

BREEDING BIOLOGY OF LEAST AUKLETS ON THE PRIBILOF ISLANDS, ALASKA¹

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Abstract. Aspects of Least Auklet (*Aethia pusilla*) breeding biology that pertain to the growth and development of chicks were studied on St. George Island, Bering Sea, Alaska, during the 1981 and 1982 breeding seasons. Yolk was 41% of fresh egg contents, a greater value than in the eggs of other alcid species. Adult incubation shifts averaged 24 hr, and both parents frequently spent the night together in the nest during both the incubation and chick-rearing periods. Adults brooded nestlings continuously during the day until 6 days post-hatching; diurnal brooding then declined gradually until cessation by Day 18. Chicks grew rapidly and achieved peak mass by 20 days post-hatching; most fledged at masses greater than average adult body mass. Nestlings were fed an average of 5.3 meals day⁻¹; meals averaged 5.4 g and consisted mostly of *Neocalanus* copepods. Estimates of breeding success (72% and 66% in 1981 and 1982, respectively) were about average for alcid species. The short nestling period of Least Auklet chicks is associated with frequent meal delivery and extended brooding made possible by the diurnal, nearshore foraging behavior of parents. Diurnal activity and nearshore foraging during the breeding season appear to be adaptations that minimize the duration of nesting and the associated risk of fox predation.

Key words: Least Auklet; alcids; reproduction; growth; Bering Sea; Pribilof Islands; seabirds.

INTRODUCTION

The Least Auklet (*Aethia pusilla*) is the smallest alcid and the most numerous plankton-feeding seabird in the Bering Sea. It breeds along the Siberian and Alaskan coasts of the Chukchi Sea, on offshore islands of the Bering Sea, on the Aleutian Islands, and on islands off the southern coast of the Alaska Peninsula (Sowls et al. 1978). It is the most abundant breeding seabird in the region, with an estimated population of six million breeding individuals in Alaska (Sowls et al. 1978). A colony of about 125,000 breeding pairs exists on St. George Island in the Pribilof Islands, Alaska (Hickey and Craighead 1977). Despite previous studies of Least Auklets (Bédard 1969a, 1969b; Sealy 1968, 1975, 1982, 1984; Knudtson and Byrd 1982; Byrd et al. 1983), there are gaps in our knowledge of its breeding biology, such as egg composition, incubation shifts, chick-feeding rates, and colony attendance patterns of breeding adults. Little has been published on breeding biology with regard to the Pribilof Island colonies (Hunt et al. 1981), where arctic foxes (*Alopex lagopus*) are a major predator on eggs, chicks, and adults. Most work on Least Auklets has been conducted on St. Lawrence Island, where foxes are rare at breeding colonies, and on Buldir Island, where foxes are absent.

Sealy (1973) has reviewed patterns of reproductive traits among the Alcidae, the avian family with the greatest variation in devel-

opmental mode. Alcid chick development has been classified as either precocial, semiprecocial, or intermediate, based on the stage of development at sea-going. Least Auklets are semiprecocial and chicks are fed at the nest by both parents until full-grown. The combination of rapid development rate and high fledging mass (relative to adult mass) is unique among confamilials. Sealy (1973) proposed that interspecific variation in the developmental mode of alcid chicks is primarily an adaptive response to differences in the feeding ecology of adults. This paper describes certain aspects of breeding for adult Least Auklets (nest-site fidelity, egg composition, incubation shift, colony attendance, chick brooding, and chick-feeding rate) that pertain to the growth, development, and survivorship of nestlings and to the interpretation of variation in alcid reproductive traits. In addition, it presents comparative data with which to assess the degree of variation among populations of Least Auklets.

STUDY AREA AND METHODS

We studied auklets on St. George Island (56°35'N, 169°35'W) from June to August, 1981 and 1982. The Ulakaia study site was located in the middle of a colony of about 129,000 breeding individuals (Hickey and Craighead 1977) on the north-facing slope of Ulakaia Hill. This colony is 1.5 km south of St. George Village on a 30° slope at about 125 m above sea level. Only Least Auklets currently nest there, and the size of the colony has declined over the last 40 years, apparently due to vegetation encroachment (Roby and Brink 1986). Most auklet nests were deep in crevices among the basalt talus and were accessible

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only if the nest were destroyed. However, we located 34 accessible nests in 1981 and 87 accessible nests in 1982 with the aid of a powerful flashlight, by carefully removing surface rocks. These nests were marked with stake flags and checked daily during the hatching and fledging periods and every other day in the interim.

The dock study site was a colony of about 20 breeding pairs that nested in a stone and mortar retaining wall that extended between two concrete docks at the village waterfront. The wall is about 2 m high and 20 m long and is just above high tide. None of the nests in the wall could be reached, so adults were captured in mist nets strung in front of the colony. We banded each adult with a U.S. Fish and Wildlife Service numbered monel band and a combination of colored, plastic leg bands that allowed each bird to be identified individually. By the end of the 1981 breeding season, all breeding adults (and many non-breeders that frequented the colony) had been color-banded. We located nest entrances by observing banded birds as they returned to the colony with chick meals. Each entrance was marked with spray paint and numbered.

We collected eggs at two colonies in beach rubble: one about 2 km east of St. George Village ("Airplane Wing") and the other at Zapadni Beach on the southwest coast of the island. We measured egg length and breadth to the nearest 0.1 mm with vernier calipers and weighed eggs to the nearest 0.1 g on an Ohaus triple-beam balance. The stage of embryo development was determined by candling eggs with a bright flashlight. Fresh eggs (those with no visible embryo development) were separated into shell, yolk, and albumen, were weighed to the nearest 0.1 g, and were air-dried to constant weight at 50 to 70°C. All other eggs were placed in a Hovabator portable incubator set at 38°C and were turned daily.

During the 1982 breeding season, we recorded colony attendance, incubation, and chick-feeding schedules for 32 color-banded, breeding adults at the dock study site. Breeding adults arriving at the colony invariably landed on top of the wall, where they could be identified prior to entering their nest. However, adults flew from the nest entrance directly out to sea; consequently, we could not identify individuals as they departed. We distinguished subadults from failed or nonbreeding adults using plumage differences described by Bédard and Sealy (1984). Incubation shifts were determined by continuously observing the dock study site during daylight hours from 2030 on 17 June to 2400 on 21 June 1982. We estimated the duration of incubation shifts by halving the period between consecutive ar-

rivals of color-banded individuals at the colony. The frequency of meal deliveries to chicks was determined by continuous observation for a 48-hr period in the middle of the chick-rearing period (19 to 20 July 1982). Sixteen pairs of parents were engaged in feeding nestlings during this period. Each arrival of a color-banded individual with a meal in its sublingual pouch was recorded as a meal delivery. We recorded all times as local Alaska Daylight Time, which is about 2.5 hr ahead of solar time.

We compared inter- and intra-year differences in median hatching date using the median test (Siegel 1956). Fledging dates could not be determined with certainty by the absence of a chick from its nest site, because some chicks wandered into adjoining crevices as they neared fledging, particularly if disturbed. In 1982 we verified fledging dates at the Ulakaia study site by excavating 25 nests after the nestlings had disappeared.

We were able to capture some nestlings at the Ulakaia study site by hand or with the aid of a small net on the end of a flexible rod. We weighed chicks to the nearest 0.5 g using a Pesola spring scale (50-g or 100-g capacity), and measured wing chord and 10th primary to the nearest 1 mm with a flexible plastic ruler. These data were fitted by logistic and Gompertz growth models using non-linear regression programs in the SAS package (1982). We determined the incidence of diurnal chick brooding by carefully approaching nests and quickly shining a flashlight into the chamber so that wary adults could be detected if present.

Chick meals were collected at three colonies: Ulakaia Hill, dock study site, and Zapadni Beach. We erected mist nets perpendicular to the flight paths of incoming adults and spread plastic sheeting under the nets. Examination of adults after disentanglement from the net insured that the entire chick meal had been ejected from the sublingual pouch while in the net. Only complete meals were collected from the plastic sheeting. Each meal was placed in a pre-weighed plastic bag (weighed to the nearest 0.1 g) and frozen.

We measured adult body mass during the chick-rearing period as part of a separate study of daily energy expenditure. Adults were captured in mist nets at the dock study site and weighed to the nearest 0.1 g on a triple-beam balance. Some adults were recaptured within 48 hr and reweighed.

We estimated hatching success at the Ulakaia study site as the percent of eggs found that eventually hatched. Chicks were removed from their nests for a separate study of body composition during the development period, so the

TABLE 1. Mass and composition of fresh Least Auklet eggs ($n = 20$) collected on St. George Island, Alaska, during 1981 and 1982.

Variable	Mean \pm SD	CV	Range
Fresh mass	17.44 \pm 1.22	7.0	14.95–19.6
Water (g)	11.58 \pm 0.85	7.3	9.85–13.0
% water	66.44 \pm 1.45	2.2	63.91–70.31
Shell mass, wet (g)	1.60 \pm 0.24	15.0	1.25–2.00
% of fresh mass	9.15 \pm 1.22	13.3	7.14–10.73
Shell mass, dry (g)	1.28 \pm 0.15	11.7	1.00–1.60
% of fresh mass	7.36 \pm 0.72	9.8	5.49–8.19
Yolk mass, wet (g)	6.50 \pm 0.69	10.6	4.95–7.80
% of fresh mass	37.25 \pm 3.27	8.8	33.07–46.15
Water (g)	3.26 \pm 0.44	13.5	2.60–4.20
% of yolk	50.12 \pm 2.66	5.3	45.38–53.85
Yolk mass, dry (g)	3.24 \pm 0.33	10.2	2.30–3.65
% of fresh mass	18.53 \pm 1.19	6.4	15.38–21.30
Albumen mass, wet (g)	9.11 \pm 1.13	12.4	6.40–11.15
% of fresh mass	52.18 \pm 4.77	9.1	37.87–57.19
Water (g)	7.77 \pm 1.08	13.9	5.20–9.60
% of albumen	85.06 \pm 1.92	2.3	81.10–88.35
Albumen mass, dry (g)	1.35 \pm 0.14	10.4	1.15–1.55
% of fresh mass	7.75 \pm 0.81	10.5	6.40–9.06
Yolk/albumen, wet	0.73 \pm 0.15	20.6	0.58–1.22
Yolk/albumen, dry	2.42 \pm 0.34	14.1	1.84–3.00

size of the nestling sample declined as the nestling period progressed. Consequently, the percentage of chick mortality was calculated on a day-by-day basis by comparing the number of chicks still alive at a given age with the number alive the previous day. To obtain an estimate of nestling mortality, these age-specific mortality rates were multiplied over the entire nestling period. Two potential sources of error in this estimation procedure are (1) chicks missing from nests may have been recorded as dead when they had only moved to an adjoining crevice and (2) chicks of fledging age that were taken by a predator may have been recorded as successfully fledged.

RESULTS

EGG STAGE

Nest site and mate fidelity. Data from the dock study site indicated high nest-site fidelity in Least Auklets. The entrances to nest crevices ($n = 11$) used by 22 adults were recorded in both 1981 and 1982. Twenty of these individuals (91%) used the same nest entrance in both years. The two adults that used different entrances also acquired new mates after the known death of their mates in 1981. Because most pairs shared their crevice entrance with at least one other pair, we could be certain of mate fidelity in only one case. One adult that bred in 1981 was apparently unmated in 1982 but continued to frequent the dock study site.

Its mate from 1981 used the same nest entrance in 1982 but was paired with a different bird.

Egg size and composition. Mean length of Least Auklet eggs ($n = 65$) was 39.4 mm (SD = 1.38, range: 35.55 to 42.65, CV = 3.5) and mean width was 28.4 mm (SD = 0.82, range: 26.70 to 30.85, CV = 2.9). In 1982, 20 fresh eggs were found at the Zapadni Beach colony, and laying dates ranged from 1 to 10 June (median = 6 June). The mean fresh mass of eggs (17.4 g) was 20.3% of average adult body mass during the chick-rearing period. The percent yolk in fresh egg contents (exclusive of shell) was 41%, and the dry yolk/dry albumen ratio was 2.4 (Table 1). These values are greater than those for other semiprecocial alcids (Birkhead and Nettleship 1984) and similar to eggs of precocial birds (Carey et al. 1980).

Attendance and incubation shifts. Continuous observations made throughout the daylight hours from 2030 on 17 June to 2400 on 21 June 1982 indicated a strong diurnal pattern of attendance by adults at the colony, with a sharp cessation of activity at nightfall (Fig. 1a). During the egg stage, activity at the colony began at about 0530 with the first departures of off-duty adults (Fig. 1b) and arrivals of adults to relieve mates began at about 0600 (Fig. 1a). Most subadults and nonbreeding adults arrived at the colony between 0800 and 1300 or between 2200 and 2330 (Fig. 1c). During the morning and early afternoon, subadults were

particularly active on the colony surface, prospecting for nest sites and interacting with other subadults and nonbreeders. From 1500 to 2200 no departures or arrivals were observed, and no birds were present on the surface of the colony. The evening activity period was short and intense, lasting from 2200 to 2330. Sixty-two percent of birds that arrived in the evening were breeding adults; the remainder were nonbreeding birds that did not spend the night in the colony.

The time interval between consecutive arrivals of breeding individuals averaged 47.4 hr (SD = 10.87, range: 24 to 72 hr, $n = 35$). If only two birds are involved (which is believed to be the case; see below), this gives 23.7 hr as an estimate of the length of the average incubation shift. This is confirmed by the fact that at six nests where the two occupants were known to comprise a pair (as they were the only birds using the crevice), the incubation shift was 23.6 hr (SD = 5.60, range: 12.5 to 36 hr, $n = 20$). Thus it seems clear that the average incubation shift for those four days in 1982 was about 24 hr, confirming Sealy's (1972) suspicion.

Off-duty breeding adults returned to the colony either between 0600 and 1200 (42%) or between 2230 and 2330. No departures from the colony in the evening were observed (Fig. 1b), indicating that both adults spent the night in the nest crevice about half the time; hence the total time that each adult spent in the nest crevice frequently exceeded the average incubation shift by about 8 hr. Incubation schedules exhibited considerable flexibility; many adults alternated relieving their mate in the evening and in the morning. Off-duty adults occasionally visited the colony around midday but were not observed relieving their mates.

CHICK STAGE

Time of hatching. At the Ulakaia study site, the median hatching date in 1981 (3 July, $n = 34$) was significantly earlier than in 1982 (13 July, $n = 87$, $P < 0.0001$; Fig. 2). Using Sealy's (1968) median incubation period of 32 days ($n = 15$), the estimated peak of laying at the Ulakaia study site was 1 June in 1981 and 11 June in 1982. In 1981, 12 partially developed eggs collected at Airplane Wing were placed in an incubator and hatched from 29 June to 9 July (median = 1 July). The estimated peak of laying for this sample was 30 May. In 1982, the estimated median hatching date of 20 fresh eggs collected at Zapadni Beach was 8 July.

Chick brooding. Diurnal nest checks throughout the chick-rearing period indicated that chicks were brooded by a parent nearly continuously for the first five days after hatch-

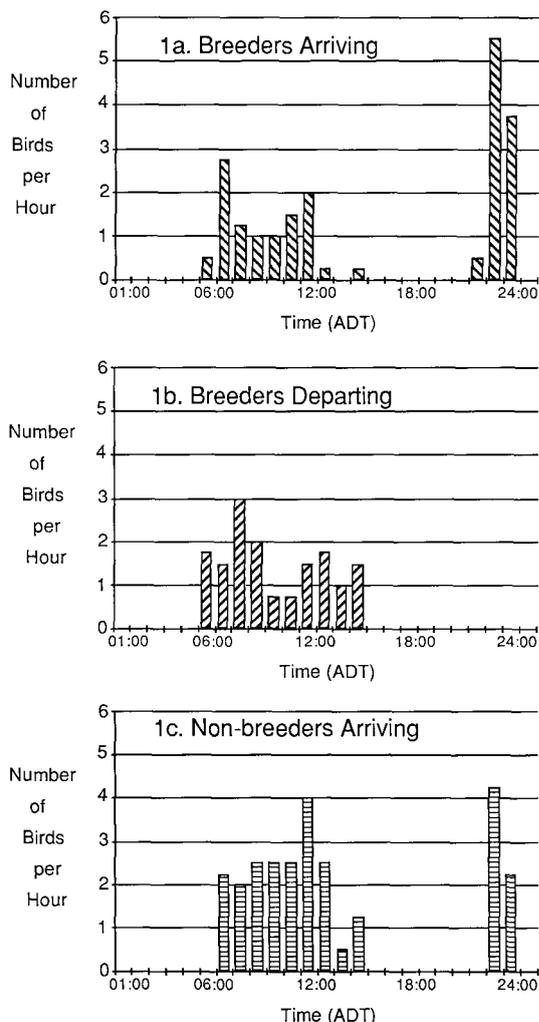


FIGURE 1. a-c. Patterns of colony attendance for Least Auklets at the dock study site during the incubation period. (Numbers are per-hr means, averaged over a four day period, 18 to 21 June 1982.)

ing. Once chicks were six days old, diurnal brooding gradually declined, and by Day 18 no young were attended by an adult during the daylight period (Fig. 3). Between Days 6 to 17, brooding of chicks was intermittent; the duration of brooding bouts decreased with chick age, probably in relation to the chick's capacity for thermoregulation. Although we did not check nests at night, observations at the dock study site during the chick-rearing period indicated that chicks were attended by at least one parent each night, regardless of chick age. Adult attendance overnight lasted at least 7.8 hr, which means that nestlings were attended a minimum of 32% of the time each day (Fig. 3).

Chick growth. Data on nestling body mass were plotted by age (Fig. 4a). On average, body mass increased up to 20 days post-hatching, after which no significant change occurred prior

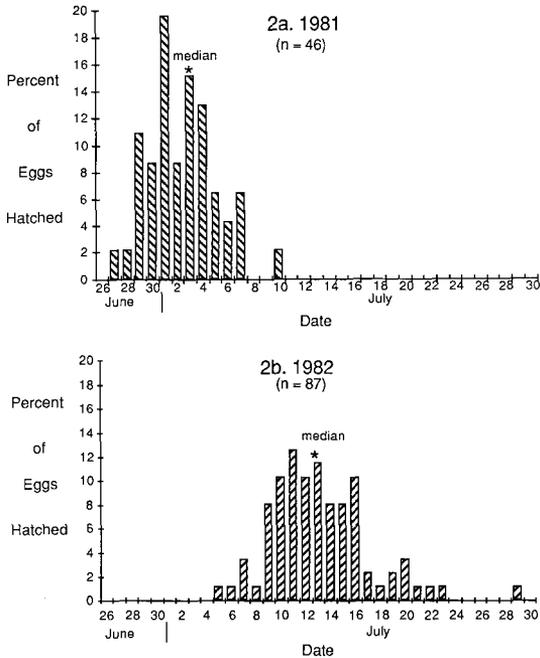


FIGURE 2. a, b. Distribution of hatching dates for Least Auklets at the Ulakaia study site on St. George Island, Alaska, in 1981 and 1982.

to fledging. Fledgling mass averaged 91.5 g (SD = 11.67, $n = 11$), or 108% of average adult body mass (84.5 g, SD = 5.23, $n = 44$) during the chick-rearing period (combined 1981 and 1982 data). Age-specific body masses of nestlings were fitted to both logistic and Gompertz growth models (Table 2) using methods outlined in Ricklefs (1983). There were no significant inter-year differences in the parameter values of the fitted curves; consequently, data from 1981 and 1982 were combined. The logistic and Gompertz growth models did not differ significantly in their goodness of fit ($P > 0.05$). However, since the two models yield somewhat different values for the same parameter, it is necessary to specify the model used when comparing fitted curves.

Wing chord and outer primary were also measured and plotted against age. Both measurements increased linearly at least up to fledging (Figs. 4b and c); however, primaries did not emerge until Days 5 to 7.

Attendance and chick feeding. Adults with chick meals arrived at the colony throughout the day (Fig. 5a). Unlike during incubation, when activity at the colony ceased completely during the afternoon, adults arrived and de-

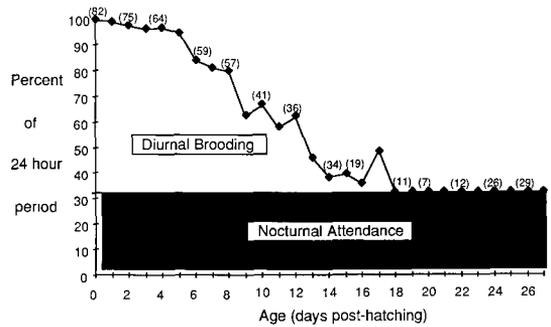


FIGURE 3. Incidence of parental brooding for Least Auklet nestlings at the Ulakaia Hill colony, 1982. (Sample sizes for even-numbered ages are shown in parentheses.)

parted the colony between 1500 and 2000. Nevertheless, there was a lull in the frequency of adults arriving with chick meals during this period of the day. Most meals were delivered from 0800 to 1430 and from 2000 to 2230. Nonbreeding birds (mostly in adult plumage) continued to frequent the colony during the chick-rearing period (Fig. 5b), but subadults were rare compared to their presence during the incubation period. Arrivals of breeding adults were most frequent from 2000 to 2230 (Fig. 5a). Of 79 recorded arrivals during the evening period, 82% were adults carrying chick meals, 8% were adults without meals, and only 10% were nonbreeders, failed breeders, or subadults.

During the evening influx of birds, when most breeding adults arrived with chick meals, few departures occurred and most of these were by nonbreeders. The incidence of departures from the colony was high between 0600 and 0700 (Fig. 5c), well before the first influx of adults carrying chick meals. Some adults departing at dawn were probably not recorded due to poor visibility and their rapid flight out to sea. Observations indicate that at least one parent, usually both, spent the night in the nest crevice with the chick.

The arrival of adults with chick meals in the evening is synchronized; and, as Manuwal (1974) found for Cassin's Auklet (*Ptychoramphus aleuticus*), the numbers of subadults accompanying the breeding birds are low compared to numbers during the incubation period. On both 19 and 20 July, 29 of 32 adults known to be feeding chicks at the dock study site (91%) arrived with a meal between 1930 and 2300. Only one individual delivered two meals during that period. Approximately 10%

FIGURE 4. a-c. Age-specific body mass, wing cord length, and outer primary length of Least Auklet nestlings at the Ulakaia Hill colony, 1981 and 1982. (Means \pm standard error, sample sizes in parentheses.)

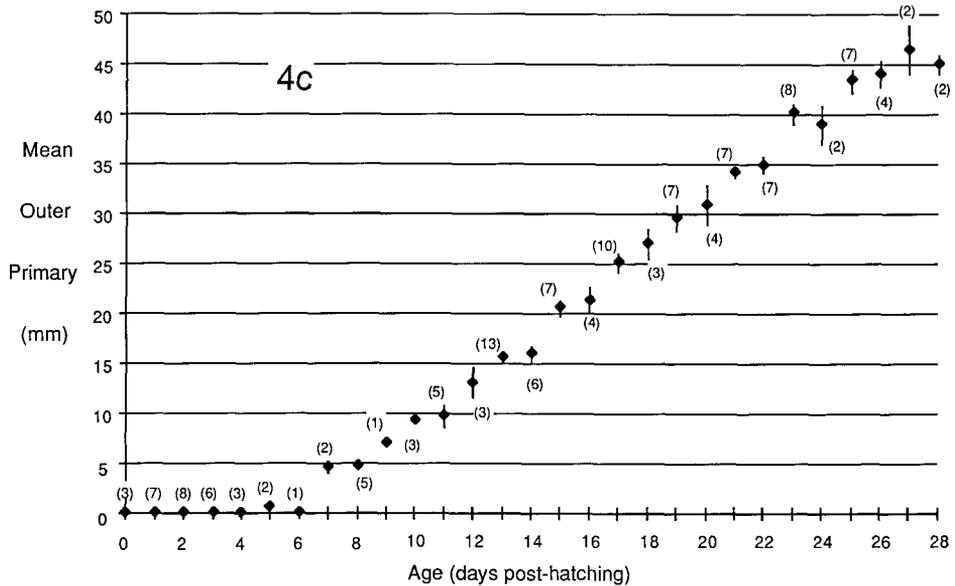
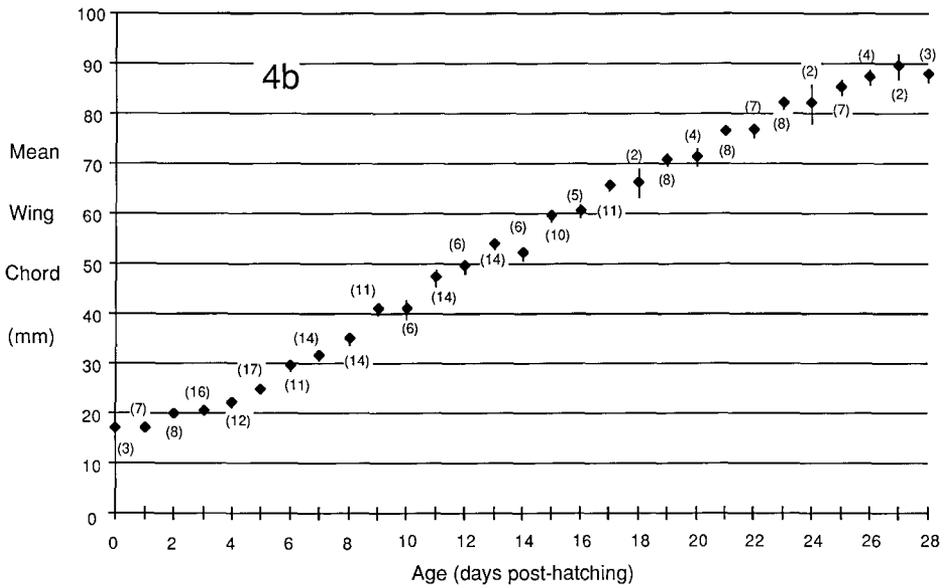
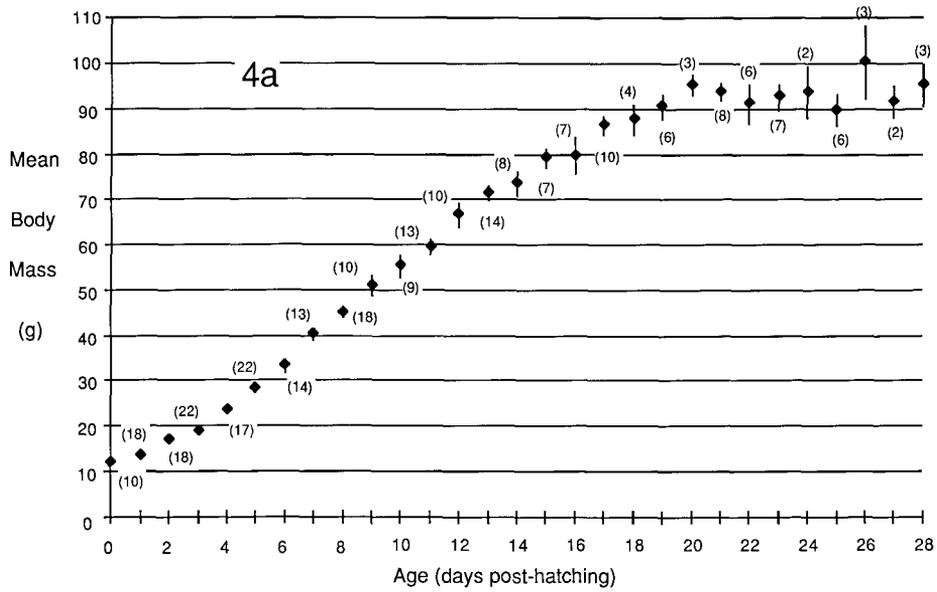


TABLE 2. Parameters of sigmoidal curves fitted to data on Least Auklet growth (age-specific body mass).^a

Model	K^b	J^c	A^d	Residual mean square
Logistic	0.239 ± 0.007	8.60 ± 0.153	95.8 ± 1.07	32.69 (df = 289)
Gompertz	0.146 ± 0.005	6.46 ± 0.160	102.3 ± 1.64	35.69 (df = 289)

^a Data from 1981 and 1982 combined; parameter values are ± standard deviation; standard deviation based on degrees of freedom of residual mean square; this underestimates variance since some chicks were weighed more than once.

^b K = a constant proportional to the overall growth rate.

^c J = the inflection point (in days post-hatching) of the fitted growth curve.

^d A = the asymptote of the fitted growth curve.

of the birds arriving in the evening were non-breeders, mostly in adult plumage. In the case of the colony at the dock study site, the net movement of individuals to the colony in the evening provides a fairly accurate estimate of the known number of successful breeders, suggesting that the number of breeding pairs is

best estimated during the mid to late chick-rearing period.

Each adult delivered an average of 2.63 chick meals day⁻¹ (SD = 0.72, range: 1 to 4 meals, $n = 64$ adult days), or an average of 5.27 meals chick⁻¹ day⁻¹ ($n = 32$ chick days). For the six known mated pairs, the average meal delivery rate was 5.33 meals chick⁻¹ day⁻¹ (SD = 1.16, range = 4 to 7 meals, $n = 12$ chick days).

Meal size and composition. The mean fresh mass of 55 complete chick meals collected in 1981 (10 July to 4 August) was 5.44 g (SD = 2.25, range: 0.9 to 12.3). In 1982, 11 chick meals (24 July) averaged 4.47 g (SD = 2.24, range: 1.3 to 7.3 g). Combined, average meal size was 5.28 g (SD = 2.26, $n = 66$), which gives an estimate of 27.8 g chick⁻¹ day⁻¹ (based on a feeding rate of 5.27 meals chick⁻¹ day⁻¹; see above). Young chicks presumably receive less food per day because of diurnal brooding by the parents.

Five chick meals were randomly selected from the 66 collected and were sorted by taxa. Four of the meals were dominated by the small, oceanic copepod *Neocalanus plumcrus*. In the fifth, the larger *N. cristatus* dominated. Small numbers of the oceanic hyperiid amphipod *Parathemisto pacifica*, euphausiids (probably *Thysanoessa* spp.), and unidentified larval forms were found in four of the five chick meals. The *Neocalanus* spp. also appeared to be the dominant prey both in numbers and % volume in all other meals ($n = 61$).

Age and time of fledging. The median and modal fledging date in 1982 was 10 August (range: 5 to 15 August, $n = 25$). Age at fledging (nestling period) was known for 20 of the 25 nestlings, and averaged 28.6 days (SD = 1.50, range: 26 to 31 days). An additional 21 nestlings were assigned a fledging age without verification by excavating the nest site. The mean fledging age of all birds ($n = 41$) was 28.5 days (SD = 1.80, range: 25 to 35 days).

At 0500 (before first light) on 11 August 1982, fledglings called from their nest sites (a characteristic shrill peeping), but there was no evidence of birds leaving the colony. By 0545, fledgling calling intensified and the first bird was heard flying toward the sea. In the darkness it was impossible to distinguish fledglings

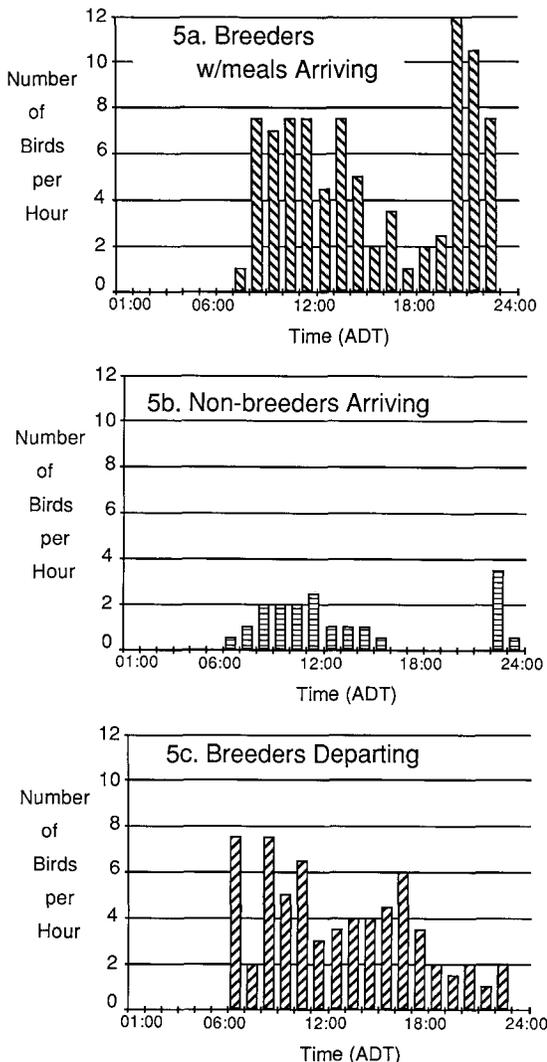


FIGURE 5. a-c. Patterns of colony attendance for Least Auklets at the dock study site during the chick-rearing period. (Numbers are per-hr means, averaged over a two day period, 19 to 20 July 1982.)

from adults, but several birds that passed close overhead flew directly and slowly toward the sea, unlike the rapid, zig-zag flight path typical of adults. Departures and loud chick calling continued until about 0615. Two fledglings were caught in a mist net at the bottom of the slope between 0605 and 0620. There was no suggestion that fledglings were accompanied by a parent during the 1.5-km flight to the sea. The first adult was netted at 0630 and from that time until 0800 (when the net was taken down) a total of 19 adults were netted as they left the colony. All birds leaving the colony after 0630 appeared to be adults. These observations suggest that most chicks fledge during the hour prior to dawn, before adults begin to depart.

Adult body mass. Average body mass of breeding adults captured at the dock study site during the chick-rearing period was 82.7 g (SD = 4.88, range: 73.3 to 94.1, $n = 30$) in 1981 and 88.5 g (SD = 3.56, range: 82.3 to 93.9, $n = 14$) in 1982. This between-year difference is highly significant ($t = 4.075$, $P < 0.01$). Combining the two years gives 84.5 g (SD = 5.23, range: 73.3 to 94.1, $n = 44$).

Body mass of some dock-study-site adults changed appreciably in less than 48 hr. For 24 banded adults that were weighed twice within 48 hr, the absolute value of the change in mass averaged 2.8 g (SD = 2.61, range: 0.1 to 11.6). This suggests that gut contents vary substantially during the day and/or that considerable body fat is deposited or metabolized over short periods.

BREEDING SUCCESS

In 1981, 90% of 49 eggs hatched, compared to 87% of 106 eggs found in 1982. These estimates of hatching success seem high, possibly because searching for nests did not begin until after the peak of egg laying, which eliminates any eggs removed from nests by foxes early in incubation.

In 1981 and 1982, the fate of nestlings was followed until the chick was: (1) found dead, (2) removed from the nest for studies of body composition, (3) missing from the nest site (prior to fledging age), or (4) fledged. Nestling survivorship was 81.7% in 1981 and 75.8% in 1982. In 1981 seven chicks out of an initial sample size of 44 hatchlings were found dead or disappeared prior to fledging age, four in the first three days after hatching. In 1982, 18 chicks out of an initial sample size of 92 hatchlings were found dead or disappeared, only two in the first three days after hatching. Overall, breeding success (i.e., fraction of eggs laid that produced fledglings) was 73.5% in 1981 and 65.9% in 1982.

DISCUSSION

INTRASPECIFIC COMPARISONS

Growth and body mass. The growth rate of Least Auklet nestlings on St. George Island ($K = 0.239$, logistic model) was not significantly different ($P > 0.05$) from average growth rate on St. Lawrence Island ($K = 0.244$; Sealy 1973). However, the asymptotic body mass of St. George nestlings (95.8 g) was greater than that of St. Lawrence nestlings (86.5 g). Also, St. Lawrence nestlings experienced an appreciable recession in body mass prior to fledging at an average mass of 81 g, whereas St. George fledglings averaged 91.5 g.

Average body mass of adults from St. George (84.5 g) was similar to those from Buldir Island (83.8 g; G. V. Byrd and R. H. Day, unpubl. data), but less than from St. Lawrence Island (92 g; Sealy 1968). However, the samples from Buldir and St. Lawrence consisted of measurements made throughout the breeding period. Bédard (1969a) and G. L. Hunt (unpubl. data) have shown for Least Auklets, and Manuwal (1979) has shown for Cassin's Auklet, that mean body mass of adults declines during the breeding season. It is thus necessary to specify the stage of the breeding cycle when comparing measurements of adult body mass from different years or colonies.

Diet composition. Hunt et al. (1981) found that the diet of Least Auklet nestlings on the Pribilof Islands consisted primarily of calanoid copepods. However, instead of *N. plumchrus* and *N. cristatus*, the neritic species complex *Calanus marshallae-glacialis* predominated. Bradstreet (1985) collected 49 Least Auklet chick meals on the Pribilof Islands in 1984, of which 15 were sorted to species. The species composition (% of total number of items) of the pooled sample was 38.5% *N. plumchrus*, 27.3% *C. marshallae*, 12.7% *N. cristatus*, 0.5% *N. glacialis*, and 18.3% unidentified copepods. The remaining 2.7% consisted of various decapods, amphipods, and euphausiids. The diet of Least Auklets on St. Lawrence Island during the breeding season consisted primarily of *Calanus finmarchicus* with small numbers of hyperiid amphipods and euphausiids (Bédard 1969a). After Bédard's (1969a) study, the species *C. finmarchicus* was split into *N. plumchrus*, *C. marshallae*, and *C. glacialis*. Thus the major prey of Least Auklets during the breeding season is consistently calanoid copepods, but the species composition of the diet may vary between years and breeding colonies.

Breeding success. On Buldir Island, Knudtson and Byrd (1982) estimated Least Auklet hatching success as 68% and nestling survival

as 75% for an overall breeding success of 51%. Peregrine Falcons (*Falco peregrinus*) and Glaucous-winged Gulls (*Larus glaucescens*) inflict considerable mortality on breeding adults on Buldir Island, but availability of breeding sites is thought to limit colony size (Knutson and Byrd 1982). While estimated hatching success was lower on Buldir Island, nestling survivorship is similar to our estimates for St. George (82% and 76%), where arctic foxes prey intensively on Least Auklets, and where population size is also apparently limited by availability of suitable breeding sites (Roby and Brink, unpubl.). Least Auklet breeding success on St. George in 1981 and 1982 (74% and 66%, respectively) was high relative to an estimate of only 20% on St. Lawrence Island in 1976, including 34% nestling survival (Searing 1977). The St. Lawrence Island population is not thought to be limited by breeding sites (Bédard 1969b), and fox predation is low (Sealy 1968). Estimates of breeding success for other alcid species range from 30 to 75%, with most estimates in the range of 65 to 75% (Asbirk 1979, Manuwal 1979, Ashcroft 1979, Vermeer 1980, Harris 1980, Gaston and Nettleship 1981, Murray et al. 1983).

INTERSPECIFIC COMPARISONS

Egg composition. Despite semiprecocial development of young, Least Auklet eggs possess more of the attributes associated with precocial post-hatching development than the eggs of other alcids. Yolk wet mass (% of total wet mass), yolk dry mass, and yolk/albumen ratio of Least Auklet eggs (Table 1) are greater than for the eggs of the Razorbill (*Alca torda*), Common Murre (*Uria aalge*), Atlantic Puffin (*Fratercula arctica*), and Rhinoceros Auklet (*Cerorhinca monocerata*); (Kuroda 1963, cited in Williams et al. 1982; Birkhead and Nettleship 1984). This is particularly unexpected because murre and Razorbills leave the breeding site at only 20% of adult mass. The high yolk content of Least Auklet eggs may be a function of the allometric relationship between body size and metabolic rate. The higher per-gram metabolic rate of Least Auklet hatchlings compared with those of larger alcid species may require relatively large yolk reserves at hatching and, consequently, higher yolk contents in fresh eggs. Egg composition data from more alcid species are needed to evaluate the significance of interspecific variation in yolk contents.

For Least Auklet eggs, shell wet mass as % of total wet mass (9.2%) is intermediate between the burrow-nesting Atlantic Puffin (8.0%) and ledge-nesting Razorbill and Common

Murre (10.4% and 13.1%, respectively; Birkhead and Nettleship 1984). These data are consistent with the hypothesis of Williams et al. (1982) that interspecific differences in proportionate shell mass reflect adaptations for breeding site substrate.

Colony attendance. During the incubation and chick-rearing periods, most Least Auklet adults spend the night in the breeding site rather than at sea. This suggests that little feeding occurs at night, perhaps due to decreased availability or detectability of prey. The fact that Least Auklets do not arrive after dark to relieve their mates or feed their chicks clearly reduces fox predation on breeding adults. Arctic foxes hunt efficiently at night, and it is significant that no nocturnal species of seabird nests on St. George Island, where the density of arctic foxes is high. Nocturnal habits in alcids apparently evolved in response to pressure from diurnal predators and in the absence of fox predation at breeding colonies. On Buldir Island, where foxes are absent and diurnal avian predators predominate, several species of nocturnal, plankton-feeding seabirds breed (Leach's Storm-Petrel [*Oceanodroma leucorhoa*], Fork-tailed Storm-Petrel [*O. furcata*], Cassin's Auklet, and Ancient Murrelet; Byrd and Day, in press). Nevertheless, Least Auklets breeding on Buldir Island maintain a diurnal chick-feeding schedule even in the face of diurnal predation pressure (Byrd et al. 1983). An apparent advantage to diurnal activities is increased frequency of chick feeding with associated higher growth rates (Sealy 1973).

Incubation shift and chick feeding. The duration of incubation shifts and the frequency of chick feeding are thought to reflect aspects of seabird feeding ecology. Alcid species that forage offshore and/or feed on unpredictable prey tend to have longer incubation shifts and lower chick-feeding frequencies than those that forage near shore (Sealy 1973, 1976). However, there are some exceptions to the correspondence between duration of the incubation shift and chick-feeding frequency. Least Auklet adults breeding on St. George forage within 5 to 10 km of the colony (Hunt et al. 1978) and deliver an average of 5.3 meals chick⁻¹/day⁻¹, similar to other diurnal, planktivorous alcids such as Parakeet (*Cyclorhynchus psittacula*) and Crested (*Aethia cristatella*) auklets (Sealy and Bédard 1973). In contrast, the chicks of nocturnal alcids, such as Cassin's Auklet, Marbled Murrelet (*Brachyramphus marmoratum*), and Rhinoceros Auklet, are only fed one to two meals each night (Summers 1970, Manuwal 1974, Sealy 1974). Yet all the above species have average incubation shifts of 24 hr. This supports the conclusion that nocturnal

activity of adults at the breeding colony limits the number of meals a chick receives.

Some nocturnal species apparently compensate for lower chick feeding frequencies by increasing meal size. For example, Cassin's Auklet chicks receive two meals averaging 27.8 g each night, or about 55 g day⁻¹ (Manuwal 1974). The similar-sized Dovekie (*Alle alle*) receives about 8.5 meals averaging 2.8 g, or a total of 23.8 g day⁻¹ (Norderhaug 1980), while Least Auklets receive 27.8 g day⁻¹ on average (this study). Clearly, nocturnal species such as Cassin's Auklet can reduce the frequency of visits to the breeding site without reducing the amount of food the chick receives. If the risk of land-based predation is proportional to the number of visits to the breeding site, then it would seem advantageous for diurnal species, as well as nocturnal, to adopt lower chick-feeding frequencies.

Growth rate and nestling period. Least Auklets have high nestling growth rates ($K = 0.24$, logistic model) and a short nestling period (28.6 days) relative to other semiprecocial alcids (Sealy 1973). Only the somewhat larger Dovekie (adult body mass = 150.5 g; Roby et al. 1981) has a higher growth rate ($K = 0.256$, mean nestling period = 28.3 days; Stempniewicz 1980, Evans 1981). Unlike Dovekies, however, which fledge at 70% of adult mass, Least Auklets fledge at about adult mass. Although the body mass of Least Auklet nestlings does not increase significantly during the last week prior to fledging, both wing chord and outer primary length increase at least up to fledging. This suggests that the duration of the nestling period is determined by developmental requirements for the fledgling's first flight to the sea, rather than the time required to reach fledging mass.

Compared with the diurnal Least Auklet and Dovekie, the nocturnal Cassin's Auklet (adult body mass = 160 g; Manuwal 1974) has a slow growth rate ($K = 0.150$; Sealy 1973) and long nestling period (45 days; Thoresen 1964, Manuwal 1974). Sealy (1973) suggested that the lower growth rates of nocturnal alcids result from lower feeding rates. However, daily food consumption by Cassin's Auklet chicks is about twice that of Dovekies and Least Auklets (see above), suggesting that growth rate is not limited by the amount of food adults can deliver to chicks.

Ricklefs et al. (1980) have suggested that the slow growth rates of some seabirds are due to the precocial development of hatchlings, rather than to limitations in food supply. This hypothesis states that growth rate is constrained by the proportion of tissues that are allocated to the competing functions of growth (cell di-

vision) and mature function (locomotion or thermogenesis; Ricklefs 1983). Thus the more precocial a neonate, the greater its mobility and thermoregulatory abilities, but the slower its growth rate. For alcid chicks that remain in the nest, variation in precocity is reflected primarily in differences in thermoregulation. Our observations of chick brooding in Least Auklets indicate that acquisition of thermal independence is a gradual process. Adults make several trips to the breeding site each day, and nestlings are apparently brooded periodically as needed until age 18 days. Dovekies also deliver several chick meals daily (Norderhaug 1980), and nestlings are brooded intermittently until 20 days after hatching (Stempniewicz 1981). Early in the nestling period there is clearly a trade-off between the brooding requirements of the chick and the number of chick meals the parents can deliver.

This trade-off is more stringent in nocturnal species. Chicks must either maintain their body temperature during the day when both parents are feeding at sea; or one parent must remain at the breeding site for the entire day, thus reducing the food delivered to the chick by at least 50%. Development of thermoregulation is apparently more precocious in Cassin's Auklet nestlings because diurnal brooding abruptly ceases once chicks are five to six days old. The cost of increased precocity in the chicks of nocturnal alcids may be slower growth rates and longer nestling periods relative to diurnal species.

In summary, by foraging near shore on abundant prey with a high energy content (Roby et al. 1986), Least Auklet adults can deliver several chick meals each day. Repeated visits to the breeding site by parents during the day and attendance by at least one of the parents at night permit chicks to remain thermally dependent on adults for much of the nestling period. High growth and development rates relative to other alcids may necessitate this delay in thermal independence. Shortening the nestling period minimizes the exposure of adults and chicks to land-based predation and concentrates breeding activities during the short period of peak food availability at high latitudes.

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