on small samples because chicks became inaccessible as they grew more mobile.

TABLE 4. Productivity of auklets on Buldir Island in 1976.

Species	Total eggs	Hatching success*	Total chicks	Fledging success**	Reproductive success***
Crested Auklet	36	76	21	67	51
Least Auklet	28	68	12	75	51
Whiskered Auklet	7	86	3	100	86

* Percent of total eggs laid that hatched.
** Percent of chicks that fledged.
*** Hatching success × fledging success.

On St. Lawrence, Searing (1977) found a lower hatching success for Crested (30%) and Least (60%) auklets than we found at Buldir. Searing was unable to determine the fate of most Crested Auklet chicks. He found that Least Auklet fledging success was only 34%, half that estimated for the species at Buldir in 1976.

MORTALITY FACTORS

Eggs. In 1976, infertility of the egg or death of the embryo were the primary causes of mortality of Crested (89%) and Least (93%) auklet eggs; the remaining dead eggs were unaccountably cracked. Disturbance of birds by investigators may have increased egg mortality by causing frightened adults to crack or temporarily abandon eggs. Most embryo death occurred during the early stages of incubation. None of the eggs we studied was taken by predators, but Glaucous-winged Gulls (*Larus glaucescens*) might prey upon a small number of auklet eggs at Buldir.

Chicks. Crested Auklets suffered higher chick mortality (35%) than Least Auklets (25%); none of the three Whiskered Auklet chicks died (Table 4). Most chick mortality occurred within the first week of life. Thermoregulation begins in Crested Auklet chicks at three to four days and in Least Auklets at five to six days of age (Sealy 1968). It seems likely that chick mortality decreases abruptly after birds develop the ability to thermoregulate. Also, severe congenital problems would be expected to cause death within the first week. In 1976 we noted ticks (up to 11 per bird) parasitizing two Crested Auklet chicks and three Least Auklet chicks. In most cases, these ticks were attached to webs of the feet or the eyelids. We were unable to learn if ticks influenced mortality, but we doubt that such low-intensity parasitism is a significant cause of chick mortality.

Most auklet chicks fledged during darkness.

TABLE 5. Number of auklet remains found in eyries of Peregrine Falcons and Bald Eagles on Buldir Island.

Predator	Total items examined	Total auklets	Crested Auklet	Least Auklet	Whiskered Auklet
Peregrine Falcon	75	61 (79)*	7 (11)**	52 (85)	2 (3)
Bald Eagle	83	33 (40)	24 (73)	8 (24)	1 (3)

* Percent of total food items in parentheses.
** Percent of total auklets in parentheses.

Glaucous-winged Gulls took two Least Auklet fledglings that remained near shore until dawn, as well as a few nestlings that were visible from the surface of the talus (R. H. Day, pers. comm.).

Adults. Peregrine Falcons (*Falco peregrinus*), Bald Eagles (*Haliaeetus leucocephalus*), and Glaucous-winged Gulls were major predators of adult auklets on Buldir. Auklets, particularly Least Auklets, were an important part of the diet of Peregrine Falcons (Table 5). White (1975) has related the distribution and abundance of Peregrine Falcons in the Aleutian Islands to the distribution of auklets. Buldir Island supported four or five breeding pairs of falcons, a particularly dense population, probably due to the large auklet population. Bald Eagles depended less on auklets than Peregrines, and unlike falcons, eagles favored Crested over Least auklets (Table 5).

Glaucous-winged Gulls hunted alcids daily at the Main Talus, and we saw gulls catch auklets on over 50 occasions. Auklets made up only 6% of the food items of gulls over the whole island (Trapp 1979), while storm-petrels (*Oceanodroma* spp.), which nested abundantly over the entire island, provided the major food source. In contrast, Trapp (pers. comm.) found that Crested and Least auklets comprised 67% and 33%, respectively, of the auklets taken by gulls at Main Talus, percentages almost identical to the estimated relative abundance of Crested and Least auklets nesting there (Byrd et al., in press). No Whiskered Auklet remains were found in gull pellets analyzed from the Main Talus, but one pellet found in another area contained the remains of such a bird.

CONCLUSIONS

Climate, predation, and the temporal and spatial availability of food exert important selective pressures on the breeding biology of auklets. Our study focused on a subarctic colony that differed from those previously studied at St. Lawrence Island in the arctic. Buldir and St. Lawrence differ in their climatic conditions and may differ in the availability of their food resources and abundance of predators. We hypothesized that the longer growing season in the subarctic would select for a longer breeding season, yet we found the breeding season at Buldir lasted as long as that at St. Lawrence. The *start* of the breeding cycle, however, was two weeks later in the arctic, probably due to snow cover on nest sites. This suggests that climate at high latitudes may dictate the timing, but not the duration of breeding.

Interspecific competition for nest sites, which has previously been recorded in the arctic, probably limited nesting populations at Buldir. Crested Auklets, owing to their large size, probably were able to secure nest crevices of a suitable size, leaving the smaller auklets crevices that Crested Auklets could not use.

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624 Fountain Ave., Redlands, California 92373. Address of second author: Aladdin Rt. Box 160 E, Colville, Washington 99114. Received 26 October 1979. Final acceptance 25 January 1982.

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RECENT PUBLICATIONS

An Annotated Bibliography of the Red-cockaded Woodpecker, *Picoides borealis*.—Jerome A. Jackson. [1981]. Savannah River Plant, National Environmental Research Park Program, U.S. Dept. of Energy. 290 p. Paper cover. Source: Librarian, Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29801. This well-compiled bibliography lists nearly 1,800 publications pertaining to the Red-cockaded Woodpecker, ranging from research articles to a bare mention. Each entry is coded to show its particular subject; reciprocally, an index lists the entries according to subject category.

International Registry of Poultry Genetic Stocks; a Directory of Specialized Lines and Strains, Mutations, Breeds and Varieties of Chickens, Japanese Quail and Turkeys.—Ralph G. Somes, Jr. 1981. Bulletin 460, Department of Nutritional Sciences, University of Connecticut, Storrs. 97 p. Paper cover. $3.00. Source: author, Dept. of Nutritional Sciences, Univ. Connecticut, Storrs, CT 06268. This fourth edition of the Registry now includes stocks from 17 different countries. Of its seven sections, Sections I, II, and V list, describe, and give sources for specialized forms of the three poultry species considered. Section III lists the known genetic traits and their gene symbols for these birds. Section IV presents the three chromosome linkage maps. Section VI describes the chicken plumage colors grouped according to the *E* locus. The last section lists the addresses of breeders and suppliers. A useful reference not just for poultry geneticists but for other scientists who use poultry for their research.

The Wading Birds of North America (North of Mexico).—Text by Allan W. Eckert, paintings and drawings by Karl E. Karalus. 1981. Doubleday & Co., Inc., Garden City, NY. 252 p. $49.95. This is a coffee-table book about North American ciconiiforms, gruiforms, and flamingos, some 31 species. The species accounts touch on the scientific and colloquial names, external morphology and coloration, habitat, enemies and defenses, feeding and nesting habits, migration, and economic role. Much space is devoted to subspecies, yet no measurements are given and the taxonomy is not considered. Overall, the treatment is superficial, diffuse, and undocumented. The list of references contains nothing later than 1975, and omits many pertinent works, notably Volume 1 of Palmer's *Handbook*. That book and others (e.g., Terres's *Encyclopedia* [noticed in Condor 83:170]) are more detailed and up-to-date sources of information about these birds. The illustrations are attractive, especially the sketches, but they are far from outstanding; the colors of many of the paintings seem too bright. The range maps are less accurate and current than those in the *Handbook* or in field guides. The book has little to recommend it, especially at such a high price.