ABSTRACT.—Daily and seasonal colony attendance patterns and census techniques for Crested (Aethia cristatella), Least (A. pusilla), and Whiskered (A. pygmaea) auklets were examined at Buldir Island, Alaska. Two daily peaks in colony activity were found throughout the breeding season: the first in the morning and early afternoon and the second just before dark. A new technique for estimating auklet populations was developed, based on the net movement of birds to and from the talus nesting area during the two peaks of activity. The new “Net Movement” technique yielded considerably higher estimates than those obtained using Bédard’s (1969) method of estimating auklet populations by observation. Both techniques have advantages and disadvantages for censusing auklets, depending on circumstances.

Populations of crevice-nesting auklets are difficult to assess for several reasons: their nests are usually inaccessible to investigators; many individuals may use a crevice entrance common to several subsurface nest sites; and birds gather in frequently immense flocks that fly over the nesting areas. Historically, most investigators have estimated auklet numbers by “guesstimating” the number of birds seen flocking over and near a colony at whatever time of the day and of the breeding season the observers happened to be present.

In the late 1960s at St. Lawrence Island, Alaska, the first intensive studies were made of colony attendance patterns (Sealy 1968) and censusing (Bédard 1969) of Crested (Aethia cristatella) and Least (A. pusilla) auklets. Sealy (1968) described the general peaks of activity, but he did not quantify patterns of activity or examine their differences between species of auklets. Bédard’s (1969) scheme for estimating populations of auklets was based on counts of birds standing on rocks at the surface of the nest habitat. This technique has subsequently been used by Hickey and Craighead (1977) and Searing (1977).

From 1974 to 1976, we studied an auklet population at Buldir Island, Alaska, that contained Crested, Least, and Whiskered (Aethia pygmaea) auklets. Our objectives were to determine when (attendance patterns) and how (estimation scheme) to estimate auklet populations. Colony attendance patterns were quantified so that both temporal changes and interspecific variations could be evaluated. A Lincoln-Peterson method of population estimation (Overton 1971) was tested, and a new estimation scheme was developed and compared with that of Bédard (1969).

STUDY AREA AND METHODS

The study was conducted at Buldir Island (52°21'N, 175°56'E), westernmost of the Rat Island group of the Aleutian Islands (see Knudtson and Byrd 1982 for a map of Buldir). Buldir’s geology (Coats 1953), vegetation (Byrd, in press), and weather (Byrd and Woolington, in press) have been characterized elsewhere.

Our study was conducted on a 4.3-ha volcanic boulder slide extending from sea level to an elevation of 90 m on the northwestern side of Buldir. In this area, called “Main Talus,” the broken rocks were poorly sorted and up to 5 m deep. Vegetation grew in shallow soil covering the periphery of the talus slope, but soil and vegetation became scarcer toward the slide’s center, which was bare rock. Besides Aethia spp., other common nesting species in the talus crevices were Parakeet Auklets (Cyclorrhynchus psittacula) and Horned Puffins (Fratercula corniculata).

In 1974 and 1975, we caught auklets as they flew from a 10 × 10-m plot on the talus slope. Two people held a 3 × 10-m mist-net, stretched between bamboo poles, parallel to the ground until an auklet flew from the plot, whereupon the net was raised in front of the bird. We marked the auklets with U.S. Fish and Wildlife Service aluminum bands and also marked a few birds with colored plastic leg bands. Subsequently, additional netting attempts were made in the plot, and we watched for birds with bands sitting on boulders in the plot.

In 1976, we made four daylight (06:00–
watches at 14- to 17-day intervals during the breeding season at each of five, randomly-selected, 10 × 10-m plots in the Main Talus colony. Observation posts were located 10 to 20 m from plot boundaries in locations affording visibility of the entire plot yet far enough away to avoid disturbing birds. At each plot we recorded the number of individuals of each species of auklet present on the surface every 15 min and the number of birds arriving and departing for one of every two 15-min periods. These data were then used to graph activity patterns. To determine the net movement of auklets during a 15-min period, we added the difference between the number of birds arriving at and departing from the plot and the difference between the number of birds present on the plot at the beginning and end of the count period, as in Table 1. This technique measured the actual flow of birds to and from subsurface nesting areas in the talus.

The estimates from all five plots were averaged for each 15-min period in order to calculate an average net movement value for the period. Since data were recorded during only 15 min of every 30 min, the average net movement values were doubled to determine the movement of auklets during a particular 30-min period. The 30-min net movement values were then summed for each of the two major activity periods—morning-early afternoon (06:00–16:00) and evening (16:00–22:30; see Results and Discussion section)—to estimate the total net movement of birds during each period.

In order to compare the “Net Movement” technique with Bédard’s (1969) estimation scheme, we analyzed the Buldir data set with both methods. In each plot, Bédard averaged the second-, third-, and fourth-highest counts of auklets standing on the surface of the talus during the first three hours after sunrise (05:00–08:00). His counts were made during the few days preceding egg laying. Since sunrise was later at Buldir than at St. Lawrence, we used data from 06:30 to 09:30 for the Bédard method of analysis. Sample sizes at Buldir were 8 to 14 counts per plot, compared with 5 to 20 counts per plot at St. Lawrence; the methods of data collection were otherwise identical. Linear regressions (Sokal and Rohlf 1969) were used to compare the two techniques.

### RESULTS AND DISCUSSION

#### ACTIVITY PATTERNS

Two pronounced peaks in activity, morning-early afternoon and evening, occurred throughout the breeding season, but the magnitude of these peaks varied (Fig. 1). Departing birds outnumbered arriving birds during the morning-early afternoon period, resulting in a net movement of birds from nesting sites to their offshore feeding areas. Conversely, during the evening, more birds arrived than departed, resulting in a net movement of birds into the talus. This suggests that both members of many pairs spent the night on land. Recently, D. D. Roby (University of Pennsylvania, pers. comm.) found that Least Auklets on the Pribilof Islands, Alaska, spend the night in the talus during the breeding season with one member of each pair leaving in early morning.

Auklet movement at the colony usually began at first light and ended abruptly at dark. Activity ceased during the afternoon prior to and during incubation, while birds foraged at sea. The period of inactivity was shorter during the pre-laying stage (14:00–19:00) than during incubation (13:30–21:00). Auklets may have spent less time foraging away from the colony during pre-laying because both birds could forage simultaneously. During incubation, breeders could feed only every other day, so more time was probably required to get enough food to last through the day of incubation. During chick-feeding, activity continued throughout the day, but a lull occurred from 15:30 to 20:30. This continual activity during chick-feeding reflects the multiple trips made by parents to feed chicks. The bimodal peak of activity in the morning (Fig. 1) suggests that two feeding trips may have been made by each parent then. Norderhaug (1980) found that Dovekies (*Alle alle*) fed their chicks 4 to 14 times per day after the chicks no longer required brooding.

Before the chick-feeding stage, the morning activity of Least Auklets peaked slightly earlier than that of Crested Auklets (this is partially masked in Fig. 1 because of hourly rather than half-hourly averages), and Least Auklets arrived later in the evening than did Crested Auklets.

### TABLE 1. Example of calculations for the “Net Movement” method of analysis of auklet counts.

<table>
<thead>
<tr>
<th>Time</th>
<th>Abbreviation</th>
<th>Calculation parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>07:00</td>
<td>B</td>
<td>No. birds present at beginning of count period</td>
<td></td>
</tr>
<tr>
<td>07:15</td>
<td>E</td>
<td>No. birds present at end of count period</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>No. birds arriving during count period</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>No. birds departing during count period</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*“Net Movement” value = (B - E) + (A - D).*
FIGURE 1. Daily and seasonal activity patterns of Crested and Least auklets at Buldir Island, Alaska, in 1976. Count dates were: 25 May (pre-laying), 8 June (early incubation), 25 June (late incubation), and 9 July (chick-feeding).

Too few Whiskered Auklets were observed in the plots to permit quantitative analysis of their attendance patterns. General observations of this species nevertheless indicated that they left the colony earlier in the morning and arrived later in the evening than their congeners. The seasonal changes in activity patterns of Whiskered Auklets seemed to be similar to those of the other two species. Recent observations of Whiskered Auklets in the eastern Aleutian Islands suggest the species is crepuscular to nocturnal there (E. Bailey, U.S. Fish
and Wildlife Service, Homer, Alaska; and D. Forsell and D. Nysewander, U.S.F.W.S., Anchorage, Alaska; pers. comm.).

The magnitude of auklet activity at the colony was higher during the pre-laying and chick-feeding periods than during incubation when one of the parents was constantly at the nest site. Throughout the season, auklet activity was more protracted during the morning-early afternoon period (7–8 h) than in the evening (2–5 h). Non-breeding auklets were present at breeding colonies on St. Lawrence (Bédard 1969) and Big Koniuji (R. H. Day, unpubl. data) islands, Alaska, from at least mid-incubation through the chick-feeding stage. At both locations, populations of non-breeders apparently increased as the season progressed. A similar pattern was noted at Buldir, where the activity of non-breeders may have been at least partially responsible for increased activity of auklets during chick-feeding and for protraction of the morning-early afternoon period of activity.

Theoretically, the net movement of birds departing from the talus in the morning-early afternoon should have equalled the net number arriving in evening if every pair exhibited an identical behavior pattern. Realistically, however, differences could be expected (e.g., some breeding birds probably remained at sea more than 24 h at a time). Weather conditions, distribution and availability of prey, and stage of the nesting cycle probably all influenced colony attendance patterns. It is not surprising, therefore, that net movement totals varied for the two major daily activity periods (Fig. 2). Breeding birds were probably most likely to follow regular patterns during incubation, and indeed morning-early afternoon and evening net movements were most similar (except for Least Auklets during early incubation) during that stage (Fig. 2). This suggests that off-duty birds left the colony in the morning, presumably foraged at sea during the day, and returned to the colony in the evening. Assuming that incubation shifts for Crested and Least auklets lasted 24 h (Sealy 1972), birds returning in the evening relieved their mates on or before the following morning and incubated the egg until at least the next evening.

During the pre-laying stage, net movement totals for the two periods of activity were particularly unequal (Fig. 2). Irregular pre-laying colony attendance patterns also occur in other alcids (Tuck 1960, Lloyd 1975, Wehle 1976).

Since our count for the chick-feeding stage occurred just after the peak of hatching, many chicks were probably still attended constantly by one parent. Chicks are normally attended until they attain endothermy. Thermoregulation begins at from three to four days of age for Crested Auklets and from five to six days of age for Least Auklets (Sealy 1968). The net movement values during early chick-feeding were similar to those during the incubation stage for Crested Auklets, but markedly different for Least Auklets (Fig. 2). Eggs of Least Auklets hatched a few days earlier than those of Crested Auklets (Knudtson and Byrd 1982); therefore, a much lower percentage of Least Auklets than Crested Auklets were still brooding chicks during our chick-feeding count. Some Crested Auklet eggs were still in the process of hatching during our count. Unfortunately, we did not make a count later in the chick-feeding stage, but the pattern of net movement for both species probably resembled that for Least Auklets during our count on 9 July.

FIGURE 2. Comparison between morning-afternoon (shaded) and evening (unshaded) periods of net arrivals and departures of Crested and Least auklets at Buldir Island, Alaska. The net values are cumulative totals for five 10 x 10-m (100 m²) plots. Positive values indicate a net arrival of birds, and negative values a net departure.

POPCULATION ESTIMATION

Early in the study, we intended to use a Lincoln-Peterson estimator (Overton 1971) by either recapturing or observing banded birds in the vicinity of a 10 x 10-m plot where intensive banding occurred (about 150 Crested, 300 Least, and 10 Whiskered auklets were marked from 1974 to 1976). Auklets were ex-
Extremely net-shy after their initial capture; therefore, capture-recapture ratios were not indicative of the population. It was also not feasible to use the ratio of marked to unmarked birds that we saw on the plot, because auklets walked and sat on their tarsometatarsi in such a way that we frequently could not see whether or not a bird was banded.

In 1976 we used the "Net Movement" technique to estimate that, during the pre-laying and incubation stages, about 200,000 auklets left the Main Talus in the morning-early afternoon period or arrived in the evening (Table 2). Our estimate exceeded 250,000 auklets in the colony during chick-feeding (Table 2). The population was composed of about 68% Crested, 32% Least, and less than 1% Whiskered auklets.

Estimates obtained from the same data, but analyzed with Bédard's (1969) method, were far lower than those from "Net Movement" calculations (Table 2). Bédard's technique is based on the assumption that all birds nesting in an area stand on the surface for an extended time in early morning. At Buldir we recorded considerable movement of birds between the colony surface and its interior. Birds spent from a few seconds to 10 min on the surface before flying out to sea or entering a crevice. Thus, we doubt that individuals remained on a plot surface long enough to be counted twice (i.e.,

<table>
<thead>
<tr>
<th>Date of count</th>
<th>Species of auklet</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crested</td>
<td>Least</td>
</tr>
<tr>
<td>25 May</td>
<td>129.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>56.8</td>
</tr>
<tr>
<td></td>
<td>19.4</td>
<td>8.9</td>
</tr>
<tr>
<td>8 June</td>
<td>124.7</td>
<td>66.2</td>
</tr>
<tr>
<td></td>
<td>12.1</td>
<td>4.8</td>
</tr>
<tr>
<td>25 June</td>
<td>146.2</td>
<td>60.2</td>
</tr>
<tr>
<td></td>
<td>11.7</td>
<td>9.9</td>
</tr>
<tr>
<td>9 July</td>
<td>175.4</td>
<td>86.9</td>
</tr>
<tr>
<td></td>
<td>10.0</td>
<td>2.4</td>
</tr>
</tbody>
</table>

<sup>a</sup> For "Net Movement" calculations the activity period was used with the highest total net movement of buds on each date. Bédard's calculations explained in methods section.

<sup>b</sup> Values expressed in thousands.

Table 2. Estimates of auklet numbers at the Main Talus site, Buldir Island, Alaska.

<table>
<thead>
<tr>
<th>Species</th>
<th>Plot number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crested Auklet</td>
<td></td>
<td>51.5 ± 17.9*</td>
<td>504.5 ± 125.5</td>
<td>109.8 ± 35.9</td>
<td>818.5 ± 150.6</td>
<td>71.8 ± 14.1</td>
</tr>
<tr>
<td>Least Auklet</td>
<td></td>
<td>47.0 ± 15.5</td>
<td>236.5 ± 89.2</td>
<td>83.3 ± 21.8</td>
<td>135.2 ± 28.4</td>
<td>51.5 ± 16.0</td>
</tr>
</tbody>
</table>

* Sample size = 8 for all plots (two count periods on four different days).

at least 15 min). Birds departing from a plot were replaced by others, so Bédard’s technique consistently yielded underestimates.

When compared graphically, the “Net Movement” and Bédard techniques had a more or less linear relationship, the correlation being much stronger for Crested Auklets (Fig. 3) than for Least Auklets (Fig. 4). This interspecific difference may have been the result of behavioral differences. Crested Auklets are larger and more aggressive than Least Auklets (Bédard 1969, Knudtson and Byrd 1982), so Least Auklets probably did not engage in courtship displays where Crested Auklets were present (Bédard 1969). Thus, the relationship between the number of Least Auklets standing on the colony surface and the number of those nesting in that area may have been influenced by densities of Crested Auklets in the same area. Bédard’s technique approximated “Net Movement” densities for Crested Auklets better than it did for Least Auklets, suggesting that the former spent more time than the latter loitering on the colony surface.

The “Net Movement” method estimated auklet breeding populations more accurately than Bédard’s scheme, but it too had drawbacks. We recorded considerable spatial and some temporal variations among sample plots (Table 3). The greatest variability was among estimates from different plots because of the heterogeneous distribution of nesting birds within the colony. In addition, interpretation of results from “Net Movement” calculations was not straightforward. We assumed that during the pre-laying stage we were seeing both members of pairs as they engaged in courtship activities (on or below the surface) in the talus and as they inspected nest sites. Since, during incubation, one member of each pair was always on the egg, each individual entering or leaving a nest site represented a pair. During chick-feeding, after chicks could thermoregulate, both members of a pair again would have been seen as they flew from and to the slopes, bringing food to chicks. Therefore, the actual population estimate during incubation was 200,000 pairs, not individuals. Interpretation of the chick-feeding count is more difficult since, as stated earlier, an unknown percentage of the pairs had one individual still brooding chicks, while other pairs had both individuals bringing food to chicks.

CONCLUSIONS

During the breeding season, auklets behaved in relatively regular patterns at the nesting colony. Despite interspecific and temporal differences, the existence of major daily periods of movement allowed sampling for population estimation.

Traditional wildlife sampling techniques (Overton 1971) proved unsatisfactory for crevice-nesting auklets. Also, Bédard’s (1969) method of estimating auklet populations yielded an underestimate of actual numbers. The new “Net Movement” technique provided a more accurate estimate than did Bédard’s scheme, but it required more labor and its results could be difficult to interpret.

We suggest that the “Net Movement” technique be used to estimate populations of auklets during the incubation stage, when activity patterns are most regular and when interpretation of counts is most straightforward. Since variation among plots is great, as many plots as possible should be censused. Counts could be made during either of the two daily activity periods. Morning-early afternoon counts require more time than do evening counts, but the light is brighter and activity is less intense than during the evening. If time and manpower constraints dictate, Bédard’s technique could be used to estimate Crested Auklet populations at other colonies, and the results adjusted by using predictor equations developed at Buldir (Fig. 3).

The “Net Movement” technique could be improved with more information about the length of time that individual auklets remain on the talus surface, the effects of weather and prey availability on auklet activity, and the presence and behavior of non-breeders.

ACKNOWLEDGMENTS

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LITERATURE CITED


