

FACTORS AFFECTING SURVIVAL OF ADULT LEAST AUKLETS (*AETHIA PUSILLA*) AT ST. PAUL ISLAND, ALASKA

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ABSTRACT.—Survival of Least Auklets (*Aethia pusilla*) was investigated at St. Paul Island, Pribilof Islands, Alaska, during three breeding seasons (1987–1989). Based on resightings of color-marked birds, an overall annual adult survival rate of about 0.75 was observed. Because of their fidelity to nesting and display sites, as well as their insensitivity to capture early in the breeding season, this estimate was unlikely to be substantially biased by emigration from the study plot or disturbance caused by handling. An index of adult body condition was highly variable during the 1988 breeding season, but was weakly correlated with subsequent survival. However, the body-condition index was significantly correlated to likelihood of breeding in the same and following years. Survival was not related to adults' variable plumage, although lightness of plumage correlated with age and dominance and functions for status signalling in this species. Survival was significantly lowered in individuals with damage to their webbed feet. Subadults (two-year-olds) showed low site fidelity compared to adults. Age of first breeding was at three years. During the breeding season, known causes of mortality included predation by foxes, gulls, and humans. The low annual survival of Least Auklets relative to other alcids, together with large year-to-year variation in reproductive performance, suggests there is greater potential for population fluctuations in this species. Survival estimation may be a partial solution to the difficulty of monitoring alcid populations directly. Received 22 April 1992, accepted 12 February 1992.

ANNUAL survival rate is a critical population parameter for theoretical investigations of avian life histories, as well as conservation of wildlife populations. Survival rate estimates will be required for a full understanding of life-history strategies of various seabird species. Furthermore, survival rates may be used to assess vulnerability of seabird populations to human and other sources of mortality, as well as for long-term monitoring of population status. However, there are few estimates of survival rates for Pacific alcids (Croxall and Gaston 1988).

The Least Auklet (*Aethia pusilla*) is the smallest member of the family Alcidae and one of the most abundant North Pacific seabirds (Sowls et al. 1978). The species is monogamous with a clutch size of one, and the chick is fed by both parents at the nesting crevice until nearly adult size. Least Auklets have both a high rate of chick development and fledging mass (Roby and Brink 1986a). There have been a number of studies of Least Auklet breeding biology (Bédard 1969, Knudtson and Byrd 1982, Byrd et al. 1983, Roby and Brink 1986a, Piatt et al. 1990a,

b), but none has attempted to estimate survival parameters. Furthermore, there is no accepted method of estimating the size of Least Auklet breeding populations or monitoring population trends (Piatt et al. 1990a, Jones 1992).

Here I present information on survival of Least Auklets obtained as part of a detailed study of behavioral ecology of the species in the Pribilof Islands, Alaska. My objectives were: (1) to estimate the annual survival rate of Least Auklets at St. Paul Island, Alaska; (2) to identify factors that influence adult survival; and (3) to examine the feasibility of long-term monitoring of auklet survival rates for conservation and management purposes.

METHODS

Field work was conducted 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 through August of 1987, 1988, and 1989. Auklets nested along a strip of habitat about 10 m wide, consisting of sparsely vegetated boulders and talus just above sea level along several kilometers of shoreline. All banding and most observations were made at one densely occupied 10 m × 15 m study plot on this talus.

With help from field assistants, I captured and color marked 263 Least Auklets (234 adults, 29 subadults)

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in 1987, 369 (306 adults, 63 subadults) in 1988, and 145 (all adults) in 1989 using mist nets and noose carpets (totals include recaptures). To minimize disturbance, birds were banded, measured and released as quickly as possible after capture; banding was restricted to every fourth day during the prelaying period. Subadults (two years old) were distinguished by their worn forehead and flight feathers and spotted throats (Bédard and Sealy 1984). Each auklet was given a numbered U.S. Fish and Wildlife Service stainless-steel band and a unique combination of three Darvik plastic color bands. Upon capture, auklets were weighed to the nearest 1 g using a Pesola spring scale, and tarsus length was measured to the nearest 0.1 mm using calipers.

Damage to foot webbing, consisting of holes or tears (always fully healed and appearing to be a result of past injuries or disease), was recorded for each bird captured in 1987 and 1988. The condition of each birds' webbing was scored as: (0) webs between toes completely intact; (1) small holes or a minor (<1 cm) tear in webbing of one foot; or (2) major tears or large holes (>1 cm) in webbing of both feet. Later, I examined the relation between web damage and subsequent survival. Ventral plumage coloration varies greatly in Least Auklets, so each marked auklet was classified into one of four plumage categories (white, lightly flecked, intermediate, or heavily flecked; see Jones 1990). I checked for a relationship between plumage and survival.

Since sexual dimorphism is slight in Least Auklets (Bédard and Sealy 1984, Jones and Montgomerie 1992), captured birds could not be sexed with certainty from external measurements. However, I identified a large sample of males by watching for vocal advertising displays (restricted to males; Jones 1992). Female members of mated pairs were identified by association with males. Mated pairs were identified by repeated association and courtship behavior prior to laying (Jones and Montgomerie 1991). To monitor attendance of marked birds and observe their behavior, 4-h watches covering the time of peak auklet activity (1100–1500 Alaska Standard Time) were conducted daily from mid-May to early August. Peak auklet activity occurred later in the day at St. Paul compared to either St. George Island (Roby and Brink 1986a) or St. Lawrence Island (Piatt et al. 1990a). Birds observed delivering food to chicks on at least two occasions were classified as breeders; those that were never seen delivering food were classified as non-breeders. Use of the term breeder implies success at least to hatching of the chick. Reproductive performance of marked auklets was quantified by monitoring chick provisioning during daily 7-h watches at the study plot throughout the chick-provisioning period, timed to coincide with most food deliveries (Jones and Montgomerie 1992). To minimize disturbance, all observations were made from a blind set near the study plot.

An index of body condition was obtained for many birds using measures of body mass corrected for variation in body size. Mass measurements were obtained during prelaying and incubation periods when birds' mass was relatively constant (breeding Least Auklets lose mass after hatching; Jones unpubl. data). Mass was measured at capture and by repeated weighings of marked birds using four electronic balances (Ohaus D 1000 LA, accurate to ± 1 g) placed on the study plot. Variation in both mass and tarsus length within individuals was less than variation between individuals because repeatability of mass ($r_t = 0.50 \pm \text{SE of } 0.05$, $F_{109,413} = 5.61$, $P < 0.0001$) and tarsus ($r_t = 0.73 \pm 0.05$, $F_{74,75} = 6.27$, $P < 0.0001$) were significant and greater than zero (see Zar 1984:323–325). The repeatability of tarsus length, based on measures of 75 individuals in both 1988 and 1989, suggests that this measure could provide a reliable indication of body size. I regressed mean mass on tarsus length and used the residuals (the difference between actual mean mass of each bird and predicted mean mass of a bird of its tarsus length) as the condition index (for further details, see Andersson 1989, Jones and Montgomerie 1992).

Survival was evaluated by resighting color-marked birds at the colony in years following banding. Daily watches during prelaying, laying, incubation, chick rearing and chick departure periods (mid-May to early August) were conducted to identify marked birds that bred, or were in regular attendance on the study plot in each year of the study (plot residents). Birds that did not appear in one season, but had been in regular attendance or breeding on the study plot in the previous year, were classified as having disappeared. These individuals must either have died or moved from the study plot to another part of the colony. To see if disappearances resulted from birds moving off the study plot, I looked for banded birds during daily walks along most of the length of the Tolstoi Point colony throughout the study. To make further checks for marked birds, I searched for color-marked Least Auklets throughout colonies at Tolstoi Point, Village Cove (1 km distant) and Zapadni Point (4 km distant) at least three times each breeding season. Additional checks of the colony 100 m on either side of the study plot were made from the blind. Further evaluation of breeding-site and display-territory fidelity was made by comparing the exact locations of nesting crevices and display areas of color-marked birds among years from plot photographs.

Wear of both plastic and stainless-steel bands was observed, but this led to few band losses. Of the total of 480 individuals color marked, 14 lost one of their three color bands during the study period, but all were still identifiable, and 9 of these were recaptured and the missing band replaced. Band wear of birds originally marked in 1987 probably led to significant losses of color bands by 1990 (Art SOWLS, pers. comm.), but resightings from that year were not included in (or available for) this analysis of survival.

TABLE 1. Survival of Least Auklets at Tolstoi Point, St. Paul Island.^a

	Breeding season		
	1987	1988	1989
Banded resident population	208	233	209
Breeding adults	172	125	155
Nonbreeding adults	36	108	54
Adults surviving to following season	152 (73%)	177 (75%)	—
Breeding adults surviving to following season	128 (74%)	104 (83%)	—
Nonbreeding adults surviving to following season	22 (61%)	70 (64%)	—
Surviving breeders that bred again in following year	83	84	—

^a Annual survival rate given in parentheses.

I used unpaired two-tailed *t*-tests to assess differences in body condition between auklets that survived and disappeared. Log-likelihood ratio tests (see Zar 1984:52) were used to compare survival frequency data between the sexes, between breeders and nonbreeders, and between captured and uncaptured auklets in 1988 and 1989. To further assess investigator disturbance effects of capture and handling, reproductive performance measures of captured and uncaptured auklets were compared with Mann-Whitney *U*-tests. Throughout this paper, two-year ranges (e.g. 1987–1988) refer to overwinter survival, while references to a single year (e.g. 1988) refer to a particular breeding season.

RESULTS

Estimation of survival rate.—Minimum annual survival of adult Least Auklets was close to 75% in each year, the first estimate for this species (Table 1). At St. Paul, fewer nonbreeding auklets survived than breeding birds in both years, but these differences were not significant (1987–1988, $G = 0.45$, $df = 1$, $P = 0.6$; 1988–1989, $G = 1.52$, $df = 1$, $P = 0.2$; Table 1). Similarly, there was no evidence of a relationship between survival rate and sex. Over 1987–1988, survival of a sample of known-sex males was 86% (56/65) and female survival was 90% (43/48; $G = 0.30$, $df = 1$, $P = 0.8$). Over 1988–1989, male survival was 86% (43/50) and female survival 95% (38/40; $G = 2.14$, $df = 1$, $P = 0.2$).

The proportion of adults classified as breeders differed significantly among years. The 1988 breeding season was poor for reproduction, with a smaller proportion of adults attempting to breed; 54% (125/233) of marked adults bred in 1988, compared to 83% (172/208) in 1987 and 74% (155/209) in 1989 (overall $X^2 = 8.77$, $df = 2$, $P = 0.01$).

Careful checks at Tolstoi Point revealed that of the adults resident on the plot in one year none were found elsewhere in subsequent years.

Site fidelity of both breeders and nonbreeders was high. For example, among 83 birds that bred in 1987 and returned to breed again in 1988, none moved to a nesting crevice more than a meter away. Most appeared to use the same crevice entrance from year to year. No resident birds moved to a nesting site outside the boundaries of the study plot between years, although the plot was small and densely occupied by marked breeding birds; this was true even when erosion by winter-storm waves altered the nesting habitat. Similarly, nonbreeding adult residents were faithful to a small area occupied year after year. Each year a number of adults, presumably prospectors, were not resighted on the plot after capture and color marking: 12 (5.1% of birds captured) in 1987; 73 (23.8% of adults captured) in 1988; 6 (4.1% of birds captured) in 1989. This proportion differed significantly among years ($X^2 = 39.6$, $df = 2$, $P < 0.0001$), possibly an artifact of the extra capture effort in 1988. Intensive efforts in 1988 using mist nets were likely to have captured a higher proportion of adult prospectors. Non-resident birds were excluded from further analysis because either mortality or emigration could explain their disappearance; therefore, my survival estimates include only resident adult breeders and nonbreeders. Subadults (two-year-old nonbreeders) showed little site fidelity, and most were not seen again on the study plot after banding. For example, 4 of 29 subadults banded in 1987 became plot residents and only 4 of 63 subadults banded in 1988 were later seen regularly. During the three years of this study, five birds banded as subadults were later observed on parts of the colony as far as 1 km from the study plot. Three of the total of four marked subadults resident on the plot in 1988 returned in 1989, and two of these three-year-olds bred, suggesting that first breeding in Least Auklets occurs at three years of age. The third three-

TABLE 2. Number and percent of adult Least Auklets (1987–1989) of different plumage categories that survived to subsequent season.

Years	Fate	Plumage category ^a			
		White	Lightly flecked	Intermediate	Heavily flecked
1987–1988	Survived	8 (67%)	30 (91%)	68 (71%)	26 (65%)
	Disappeared	4 (33%)	3 (9%)	28 (29%)	14 (35%)
1988–1989	Survived	16 (80%)	33 (81%)	79 (78%)	26 (65%)
	Disappeared	4 (20%)	8 (19%)	22 (22%)	14 (35%)

^a See Jones (1990) for further explanation of how plumage categories were scored.

year-old that returned remained as a nonbreeder. In 1987, several two-year-olds were observed at the study plot with throat pouches full of food, but none obtained mates or bred. Nearly all subadults arrived at the colony for the first time well after the peak of laying (Jones 1992). Because of their low site fidelity, it was not possible to estimate subadult survival quantitatively. However, anecdotal evidence suggests that immature and subadult auklets may have a survival rate as high or higher than adults. The number of breeders on the plot in 1987 was about 170 pairs (Jones 1992), which produced an estimated 130 fledglings. Two years later in 1989, up to 125 two-year-olds attended the study plot simultaneously (50% of auklets present; Jones 1992). This proportion of subadults attending seemed to hold for all parts of the colony. The presence of these remarkably large numbers of two-year-old subadults on the colony can only be explained by a high survival rate between fledging and two years of age.

To evaluate possible disturbance effects, I investigated the relationship between capture and handling of birds and their likelihood of breeding later the same season and returning to the study plot the following season. In 1988, 50 birds that were color marked in the previous year bred on the study plot, but were not captured (i.e. not disturbed), and another 173 breeders were captured in the prelaying period (disturbed). Capture and handling had no detectable effect on survival or on the likelihood of returning the following season: among undisturbed birds 43 of 50 (86%) returned the next year; among disturbed (i.e. captured) birds 138 of 173 (79.8%) returned ($G = 1.53$, $df = 1$, $P = 0.2$). Auklets captured in 1988 were not significantly less likely to breed in 1989 than the undisturbed sample: among disturbed birds 92 of 138 (66.7%) bred; among undisturbed birds 33 of 43 (76.7%) bred ($G = 1.63$, $df = 1$, $P = 0.3$). Similarly, disturbance caused by capturing

and handling birds had no detectable effect on timing of breeding, chick provisioning rate or reproductive success (for further details on measures of reproductive effort and success, see Jones and Montgomerie 1992). For example, the mean hatch date did not differ between captured and uncaptured auklets in 1988 (Mann-Whitney U , $Z = 1.3$, $n = 129$, $P = 0.2$) or 1989 ($Z = 0.4$, $n = 141$, $P = 0.7$). In addition, capture had no detectable effect on chick provisioning rate in 1988 (Mann-Whitney U , $Z = 0.4$, $n = 128$, $P = 0.7$) or 1989 ($Z = 0.9$, $n = 141$, $P = 0.4$), nor on reproductive success later the same season as measured by chick feeding interval (Mann-Whitney U : 1988, $Z = 1.9$, $n = 129$, $P = 0.1$; 1989, $Z = 1.4$, $n = 144$, $P = 0.3$).

Factors affecting survival.—In 1988, the mean body-condition index of Least Auklet survivors was somewhat greater than that of birds that failed to return the following year, but this difference was not significant (survivors' body condition = $1.86 \pm SE$ of 0.41 g; disappeared birds' condition = 0.63 ± 0.70 g; $t = 1.48$, $df = 159$, $P = 0.07$; Fig. 1A). However, among birds that did return, mean body condition was significantly greater in 1988 among auklets that bred in the following year (breeder body condition = 2.30 ± 0.51 g; nonbreeder body condition = 0.83 ± 0.48 g; $t = 2.10$, $df = 159$, $P = 0.02$; Fig. 1B).

The variable ventral plumage color of Least Auklets is correlated with reproductive performance and dominance status, and lightens with age (Jones 1990). However, there was little evidence that plumage variation correlated with survival (1987–1988, $X^2 = 7.13$, $df = 3$, $P = 0.07$; 1988–1989, $X^2 = 0.87$, $df = 3$, $P = 0.83$; Table 2). There may be a weak trend towards darker-plumaged (i.e. heavily flecked plumage) birds having lower survival, but this was not statistically significant.

In both years, fewer Least Auklets with damaged webs survived than did birds with un-

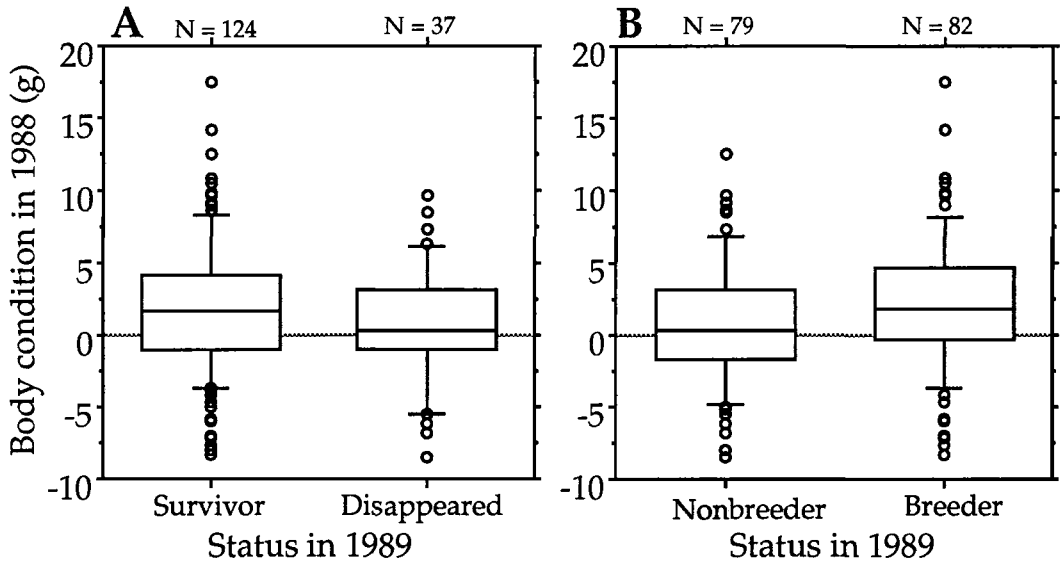


Fig. 1. Box plots showing: (A) body condition during 1988 breeding season of birds that survived to 1989 breeding season and of those that disappeared; (B) body condition during 1988 breeding season of surviving birds that subsequently bred during 1989 breeding season compared to those that returned as nonbreeders. Horizontal lines indicate 5th percentile, 25th percentile, median, 75th percentile and 95th percentiles; open circles represent outliers.

damaged webs (1987–1988, $X^2 = 6.35$, $df = 1$, $P = 0.01$; 1988–1989, $X^2 = 9.51$, $df = 1$, $P < 0.01$; Table 3). This effect was remarkably consistent among years. Birds with severely damaged webs had lower survival than birds with minor damage, but the sample of birds with severe web damage was small and the difference among these groups was not significant (Table 3). Web damage occurred at a low rate (4 of 65 [6.2%] adults examined in 1987 had additional damage in 1988), but there were few clues as to how auklets incur web damage. Some auklet chicks had similar damage to their feet, so injuries may occur in nesting crevices. Web damage may also result from bumblefoot, a condition that can result from the septic conditions in the nesting crevice (D. D. Roby, pers. comm.). The mean body-condition index during the breeding sea-

son was not correlated with web damage (undamaged condition = -0.05 g, $n = 249$; slightly damaged condition = 0.21 g, $n = 14$; extensively damaged condition = -0.24 g, $n = 6$; ANOVA, $F = 0.02_{2,226}$, $P = 0.98$), but the sample size of web-damaged auklets of known condition was small; thus, this test has very low power.

Arctic foxes (*Alopex lagopus*) were abundant at St. Paul Island at the time of this study and were a predator of adults, eggs, and chicks at the study plot. Foxes may be the single largest source of auklet mortality at St. Paul Island and nearby St. George Island (Roby and Brink 1986b). Predation by Glaucous-winged Gulls (*Larus glaucescens*) occurred at St. Paul, but this species rarely breeds in the Pribilofs and few individuals specialized in capturing auklets. Least Auklet remains were found in stomachs of halibut

TABLE 3. Number and percent of Least Auklets (1987–1989) with different degrees of web damage that survived to subsequent year.

Years	Fate	Condition of webbing between toes		
		Undamaged	Slight damage	Extensive damage
1987–1988	Survived	110 (80%)	11 (58%)	2 (40%)
	Disappeared	27 (20%)	8 (42%)	3 (60%)
1988–1989	Survived	115 (80%)	7 (58%)	1 (25%)
	Disappeared	28 (20%)	5 (42%)	3 (75%)

(*Hippoglossus stenolepis*) at a fish-processing plant at nearby St. George Island (Vernon Byrd, pers. comm.). Hunting of Least Auklets by Aleuts occurs at several breeding sites close to roads at St. Paul Island, but no auklets were taken at my study plot, so this source of mortality probably did not affect my survival estimates. During the 1988 breeding season, many birds returned to the colony with their plumage fouled by oily waste discharged from fish-processing vessels anchored off St. Paul Island. This may have caused some mortality, but no disappearance of a marked auklet was attributable to this fouling.

DISCUSSION

My survival-rate estimates for Least Auklets were derived from resightings of color-marked birds, so they must be evaluated in light of various biases that are known to influence estimates of survival rates (Hudson 1985). Marked auklets were presumed to have died if they were resident on the study plot in one year and did not return the following year. This method would underestimate natural survival rate if any birds emigrated from the plot, either naturally or due to investigator disturbance (Hudson 1985). This is a confounding factor in all methods of survivorship estimation (Clobert and Lebreton 1991). Because of the large population of auklets at St. Paul, I cannot eliminate the possibility that a small proportion of banded birds that disappeared were actually alive and attending some remote part of the colony, or remained at sea through the breeding season. However, because color-marked breeding and nonbreeding adults were highly faithful to their nesting and display sites, and because no plot residents categorized as having disappeared were found elsewhere during extensive checks of the colony, I believe emigration was unlikely to have significantly biased the survival estimate. Roby and Brink (1986a) recorded similarly high nest-site fidelity of Least Auklets at St. George Island. The low subadult site fidelity in Least Auklets follows a trend among other alcids (i.e. where site fidelity is extremely high among adults, but low among young birds; Hudson 1985).

Disturbance associated with capture and banding of the study population appeared to have a negligible effect on Least Auklet behavior and on rates of return and survival. Direct disturbance of nesting crevices does have a sig-

nificant impact on breeding success and probably other behavior of auklets and other cavity-nesting seabirds (Roby and Brink 1986a, Piatt et al. 1990b, Gaston et al. 1988). However, this was not a factor in the present study because nesting crevices were left entirely undisturbed. Ancient Murrelets (*Synthliboramphus antiquus*) are very sensitive to disturbance, probably even to capture and handling away from their burrow (Gaston 1990). This did not appear to be the case with Least Auklets. Band wear occurred but resulted in few band losses and, thus, could not have biased survival estimates during the short duration of this study. However, alternative color-band material will have to be used for long-term studies of Alaskan auklets because of the highly abrasive volcanic talus at many nesting colonies.

If my estimate of survival rate is representative of Least Auklet populations generally, the species may have lower adult survival than all other alcids except Ancient Murrelets. Gaston (1990) calculated that annual survival of breeding adult Ancient Murrelets averaged about 0.77. Ancient Murrelet body size (mean mass about 200 g) is more than double that of Least Auklet, so their apparently similar survival rate is noteworthy. Mean annual survival for breeding Least Auklets at St. Paul was similar at 0.79. Inclusion of all adult Least Auklets in the analysis yielded a mean survival rate of 0.75. One year of Least Auklet survival data from Buldir Island in the Aleutian Islands (52°21'N, 175°56'E) indicated a similar survival rate of 77% (unpubl. data). Additional estimates of Least Auklet survival from other parts of their range such as St. Lawrence Island, where there are larger colonies with different predators, will be required before any generalizations about their demography can be made. Furthermore, it will be useful to investigate the degree of interyear fluctuation in adult survival in a longer-term study. With a population of about 25,000 (pers. observ.), the Least Auklet colony at St. Paul Island is small relative to that at nearby St. George, and to other Alaskan colonies. Only further work on survival at other colonies will reveal whether the St. Paul population of 1987-1989 is typical.

Survival data have been collected for two other auklet species. The Cassin's Auklet (*Ptychoramphus aleuticus*) had adult survival rates of 0.83 in California (Speich and Manuwal 1974) and 0.86 in British Columbia (Gaston, unpubl. data). The survival rate of Crested Auklets (*Aethia cris-*

tatella) was 0.86 at Buldir Island, Alaska (one year of monitoring; unpubl. data). Large alcids such as murres (*Uria* spp.), Razorbill (*Alca torda*) and puffins (*Fratercula* spp.), like most other seabirds, have survival rates of 0.87 to 0.96 (Hudson 1985, Croxall and Gaston 1988, Hatchwell and Birkhead 1991). Given their single-egg clutch, the low survival rate of Least Auklets relative to most other alcids must be compensated for by relatively high reproductive success, an earlier age of first breeding, and/or high recruitment. Breeding-success estimates for Least Auklets have varied between 50 and 72% (Roby and Brink 1986a, Piatt et al. 1990b), similar to other alcids. However, Least Auklets, with some individuals breeding at three years of age, breed early compared to most other alcids (Hudson 1985). Furthermore, there is evidence that recruitment rate may be unusually high as well, because survival from fledging to two years of age seems to be high. Overall, these data suggest that with low adult survival and a clutch of but one egg, Least Auklet populations may be vulnerable to additional adult mortality or breeding failure.

The low survival rate of breeding Least Auklets may result partly from their small body size and diurnal colony attendance, which may make them vulnerable to predators. Foxes were a major source of auklet mortality at St. Paul. This contrasts with some Aleutian Island breeding sites, where foxes are absent, and St. Lawrence Island, where few foxes are present (Roby and Brink 1986a). Overall, human predation takes place at such a low level in the Pribilofs that its impact on the overall auklet population is probably negligible. Marine pollution represents a significant threat to auklet populations, particularly in the Pribilofs where large numbers of fish-processing vessels operate close to shore. Causes of mortality outside the breeding season remain unknown.

My index of Least Auklet body condition during one breeding season did not significantly correlate with survival to the following year, although it was significantly correlated with likelihood of breeding the following year. This finding is somewhat surprising, because in general a relationship between body condition and survival would be expected. However, body condition in autumn and winter, when plankton populations are low and weather conditions are harsh, is likely to be most crucial to survival. Measures of body condition in May and June

may weakly correlate with subsequent survival because considerable seasonal changes in mass and, consequently, body condition occur by the end of the breeding season, and these changes vary according to breeding status (unpubl. data). I also found little indication that plumage-color differences, which relate to age and differences in social status (Jones 1990), were related to survival. This finding would be surprising if plumage status signals were used in competition for food. However, status signalling by plumage is presumably used only on the colony, probably in competition for nest sites and mates (Jones 1990).

Reduced survival of Least Auklets with small injuries to their feet indicates the degree to which defects may determine individuals' fitness. This effect could have been due to reduced foraging success of individuals with damaged feet. Alcids use their feet as rudders when pursuing prey underwater, so web defects could reduce underwater maneuverability and ultimately foraging success. If this is true, the lack of a relationship between web and body condition in May and June suggests that when food is abundant the effect of web damage is not important (some auklets with damaged webs were able to breed successfully). Mortality due to web damage may be more likely to occur in winter, when conditions are harsher. Web defects may have a particularly significant effect on fitness in Least Auklets because of their high buoyancy and poor diving ability compared to other alcids (Haney 1991). An alternative explanation for the effect of web damage is that it indicates past disease, and is present in weakened individuals that are more likely to die. The penalty correlated with web defects also raises the question of whether bands could have a similar effect, by increasing underwater drag. This could not be assessed in this study because it was impossible to monitor survival of unbanded individuals.

Because of many statistical and logistical difficulties inherent in attempts to directly monitor auk populations using counts of birds on the surface of colonies (Gaston et al. 1988, Piatt et al. 1990a, Jones 1992), measurement of adult survival may be a useful additional method of monitoring auklet populations. This may be particularly true for Least Auklets, because surface counts in this species provide only a weak indication of population changes (Jones 1992). Monitoring of adult survival in color-marked

populations of auklets with diurnal colony attendance (e.g. Least Auklets, Crested Auklets, and Parakeet Auklets [*Cyclorhynchus psittacula*]) could alert us to trouble before our relatively weak census techniques detect a population decline. An initial effort to establish a marked population of several hundred birds would be required in the first year of such a study. Afterwards, researchers would need only return for a few weeks each summer to resight survivors and band new birds to maintain the marked population. This would permit year-to-year monitoring of adult survival, a crucial population parameter. Information on reproductive performance, such as proportion of adults breeding and even fledging success, could be obtained by observation of marked birds carrying food to chicks (Jones and Montgomerie 1992).

Recruitment, an additional component of a population-dynamics model, would remain unmeasured. This could be a problem if differing population trends among colonies relate to recruitment, such as may be the case for Common Murres (*Uria aalge*; Harris and Wanless 1988, Hatchwell and Birkhead 1991). Least Auklet chicks are difficult to capture in their usually inaccessible crevices, so recruitment is unlikely to be easy to measure in this species. Nonetheless, annual estimates of survival and reproductive performance may provide valuable measures for population monitoring.

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