

BREEDING BIOLOGY OF CRESTED AUKLETS AT BULDIR AND KASATOCHI ISLANDS, ALASKA

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ABSTRACT.—We quantified breeding parameters of Crested Auklets (*Aethia cristatella*) at Buldir and Kasatochi islands in the Aleutian Islands, Alaska, in 1996 and 1997. Crested Auklets incubated their eggs for about 36 days and chicks weighed about 35 g within the first three days of hatching (14% of adult mass; Buldir, $n = 58$). Growth rates averaged about 9.9 g per day during the linear phase (Buldir, $n = 58$; Kasatochi, $n = 17$), and chicks fledged at an average mass of 248 g (95% of adult mass; Buldir, $n = 63$) and a wing length of 123 mm (88% of adult wing length; Buldir, $n = 37$) at 34 days after hatching. We found no differences in intrainland and intrayear chick growth for Buldir and Kasatochi. Productivity (the product of hatching success and fledging success) averaged more than 60% for the two years at Kasatochi and for eight years (1990 to 1997) at Buldir. Intercolony comparisons of productivity parameters revealed differences in hatching date, age of chicks at fledging, and hatching and fledging success. Adult mass differed significantly between the sexes (267 g for males, 253 g for females) and among years. At Buldir, we observed no effect of various levels of investigator disturbance on hatching and fledging success or on other breeding parameters. We found no negative relationships between hatching date and fledging age, hatching date and fledging mass, or fledging mass and fledging age, contrary to the predictions of Ydenberg's (1989) model of intraspecific variation in timing of fledging of alcid chicks. Crested Auklet chicks, like those of other diurnally active species of auklets, grow relatively fast and depart at a younger age compared with chicks of two nocturnal species of auklets. Received 24 April 1998, accepted 17 November 1998.

CRESTED AUKLETS (*Aethia cristatella*) are colonial seabirds that lay a clutch size of one and have semiprecocial chicks that are provisioned by both parents (Jones 1993b, Gaston and Jones 1998). This species is part of a remarkable adaptive radiation of five small planktivorous auklets (Cassin's [*Ptychoramphus aleuticus*], Parakeet [*Aethia psittacula*], Least [*A. pusilla*], and Whiskered [*A. pygmaea*] auklets) that are endemic to the North Pacific Ocean and Bering and Okhotsk seas. These auklets range in mean body mass from the Least Auklet at 85 g to the Parakeet Auklet at 289 g. Adult and chick diets and chick development patterns (Gaston 1985, Gaston and Jones 1998) also vary among species. The biology of Cassin's and Least auklets have been relatively well studied (see Manuwal and Thoresen 1993, Jones 1993c), whereas Parakeet and Crested auklets are less well known

(e.g. Bédard 1969, Hipfner and Byrd 1993, Jones 1993b), and the Whiskered Auklets is the least well known (Byrd and Williams 1994). Detailed knowledge of the biology of these auklets is required for an understanding of their life-history variation, adaptive radiation, and ecological relationships.

Alcids show considerable inter- and intraspecific variation in the age and mass of their chicks at the time of departure from nesting colonies. For example, the tiny precocial chicks of Ancient Murrelets (*Synthliboramphus antiquus*) depart two days after hatching, whereas the semiprecocial chicks of Rhinoceros Auklets (*Cerorhinca monocerata*) depart close to adult size at 38 to 58 days old (Gaston 1985, Gaston and Jones 1998). Ydenberg (1989) and Ydenberg et al. (1995) provided the first comprehensive model that explained variation in life-history traits in alcids and offered testable predictions. Two main assumptions of the model

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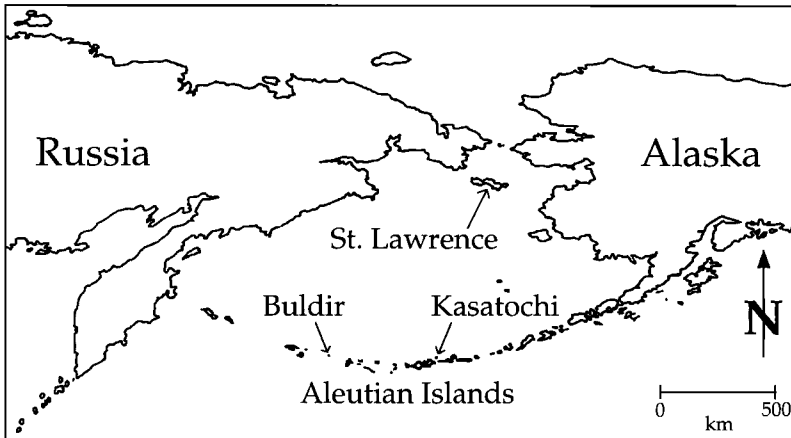


FIG. 1. Map of the North Pacific, including St. Lawrence Island and our study sites in the Aleutians.

were that juvenile mortality is lower at the nest and growth rate is higher at sea. Here, we test two of the model's predictions about intraspecific variation in life-history traits using data from Crested Auklets: (1) fast-growing chicks depart the nest younger and heavier (i.e. a negative relationship exists between fledging age and fledging mass), and (2) late-hatching chicks depart the nest younger and lighter. Although some data from Cassin's and Rhinoceros auklets are consistent with these predictions (Harfenist 1995, Harfenist and Ydenberg 1996, Morbey and Ydenberg 1997), further testing of the model is needed (Gaston and Jones 1998, Hipfner and Gaston 1999). Crested Auklet chicks are semiprecocial, depart the nest at close to adult size, fit all of the assumptions of the model (Ydenberg et al. 1995), and thus provide an opportunity to examine the model's predictions for the first time within the genus *Aethia*.

Much of the information on Crested Auklet breeding parameters comes from northern colonies on St. Lawrence Island (Bédard 1969, Piatt et al. 1990; see Fig. 1) where the birds nest later than their Aleutian counterparts. The Aleutian Islands comprise a substantial portion of the Crested Auklet's breeding range. Nevertheless, Knudtson and Byrd's (1982) and Hipfner and Byrd's (1993) reports on laying and hatching dates, productivity, and nest-crevice attributes provide the only published data from the Aleutians. Here, we present the first comparisons across years and colonies of

chick growth, productivity, and breeding chronology in Crested Auklets, including eight years of data from a single colony in the Aleutians.

The objectives of our study were to (1) quantify chick growth; (2) examine eight years of variation in reproductive performance and breeding chronology from one colony in the western Aleutians (1990 to 1997) and make interyear and intercolony comparisons with another site located in the central Aleutians (1996 to 1997); (3) evaluate the effects of investigator disturbance on breeding success; and (4) test two key predictions of Ydenberg's (1989) model to explain timing of chick departure for a semiprecocial species of auklet.

STUDY AREA AND METHODS

Study areas.—We studied auklets on Buldir (52°21'N, 175°56'E) and Kasatochi (52°11'N, 175°30'W) islands in the Aleutian chain of Alaska (Fig. 1). Buldir, located in the western part of the chain, contains one of the largest and most diverse concentrations of seabirds in the Aleutians (Sowls et al. 1978, Byrd and Day 1986). Our study area on Buldir was located at "Main Talus," a colony with approximately 250,000 Crested and Least auklets (ratio of 2:1 Crested to Least; Knudtson and Byrd 1982, Byrd et al. 1983). Kasatochi is located in the central Aleutians about 480 km east of Buldir. Our study area there was in a colony on a northeast-facing talus slope with a minimum of 35,000 Least and Crested auklets (2:1 Least to Crested; Scharf et al. 1996).

Chick growth, productivity, and breeding chro-

nology were recorded on both islands, whereas investigator disturbance and effects of crevice location were evaluated only on Buldir. We selected crevices that were configured so that parents or chicks in nests could not easily hide from view. Because our samples of crevices were taken from large areas and were of different crevice types (except for very deep crevices), we believe that the crevices we monitored were representative of the entire colonies at Buldir and Kasatochi. For all crevices, chicks were considered fledged (i.e. left the nest) if they were 26 days or older upon disappearance (i.e. the crevice failed if chicks disappeared at less than 26 days of age).

Incubation and chick growth.—In 1997, we followed eight pairs from laying until hatching to determine the duration of incubation on Buldir. We selected previously used crevices that were unoccupied in mid-May and checked them daily until an incubating bird was present. To minimize disturbance early in incubation, we checked occupied crevices only once a week for the first 29 days. After 29 days, we checked crevices daily to obtain the exact date of hatching.

In 1996 and 1997, we studied chick growth on Buldir and Kasatochi. Because we had larger sample sizes and wanted more precise data from Buldir, our methodology varied slightly between the two colonies. To determine hatching dates on Buldir, nests were checked once a week until mid-June (again, to minimize disturbance early during incubation), then every two days until hatching. Chick age was estimated to within one day based on appearance (Jones 1993b). Chicks were then measured every three days until they departed from their crevice; in most cases, fledging dates were known to the nearest day. On Kasatochi, we determined hatching dates by checking nests at four-day intervals prior to hatching and estimated chick age to within two days. We measured chicks only during the linear growth period on Kasatochi; therefore, chicks were handled every four days (from ages 6 to 24 days), and fledging dates were estimated to within two to four days. We measured chick mass to the nearest 1 g, flattened wing (Buldir) and wing chord (Kasatochi) to the nearest 1 mm, and tarsus length to the nearest 0.1 mm.

We used regression residuals from mass versus age and wing versus age to estimate the linear portion of the growth curve from composite data. We assumed linear growth when the residuals were randomly distributed around zero. The slopes of simple linear models for mass and wing length from each chick provided comparative statistics. The sample units were individual chicks with at least three measurements collected during the linear growth period. We used $P < 0.05$ as a threshold for concluding statistical significance.

To compare our growth data with those from studies of Crested Auklets on St. Lawrence Island (Sealy 1968, Piatt et al. 1990), we fitted individual growth

data from Buldir to a logistic model (Ricklefs 1967). The model's products (asymptotic mass [a] and the growth constant [k]) were used to calculate the instantaneous growth rate at the point of inflection (i.e. $k(a)/4$; Hussell 1972), which is considered to be the maximum growth rate (Hussell 1972, Sealy 1973, Gaston 1985, Piatt et al. 1990).

Adult mass.—To quantify variation in adult mass within and between breeding seasons and islands, and to compare adult mass with chick mass at fledging, we caught birds at a single study plot centrally located on Main Talus, Buldir Island, and at a similar plot on Kasatochi Island. We determined the sex of these birds using bill shape (Jones 1993a) and weighed them to the nearest 1 g with a spring scale. Measurements of adults were taken between May and August from 1990 to 1997 on Buldir and from 1996 to 1997 on Kasatochi.

Productivity and breeding chronology.—Crested Auklet crevices were checked approximately every seven days throughout each breeding season between 1990 and 1996 (1996 to 1997 at Kasatochi). In 1997, we checked crevices every four days between the onset and termination of hatching and fledging periods to obtain more precise estimates of the timing of these events. To minimize bias resulting from nest failures early in the breeding season (i.e. overestimating hatching success), only crevices found prior to 15 June were used to estimate productivity. We used the midpoint between visits to estimate hatching and fledging dates and the even-numbered Julian date when an even number of days occurred between visits.

Effect of crevice location and investigator disturbance.—We evaluated differences in habitat quality and compared various parameters of productivity, nesting chronology, and chick condition between sites located in different types of habitat on Main Talus, Buldir. We subdivided the area into three sections (1) the low area (27×45 m), which was characterized by large boulders (>1 m³) that provided deeper and larger crevices apparently preferred by Crested Auklets (Knudtson and Byrd 1982, Bédard 1969); (2) the middle section (42×45 m), which contained a mixture of large and small boulders; and (3) the high section (67×35 m), which was composed primarily of small boulders with more vegetation.

We evaluated the disturbance caused by our monitoring activities by comparing success of nests visited at different frequencies during the incubation and chick-growth periods. In 1996, we visually checked crevices during incubation (1) once a week (i.e. low disturbance), (2) every two days (medium disturbance), or (3) twice a day for 15 days before hatching (high disturbance). During 1997, we had two levels of disturbance during the incubation period (1) weekly checks (low disturbance) and (2) every two days (medium disturbance). During the chick-rearing periods of both years, we evaluated

three levels of disturbance (1) crevices that we visually checked approximately every seven days (low disturbance), (2) crevices in which we captured a chick every three days (medium disturbance), and (3) crevices in which we captured a chick every three days and in which we captured at least one adult once within six days after hatching (high disturbance; 1996, $n = 16$ nests; 1997, $n = 36$ nests). To assess the effects of handling chicks, we compared mass, wing, and tarsus measurements of chicks handled regularly throughout the rearing period with chicks that we checked visually every three days, but captured and measured only once between ages 28 and 30 days (i.e. control chicks).

RESULTS

Incubation period and chick growth.—In 1997, the duration of incubation averaged $35.9 \pm$ SD of 4.8 days ($n = 8$, range 29 to 44 days) on Buldir. On average, Crested Auklet chicks on Buldir weighed about 35 g within three days of hatching (13.4% of adult mass) and gained approximately 10 g per day during the linear phase of growth. They remained in their crevices for about 35 days (range 26 to 41 days) and fledged at a mass of 248 g (95% of adult value; Tables 1 and 2, Figs. 2A, B) and a wing length of 123 mm (88% of adult value; Fig. 2C). Chick mass declined prior to fledging by 5% in 1996 and by 3% in 1997.

At Buldir, we found no significant differences between years in hatching mass ($P = 0.07$), growth rate ($P = 0.60$), maximum mass ($P = 0.20$), fledging mass ($P = 0.70$), and fledging age ($P = 0.10$). Hatching date ($t = 2.4$, $df = 1$, $P = 0.005$, $n = 91$) and fledging date ($t = 2.3$, $df = 1$, $P = 0.02$, $n = 67$) differed significantly between years (Table 1).

We found no significant relationships in 1996 or 1997 between hatching dates and the following: fledging mass, fledging age, fledging wing length, and linear growth rate for mass (Table 3). When we controlled for linear growth in 1997, we found that fast growing chicks fledged at a heavier mass, but not at an earlier age (i.e. a positive relationship between linear growth and fledging mass exists, but no significant relationship between hatching date and fledging mass, or fledging age; Table 3). We also found a significant negative relationship ($r^2 = 0.32$, $P = 0.02$, $n = 17$) between wing length and age of fledging in 1997 (i.e. day 25, which is one day before the first fledging age; see Hipfner and Gaston 1999). However, we found no signifi-

cant relationship between mass and age of fledging (day 25 only) in either 1996 or 1997 (1996, $P = 0.60$; 1997, $P = 0.10$).

On average, Crested Auklet chicks at Kasatochi gained approximately 9 g per day during the linear growth phase and remained in their crevice for 35 days (range 26 to 40; Table 1). We found no significant differences between years for the linear phase of growth in mass ($P = 0.20$) or wing length ($P = 0.08$), nor any significant differences between islands or years for the linear phase of growth in mass (island, $P = 0.30$; year, $P = 0.20$; island \times year, $P = 0.06$) or fledging age (island, $P = 0.10$; year, $P = 0.90$; island \times year, $P = 0.80$). We were unable to statistically compare linear growth of the wing because of differences in methodology for wing measurements (Buldir, $\bar{x} = 4.5 \pm 0.36$ mm per day; Kasatochi, $\bar{x} = 3.1 \pm 0.61$ mm per day).

Adult mass.—On average, male Crested Auklets ($\bar{x} = 267 \pm 19$ g, range 211 to 314 g, $n = 347$) were 14 g heavier than females ($\bar{x} = 253 \pm 1.0$ g, range 210 to 322 g, $n = 345$; $t = 10.1$, $df = 1$, $P < 0.0001$; Fig. 3). Mass varied significantly among years on Buldir (1990 to 1997; $F = 6.2$, $df = 6$ and 565, $P < 0.0001$), being highest in 1993 and 1997, which corresponded with two years of high breeding productivity (Table 4). We found no evidence that mass differed between islands in 1996 and 1997 ($P = 0.20$).

Productivity and breeding chronology.—Over an eight-year period at Buldir, hatching success averaged 81%, fledging success 76%, and productivity 67% (Table 4). For the two study years on Kasatochi (1996 and 1997), Crested Auklets averaged 85% hatching success, 76% fledging success, and 65% for productivity (Table 5).

The annual breeding chronology for Crested Auklets on Buldir was somewhat flexible during the eight years we monitored the colony (Table 4). The median hatching date was 26 June, but hatching dates varied by nine days among years; typically, the first eggs hatched in mid-June, and the last eggs in mid-July. The median fledging date was 29 July. Median fledging dates differed as much as seven days between breeding seasons, but generally the first chicks fledged on about 19 July, and the last chicks fledged on around 12 August. On average, the auklets on Kasatochi appeared to be on a slightly later schedule than on Buldir (Table 5). The first chicks hatched on 26 June, the last chicks on 15 July, and the median hatching date

TABLE 1. Summary of Crested Auklet chick growth at Buldir and Kasatochi islands, 1996 and 1997. Data are $\bar{x} \pm SD$, with range and n in parentheses. Measures of mass in g, wing length in mm, and age in days.

Hatching date ^a	Hatching mass ^b	Hatching wing length ^b	Slope mass ^c	Slope wing length ^c	Maximum mass	Age at maximum mass	Fledging age	Fledging date	Fledging mass ^d	Fledging wing length ^d
Buldir 1996										
26 June (45)	37.7 ± 10.95 (22-60, 29)	—	9.7 ± 1.45 (7.5-12.3, 25)	—	262.0 ± 36.6 (199-329, 20)	29.3 ± 3.3 (25-35, 20)	33.9 ± 3.7 (27-40, 30)	1 August (30)	248.8 ± 31.3 (173-298, 26)	—
Buldir 1997										
24 June (46)	33.1 ± 7.93 (20-51, 29)	19.6 ± 1.97 (15-23, 27)	10.1 ± 1.71 (7.4-13.7, 33)	4.46 ± 0.36 (3.7-5.1, 35)	252.0 ± 32.2 (195-298, 32)	30.1 ± 3.6 (20-35, 32)	35.27 ± 3.2 (26-41, 37)	30 July (37)	245.8 ± 27.0 (195-298, 37)	123.4 ± 8.33 (102-135, 37)
Kasatochi 1996										
30 June (7)	—	—	10.2 ± 2.60 (7.7-12.7, 7)	3.7 ± 0.32 (3.2-3.9, 7)	—	—	33.8 ± 3.4 (26-40, 6)	2 August (6)	—	—
Kasatochi 1997										
2 July (10)	—	—	8.5 ± 2.60 (4.0-11.7, 10)	3.2 ± 0.60 (1.9-3.9, 10)	—	—	35.6 ± 5.7 (27-36, 8)	6 August (8)	—	—

^a Hatching date known to within 1 day for Buldir, 2 days for Kasatochi.

^b From chicks measured within three days of hatching.

^c From the linear portion of growth curve (g per day). Includes chicks with three or more data points during linear growth period.

^d From chicks within three days of fledging.

TABLE 2. Crested Auklet chick growth data (logistic model) from Buldir and St. Lawrence islands.

Asymp- totic mass (g)	Adult mass (g) ^a	Fledging age (days)	Fledging mass (g)	<i>k</i> ^b	<i>k(a)/4</i> ^c	Island	Source
254.4	286	34	228 (80) ^d	0.197	12.5	St. Lawrence	Sealy (1968, 1973)
269.0	260–283	—	—	—	12.8	St. Lawrence	Piatt et al. (1990)
—	267	—	—	—	11.1	St. Lawrence	Searing (1977)
260.8	262	34	244 (93)	0.184	12.0	Buldir	This study (1996)
258.5	262	35	246 (94)	0.172	11.1	Buldir	This study (1997)

^a Mass of incubating adults (see Fig. 2).

^b Mean instantaneous growth rate calculated from individual chicks fit to model.

^c Maximum instantaneous growth rate, where *a* = asymptotic mass (Hussell 1972, Sealy 1973).

^d Fledging mass at % of adult mass in parentheses.

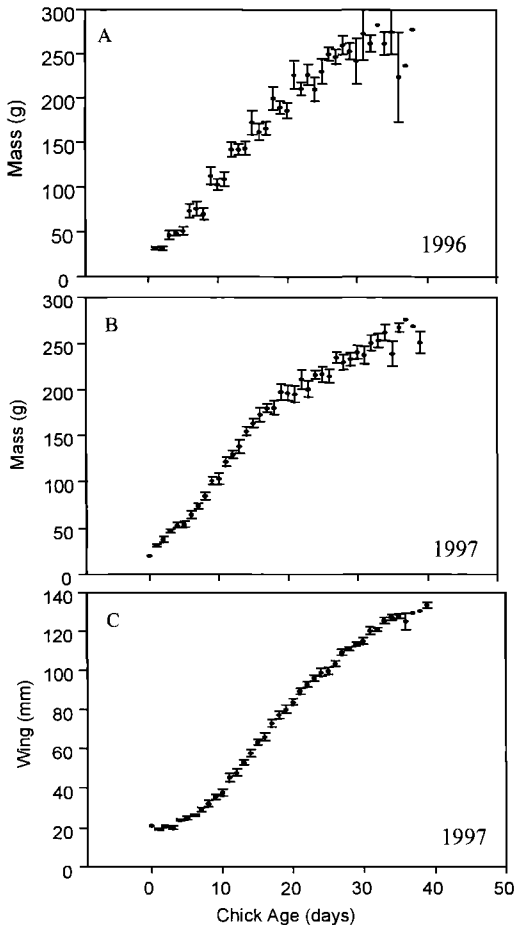


FIG. 2. Growth of Crested Auklet chicks on Buldir Island. Changes in body mass in (A) 1996 and (B) 1997; (C) wing length in 1997. Values are $\bar{x} \pm SE$.

was 30 June. The first chicks fledged on 22 July, the last ones by 12 August, and the median fledging date was 4 August.

Interisland comparisons of breeding chronology and productivity.—In comparing reproductive variables for four colony-year combinations, we found significant differences in hatching date ($F = 68.9$, $df = 1$ and 229 , $P < 0.0001$; Tables 4 and 5) and hatching and fledging success in 1997 (hatching, $\chi^2 = 3.86$, $P = 0.05$; fledging, $\chi^2 = 4.0$, $P = 0.05$). We also found a significant interaction between year and island for fledging age (year, $F = 0.05$, $df = 1$ and 171 , $P = 0.80$; island, $F = 3.0$, $df = 1$ and 171 , $P = 0.08$; year \times island, $F = 16.9$, $df = 1$ and 171 , $P < 0.0001$), and pairwise comparisons revealed significant differences in fledging age between islands (1996, $F = 12.9$, $df = 1$ and 69 , $P = 0.0006$; Buldir, $\bar{x} = 35.2$ days; Kasatochi, $\bar{x} = 31.7$ days; 1997, $F = 3.8$, $df = 1$, 102 , $P = 0.05$; Buldir, $\bar{x} = 32.6$ days, Kasatochi, $\bar{x} = 34.0$ days). We found no differences in hatching and fledging success in 1996 or in fledging date in either year ($P_s > 0.05$).

Effect of crevice location on productivity.—The location of a nesting crevice on Main Talus had some influence on when a chick hatched and on the likelihood that it would survive to fledging age. Chicks in crevices in the low or middle areas on Main Talus hatched earlier ($F = 6.2$, $df = 2$ and 115 , $P = 0.002$; Scheffe's post-hoc, high vs. low, $P = 0.005$; high vs. middle, $P = 0.04$; middle vs. low, $P = 0.90$; low, $\bar{x} = 24$ June; middle, $\bar{x} = 24$ June; high, $\bar{x} = 27$ June) and had a greater chance of fledging (both years combined, $\chi^2 = 16.9$, $P = 0.0002$; high = 53.3%, middle = 92.6%, low = 83.7%) than chicks located high on the talus. We found no location effects (all $P_s > 0.05$) in either year for hatching

TABLE 3. Data from Crested Auklets with respect to Ydenberg's predictions for timing of fledging in alcid chicks. Dependent variables centered in bold.

Year	Hatching date			Hatching date; linear growth of mass ^a			Linear growth of mass		
	<i>n</i>	<i>P</i>	<i>r</i> ²	<i>n</i>	<i>P</i>	<i>r</i> ²	<i>n</i>	<i>P</i>	<i>r</i> ²
Fledging mass									
1996	25	0.8	0.003	25	0.8, 0.3	0.05	23	0.3	0.04
1997	35	0.2	0.04	35	0.5, 0.02	0.14	35	0.01	0.18
Fledging age									
1996	25	0.8	0.01	25	0.6, 0.4	0.04	26	0.4	0.03
1997	35	0.9	0.001	35	0.9, 0.7	0.01	35	0.6	0.01
Fledging wing length									
1996	—	—	—	—	—	—	—	—	—
1997	35	0.4	0.02	35	0.3, 0.5	0.04	35	0.6	0.01
Linear growth of body mass									
1996	24	0.7	0.01	—	—	—	—	—	—
1997	32	0.1	0.09	—	—	—	—	—	—

^a Hatching date and linear growth as independent variables in a multiple regression.

mass, hatching wing length, hatching success, or for the slope of the linear growth for mass and fledging mass, fledging wing length, fledging age, or fledging date.

Investigator disturbance.—Crested Auklets tolerated large amounts of disturbance during the incubation period; hatching success did not differ significantly with low, medium, or high levels of disturbance (1996, *P* = 0.40; 1997, *P* = 0.20). Crevices where we either captured an adult (once after hatching), and/or handled a chick regularly did not experience lower fledging success in 1996 (*P* = 0.40). In contrast,

fledging success varied with disturbance level in 1997, although in a direction we would not have predicted: nests with higher levels of disturbance appeared to have higher fledging success ($\chi^2 = 7.4$, *P* = 0.03; low = 82%, medium = 55.6%, high = 92.3%).

Crested Auklet chicks that were handled regularly were the same size between days 28 to 30 as chicks that we handled only once. Chicks handled only once (*n* = 10) were similar in mass (*P* = 0.10), wing length (*P* = 0.20), tarsus length (*P* = 0.70), and fledging date (*P* = 0.40) compared with chicks handled every three days (ages 28 to 30 days in both cases).

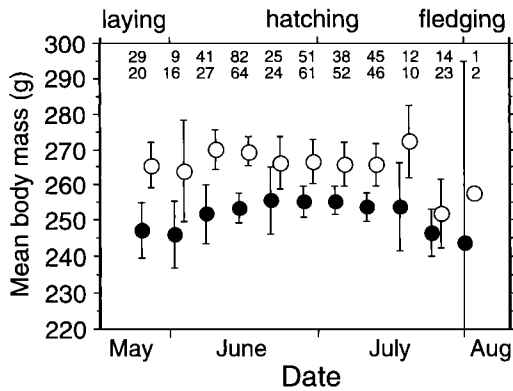


FIG. 3. Variation in mass of adult male (open circle) and female (closed circle) Crested Auklets at Buldir and Kasatochi Islands, Alaska (values are $\bar{x} \pm 95\%$ confidence limit; sample sizes indicated for each week).

DISCUSSION

Incubation and chick growth.—Similar to other studies (Sealy 1984, Piatt et al. 1990), we found the duration of the incubation period to be highly variably, although the mean duration on Buldir was comparable to that on St. Lawrence Island. We believe that the wide range in incubation periods is related to egg neglect, as Sealy (1984) reported for Crested Auklets, Least Auklets, and Ancient Murrelets. Crested Auklet eggs can endure periods of cooling and still hatch; an egg that we found unattended several times hatched after 44 days. The ability of eggs to endure cooling likely is important for a species that forages far from the colony on ephemeral patches of food.

We observed no intracolony differences in

TABLE 4. Reproductive performance and variation in adult mass in Crested Auklets at Buldir Island, 1990 to 1997.

Parameter ^a	1990	1991	1992	1993	1994	1995	1996	1997
No. eggs found	67	74	79	49	67	66	66	82
No. eggs hatched	48	56	70	44	59	59	57	77
No. chicks fledged	33	43	57	38	46	51	40	62
Median hatching date	—	30 June	27 June	24 June	25 June	26 June	29 June	25 June
Range hatching date	21 June to 19 July	21 June to 12 July	12 June to 7 July	16 June to 15 July	14 June to 15 July	21 June to 21 July	16 June to 12 July	15 June to 15 July
Median fledging date	29 July	1 August	26 July	27 July	28 July	30 July	3 August	29 July
Range fledging date	19 July to >1 August	25 July to 8 August	13 July to >10 August	23 July to >31 July	15 July to 14 August	26 July to 16 August	20 July to 14 August	16 July to 8 August
Hatching success ^b	0.72	0.76	0.87	0.9	0.88	0.89	0.86	0.94
Fledging success ^c	0.69	0.77	0.81	0.86	0.78	0.86	0.70	0.81
Productivity ^d	0.49	0.59	0.70	0.78	0.69	0.77	0.60	0.76
Male mass ^e	260.8 ± 23.0 (17)	259.4 ± 16.5 (16)	266.6 ± 16.4 (58)	273.5 ± 18.0 (48)	264.8 ± 19.9 (41)	268.2 ± 21.3 (44)	267.1 ± 18.1 (49)	267.6 ± 19.7 (63)
Female mass ^e	252.1 ± 20.6 (30)	252.4 ± 22.7 (14)	246.9 ± 15.8 (42)	260.5 ± 13.6 (38)	258.4 ± 11.5 (5)	250.9 ± 18.1 (55)	253.2 ± 14.4 (62)	253.5 ± 19.7 (42)

^a Data are from nest sites every 11 days or less during hatching and fledging.

^b Proportion of eggs that hatched.

^c Proportion of chicks that survived to fledging age (26 days before disappearing or 22 days at the time of the last visit).

^d Hatching success × fledging success.

^e $\bar{x} \pm SD$, with *n* in parentheses.

TABLE 5. Reproductive performance and variation in adult mass of Crested Auklets at Kasatochi Island, 1996 and 1997.

Parameter	1996	1997
No. eggs found	43	76
No. of eggs hatched	37	64
No. chicks fledged	32	42
Median hatching date	30 June	1 July
Range hatching date	26 June to 17 July	27 June to 14 July
Median fledging date	31 July	8 August
Range fledging date	22 July to 8 August	27 July to 12 August
Hatching success ^a	0.86	0.84
Fledging success ^b	0.86	0.66
Productivity ^c	0.74	0.55
Male mass ^d	269.1 ± 17.6 (29)	256.2 ± 18.6 (19)
Female mass ^d	259.1 ± 19.5 (30)	248.8 ± 15.1 (31)

^a Proportion of eggs that hatched.

^b Proportion of chicks that survived to fledging age (26 days before disappearing or 22 days at the time of the last visit).

^c Hatching success × fledging success.

^d $\bar{x} \pm SD$, with *n* in parentheses.

growth parameters (Table 1). Although Buldir Crested Auklet chicks fledged at a similar age and grew at rates comparable to St. Lawrence Island chicks, fledging mass differed between the two sites (Sealy 1968, 1973; see Table 2). We would predict that fledglings on St. Lawrence are heavier than those on Buldir because adult mass, on average, was greater in the northern part of their range (Sealy 1968, Jones 1993b). However, St. Lawrence Island chicks weighed less at fledging (228 g) and lost more mass prior to fledging (11% decline) than chicks on Buldir (Sealy 1968, 1973). The Ydenberg model (Ydenberg et al. 1995) for intraspecific variation predicts that in colonies with faster growth, nestlings will fledge heavier and younger; however, Buldir chicks fledged heavier but not at a younger age. There are three possible reasons for the observed differences in fledging mass between chicks from St. Lawrence Island and those from the Aleutians: (1) methods differed between the two studies (i.e. chicks that were handled every day fledged lighter than those handled less frequently), (2) environmental differences between the two areas resulted in the Aleutian chicks being fed more often or on higher-quality food, or (3) differences resulted from inter-year variation related to differences in prey availability.

Ydenberg's model (Ydenberg 1989, Ydenberg et al. 1995), concerning the transition from nest site to sea by alcid chicks, predicted three negative relationships: (1) between hatching date and fledging mass, (2) between hatching date and fledging age, and (3) between fledging age

and chick growth. The model also predicted a positive relationship between fledging mass and chick growth. Studies on two semiprecocial species, Cassin's Auklet (Morbey and Ydenberg 1997) and Rhinoceros Auklet (Ydenberg et al. 1995, Harfenist 1995), supported the model's predictions. However, we found no significant negative relationships between these variables for Crested Auklets at Buldir Island in either of our two study years. When we controlled for linear growth, we observed a positive relationship between linear growth and fledging mass only in 1997, which implied that faster-growing chicks fledged heavier, but not earlier (Table 3). The lack of a seasonal decline in fledging mass with age at Buldir could have resulted from the lack of a strong seasonality in food abundance around this near-oceanic island.

Hipfner and Gaston (1999) suggested that wing length is a better predictor of the timing of chick departure than body mass and predicted a negative relationship between wing length at minimum fledging age minus one day and fledging age. We observed this relationship for Crested Auklet chicks on Buldir. Crested Auklets have a higher survival rate if they are able to fly to sea rather than walk, because fliers are more adept at avoiding predators and at getting past the surf (G. Fraser pers. obs., Jones 1993b). Therefore, wing length might be more crucial than body mass in determining the timing of departure of Crested Auklet chicks.

Among the five planktivorous auklets (Cassin's, Parakeet, Least, Whiskered, and Crested)

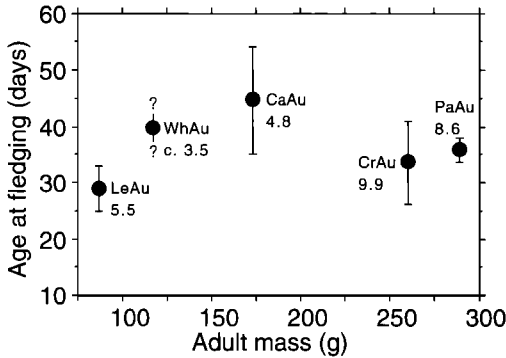


FIG. 4. Relationship between adult mass, fledging age (bars indicate range of values recorded in published studies), and maximum growth rate (below acronyms, in g per day) of auklet chicks in the Aethiini (see Gaston and Jones 1998 for references). LeAu = Least Auklet, WhAu = Whiskered Auklet, CaAu = Cassin's Auklet, CrAu = Crested Auklet, PaAu = Parakeet Auklet.

that coexist in the Bering Sea and adjacent parts of the North Pacific, the major dichotomy in chick provisioning occurs between species with nocturnal versus diurnal colony attendance (Fig. 4). The nocturnal Cassin's and Whiskered auklets, which are constrained to feeding their chicks no more than once or twice per day during the hours of darkness, have relatively slow-growing chicks that fledge at 40 days or older, whereas the diurnal species (particularly Least Auklets) have relatively fast-growing chicks that fledge between 29 and 36 days after hatching. A nocturnal lifestyle for Cassin's and Whiskered auklets, while presumably reducing adult mortality from predation, prolongs the nestling period of their chicks (Sealy 1973). Diurnal activity at colonies is the ancestral character state for planktivorous alcids (Gaston and Jones 1998). The evolution of nocturnal colony activity by these two species may have been favored because it reduced competition for nest sites, permitted colonization of areas with large numbers of avian predators, and/or enhanced diurnal foraging opportunities.

Productivity and breeding chronology.—Crested Auklet productivity and breeding chronology appear to be somewhat flexible. Productivity on Buldir steadily increased for the first four years (1990 to 1993) and then fluctuated in alternating years (1994 to 1997). A relationship between productivity and breeding chronology may exist; in two of three years, lower pro-

ductivity corresponded with later hatching and fledging dates (Table 3). Although hatching dates did not vary much across years, lower productivity coincided with a later fledging date on Kasatochi (Table 4). Knudtson and Byrd (1982) reported productivity from Main Talus on Buldir from 1976 as 51% (proportion of eggs resulting in fledged chicks), which is 31% lower than the average productivity during the 1990s. Lower productivity in 1976 also corresponded with a very late peak hatching date (July 8). During our study, intercolony and interyear differences in productivity were dramatic. On Buldir, productivity increased by 27% between 1996 and 1997, whereas on Kasatochi, productivity dropped by 26%. The timing of breeding and the productivity of an auklet colony were almost certainly related to local prey availability. Data on prey types, prior to and during chick rearing, between islands and years would allow us to further examine these relationships. Another factor that could influence timing and success of breeding are local weather conditions such as sea state, sea temperature, wind speed, and rainfall during the winter and summer months.

Other productivity data for Crested Auklets are scarce. From St. Lawrence Island, Piatt et al. (1990) reported productivity for 1987 at 48%. Although this value fell within the range observed at Buldir (1990), it is 19% lower than the average productivity at Buldir during the 1990s. One major difference between our study sites and the colonies on St. Lawrence Island is a lack of mammalian predators. We would predict that productivity would be lower at colonies that have mammalian predators. Sealy (1968) and Piatt et al. (1990) documented that predation on auklet chicks by voles (*Clethrionomys rutilus* and *Microtus oeconomus*) and arctic foxes (*Alopex lagopus*) was an important factor that depressed productivity on St. Lawrence Island.

Effect of crevice location and investigator disturbance.—Knudtson and Byrd (1982) showed that auklets selected nest sites based on crevice volume and substrate type. The differences in hatching dates and fledging success we observed were somewhat correlated with rock size on Main Talus. Crested Auklets that selected crevices in larger boulder areas had earlier hatching dates and higher fledging success than ones that nested in areas of smaller-sized

boulders. These differences could also be related to other microsite features, such as proximity to the sea and exposure to predators. For instance, lower areas might be preferred because they are closer to the sea, or because areas high on the talus slope may experience higher rates of predation by Glaucous-winged Gulls (*Larus glaucescens*).

Our finding that investigator disturbance had no significant influence on fledging success of Crested Auklets was similar to that for Parakeet Auklets (Hipfner and Byrd 1993), but it differed from Piatt et al.'s (1990) study at St. Lawrence, where hatching and fledging success of Least Auklets decreased in highly disturbed plots. Again, mammalian predators may explain the difference in our results; higher levels of human disturbance on St. Lawrence Island may have caused auklet chicks to be more vulnerable to mammalian predation.

Regular handling of chicks often can retard chick growth and cause chicks to fledge prematurely (e.g. Harris and Wanless 1984, Lyngs 1994). However, we found no differences in tarsus length, wing length, or body mass between regularly handled chicks and chicks measured only once. This suggests that measuring chicks once every three days is an appropriate protocol, although a longer interval between measurements during the linear growth phase would suffice (Harfenist 1995).

Conclusions.—The paucity of data on breeding biology of Whiskered Auklets presents the biggest gap in knowledge within the *Aethia* group; once this gap is bridged, a more in-depth comparison of auklet life-history strategies will be possible. Furthermore, an understanding of how productivity, breeding chronology, and growth parameters correspond with interyear variation in prey types, and ideally, how the availability of prey types changes throughout the breeding season, is essential for a comprehensive examination of auklet ecology, including how large changes in the marine ecosystem may influence breeding parameters.

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