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COLONY ATTENDANCE AND POPULATION MONITORING OF LEAST AND CRESTED AUKLETS ON ST. LAWRENCE ISLAND, ALASKA[1]

JOHN F. PIATT, BAY D. ROBERTS, AND SCOTT A. HATCH
Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, AK 99503

Abstract. Diurnal and seasonal patterns of attendance of Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) were studied in 1987 at breeding colonies on St. Lawrence Island, Alaska. Numbers of auklets attending eight 200-m² plots on talus slopes were counted throughout the day by observers on 11 occasions through the breeding season. Numbers attending smaller plots were recorded on time-lapse film on 71 different days. Another 16 200-m² plots were censused for auklets using surface counts. Within-day patterns of attendance were extremely variable over small and large temporal scales. Peaks of attendance occurred in late morning and late evening, with a 7- to 12-hr period of absence in the middle of the day. Attendance varied markedly between days, and numbers were negatively correlated with wind speed and the magnitude of tidal oscillations. Patterns of attendance also varied with stage of breeding, and counts were least variable during incubation and early chick rearing. Whereas Least Auklet numbers peaked during prelaying, Crested Auklet numbers peaked during incubation. Counts indicated that auklets at Kongkok Bay have increased about twofold since studies in the mid-1960s. Recommendations are made for future monitoring of auklet populations.

Key words: Least Auklet; Aethia pusilla; *Crested Auklet;* Aethia cristatella; *census; population monitoring; St. Lawrence Island; time-lapse photography.*

INTRODUCTION

Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) are two of the most abundant seabirds in the North Pacific, but numbers are difficult to census and population estimates for most colonies are still tentative (Sowls et al. 1978). Both species lay their eggs in natural crevices among the rubble of boulder fields or glacially-formed talus slopes, and attendance at colonies is extremely variable. Those factors make it difficult to estimate numbers of breeding birds or monitor population trends.

Bédard (1969b) was the first to develop methods for censusing auklets. He counted birds attending 200-m² plots on talus slopes and extrapolated to estimate total population sizes of colonies on St. Lawrence Island, Alaska. However, Bédard did not quantify diurnal or seasonal variations in attendance. Byrd et al. (1983) and Roby and Brink (1986) demonstrated that the numbers of Least and Crested auklets in attendance on slopes varied widely both daily and seasonally. They also monitored the movements of breeding and nonbreeding auklets to and from breeding sites and related attendance at the surface to activities of birds below the surface of talus slopes. Despite these advances, no consensus has been reached on the best methods for monitoring auklet populations.

We studied diurnal and seasonal attendance patterns of Least and Crested auklets on St. Lawrence Island in summer 1987, using surface counts of auklets and time-lapse photography. The purpose of the study was to identify sources of variation in attendance and refine methods for monitoring populations. We compare our data with results of previous studies to assess changes in the populations of auklets at St. Lawrence Island.

METHODS

We worked at Kongkok Bay (63°24′N, 171°49′W) near the southwest cape (Fig. 1); in the area described in detail by Bédard (1969b). We established 16 200-m² auklet study plots on: (1) the inland talus slopes of Owalit Mountain to study breeding biology (Piatt et al., in press) and attendance patterns, and (2) the northern and southern slopes of Kongkok Basin for censusing (Fig. 1).

We counted birds sitting on the surface of talus

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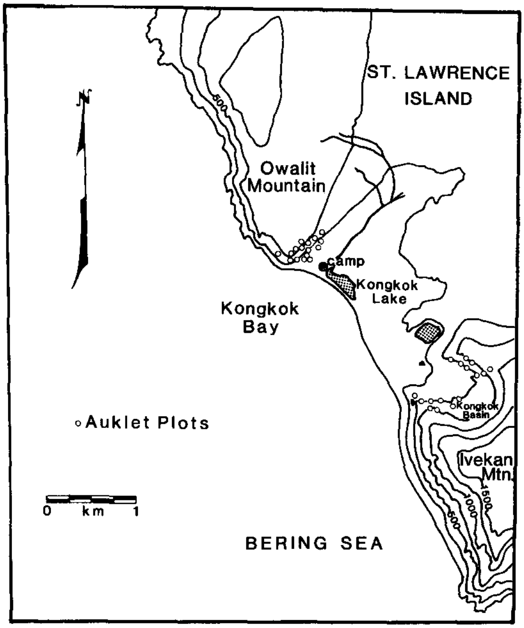

FIGURE 1. Study area and location of auklet plots on St. Lawrence Island. Contour intervals in feet.

habitat (hereafter called "surface counts") on eight of the Owalit study plots every 0.5 hr on 11 different days. We also placed 8-mm time-lapse cameras on three Owalit plots with about 10-m^2 areas to take time-lapse photos every 5 min. Birds recorded by observers or time-lapse film represent only that portion of the population present on top of the talus rocks (i.e., birds in crevices, flying about the colony, foraging, or loitering at sea near the colony are excluded). Auklet numbers were later counted from the films using a time-lapse projector. Complete diurnal counts were obtained for 71 different days from 30 May to 26 August. Attendance patterns were analyzed with nested ANOVA and variance component procedures in SAS (1985). We used the 5% level of statistical significance and the term "significant" is used hereafter in its statistical sense only.

Bédard (1969b) censused auklets prior to egg laying by counting numbers attending a number of 200-m^2 plots during the early morning, selecting the second to fourth highest counts to get a mean density per plot, and extrapolating from plots to the total area of habitat used by auklets to get a population estimate. He adjusted surface counts for the total area of plots covered with suitable substrate, and the depth of the talus rock layer. Searing (1977) used exactly the same procedure as Bédard (1969b).

For comparing our surface counts with those of Bédard and Searing, we averaged the second, third, and fourth highest counts of auklets at each plot to calculate peak densities. Counts were conducted between 05:00–11:00 Bering Daylight Time (BDT). We found two of the same plots used by Searing, and located other plots in the same vicinity (Lane Iyakitan, pers. observ.). Surface counts at Owalit were conducted during June (prelaying) and at Kongkok in late July (chick rearing). We corrected for seasonal variation by counting at Owalit and Kongkok simultaneously in July, and extrapolating from the June and July counts at Owalit. We extrapolated from surface counts to total populations by using our measures of average auklet densities and Bédard's estimates of total colony areas for Owalit and Kongkok.

RESULTS

ATTENDANCE PATTERNS

Diurnal patterns of auklet attendance were typically erratic at small temporal (5 min) and spatial scales (Fig. 2). Least and Crested auklet numbers on time-lapse plots were negatively correlated on 73% of 77 count-days observed, and 48% of those negative correlations were significant. At larger (30 min) time scales, Least and Crested auklet numbers were positively and significantly correlated each day on all eight Owalit plots (Fig. 3) and on 94% of time-lapse count-days when the data were averaged over 0.5-hr time intervals. Strongly significant correlations (Least: mean $r = 0.67 \pm 0.096$ SE; Crested: $r = 0.62 \pm 0.23$) between time-lapse counts averaged over 0.5 hr and observer counts on eight Owalit plots were observed on all days except 23 August, when few auklets attended the colony (Fig. 3). Time-lapse and surface counts revealed that auklet attendance increased rapidly and plateaued during the morning hours, declined slowly in early afternoon until no birds were present for 7–12 hr, and peaked again at lower levels late in the evening.

Analysis of the components of variation in numbers of auklets on Owalit plots indicated that within-day fluctuations accounted for most of the total explained variance in auklet attendance (Least: 78%, Crested: 53%). After removing within-day variation from the analysis, and using only data from 06:00–09:00 BDT (period used for censusing by Bédard 1969b), between-day and between-plot variance accounted for most of the variation (Table 1). By grouping time-lapse data

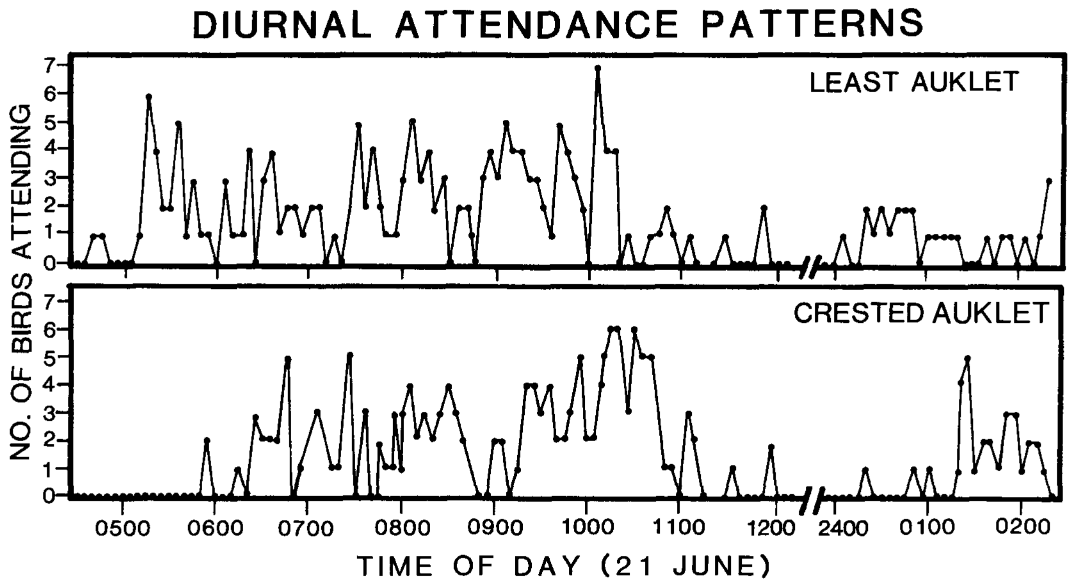

FIGURE 2. Diurnal attendance of Least and Crested auklets at plot 3, Owalit Mountain on 21 June 1987. Counts are for a 10-m² area every 5 min from time-lapse film. Note break in time between 12:10–23:55, when no auklets were present.

into hours and months, we obtained an integrated picture of auklet attendance (Fig. 4), which was more accurate than the observer counts (Fig. 3) because between-day variance was smoothed out by the large sample size. In most respects, patterns revealed by time-lapse and surface counts were similar. Attendance shifted from early morning to afternoon hours as the breeding season progressed, and Crested Auklet attendance peaked in July whereas Least Auklet attendance was similar in June and July.

Integration of time-lapse data within days (Fig. 5) revealed that Least Auklet attendance peaked during prelaying whereas Crested Auklet attendance slowly built up to a peak during incubation. Both species stopped attending the surface of talus slopes after mid-August, although chicks did not fledge until late August and early September (Piatt et al., in press). Figure 5 also illustrates the magnitude of daily variation in surface attendance. Coefficients of variation in auklet attendance over 2-week intervals indicated that attendance was least variable during late incubation or early chick rearing (Table 2).

The influence of environmental conditions on attendance were assessed by measuring correlations between daily mean attendance values from time-lapse plots (excluding the fledging period) and environmental variables (Table 3). Attendance of both species was negatively correlated with wind speed, which accounts for many days of low attendance, particularly in June (Figs. 3 and 5). Attendance also was negatively correlated with the range of daily tidal oscillations. Correlations improved when data were grouped over 7-day intervals. Crested Auklet attendance was also positively correlated with daily maximum air temperature and rainfall, although those correlations were probably an artifact of analysis due to a seasonal trend of increasing air temperature and rainfall.

POPULATION TRENDS

At Kongkok Basin, we observed higher densities of Least Auklets, but similar densities of Crested

TABLE 1. Components of variation in attendance of Least and Crested auklets at plots on Owalit Mountain, St. Lawrence Island. Nested ANOVA on counts conducted between 06:00–09:00 BDT.

Source	% variance explained	
	Least Auklet	Crested Auklet
Plot	11.8	22.9
Period of summer	0.0	10.2
Day (within period)	45.7	13.4
Plot•period	0.0	1.7
Plot•day	8.2	8.1
Within day (error)	34.3	43.7

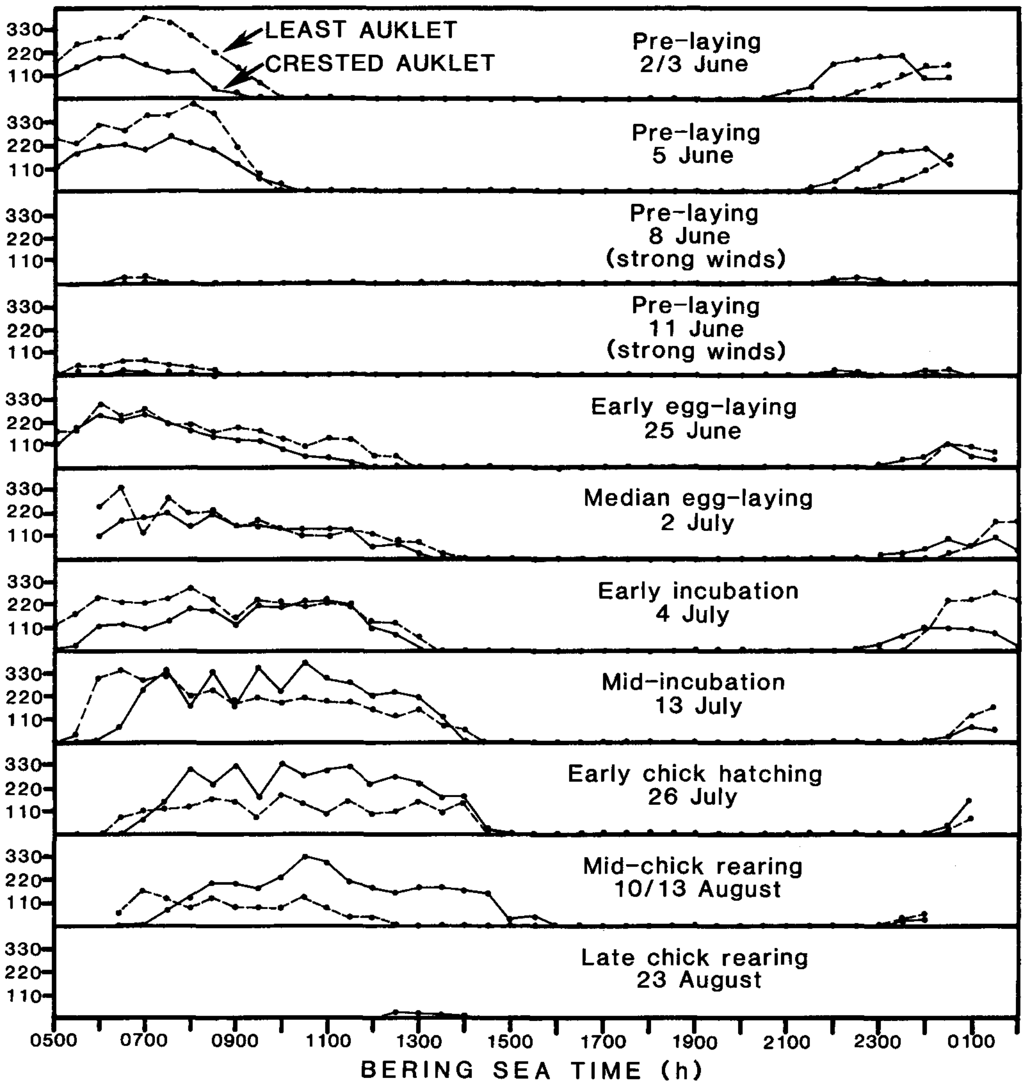

FIGURE 3. Diurnal attendance of Least and Crested auklets at eight 200-m² plots on Owalit Mountain at different stages of the breeding season.

Auklets in 1987 compared to Searing's estimates in 1976 (Table 4). The mean densities of both species decreased on the north side, but increased on the south side of Kongkok. The density of Least Auklets on Owalit did not change since Searing's investigation, but we noted a large increase in density of Crested Auklets. At both locations, Searing observed higher densities of Least and Crested auklets in 1976 than Bédard had in 1964.

Based on Bédard's (1969b, p. 391) original estimates, the overall density of Least Auklets increased 1.6- and 2.7-fold at Owalit and Kongkok, respectively, whereas Crested Auklets increased 1.7- and 1.4-fold, respectively, over the 20-year interval since Bédard's investigation. Extrapolating to the total area surveyed by Bédard, total auklet populations in Owalit (21,000 birds) and Kongkok (730,000 birds) are now about twice what they were during Bédard's time.

DISCUSSION

ATTENDANCE PATTERNS

Breeding auklets arrive at Kongkok Bay in May and early June, and establish breeding territories

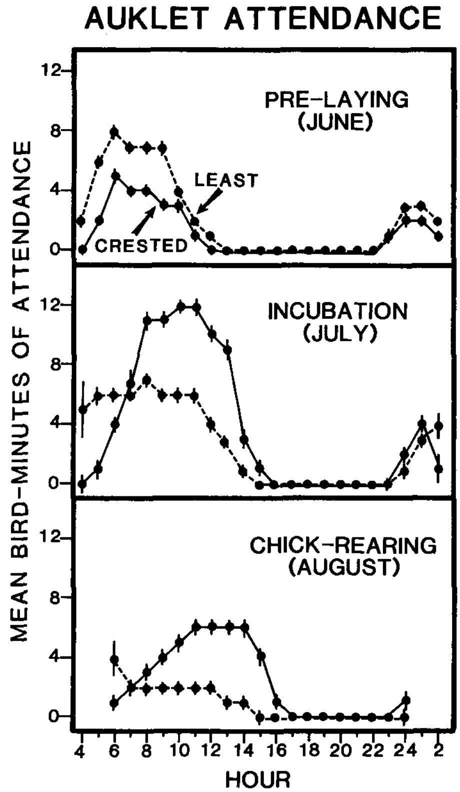

FIGURE 4. Diurnal attendance of Least and Crested auklets integrated over time during prelaying, incubation, and chick rearing. Each data point is the mean (±SE bars) attendance per hour per month calculated from time-lapse counts on all plots conducted at 5-min intervals.

on talus slopes where they engage in courtship activities, defend against competitors, and select sites to lay their eggs in crevices under the talus rocks (Bédard 1969b, Sealy 1975). Subadults arrive during incubation and remain until fledging. They also loiter on talus slopes during the day, interacting with other auklets and prospecting for breeding sites (Bédard 1969b, Roby and Brink 1986).

During prelaying and incubation periods, at least one adult stays in the breeding crevice during the day and frequently both adults occupy egg sites overnight (Sealy 1968, Roby and Brink 1986). Adults exchange incubation duties about every 24 hr (Sealy 1968, Roby and Brink 1986). During chick rearing, one adult auklet stays with the chick for most of the day during the first 5–10 days of life (Roby and Brink 1986; Piatt et al., in press), and thereafter chicks are increasingly left unattended during the day while adults forage or sit on talus slopes.

On the basis of those observations, one might expect the numbers of auklets on talus slopes to be highest during prelaying when neither mate is restricted to an egg site, and lowest during chick rearing when both parents are foraging for chick meals. This was true for Least Auklets, even though the arrival of subadults during incubation may inflate slope attendance by 10–50% (Bédard 1969b; Roby and Brink 1986; Ian Jones, pers. comm.). Crested Auklet attendance, however, was markedly lower during the prelaying period. At St. Lawrence Island, Crested Auk-

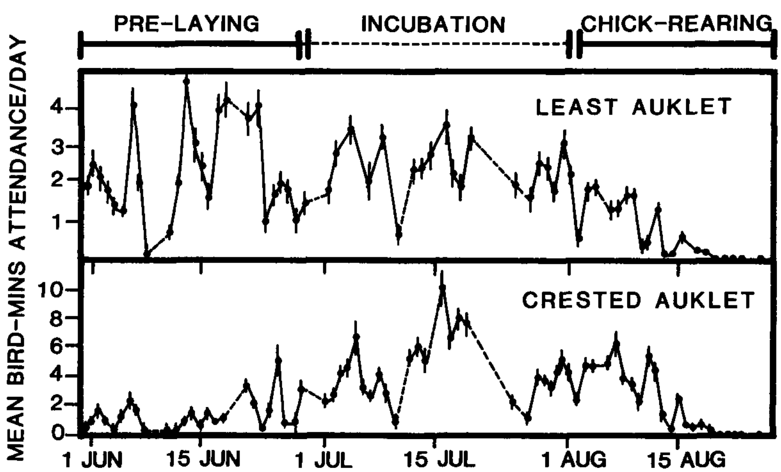

FIGURE 5. Seasonal attendance of Least and Crested auklets as determined from time-lapse film. Each data point is the mean (±SE bars) attendance per day on 10-m² surface plots calculated from time-lapse counts on all plots conducted at 5-min intervals.

TABLE 2. Variation in Least and Crested auklet attendance during different periods in their breeding cycle at St. Lawrence Island (counts of auklets at 5-min intervals on time-lapse film plots).

Period	Date	n	Least Auklet $\bar{x}$	Least Auklet SE	Least Auklet CV	Crested Auklet $\bar{x}$	Crested Auklet SE	Crested Auklet CV
Prelaying	1–15 Jun	1,289	0.51	0.03	229	0.10	0.01	426
	16–30 Jun	2,846	0.48	0.02	238	0.37	0.02	278
Incubation	1–15 Jul	3,139	0.49	0.02	216	0.76	0.03	224
	16–31 Jul	2,095	0.67	0.03	188	1.58	0.06	175
Chick rearing	1–15 Aug	2,171	0.49	0.02	199	1.43	0.05	166
	16–31 Aug	1,470	0.05	0.01	549	0.07	0.01	526

let egg sites are deeper and less accessible to the surface than Least Auklet egg sites, and Crested Auklets might spend more time under the talus during prelaying and therefore were underrepresented on surface counts compared to Least Auklets. Alternatively, Crested Auklets (ca. 270 g) may have to forage longer than Least Auklets (ca. 85 g) because of their higher food demands, and attendance may not peak until zooplankton blooms result in densities of prey sufficient to support the extra cost of commuting from the colony (Bédard 1969b; Piatt, in press). In support of this hypothesis, Byrd et al. (1983) noted a nearly twofold increase in Crested Auklet activity (total movement in and out) between pre-egg laying and late incubation at Buldir Island whereas Least Auklet activity remained similar over that time.

Attendance by both species diminished after hatching of chicks and apparent attendance stopped completely during late chick rearing. Most of the birds attending the surface at that time may have been subadults (Dan Roby, pers. comm.). Although the attrition in numbers was partly a result of fledging chicks and adults leaving the colony, breeding birds stopped loitering on slopes at that time. The total movement of adults actually increases two- to fourfold during chick rearing as adults bring four to six meals a day to chicks (Byrd et al. 1983, Roby and Brink 1986).

Crested Auklets may suppress the numbers of Least Auklets attending shared talus slopes through aggressive intimidation (Bédard 1969b, Knudtson and Byrd 1982). Our data support this hypothesis because on a 5-min time scale, Least and Crested auklet numbers on 10-m^2 time-lapse plots were negatively correlated about 75% of the time. Attendance at plots was often synchronized; auklets of the same species often arrived and departed together in groups of 20–50, as they do while foraging at sea (Bédard 1969a). This partially accounts for the erratic diurnal attendance data (Figs. 2, 3), and, in light of the negative correlations in fine-scale attendance, further suggests that Least Auklets may conduct their activities at the surface in short bouts between periods of intense Crested Auklet activity.

Diurnal patterns of attendance changed seasonally for two reasons. First, seasonal variations in day length determine the timing of departure in morning and return in evening. Auklets apparently do not forage at night (Bédard 1969a, 1969b; Roby and Brink 1986). Similarly, day length determines the total amount of time available for foraging, and therefore the duration of the midday break in attendance. This may explain why the midday gap in attendance at St.

TABLE 3. Spearman's rank correlations between mean numbers of auklets attending time-lapse plots per day and environmental variables (ns = nonsignificant).

Variable	n	Least Auklet r	Least Auklet P	Crested Auklet r	Crested Auklet P
Wind speed	55	−0.29	<0.05	−0.31	<0.05
Tide range	55	−0.07	ns	−0.28	<0.05
Tide (7-day means)	9	−0.69	<0.05	−0.54	ns
Maximum temperature	55	0.26	ns	0.48	<0.05
Fog	55	0.04	ns	0.41	ns
Rain	55	0.21	ns	0.52	<0.05

TABLE 4. Mean densities of Least and Crested auklets on Owalit Mountain and in Kongkok Basin, St. Lawrence Island. Counts from 1987 indicated to be significantly higher (**** $P < 0.0001$) or not significantly different (ns) from counts in 1976 by Searing (1977). Differences tested using two-tailed t-tests. Counts in 1964 from Bédard (1969b).

Location	1987				1976			1964	
	n	$\bar{x}$	SE		n	$\bar{x}$	SE	n	$\bar{x}$
Least Auklet									
Owalit Mtn.	24	53	3.0	ns	24	64	4.9	?	36
Kongkok Basin	48	90	5.9	****	48	56	5.0	39	34
Crested Auklet									
Owalit Mtn.	24	32	4.4	****	24	13	1.7	?	19
Kongkok Basin	48	42	6.0	ns	48	40	12.6	39	30

Lawrence Island (7–12 hr) is greater than that observed further south at the Pribilofs (5–9 hr; Roby and Brink 1986) or Buldir Island (5–8 hr; Byrd et al. 1983). Secondly, auklets must make more visits to the colony during chick rearing to deliver chick meals, and activity stretches over a longer portion of the day at that time. Although a midday gap in attendance continues through chick rearing, this is deceptive because adults still come and go at reduced levels, but they do not loiter on slopes after delivering food (Byrd et al. 1983, Roby and Brink 1986). Like Byrd et al., we found that Least Auklets usually returned about 1 hr earlier in the morning than Crested Auklets. Some Least Auklets use prey patches closer to the colony (e.g., at sites of coastal upwelling) than patches exploited by Crested Auklets (Bédard 1969a), and therefore may be able to get back to the colony more quickly after the dawn exodus.

Auklets from Kongkok Bay may regularly forage over 60 km from their colonies, and by late chick rearing as far as 150 km from colonies (Piatt et al. 1988; Hunt et al., in press). Some auklets must forage within about 30 km of Kongkok to be able to return within an hour or so after the dawn exodus (assuming flight speeds of ca. 60 km/hr). For auklets to make a return trip to foraging areas 150 km away would require about 6 hr (allowing 1 hr for feeding), which may explain the total absence of loitering adults during late chick rearing. At that time, delivery of five chick meals per day (Roby and Brink 1986) would require a commitment of about 30 hr/day, or about 15 hr of a 17- to 18-hr day for each adult.

Tidal conditions also may influence attendance behavior via its effect on prey availability. Tide rips near headlands and turbulence at offshore fronts increase in intensity as tidal oscillations become larger, and this may serve to concentrate zooplankton in predictable locations (Alldredge and Hamner 1980, Brown 1980, Haney 1988). We found that auklet attendance was negatively correlated with the range of tidal oscillations when the data were grouped over 7-day intervals. This suggests that birds were foraging more during periods when tidal action was strongest, and spent more time at the colony when tidal movements were minimal and prey were presumably less available. Wind speed was also negatively correlated with auklet attendance, particularly during the prelaying period. This may have been because high winds interfered with activities at the colony so birds just stayed away, or high winds may interfere with foraging activities at sea, so birds are forced to spend more time foraging.

MONITORING AND CENSUSING POPULATIONS

Bédard's (1969a, 1969b) 'surface count' technique is relatively simple to apply and interpret, large numbers may be counted by a single observer, and there may be a direct relationship between birds at the surface and the number of breeding pairs occupying the talus (Sealy 1975; Ian Jones, pers. comm.), although the ratio remains to be determined. On the negative side, our study indicated that Crested Auklets were least abundant before egg laying and counts of both auklet species were most variable at that time. Furthermore, the deletion of the highest count to estimate mean densities seems arbitrary (Byrd et al. 1983).

At Buldir Island, Byrd et al. (1983) estimated auklet numbers by mark-recapture and net movement techniques, and compared those with estimates from surface counts. Mark-recapture efforts were unsuccessful because auklets became net-shy after initial capture and leg bands were difficult to see on birds walking or resting on talus slopes. The net movement of unmarked birds to and from study plots was used to estimate numbers of auklets, and results suggested that surface counts underestimated numbers about 10-fold. Furthermore, results indicated that count variability was lowest during late incubation and early chick rearing. Theoretically, the net movement technique should provide reasonable estimates of total birds using breeding habitat. However, the technique is difficult to apply in areas of high auklet density, requires a substantial observer effort, yields highly variable counts, and is difficult to interpret without knowledge of breeding phenology and the activities of adult birds (Byrd et al. 1983).

At the Pribilofs, Roby and Brink (1986) also monitored the net movement of marked birds over brief periods at a small colony. They concluded that the best time to census breeding adults was in the evening during late chick rearing because at that time, only adults with meal deliveries were observed arriving at the colony. However, our study indicated that attendance during late chick rearing was more variable than at any other time, and more work is required to determine what proportion of breeding adults would be counted on those evening arrivals. To extrapolate from net movements to total population size, this method requires that birds be captured and banded, and only small numbers can be monitored by a single observer. One similar and promising approach is to count the numbers of banded adults carrying food in gular pouches throughout the chick-rearing period to estimate the numbers of auklets per unit area that successfully rear chicks (Ian Jones, pers. comm.). Like the net movement technique, however, this requires a considerable time investment and is limited by the number of individual birds that can be monitored at one time.

Based on our experience and the results of previous investigations, we recommend the following approach for censusing and monitoring auklet populations. Censusing should be conducted by using the surface-count technique over at least a 2-week period during late incubation and early chick rearing (i.e., when Crested Auklet attendance is maximal and variability in counts is minimal). Counts on 200-m^2 plots (a workable and convenient size) should be conducted over morning and early afternoon, and for statistical purposes, the top 10 counts should be used to get a mean value of attendance per day. Counts should be conducted over at least a 14-day period to get a mean value of attendance over a complete tide cycle. Days with strong winds (e.g., >40 km/hr) should be avoided for censusing. The number of plots counted will depend on manpower available, but a reasonable number (e.g., ≥ 10) in representative habitat should be established and permanently marked for later comparisons. For monitoring purposes, it is sufficient to apply these methods to sample plots over succeeding years.

Extrapolation to total numbers of breeding birds requires knowing the ratio between the number of adult birds present on talus slopes and the number of breeding sites below the talus, and measuring the total habitat used by auklets. We recommend the use of the net movement technique for determining ratios of attending (adults and subadults) to breeding birds. Although difficult to apply to large areas or in areas of high auklet density (Byrd et al. 1983), this technique could be used to establish ratios in relatively small areas (e.g., 10 to 20 m^2) of larger surface count plots. Besides obtaining a correction factor for surface counts, subadult birds could be identified on net movement watches, and that would help in interpreting seasonal and annual variations in attendance.

For monitoring, we also recommend the use of 35-mm time-lapse photography. Whereas the 8-mm cameras we used were adequate to quantify some aspects of attendance behavior, and time-lapse counts were strongly correlated with surface counts, the number of birds monitored was quite small. The 35-mm camera could be used to monitor attendance in much larger plots (e.g., 50 to 200 m^2) with permanent boundaries highlighted by rope or flagging tape during the study period. We recommend that photos be taken about every 20 min through morning hours of attendance over the same 2-week period that surface counts are conducted. Establishing one or more permanent time-lapse plots would provide a valuable secondary source of information for monitoring populations because the time-lapse technique provides a measure of attendance that integrates far more data over days and weeks than can be obtained from surface counts. Furthermore, it can yield a single average value of attendance with known variance for comparison between years, and the influence of diurnal and daily variations in attendance is minimized because data are integrated over the whole period.

POPULATION TRENDS

If the density estimates of Bédard (1969b), Searing (1977), and ourselves in 1987 are comparable, then it appears that over the period 1967–1987, Least Auklet densities increased dramatically at Kongkok and slightly at Owalit, whereas Crested Auklet densities increased markedly at Owalit, but only slightly at Kongkok. Overall, the densities of both species increased about two-fold since Bédard's study was conducted. Our estimates for 1987 would be slightly higher if we had made the corrections for percentage of plots covered by suitable breeding substrate and the depth of talus, as described by Bédard (1969b). However, Bédard apparently did not measure talus depths at Kongkok (he made no mention of Owalit where the talus is much deeper), and his corrections for percentage cover were minimal, so our estimates were probably conservative.

Although statistically significant, we are cautious in suggesting that the changes observed were biologically significant. We still know little about interannual variations in attendance patterns, and particularly about how subadult numbers contribute to total variability. Attendance behavior of subadults needs further study. Subadult plumages are confusing, however, and we often found it difficult to distinguish subadults from adults. Plumages need to be better described before attendance patterns of different age classes can be studied with confidence.

We can only speculate on the causes of the apparent increase in auklets at Kongkok and Owalit. If populations were limited by food, it is possible that zooplankton became increasingly more abundant or available to auklets over the 20-year period examined because of favorable oceanographic conditions or a reduction in fish species that could compete with auklets for zooplankton (Springer and Roseneau 1985). However, a reduction in predation on auklets by arctic foxes (*Alopex lagopus*) and humans is the most likely explanation for the apparent increase in auklet numbers. The trapping of foxes by native Yup'ik eskimos increased on St. Lawrence Island with the arrival of modern traps and snowmobiles in the 1960s, and the population of foxes has been reduced since Bédard's time (Lane Iyakitan, pers. comm.). Perhaps more importantly, the traditional Yup'ik method of capturing auklets in nets on talus slopes, and removing chicks from crevices, had fallen into disfavor at Kongkok even in Bédard's time (Bedard 1969b). We found numerous stone walls and blinds at both Owalit and Kongkok that were used in the past for hiding while netting birds, but those appeared not to have been used for many years, and we observed no netting in 1987. Thus, the indirect (disruption of adult attendance and chick feeding) and direct (loss of breeding adults) effects of netting have been reduced or eliminated since Bédard's time.

Finally, the different patterns of population increase at Kongkok and Owalit exhibited by Least and Crested auklets may result from competitive interactions between species and habitat differences between those sites. The habitat at Kongkok is definitely favored by Least Auklets, especially on the south side, because the talus is composed of a shallow layer of small boulders (Bédard 1969b, Searing 1977). The reverse is found on Owalit, where a deep layer of talus composed of large boulders would be favored by Crested Auklets (Bédard 1969b, Searing 1977). The fact that Crested Auklet densities have remained the same despite a large increase in Least Auklets at Kongkok, and that Least Auklet densities declined slightly while Crested Auklets increased at Owalit (1976–1987), supports the idea that asymmetric interference competition exists between species for breeding habitat, with Crested Auklets being superior in their favored habitat because of their larger size and aggressive behavior (Bédard 1969b, Byrd et al. 1983, this study).

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