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COLONY ATTENDANCE OF LEAST AUKLETS AT ST. PAUL ISLAND, ALASKA: IMPLICATIONS FOR POPULATION MONITORING[1]

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Abstract. Colony attendance by Least Auklets (*Aethia pusilla*) was monitored during three breeding seasons at St. Paul Island, Alaska. Maximum counts of birds attending one 150-m^2 study plot varied significantly from year to year, with a nearly two-fold difference between highest and lowest years. Maximum numbers on the surface at any one time amounted to about half of the local breeding population. Attendance was high in the year with greatest proportion of adults breeding, low in the year with lowest proportion of adults breeding, and the proportion of adults breeding differed significantly among years. Adult attendance both early and late in breeding season differed significantly among years, but there was no evidence that varying attendance related to changes in the overall adult population. Counts during incubation and chick-rearing stages were affected by sub-adults (two-year-olds), which differed significantly in attendance from year to year and sometimes represented up to half the birds on the colony surface. Year-to-year changes in surface counts probably related to strength of this sub-adult cohort and to varying attendance behavior of adults and sub-adults that correlated with food availability. These data suggest that, taken alone, surface counts at Least Auklet colonies must be interpreted cautiously in assessing population changes. Suggestions for improvement of counting techniques and an alternative approach to population monitoring are discussed.

Key words: Alcidae; Aethia pusilla; *census; colony attendance; Least Auklet; population monitoring; reproduction; seabird; survival.*

INTRODUCTION

The Least Auklet (*Aethia pusilla*) is a plankton-feeding seabird endemic to the Bering Sea and adjacent North Pacific waters and is the most abundant breeding seabird of the region (Sowls et al. 1978). Least and other auklets represent an important component of the local marine ecosystem, which is thought to be in a dynamic state due to natural and man-made disturbances (Springer and Roseneau 1985). However, auklet populations have proved to be difficult to census, population estimates for most colonies are rough estimates, and as yet there is no accepted method of monitoring population changes (Sowls et al. 1978, Piatt et al. 1990a). Problems with counting auklets arise because most breeding sites are concealed in inaccessible crevices in talus that may be several meters deep; therefore, populations must be estimated indirectly from the number of birds on the colony surface. Further difficulties result from extreme within-day, daily and seasonal variability of colony attendance.

Attempts to monitor auklet populations have involved counts of birds active on the surface of rocky slopes of breeding colonies (Bédard 1969, Searing 1977, Byrd et al. 1983, Piatt et al. 1990a). These counts are normally timed to coincide with daily peak periods of abundance and replicate counts are normally conducted during the period of breeding season when day-to-day variation in attendance is lowest. The mean of these counts is presumed to be useful for population monitoring. For example, changes in counts of auklets at Kongkok Bay, St. Lawrence Island, in 1964 (Bédard 1969), 1976 (Searing 1977) and 1987 (Piatt et al. 1990a) have been interpreted as possible evidence for a massive population increase (auklet counts increased two-fold over the period). However, there are few data available on inter-annual variability in colony attendance. A key question is whether changes in surface counts from one year to the next, or over longer periods, reflect real changes in auklet populations.

Here I present information on colony attendance of Least Auklets obtained as part of a study of behavioral ecology of the species in the Pribilof Islands, Alaska. Previous studies have in-

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volved counting large numbers of auklets on the surface at many plots. Here I report results of an intensive investigation of colony attendance behavior at a single study plot, utilizing a population of color-marked auklets. The objectives of this study were (1) to document inter-annual variation in colony attendance, (2) to identify factors that influence attendance and ultimately (3) to assess the value of surface counts for monitoring auklet population changes.

METHODS

Colony attendance was monitored at a colony of more than 10,000 Least Auklets near Tolstoi Point, St. Paul Island, Pribilof Islands, Alaska (57°08′N, 170°17′W) during May to August of 1987, 1988 and 1989. At this site, auklets nest among sparsely vegetated beach boulders and talus, and in adjacent cliff crevices. I made counts of auklets visible on the talus ("surface counts") at one densely occupied 10 m × 15 m study plot on a talus slope about 5 m above sea level. This site appeared to be representative of auklet habitat at St. Paul and had similar densities of auklets on the surface to those reported in previous studies (e.g., Piatt et al. 1990a). Auklet counts were made within the boundaries of one study plot between 25 May–1 August 1987, 15 May–9 August 1988, and 8 May–12 August 1989 (Fig. 1) during a four-hour monitoring period timed to include the daily peak of auklet attendance (11:00–18:00 hr Alaska Daylight Saving Time). Surface counts were made regularly during the pre-laying and laying periods, and daily after June 27 in 1987, June 26 in 1988 and June 25 in 1989 until auklet surface activity ceased at the end of the breeding season (Fig. 1). The plot boundaries remained the same throughout the study. The monitoring period was shifted later in the day as the breeding season progressed, to parallel the shift in peak colony attendance. All birds within plot boundaries were counted at least every 30 min and then as frequently as necessary at time of peak attendance to estimate each day's highest number of birds attending at one time. This involved repeated counts every few minutes about the time of peak numbers on the surface. I used single highest counts of adults and sub-adults made each day to estimate day-to-day variability in attendance of each age group. Bédard (1969), Searing (1977) and Piatt et al. (1990a) all used the average of second, third, and fourth highest regular counts of all birds made throughout the daytime activity period to estimate the daily activity peak. Although I never directly compared the results of these two counting methods, my counting technique is likely to compare favorably with auklet counts made in previous studies because it also estimates peak numbers (John Piatt, pers. comm.). In this study, sub-adults (two year old birds) were distinguished by their brown foreheads with restricted nuptial plumes, worn flight feathers and spotted throats (Bédard and Sealy 1984, Jones and Montgomerie, in press further details below).

To monitor activity of individual auklets at the study plot, a color-marked population of a minimum of about 200 regularly attending birds was maintained. With help from field assistants I captured and color-marked 248 auklets (219 adults, 29 sub-adults) in 1987, 369 (306 adults, 63 sub-adults) in 1988, and 145 (all adults) in 1989. To minimize disturbance, banding was restricted to the pre-laying period, banding took place every fourth day, and birds were processed and released as quickly as possible after capture. Capture and handling of these birds did not affect their reproductive performance or likelihood of returning in following years (Jones, unpubl. manuscript). Each auklet was given a numbered USFWS stainless steel band and three Darvik® plastic color bands (see Jones and Montgomerie 1991, in press, for further details).

Chick growth and fledging success were not monitored directly because most Least Auklets nested in inaccessible crevices at Tolstoi, and because disturbance of nesting crevices reduces reproductive success (Roby and Brink 1986a, Piatt et al. 1990b). Consequently, breeding performance and phenology were evaluated by observing chick-provisioning behavior of color-marked birds. Least Auklets have a clutch size of one, and food is delivered to the chick until it fledges 26–31 days after hatching (Roby and Brink 1986a). Starting on the day when the first auklet was seen delivering food, watches at the plot were extended to seven hours daily, encompassing the daytime and evening peaks of food delivery (see Jones and Montgomerie, 1991; in press). Marked auklets that delivered food to chicks on at least two occasions were classified as active breeders, those never seen delivering food were classified as non-breeders. Use of the term "active breeder" implies success at least to hatching. Hatching dates were estimated from date of first appearance of each marked breeding

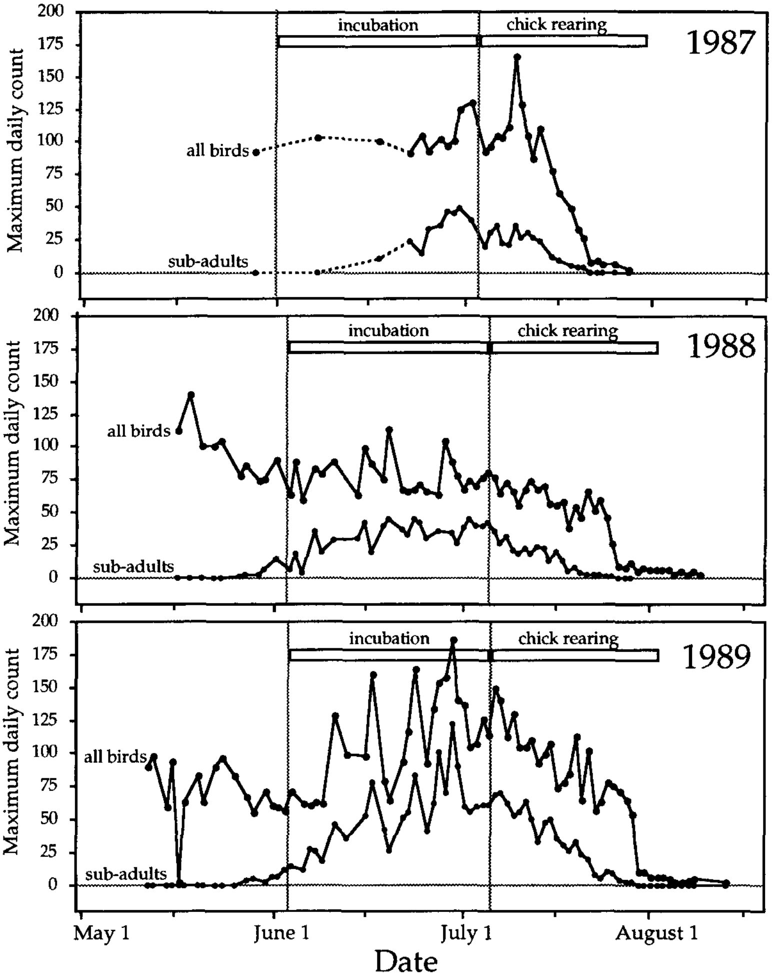

FIGURE 1. Patterns of daily variation in colony attendance of Least Auklets at Tolstoi Point, St. Paul Island, 1987–1989. Daily adult counts may be determined by subtracting the sub-adult count from the count of all birds.

auklet with a food load and fledging success was assumed if a marked bird was observed delivering food for at least 25 consecutive days. The date of the peak of hatching for each year of this study was inferred from the distribution of estimated hatch dates (n = 184 in 1987, n = 131 in 1988, n = 163 in 1989). Each year's peak of laying date was assumed to be 32 days (the mean duration of incubation) prior to the peak hatch date.

RESULTS

COLONY ATTENDANCE

Maximum daily counts of Least Auklets fluctuated day to day and seasonally in each year at the study plot and throughout the colony. In 1988, attendance was highest during laying and prelaying periods, while in 1989 attendance peaked late in the incubation period (Fig. 1). Day-to-day fluctuation in attendance was high in 1989 compared to 1988 (Fig. 1). In contrast with observations of Roby and Brink (1986a) from nearby St. George Island, timing of breeding at Tolstoi Point, St. Paul Island, differed little among years in this study; based on hatching dates estimated for marked active breeders, peak (modal) dates of hatching were: 2 July in 1987, and 4 July in 1988 and 1989.

Before assessing variability in attendance of adults and sub-adults, it is necessary to consider

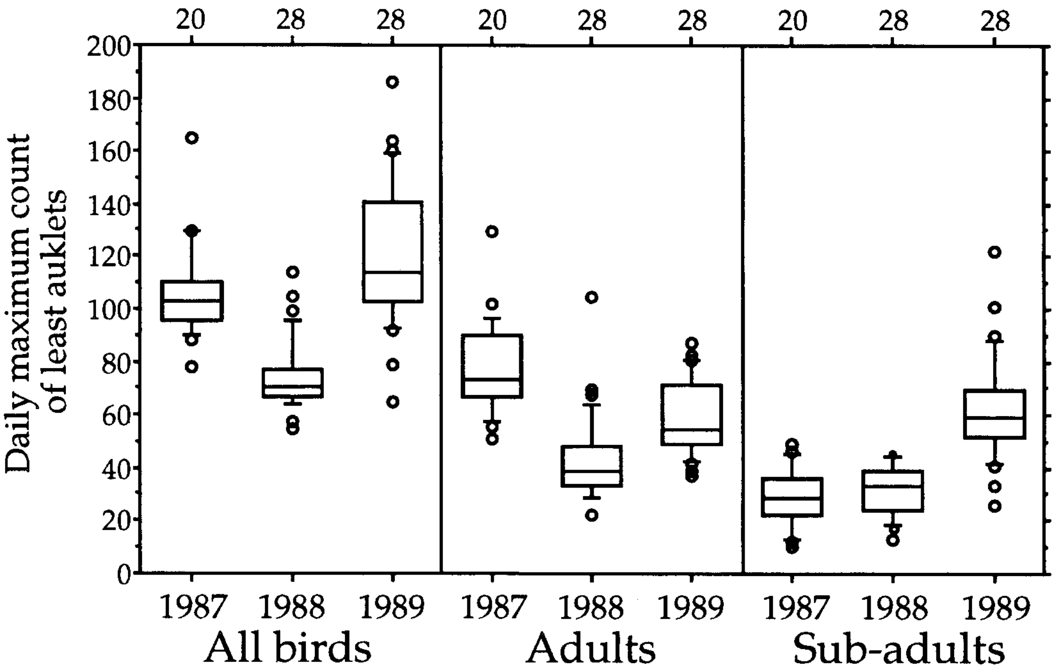

FIGURE 2. Box plots showing colony attendance (1987–1989) of adults, sub-adults and all birds combined. Counts compared for the period June 15 to July 15, when attendance had the lowest day to day variability (see text). The horizontal bars of each box-plot indicate the tenth, twenty-fifth, fiftieth (the median), seventy-fifth and ninetieth percentiles, small circles indicate outliers.

the reliability of their identification in the field. Sub-adults were identified by their brown foreheads with restricted nuptial plumes and worn flight feathers (Bédard and Sealy 1984). About 50% (14 of 29 captured in 1987) of sub-adults also had entirely dark or heavily spotted throats. Adults never showed any of these characteristics, and all color-marked sub-adults that returned in years following banding did so in adult plumage. Adults and sub-adults also differed strikingly in behavior. Sub-adults were socially subordinate to adults (Jones 1990), were not site faithful (Jones, unpubl. manuscript), did not obtain mates or breed, rarely vocalized, and were lighter in mass (by about 7%) than adults (mean adult mass = 85.7 ± 0.32 g, mean sub-adult mass = 79.8 ± 0.61 g; $t = 8.32$, df = 312, $P < 0.0001$). Thus, sub-adults represented a morphologically and socially distinct sub-group of the overall auklet population.

To compare attendance levels among years statistically, I compared (1) daily maximum counts of all birds (combined counts of adults and sub-adults, similar to previous studies), (2) counts of adults only, and (3) counts of sub-adults only. Comparisons of surface counts were made during late incubation to early chick-rearing stage (June 15–July 15, Fig. 1, 2), when attendance may be least variable (Piatt et al. 1990a), and during the pre-laying period, as in previous studies. Daily maximum counts of all birds on the Tolstoi study plot between June 15–July 15 differed significantly among years (Kruskal-Wallis ANOVA, H = 41.6, $P < 0.0001$, df = 2). Maximum daily counts of all birds in 1987 ($\bar{x}$ = 106.3 birds, n = 20 days sampled), 1988 (74.3 birds, n = 28) and 1989 (120.6 birds, n = 28) were significantly different from each other ($P < 0.001$ for each comparison, Fig. 2) using nonparametric multiple comparisons (NPMC, see Zar 1984, p. 199–201).

Maximum counts of adults also differed significantly among years (Kruskal-Wallis ANOVA, H = 34.9, $P < 0.0001$, df = 2, Fig. 2). Maximum daily counts in 1987 ($\bar{x}$ = 77.3 birds, n = 20 days sampled), 1988 (43.4 birds, n = 28) and 1989 (59.0 birds, n = 28) were significantly different from each other (NPMC, $P < 0.001$ for each comparison). Adult attendance during prelaying was used by Bédard (1969), Searing (1977), and Piatt et al. (1990a) to monitor possible population changes. Few sub-adults were present on the colony at this time (Fig. 1). Adult attendance during pre-laying differed significantly between 1988 (mean = 91.4 birds, n = 9 days sampled) and 1989 (mean = 72.4 birds, n = 16 days sampled, Mann-Whitney U, U = 110, P = 0.03). There was no indication that the actual total number of individual adult Least Auklets attending differed among years (Jones, unpubl. manuscript).

Attendance of sub-adults (two-year olds) also differed among years (Fig. 1, 2). Sub-adult attendance between June 15–July 15 differed significantly among years (Kruskal-Wallis ANOVA, H = 42.4, P < 0.0001, df = 2, Fig. 2). Maximum daily counts in 1987 (mean = 19.1 birds, n = 20 days sampled) and 1988 (32.0 birds, n = 28) were significantly different from counts in 1989 (61.6 birds, n = 28, NPMC, P < 0.001 for each comparison), but 1987 and 1988 were not significantly different (NPMC, P > 0.05). There was also a significant difference comparing the highest 20 daily counts of sub-adults made in each year (Kruskal-Wallis ANOVA, H = 42.0, P < 0.0001, df = 2). At their period of peak attendance (in late June, just before peak of hatching), two-year olds comprised about half the birds on the colony surface (Fig. 1).

Based on observations of color-marked breeding and non-breeding birds and of the sub-adult population, it was possible to estimate their relative contributions to surface counts through the breeding season. Before peak of laying, surface counts consisted entirely of adult breeders. About the time of peak of laying there was an influx of non-breeding adults and sub-adults. Breeding pairs courted on the surface each day until laying, but were never observed together on surface during incubation. Surface activity of breeders dropped drastically as incubation commenced, while surface counts remained the same or increased due to an influx of non-breeders. During incubation and chick-rearing periods, about half the adults on the plot surface were breeders, the other half non-breeding prospectors.

In each year, I estimated the ratio of marked birds delivering food to unmarked birds delivering food to be about 60% and used this figure to estimate the total number of auklets breeding on the study plot. The population of breeding Least Auklets (including unmarked birds) on plot was probably about 340 birds in 1987, 200 in 1988 and 300 in 1989. These numbers are approximations because unmarked birds delivering food to chicks were difficult to count. However, maximum surface counts represented at most about half the number of birds breeding on plot and the number of *pairs* breeding on the study plot normally exceeded highest daily maximum counts of all *individuals* on the surface.

REPRODUCTIVE PERFORMANCE AND SURVIVAL

Overall, surface counts were highest in the best year for reproduction (1989) and lowest in the worst year (1988). The 1988 breeding season was a poor year for reproduction compared to other years of study. In 1988, 59% (138/236) of adult birds regularly attending the plot were classified as active breeders, whereas a significantly higher proportion were classified as active breeders in both 1987 (72%, 174/242; log-likelihood ratio test, $G^2 = 9.54$, $P < 0.002$), and 1989 (84%, 151/180; $G^2 = 32.6$, $P < 0.0001$). A smaller proportion of birds bred in 1988 than 1989 ($G^2 = 8.6$, $P > 0.004$). Among those birds that did reach the chick-rearing stage, fledging success was lowest in 1988 (70/138, 51% success) compared to 1987 (99/174, 57% success) and 1989 (94/151, 62% success), but these differences were not statistically significant ($\chi^2 = 3.91$, df = 2, $P = 0.15$).

It was impossible to determine the total number of auklets using the study plot in each year. However, observations of marked and unmarked auklets were consistent with a stable population. For example, based on re-sightings of color-marked birds, annual adult survival remained the same, at about 0.80 for breeding birds and 0.75 for all adults, over both 1987–1988 and 1988–1989 (Jones, unpubl. manuscript). Although my estimate of the number of breeding pairs dropped considerably between 1987 and 1988, most pairs in 1987 survived and returned in 1988 (of 172 active breeders in 1987, 128 survived [74.4%], but only 83 [64.8%] of the survivors bred in 1988).

To assess whether a change in adult attendance behavior could explain the change in attendance among years, I examined the attendance of a sample of 79 individual adults that bred successfully in both 1988 and 1989. Attendance of these individuals during the incubation stage increased by about 10% between 1988 (when overall attendance was low) and 1989 (when overall attendance was higher). Based on paired comparisons of attendance on the same dates in 1988 and 1989, this increase was statistically significant (Wilcoxon signed rank test, $Z = 2.31$, $P = 0.02$)—increased adult surface counts resulted from a higher frequency of attendance within the same pool of adults.

DISCUSSION

For monitoring purposes, a censusing method that accurately measures population size is required. Thus, to evaluate the usefulness of surface counts for auklet population monitoring, we need to know relative contribution of changes in population size, and changes in population behavior, to inter-annual variation in counts. The results of this study suggest that at the Tolstoi plot, variation in Least Auklet colony attendance among years could relate as much to changes in behavior as to changes in population size, because both the seasonal pattern of attendance and number of birds on the surface varied greatly among years while adult survival, and possibly the total number of adults present, remained fairly constant.

Inter-year changes in attendance behavior related to food supply may result in variation in counts of auks at colonies, without any change in local population size (Gaston and Nettleship 1982, Hatch and Hatch 1989). In auklets, this potential is magnified because unlike murres, which remain in plain sight on their cliff ledges, most breeding auklets are normally invisible and uncountable within their nesting crevices when not foraging out at sea. At least one member of each pair of murres is present and countable at the nest-site through the breeding season, reducing day-to-day, seasonal and inter-year variability in counts. Auklet surface counts reflect the highly variable, and perhaps unpredictable, loitering of off-duty breeders and non-breeders on the colony surface. Variable food availability among breeding seasons may explain why auklets vary in reproductive performance, and have more or less time available for activity on the surface, resulting in variable colony attendance (i.e., surface counts). For example, in 1988, a relatively poor year for reproduction, colony attendance at Tolstoi was lowest, while in 1987, a good year for reproduction, colony attendance was relatively high. Adult body mass and body condition also varied over the three years of study (Jones and Montgomerie, in press), reflecting good and bad years. Colony attendance of Least Auklets is likely to vary with oceanographic conditions, which may cause Bering Sea zooplankton to vary in abundance or availability to seabirds from year to year (Springer and Roseneau 1985).

Surface counts of auklets at Kongkok Bay, St. Lawrence Island, made during the pre-laying state of three breeding seasons, 1964 (Bédard 1969), 1976 (Searing 1977) and 1987 (Piatt et al. 1990a) showed auklet numbers on the surface varying about two-fold between highest and lowest years. These observations are consistent with a doubling of the auklet population there. However, because of effects of inter-annual variation in attendance behavior, the actual change in population may be difficult to ascertain (Piatt et al. 1990a). There was considerable fluctuation among 1987, 1988 and 1989 counts made at Tolstoi during late incubation and chick-rearing, the most stable period of attendance (1.6-fold for all birds, 1.8-fold for adults, and 2.1-fold for subadults). Similarly, counts of adults made during pre-laying at St. Paul also varied significantly between years. Furthermore, the pattern of attendance differed significantly between years, suggesting that counts made in one season only have limited value. If behavior of the auklet population at the Tolstoi study plot is typical, then it is possible that variation in surface counts at St. Lawrence Island resulted from annual fluctuation in colony attendance, rather than a full two-fold population increase. Furthermore, differences in timing of breeding among years could also account for changes in surface counts made on the same dates in different years. While surface counts would indicate population crashes or reproductive failure, they are not likely to provide precise information about small changes in population status, and thus must be interpreted with extreme caution. For similar reasons, measures of surface activity (calls and numbers of birds present) at Ancient Murrelet (*Synthliboramphus antiquus*) colonies have proved to be of limited use for population monitoring (Jones et al. 1989).

Clearly, an auklet population monitoring technique that minimizes the effect of annual variation in colony attendance is required. Surface counts are indispensable because they have the advantage of being simple to perform, can cover a large number of birds on replicate plots throughout a large colony and could provide evidence for drastic changes in population size. This technique could be improved upon by making surface counts during pre-laying, when sub-adults are absent and most birds on the surface are likely to be breeders, or by identifying sub-adults and counting them separately after peak of laying. Sub-adults contributed greatly to total surface counts made at Tolstoi Point and their numbers fluctuated from year to year, influencing the changing pattern of colony attendance among years. For example, including sub-adults, attendance was highest in 1989, but excluding these birds, 1987 was the year with greatest attendance. Although it was not possible to test whether inter-annual variation in sub-adult colony attendance resulted mostly from strength of this cohort (i.e., total number of two-year olds alive), or alternatively from variation in behavior, anecdotal evidence lends support to the former possibility: highest counts of two-year olds (in 1989) occurred two years after the best year for breeding (1987). Thus, separate counts of sub-adults could be useful for population monitoring by providing an index of past reproductive performance, and current recruitment of two-year olds into the population.

The status of an alcid population depends partly on the survival of adults and their reproductive success. Ideally, monitoring of alcid populations would include regular measurement of these parameters (Evans and Nettleship 1985). Long-term observation of color-marked populations of auklets with diurnal colony attendance (e.g., Least or Crested Auklets *Aethia cristatella*), could be used to monitor survival and reproductive performance. Least Auklets are site faithful, so survival can be estimated from re-sighting individually color-banded birds from year to year (Jones, unpubl. manuscript). With marked populations of about 200 birds as in this study, which are not difficult to establish, differences in annual adult survival of 13% are statistically detectable (see Zar 1984, p. 399 for estimating required sample sizes). To properly monitor a large colony, replicate plots with color-marked birds would be required, because within-colony variation in reproductive parameters is frequently observed in auks (e.g., Gaston et al. 1983). Information on reproductive performance, such as proportion of adults breeding, fledging success, and phenology, could be obtained by observation of marked birds carrying food to chicks (Jones and Montgomerie, in press). This would allow reproductive performance to be monitored without time-consuming examination of nesting crevices, which may give biased estimates of reproductive success due to disturbance (Piatt et al. 1990b). An initial effort to establish marked population(s) would be required in the first year of such a program. Afterwards, researchers would need only return for a few weeks each summer to re-sight survivors, monitor performance of active breeders and band new birds to maintain marked populations.

Another potentially useful method of monitoring auklet populations involves documenting extent of occupied habitat at colonies, then rechecking in later years to assess changes in area occupied. This technique would appear to be insensitive to inter-year changes in attendance, but could be used to assess long-term changes in populations. For example, Roby and Brink (1986b) provided convincing evidence that the Least Auklet colony at Ulakaia Hill, St. George Island, has decreased in size due to encroachment of vegetation.

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