

## AGE AT FIRST BREEDING AND NATAL DISPERSAL IN A DECLINING POPULATION OF CASSIN'S AUKLET

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**ABSTRACT.**—Age of first breeding (AFB) and natal dispersal distance (NDD) were investigated relative to proximate and ultimate factors in 276 known-age Cassin's Auklets (*Ptychoramphus aleuticus*) breeding during 1981–1999 on Southeast Farallon Island, California. Breeding density in 446 study boxes declined significantly during the period 1987–1999, confirming other information indicating a long-term decline (since at least the 1970s) in the population. Mean AFB was 3.34 years when sexes were combined, ranging from 2–10 (mean 3.36) years in females and 2–9 (mean 3.36) years in males. AFB showed a significant linear increase with decreasing colony density, suggesting that increased stress on the entire population, such as that caused by decreasing food availability, may have prevented younger birds from attaining breeding condition at an early age. Median NDD was 8.84 m, ranging from 0–448.7 m; two individuals of each sex recruited into their natal boxes. NDD showed a significant linear increase with decreasing breeding density but no significant linear or curvilinear correlations with mate fidelity, annual reproductive success, or lifetime reproductive output. A significant proportion (66.9%) of movements after recruitment (breeding dispersal) resulted in closer proximity to the natal site. Thus, although natal philopatry was strongly developed in the Cassin's Auklet, it did not seem to be adaptive. Those paradoxical results suggest that selective equilibrium may be acting on natal philopatry in response to the population decline: a low-philopatry, low-cost (later breeding and increased survival) strategy has become increasingly adaptive in Cassin's Auklets, explaining increases in AFB and NDD with the declining breeding densities. The lack of sex-specific effects on AFB and NDD suggests that an even sex-ratio and roughly equal roles in reproduction among Cassin's Auklets exists on Southeast Farallon Island, and that inbreeding avoidance may be counterbalanced by relatively low mate fidelity in this species. Received 29 June 2000, accepted 11 June 2001.

DEFERRED BREEDING, DOCUMENTED in many seabirds (Furness and Monaghan 1987, Newton 1989), could be adaptive for long-lived organisms because potential benefits of breeding early in life are outweighed by costs to early reproduction (Lack 1968, Nur 1988, Partridge and Harvey 1988, Reznick 1992, Pyle et al. 1997, Caswell 2000). Natal dispersal (movement between natal site and recruitment site) is relatively undocumented in seabirds (Greenwood 1980, Greenwood and Harvey 1982, but see Chabrzyk and Coulson 1976; Ainley et al. 1983, 1990; Rabouam et al. 1998; Spear et al. 1998). Depending on population demography, natal philopatry in birds could be adaptive due to local experience with breeding parameters and proximity of successful and related individuals, or it could be maladaptive due to a higher risk of inbreeding and increased competition for mates, nesting sites, or food re-

sources (Oring and Lank 1984, Dobson and Jones 1985, Johnson and Gaines 1990, Pärt 1991, Perrin and Mazalov 2000).

In most studies of long-lived organisms, variation in age of first breeding or natal dispersal distance has been documented in populations that are stable or in which trends in size or breeding density are unknown. Theory predicts that distributions in those traits may vary in species undergoing population change (Mertz 1971, Caswell 2000, Ricklefs 2000). For example, age of first breeding (AFB) could increase with population decline if increased stress on the entire population, such as that caused by decreasing food availability, prohibits younger birds from attaining breeding condition at an early age. Alternatively, if a population decline is caused by increased adult mortality (e.g. due to interactions with fisheries or increased predation pressure), AFB could decrease as a population decreases due to less competition among potential recruits for breeding sites and experienced mates. For sim-

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ilar reasons, natal dispersal distance (NDD) could also decrease with population decline, assuming that natal philopatry is advantageous. Evidence based on long-lived birds indicates that AFB can either increase (Wyllie and Newton 1991) or decrease (Bendell et al. 1972; Coulson et al. 1982; Weimerskirch and Jouventin 1987; Kress and Nettleship 1988; Croxall et al. 1990, 1998) with reduced breeding densities, and that NDD tends to decline with declining densities (Greenwood 1980, Greenwood and Harvey 1982, Negro et al. 1997), although sex-specific differences have been noted (Greenwood et al. 1979).

Both age of first breeding and natal dispersal distance can show sex-specific variation. Depending on the population, AFB in seabirds can be significantly younger in either males (e.g. Wooller and Coulson 1977, Mills 1989, Spear et al. 1995) or females (e.g. Ainley et al. 1983, Gaston et al. 1994), or it can show no sex-specific bias (e.g. Chabrzyk and Coulson 1976, Wooller et al. 1989). Sex-specific variation in AFB could relate to skewed sex-ratios in recruiting populations, resulting from differential survival in prebreeding birds (Spear et al. 1987, 1995; Newton 1989). In birds, females usually show greater natal dispersal and breeding dispersal (movement between successive breeding attempts) distances than males whereas the reverse tends to be true in mammals (Greenwood 1980, Johnson and Gaines 1990, Perrin and Mazalov 2000). Sex-specific differences in dispersal have been explained as a means to avoid inbreeding (Pusey 1987), and the difference between birds and mammals correlates with whether or not mate selection is based on a resource-defense breeding system (most birds) or a mate-defense system (most mammals). The breeding system (nomadic, polyginous, or monogamous) as well as skewed sex-ratios may also affect sex-specific natal dispersal distances (Greenwood 1980, Liberg and von Shantz 1985, Johnson and Gaines 1990, Spear et al. 1998, Perrin and Mazalov 2000).

Due to their habit of nesting in dense colonies and sensitivity to human disturbance, little is known about age of first breeding or intracolony natal dispersal in alcids (Gaston and Jones 1998). Frequency distributions in AFB have been examined only in the Razorbill (*Alca torda*; Lloyd and Perrins 1977), Thick-billed Murre (*Uria lomvia*; Gaston et al. 1994), and At-

lantic Puffin (*Fratercula arctica*; Petersen 1976, Kress and Nettleship 1988), whereas age of youngest breeding is known for a few other species (Gaston and Jones 1998). Along with Ancient Murrelet (*Synthliboramphus antiquus*; Gaston 1990), Cassin's Auklet (*Ptychoramphus aleuticus*) is the only alcid known to breed as young as two years (Speich and Manuwal 1974), but variation in that trait has not been measured.

Cassin's Auklet has been declining on Southeast Farallon Island, off San Francisco, California, from an estimated 105,000 individuals in the breeding population in 1972 (Manual 1974a) to 46,000 in 1989 (Carter et al. 1992), with the decline continuing through the 1990s, on the basis of decreases in burrow densities within study plots and decreased occupancy of nest boxes (Ainley et al. 1994, Sydeman et al. 1996, this study). Declines may be the result of predation at the breeding colony by an increasing (during the 1970s) population of Western Gulls (*Larus occidentalis*) or shifts in prey resources caused by ocean warming (Ainley et al. 1996, Sydeman et al. 1996). Generally, breeding densities and annual reproductive success by Cassin's Auklets are inversely correlated with sea surface temperature (Ainley and Boekelheide 1990, Ainley et al. 1995), an effect most pronounced during warm-water, El-Niño-Southern-Oscillation (ENSO) events (see Ainley et al. 1995). Cassin's Auklets on Southeast Farallon Island exhibit moderately low mate fidelity; that is, birds often divorce (and at times remate after divorce) during consecutive breeding attempts (Emslie et al. 1992, Sydeman et al. 1996).

In this paper, I investigate age of first breeding and natal dispersal in 276 known-age Cassin's Auklets breeding on Southeast Farallon Island between 1981 and 1999. I examine those traits relative to each other, sex, natal fledging date, interannual variation in colony density, and ultimate factors such as mate and site fidelity, annual reproductive success, and lifetime reproductive output. I also assess changes in age of first breeding and natal dispersal distance during the 17 year study period as related to the declining population trend.

#### METHODS

The breeding biology of the Cassin's Auklet on Southeast Farallon Island has been described by Manuwal (1974a, b) and Ainley and Boekelheide (1990).

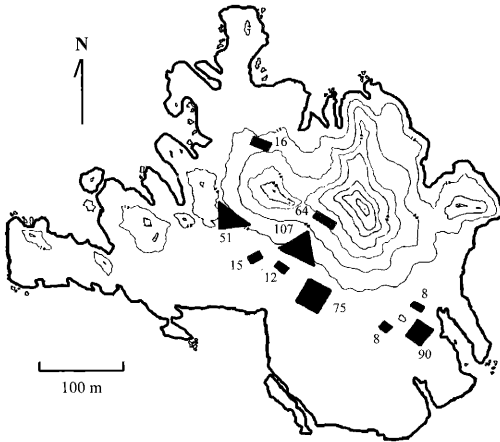


FIG. 1. Locations of 10 known-age Cassin's Auklet study plots on Southeast Farallon Island including number of boxes per plot (1987–1999).

Between 1978 and 1983, ~700 nest boxes were installed for oil-related studies (e.g. Ainley et al. 1981) and subsequently used by Cassin's Auklets. Boxes were unevenly distributed among 10 plots throughout accessible portions of the island (Fig. 1). In 1987, boxes that had not been occupied by auklets since installation were removed, resulting in a total of 446 boxes that were subsequently maintained throughout the study period (Fig. 1). This study is based on recruitment and breeding attempts within those 446 boxes, as monitored by Point Reyes Bird Observatory (PRBO) biologists. Although a few unmonitored burrows were present in the vicinity of boxes during the early years of the study, by 1987 there were virtually no burrows within the maximum breeding dispersal distance (14.45 m; see below) of boxes; thus, it is assumed that biases in the data due to movement between burrows and boxes were negligible.

Throughout the study period (beginning in 1978), band numbers of breeding auklets in all boxes were recorded each year. Between 1978 and 1999, all unbanded breeding adults were banded, and between 1987 and 1999 unbanded mates of known-age birds were banded. All fledging chicks were banded each year. The bands were stainless steel, and a double-banded bird experiment conducted by PRBO (P. Pyle unpubl. data) from 1978 to 1988 indicated that band loss was absent or virtually so (<0.1% per year). Between 1981 (when the first known-age adult was observed) and 1986, annual reproductive success was determined for only a few breeding attempts by known-age auklets. Between 1987 and 1999, breeding success was determined for most or all attempts per year. Beginning 15 March each year (1987–1999), each box was checked once every 15 days for breeding auklets. When a known-age bird was found, the band status of its mate was determined and the site

was monitored on a five day schedule to determine hatching and fledging success (see Ainley and Boekelheide 1990 for details). Sex of known-age birds was determined by bill depth (Nelson 1981). Bill depths of <9.8 mm indicated females and those >10.2 mm indicated males; only a small proportion of known-age individuals could not be sexed after pairs were measured during one or more years of data collection.

Natal dispersal distance (NDD) and breeding dispersal distance (BDD) were measured directly as the distance (nearest 0.01 m) between entrances of natal and recruitment boxes and of nest boxes used by known-age individuals between years. Breeding colony density was defined as proportion of the 446 study boxes that were occupied by an incubating bird each year. Estimated natal fledging date was calculated to the nearest 15 days for most known-age birds on the basis of information on egg-laying, chick-hatching, and chick-fledging dates during the known-age bird's natal year. Mate fidelity was scored (for birds with at least three years of breeding) as  $1 - (\text{total number of mates} / \text{total number years breeding})$ ; thus, birds with a different mate each year have mate fidelity of 0, and those with the same mate throughout their lives have mate fidelity approaching 1. Site fidelity was assessed (for birds with at least two years of breeding) as an individual's mean breeding dispersal distance during the study.

Mean annual reproductive success was determined (in birds that had bred at least two years) as total number of chicks fledged divided by years of breeding (Cassin's Auklets can fledge up to two chicks per year; Ainley and Boekelheide 1990). Fledging status for attempts with missing data (4.8% of all attempts) were calculated with a model including year and age and experience terms of both the known-age bird and its mate (see Pyle et al. in press for details). Lifetime reproductive output of known-age birds was calculated, for birds that initiated breeding in 1993 or earlier, as mean reproductive success  $\times$  number of years breeding. A small proportion of those birds (7.2%) were still breeding at the end of the study period (1998 or 1999), but there is no reason to assume that the potentially underestimated lifetime reproductive output of those birds would be biased with respect to AFB or NDD.

Using STATA (Stata Corporation 1997), analysis of variance (ANOVA) and simple and multiple regression were used to examine effects and model dependent variables. To normalize natal and breeding dispersal distance, these terms were log-transformed ( $\log[n + 0.5 \text{ m}]$ , because NDD and BDD both included values of 0). Residuals of all variables met assumptions for normality (skewness/kurtosis tests,  $P > 0.05$ ; Stata Corporation 1997). Nonlinearity (curvilinearity) was tested by examining significance of quadratic terms. Sex-specific effects were tested using analyses of covariance (ANCOVA) which exam-

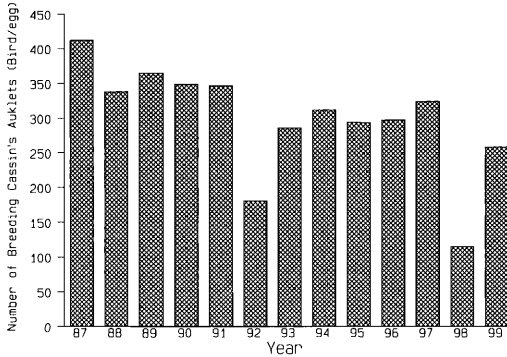


FIG. 2. Number of breeding Cassin's Auklets recorded per year in the 446 study boxes. Breeding density, defined as proportion of occupied boxes, declined significantly during this period, indicating a population decline of  $-2.8\%$  per year.

ines interaction terms between dependent variables and sex; additionally, analyses were performed separately on each sex to look for significant effects of a term on one sex but not the other.

## RESULTS

**Colony density.**—Number of occupied boxes within the 10 plots (Fig. 1) varied from 115 (25.8%; 1998) to 412 (92.4%; 1987) during 1987–1999 (Fig. 2), resulting in a mean breeding density of 66.9%. Breeding density was significantly lower during the two years affected by warmer sea surface temperatures associated with ENSO events, 1992 (40.6%) and 1998 (25.8%), than in the other 11 years (mean 73.1%; ANOVA,  $F = 29.02$ ,  $df = 1$  and  $11$ ,  $P < 0.001$ ). Breeding density declined significantly during the 13 year period, both with (linear regression,  $t = -2.71$ ,  $P = 0.020$ ) and without ( $t = -4.71$ ,  $P = 0.001$ ) inclusion of data from the two ENSO years. Skipped years, defined as years of absence between years of breeding, occurred 74 times among 47 birds (23 males and 24 females), and included 64 skipped episodes of 1–4 consecutive years. Thirty of the 74 skipped years (40.5%) occurred during the ENSO events of 1992 and 1998. Skipping did not increase during the study period (linear regression,  $t = 0.45$ ,  $P = 0.67$ ); thus, decreasing breeding density was not caused by an increasing rate of skipping. Without including data from 1992 and 1998 (clearly years of reduced attendance rather than population fluctuation), average decline was 2.8% per year.

**Known-age birds.**—Between 1981 and 1999, 276 known-age Cassin's Auklets were recorded in the breeding plots (144 males, 123 females, and 9 of undetermined sex). A total of 794 breeding attempts was recorded, by birds 2–14 yrs of age and 0–11 years of previous breeding experience. Annual reproductive success was determined for 756 of those attempts including 688 attempts (91.0%) between 1987 and 1999. Among known-age birds with at least three years breeding ( $n = 116$ ), mean mate fidelity was 0.484 (range 0–0.857). Mean breeding dispersal distance ( $n = 511$  between-year attempts by 161 individuals) was  $1.16 \pm 2.21$  (SD) m with a range of 0–14.45 m; breeding dispersal occurred during 34.2% of between-year attempts. Among known-age birds with at least two years of breeding data ( $n = 160$ ), mean annual reproductive success was  $0.63 (\pm 0.34$  [SD]; range 0–1.5) chicks fledged. Lifetime reproductive output for auklets first breeding in 1993 or earlier ( $n = 166$ ) was  $2.74 (\pm 2.66$ ; range 0–9.34).

**Age of first breeding.**—Mean AFB was 3.34 years ( $\pm 1.32$  SD;  $n = 276$ ) when sexes were combined. AFB ranged from 2–10 years (mean 3.357, median 3 years;  $n = 123$ ) in females and 2–9 years (mean 3.36, median 3 years;  $n = 144$ ) in males (Fig. 3). The sex-specific difference was not significant (ANOVA,  $F = 0.60$ ,  $df = 1$  and  $266$ ,  $P = 0.44$ ), although a slightly higher proportion of females (29.3%) than males (24.1%) recruited at the youngest age, 2 years (Fig. 3). A majority of birds (95.5%, sexes combined) initiated breeding between 2 and 5 years (Fig. 3); thus, in the following analyses, data from birds with AFBs of 6–10 years have been pooled.

Correlations of AFB with both proximate and ultimate factors are shown in Table 1. No significant linear or curvilinear correlations or sex-specific effects were found between AFB and NDD or natal fledging date. Mate fidelity showed significant positive linear correlations with AFB, and mean BDD (log transformed) showed significant linear decreases with AFB, overall and in both sexes. Those correlations, confounded by affects of age and previous breeding experience on mate and site fidelity, were discussed in more detail in a separate paper (Pyle et al. in press).

When sexes were combined, AFB of recruiting individuals showed a significant linear in-

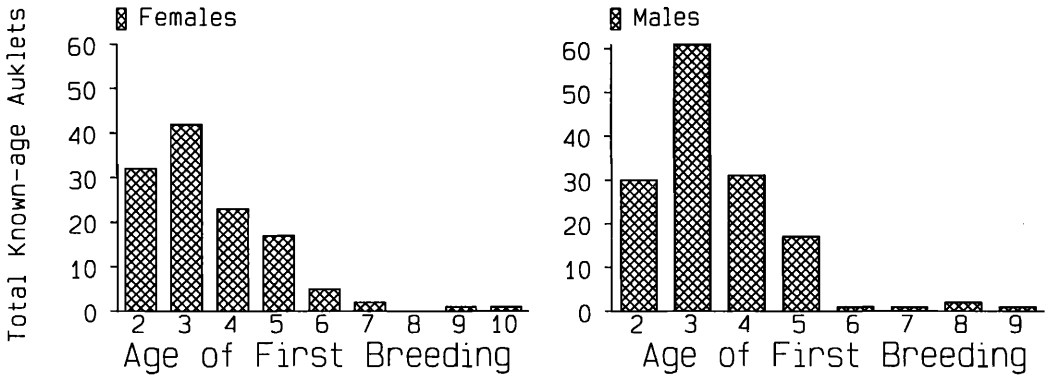


FIG. 3. Age of first breeding in female and male Cassin's Auklets.

crease with year (1987–1999 only, to remove bias associated with sample of potential recruits) and a significant linear decrease with colony density; in each case, quadratic terms were significant and negative indicating that year trend was decelerating and density trend was accelerating (Fig. 4). AFB showed a significant linear increase but no curvilinear relationship with year in females, whereas in males, no linear trend but a significant negative curvilinear trend was found; however, ANCOVA revealed no significant sex-specific differences in those relationships (Table 1). Relative to colony density, AFB showed a significant linear and curvilinear decrease in females, and no linear trend but a significant negative curvilinear trend in males; again, however, sex-specific effects were not significant (Table 1). When sexes were combined, multiple regression indicat-

ed confounding between linear effects on AFB of year ( $t = 1.24, P = 0.22$ ) and density ( $t = -1.20, P = 0.23$ ); that is, it could not be determined which of the two variables (or both) resulted in significant correlations with AFB. Similar results were obtained with each sex separately. Examination of AFB during ENSO events (1992 and 1998;  $n = 17$ , mean AFB 3.59), when colony density was reduced (Fig. 2), versus the other 11 years ( $n = 208$ , mean AFB 3.45) indicated no significant difference (ANOVA,  $F = 0.07, df = 1$  and  $222, P = 0.79$ ).

*Natal dispersal distance.*—Median NDD in known-age Cassin's Auklets was 8.84 m ( $n = 273$ ; mean =  $17.6 \pm 36.2$  [SD] m; range 0–448.7 m), 9.39 m ( $n = 121$ ; mean =  $19.1 \pm 28.6$  m) in females and 8.11 m ( $n = 144$ ; mean =  $16.8 \pm 44.6$  m) in males. Two individuals of each sex recruited into their natal boxes (NDD = 0).

TABLE 1. Relationships between age of first breeding and natal fledging date, year, breeding density, natal dispersal distance (NDD), mate fidelity, and breeding dispersal distance (BDD), in Cassin's Auklets on Southeast Farallon Island. See text for definitions of variables and certain restrictions; AFB's of 6–10 years were pooled. For overall (both sexes), females, and males,  $t$ -values based on linear regression or multiple regression including quadratic terms (e.g.  $\chi^2$ ) are presented. Results of analyses including quadratic terms are presented only when significant curvilinear effects were found. Linear effects were calculated without including quadratic terms. For sex-specific effects,  $F$ -statistics are presented on the basis of analysis of covariance. Significant effects are indicated by asterisks: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Variable	$n$	Overall		Females	Males	Sex-specific effect $F$
		$r$	$t$	$t$	$t$	
Fledging date	270	0.07	0.73	1.47	-1.03	3.70
Year $\times$ year	224	0.17	3.04**	2.80**	1.35	1.22
		0.31	-2.02*	-0.85	-2.56*	0.81
Density $\times$ density	224	0.19	-3.02**	-2.83**	-1.36	1.72
		0.34	-3.42***	-2.03*	-2.58*	0.59
NDD	273	0.00	0.25	-0.13	0.78	0.45
Mate fidelity	116	0.22	3.62***	2.59*	2.63*	0.01
Mean BDD	161	0.23	-3.17**	-1.98*	-2.23*	0.06

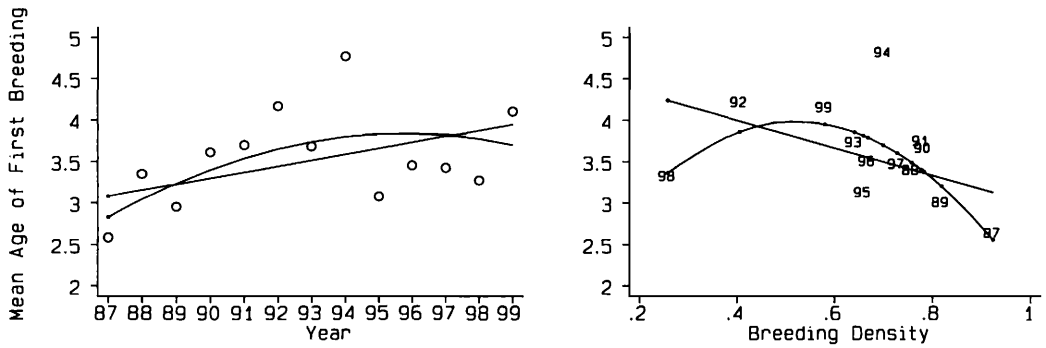


FIG. 4. Linear and curvilinear correlations between mean age of first breeding and year and density in Cassin's Auklets. See Table 1 for statistical analyses.

NDD was >75 m in only seven individuals (three males and four females that recruited into nonnatal plots; see Fig. 1); excluding those, mean NDD was  $13.5 \pm 13.0$  m in females and  $12.8 \pm 13.8$  m in males. Those values were likely biased downward, compared with overall dispersal distances, by the nonrandom distribution of plots and boxes within plots (Fig. 1) and the fact that dispersal away from Southeast Farallon Island was unknown; however, comparisons of NDD between sexes and with other parameters should not be subject to that bias. The sex-specific difference in NDD (log transformed) was not significant either with ( $F = 0.31$ ,  $df = 1$  and  $263$ ,  $P = 0.58$ ) or without ( $F = 0.42$ ,  $df = 1$  and  $256$ ,  $P = 0.52$ ) the inclusion of birds with NDD > 75 m. There also was no sex-specific difference in natal philopatry when defined as NDD < 5 m ( $\chi^2 = 1.28$ ,  $P = 0.72$ ), NDD

< 10 m ( $\chi^2 = 0.40$ ,  $P = 0.53$ ), or NDD < 15 m ( $\chi^2 = 0.20$ ,  $P = 0.89$ ).

Correlations of NDD (log transformed) with both proximate and ultimate factors are shown in Table 2. No significant linear or curvilinear correlations, or sex-specific effects, were found between NDD and natal fledging date, year, mate fidelity, annual reproductive success, or lifetime reproductive output. When sexes were combined, NDD showed a significant linear decrease with breeding density (Fig. 5). Multiple regression showed that effect remained significant ( $t = -2.12$ ,  $P = 0.035$ ) with inclusion of the year term, which was not significant ( $t = -0.58$ ,  $P = 0.56$ ). The decrease in NDD with density was significant in females and not significant in males, but sex-specific difference in that correlation was not significant (Table 2). NDD also showed a significant increase with

TABLE 2. Relationships between natal dispersal distance at recruitment and natal fledging date, year, breeding density, mate fidelity, breeding dispersal distance (BDD), mean reproductive success (RS), and estimated lifetime reproductive success (LRS) in Cassin's Auklets on Southeast Farallon Island. See text for definitions of variables and certain restrictions; natal dispersal distance (meters) represented as log (NDD + 0.5). For overall (both sexes), females, and males,  $t$ -values based on linear regression are presented. Quadratic analyses were performed on each variable and no significant curvilinear effects were found. For sex-specific effects,  $F$ -statistics are presented on the basis of analysis of covariance. Significant effects are indicated by asterisks: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Variable	<i>n</i>	Overall			Sex-specific	
		<i>r</i>	<i>t</i>	Females <i>t</i>	Males <i>t</i>	effect <i>F</i>
Fledging date	269	0.06	1.32	1.71	-0.37	1.06
Year	273	0.08	0.54	0.32	0.50	1.97
Density	223	0.16	-2.34*	-2.00*	-1.41	0.76
Mate fidelity	114	0.00	1.07	1.23	0.41	0.43
Mean BDD	161	0.16	1.25	2.84**	-0.67	5.37*
Mean RS	160	0.07	-0.59	-1.15	0.06	0.75
Estimated LRS	164	0.09	0.56	-0.57	1.39	2.04

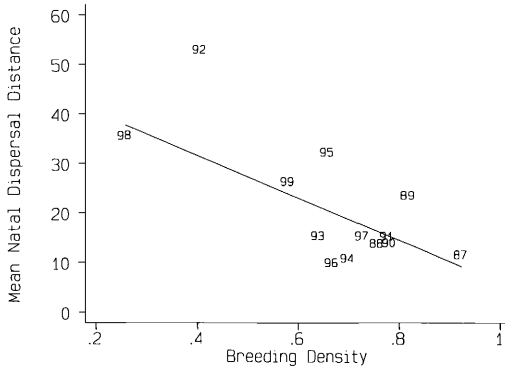


FIG. 5. Mean natal dispersal distance as compared with annual breeding density in Cassin's Auklets on Southeast Farallon Island. See Table 2 for statistical analyses.

mean breeding dispersal distance (log transformed) in females but not in males (Fig. 6) and that sex-specific difference was significant (Table 2). However, the female with the largest NDD (181.4 m) also had the largest mean BDD (13.78 m; Fig. 6); removing that individual from the sample resulted in a marginally non-significant correlation ( $t = 2.01$ ,  $P = 0.051$ ) between NDD and BDD in females and no sex-specific effect (ANCOVA,  $F = 1.19$ ,  $df = 3$  and  $155$ ,  $P = 0.28$ ).

Change in distance from the natal site was analyzed after breeding dispersal events. During 111 of 166 events (66.9%), known-age Cassin's Auklets moved closer to their natal box, whereas during 55 events they moved farther from their natal box; that proportion was significantly different from 0.50 ( $\chi^2 = 9.72$ ,  $P = 0.002$ ). When sexes were separated this tenden-

cy was stronger in males (65 closer, 27 farther) than females (45 closer, 28 farther), although the sex-specific difference was not significant ( $\chi^2 = 1.48$ ,  $P = 0.22$ ). Mean change in distance from the natal box was  $-0.52 \pm 3.20$  (SD) m with a range of  $-11.73$  to  $9.20$  m.

## DISCUSSION

*Declining population and age of first breeding.*—The significant decrease in breeding density between 1987 and 1999, coupled with lack of an increase in skipped breeding, confirms other information (Carter et al. 1992; Ainley et al. 1994, 1996) that the Cassin's Auklet population is declining on Southeast Farallon Island. Our calculated annual percentage change of  $-2.8\%$  is similar to the  $-2.6\%$  preliminarily reported by Nur et al. (1998) based on mark-recapture analysis. Similar declines have been noted for other planktivorous species of alcids in the North Pacific (Kitaysky and Golubova 2000), and for Cassin's Auklets in British Columbia (Bertram et al. 2000).

The significantly lower breeding densities observed during the two years affected by ENSO support findings by Ainley and Boekelheide (1990) and Ainley et al. (1995) that breeding-population sizes are inversely correlated with sea-surface temperature (SST). The high rates of skipping during ENSO years suggest that warmer SST associated with ENSO events result in decreased colony attendance rather than reduced population per se. However, correlations between warmer SST and reduced zooplankton abundance off California (Roemich and McGowan 1995), coupled with the

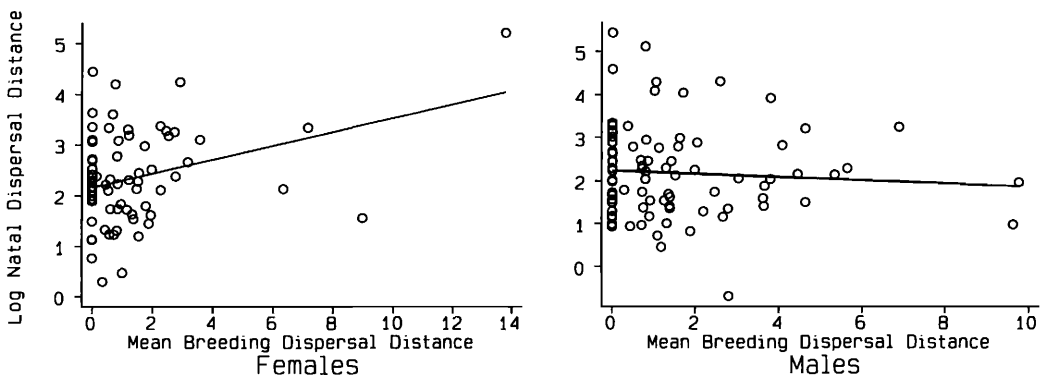


FIG. 6. Natal dispersal distance (log transformed) compared with mean breeding dispersal distance in female and male Cassin's Auklets. See Table 2 for statistical analyses.

fact that SST in the eastern North Pacific has increased during this study (McGowan et al. 1998) suggests that the long-term population decline is correlated with ocean-temperature-related shifts in prey resources (primarily krill [*Euphausia*]) as suggested by Ainley et al. (1995, 1996; see also Bertram et al. 2000), rather than (or in addition to) predation by Western Gulls (cf. Nelson 1989, Emslie and Messenger 1991). Nur et al. (1988) also report that adult survival was lower during ENSO events.

Results of this study support the premise that shifts in prey resources are contributing to the population decline. Mean AFB in Cassin's Auklets increased significantly with declining breeding density during 1987–1999. Although confounded with year, we believe that density effects on life-history traits in the population are genuine, as shown for NDD in this study (see also Pyle et al. in press more details). These findings are opposite to results of other studies indicating decreased AFB with lower breeding densities in Blue Grouse (*Dendragapus obscurus*; Bendell et al. 1972, Zwickel 1972), Herring Gulls (*Larus argentatus*; Coulson et al. 1982), Atlantic Puffins (Kress and Nettleship 1988), and Wandering Albatross (*Diomedea exulans*; Croxall et al. 1990), but similar to results suggesting increased AFB in a declining population of European Sparrowhawks (*Accipiter nisus*; Wyllie and Newton 1991). Explanations for a positive relationship between AFB and breeding density have included reduced competition for nest sites and food resources and a greater availability of experienced mates, situations that arise due to decreased survival or increased (often human-induced) mortality of breeding adults, as was the case in the study populations of grouse, gulls, puffins, and albatross mentioned above. A similar relationship in Cassin's Auklet might be expected if predation by Western Gulls on breeding adults was the primary factor causing decline. Instead, increase in AFB with decreased density in Cassin's Auklets suggests that increased stress on the entire population, such as that caused by decreasing food availability, may have prevented younger birds from attaining breeding condition at an early age. A similar situation may have occurred in the declining population of sparrowhawks (Wyllie and Newton 1991).

*Natal Philopatry.*—The median natal dispersal distance of 8.84 m is likely biased downward by the nonrandom distribution of study boxes and lack of information on intercolony dispersal. However, several lines of evidence suggest that natal philopatry is strongly developed in Cassin's Auklets on Southeast Farallon Island (cf. Baker 1978, Greenwood and Harvey 1982). What little is known about natal dispersal in alcids suggests that most breeders recruit into their natal colony, at least in murre (Birt-Friesen et al. 1992, Gaston and Jones 1998). The nearest significant colony of Cassin's Auklets to Southeast Farallon Island is that of Castle Rock, almost 400 km to the north (Carter et al. 1992), suggesting that the Southeast Farallon Island colony likely experiences little immigration or emigration. That four birds recruited into their natal sites and that a significant proportion of auklets moved closer to their natal site after breeding dispersal events further supports the conclusion that natal philopatry is advantageous in the population. Paradoxically, however, neither AFB nor any of the proximate or ultimate estimators of fitness (mate fidelity, annual reproductive success, lifetime reproductive output) were correlated with NDD, except for a marginally significant relationship between breeding dispersal distance and NDD in females. Furthermore, NDD increased with decreasing breeding density, a result that might be expected if NDD was constrained by mate availability but is opposite to that expected in most birds (Greenwood 1980), assuming auklets are selected for natal philopatry and NDD is constrained by competition.

A study of NDD in Western Gulls on Southeast Farallon Island from 1979 to 1994 (Spear et al. 1998) indicated similar results: natal philopatry was well developed but appeared to be nonadaptive, if not maladaptive, due to lower lifetime productivity in more philopatric gulls. Spear et al. explained those results in terms of relatively poor food availability in the Gulf of the Farallones during 1989–1994. Natal philopatry may have been selected for, especially in male Western Gulls, as part of a high-cost reproductive strategy (earlier breeding and poorer long-term survival) developed during a period of good food availability in the 1970s and early 1980s. Once food availability decreased, however, that strategy was no longer adaptive. A similar situation may be occurring in Cas-



sin's Auklets, given decreasing breeding densities that are likely related to decreases in food availability (see above). Thus, as in the Western Gull, a low-philopatry, low-cost strategy (later breeding and increased survival) may now be adaptive in Cassin's Auklets, explaining both accelerating increases in AFB and linear increases in NDD with declining breeding densities, and lending support to the theory that selective equilibrium may be acting on such traits as natal philopatry, depending on periodicities in breeding densities and food availability (Stearns 1992, Spear et al. 1998).

*Sex-specific effects.*—A sex-specific effect in the positive correlation between NDD and mean breeding dispersal distance became non-significant with the removal of the individual female with the greatest NDD. Otherwise, there were no sex-specific effects on AFB, NDD, or their correlations with proximate and ultimate factors in known-age Cassin's Auklets on Southeast Farallon Island.

It is again instructive to contrast those results with the many sex-specific results found in Western Gulls breeding on Southeast Farallon Island during roughly the same period of time. Age of first breeding was significantly lower in male than female Western Gulls (Spear et al. 1995, Pyle et al. 1997). That difference was correlated with a skewed sex ratio in the recruiting population, the result of differential survival among prebreeding birds (Spear et al. 1987), and with differences in roles of reproduction (Pierotti 1981, Pyle et al. 1991; see also Chabrzyk and Coulson 1976, Wooller and Coulson 1977, Ainley et al. 1983, Mills 1989). The lack of sex-specific effects on AFB in Cassin's Auklets may indicate an even sex-ratio and roughly equal roles in reproduction on Southeast Farallon Island. That corresponds with what we know of the breeding biology of that species (and of alcids in general; Gaston and Jones 1998): incubation and chick-provisioning are shared (Manual 1974a, b) and the relatively low (compared with other long-lived seabirds) mate and site fidelity (Emslie et al. 1992, Sydeman et al. 1996, Pyle et al. in press) suggests that territoriality and sex-specific roles in reproductive effort are not well developed.

Except in nomadic species and waterfowl (Anatidae), most birds show female-biased natal dispersal; that is, females disperse in greater proportions and farther than males (Green-

wood 1980, Spear et al. 1998). Sex-specific differences in natal dispersal have been explained as a means to avoid inbreeding, and female-biased dispersal in most birds correlates with the fact that mate selection is based primarily on resource-defense breeding systems (Greenwood 1980, Pusey 1987). During territory establishment and defense, males may benefit from natal philopatry due to local experience with breeding parameters and proximity of successful and related individuals, whereas females disperse to avoid inbreeding with philopatric male siblings.

Cassin's Auklets show little tendency toward sex-specific roles in reproduction. Unlike Western Gulls, where quality of territory (amount of cover for chicks) correlates with successful reproduction, nest boxes (and perhaps breeding burrows) are all relatively similar in quality. Lack of sex-specific effects in both AFB and NDD in Cassin's Auklets may support a theory proposed by Johnson (1986) correlating sex-specific effects in philopatry with those of delayed breeding in mammals (see also Johnson and Gaines 1990). In addition, the relatively low mate fidelity in Cassin's Auklets may lessen importance of inbreeding avoidance in that species (cf. Liberg and von Schantz 1985, but see also Marks and Redmond 1987). Should inbreeding occur at a low level in Cassin's Auklets, as has been documented in Cory's Shearwaters (*Calonectris diomedea*; Rabouam et al. 1998), frequent mate switching ensures increased genetic heterogeneity at the level of both the individual and the population. Relationships between mate fidelity and age, breeding experience, site fidelity, and ultimate measures of fitness in Cassin's Auklets on Southeast Farallon Island, which shed further light on those issues, have been treated in a separate analysis (Pyle et al. in press).

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