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DEMOGRAPHY OF THE PIGEON GUILLEMOT ON SOUTHEAST FARALLON ISLAND, CALIFORNIA[1]

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Key words: Demography; Pigeon Guillemot; Cepphus columba; *seabirds; survivorship.*

Auks (Alcidae) form an important component of marine avifaunas in the Northern Hemisphere, in terms of numbers of both individuals and species. In order to effectively manage and protect alcid populations, basic demographic data are vital (Nisbet 1979). Demographic parameters have been estimated for five of the six species in the North Atlantic (Hudson 1985). In contrast, survivorship of banded birds is known for only one Pacific Ocean alcid species (Ancient Murrelet, *Synthliboramphus antiquus,* Gaston 1990). In this note, I report survivorship and recruitment of a color-marked sample of Pigeon Guillemots (*Cepphus columba*) over a five-year period.

METHODS

I observed Pigeon Guillemots in 1977 and from 1979–1982 on Southeast Farallon Island, California (37°42′N, 123°00′W), a 44 ha island about 43 km west of San Francisco. Biological and physical features of the island were described by Ainley and Lewis (1974) and Ainley and Boekelheide (1990). Among the 12 species of marine birds breeding on SE Farallon is a population of approximately 1,000 Pigeon Guillemot pairs (Ainley et al. 1990). I began observations in March 1977, 1979 and 1980 before guillemots had returned to the island from their wintering areas, and continued observations until late July or August when chicks began to fledge. I also visited the island for one month in April 1981 and May 1982.

In 1977, I studied about 10 pairs of guillemots that nested atop a 40 m high ridge on Shubrick Point. After 1977, I also made observations on the southeast side of the island where approximately 20 pairs nested in or near a rubble pile at the head of a surge channel (East Landing).

Guillemots nested in natural and artificial crevices at East Landing (Nelson 1987). Eight-nine guillemots were captured with leg nooses and banded with unique combinations of two color bands and a numbered monel U.S. Fish and Wildlife Service band (Nelson 1987). To minimize nest desertion, I allowed birds to occupy a site for at least one week before capture. Additional birds were identified by unique tears or holes in their webbed feet or by plumage marks in the white wing patches. Birds were sexed by copulation position (Nelson 1987). The Point Reyes Bird Observatory (PRBO) also banded between 19 and 284 chicks annually since 1970 with unique year-class color rings (Ainley et al. 1990). Most of these birds were banded on Lighthouse Hill, about 200 m from my study sites. Several of these birds were in my study plot each year as territory owners and non-territorial "loafers."

Survivorship of territory owners was estimated by resighting banded birds and five birds with easily visible, unique natural marks at Shubrick Point and East Landing. This includes several pairs each year that held territories but did not produce eggs (Nelson 1987). Sur-

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TABLE 1. Annual survivorship estimates for territorial Pigeon Guillemots.

Year	Survivorship	n[b]
1977–1979[a]	0.89	10
1979–1980	0.84	37
1980–1981	0.62	52
1981–1982	0.76	33

[a] Annual survivorship over the two-year period was estimated as the square root of the percentage of birds that survived.

[b] n birds alive at beginning of sample period.

TABLE 2. Association between site fidelity and survival of mate.

Mate	Site fidelity	
	Stay	Move
Present	71	4
Not present	12	8

vival was defined as the proportion of birds alive in year $\bar{x}$ that were present in year $\bar{x} + 1$. I observed at East Landing almost daily, and at Shubrick Point one or two mornings a week. To estimate dispersal, I attempted to locate all banded guillemots on the island. However, much of the island was inaccessible. Band loss was not a serious problem over the relatively short term of this study. Three individuals lost single color bands but I was able to keep track of the birds. The rate of plastic band loss was about 1% per band-year. I never found a bird with plastic band(s) and no monel band.

RESULTS

Survivorship. The mean annual survival of territory holders was 0.80 (n = 5 years, Table 1). This is a minimum estimate and may include disappearance due to emigration. The value for 1980–1981 is low because I missed two birds that were present in 1982. I also captured and banded 15 loafers. Eight were not seen again after their capture. One loafer was sighted about 450 m from East Landing 22 months after I banded it (PRBO, unpubl. data). The remaining six along with many other recognizable birds visited the study sites almost every day.

Prebreeding dispersal. Two of three known-age males (one seven-year-old, one two-year-old) held territories less than five meters from the crevice where they had been banded as chicks. A seven-year-old male and two eight-year-old females bred in crevices about 200 m from where they had been raised.

Age at first breeding. The youngest guillemot known to breed on SE Farallon was a three-year-old male in 1979. This male acquired a territory and mate as a one-year-old in late June 1977, but did not breed until 1979; however, very few guillemots bred successfully in 1978 on SE Farallon (Ainley et al. 1990). In 1979, two seven-year-olds and two eight-year-olds also bred. These birds all bred in 1980, and there were no new known-age recruits in 1980. Loafers were younger than most breeders. In 1979 there were three two-year-olds, one three-year-old, one five-year-old, and one six-year old loafers. In 1980 there were three three-year-olds, and one four-year-old.

Nest-site retention and pair-bond maintenance. Of 95 year-year transitions involving 43 different territory owners, birds returned subsequently to the same nest-site in 83 cases (87%) (Table 2). Three males bred for at least six consecutive years in the same nests.

In 12 cases (13%), birds switched crevices between years. Four of these switches were associated with "divorce" (both members of the pair were alive the next year, but one or both occupied different crevices).

Most changes of nest site were associated with loss of a mate. However, loss of mate did not usually lead to a change of nest site because 12/20 birds (60%) whose mates disappeared remained at the same crevice (Table 2). Both members of the pair had to be recognizable to be included in this analysis. Males (n = 4) and females (n = 4) were equally likely to change crevices after mate loss.

Of 10 birds that lost their mates during the breeding season (April–August), nine remained at their crevices while four of six whose mates did not return in April changed crevices (Fisher's Exact Probability = 0.036). The one female who did change crevices after losing her mate in June 1980 paired with a widowed male 3 m away and also repeatedly defended her old crevice against other females in the same year.

Predators and competitors. Pigeon Guillemots had few predators on SE Farallon. Peregrine Falcons (*Falco peregrinus*) were rare on the island during the seabird breeding season but have been observed to chase and capture guillemots (PRBO unpubl. data). Western Gulls (*Larus occidentalis*) caught but never killed guillemots in the 14 captures I witnessed. Most captures by gulls seemed to be a matter of chance, although a few individual gulls stalked and attempted to capture guillemots. On one occasion a gull stole an octopus from a guillemot feeding chicks.

Six hole-nesting seabird species breed on SE Farallon, two storm-petrels (Ashy Storm-petrel, *Oceanodroma homochroa* and Leach's Storm-petrel, *O. leucorhoa*: Ainley and Lewis, 1974), and four alcids. I never saw guillemots interact with either of the nocturnal storm-petrels, but conflicts with the three other alcids were common. Cassin's Auklet (*Ptychoramphus aleuticus*) is a small species (mean mass = 165 gm; Manuwal 1979) that visits the island only at night, except when incubating eggs or brooding chicks. Egg-laying usually began during March or April, two to three months before guillemots laid. At East Landing in 1979 and 1980, auklets laid eggs in 13 of 28 nests (46%) used the same season by guillemots. None of the 13 auklet pairs successfully reared a chick. I observed male guillemots chase auklets out of their nests several times.

Of the other alcids, the Tufted Puffin (*Lunda cirrhata*: 797 gm, Sealy 1973) is considerably larger, and the Rhinoceros Auklet (518 gm, Sealy 1973) slightly larger than the Pigeon Guillemot (490 gm, Nelson 1987). Fewer than 150 pairs of either species occur on SE Farallon, although the populations of both species appear to be increasing (Ainley and Boekelheide 1990). One Tufted Puffin pair took over a guillemot crevice on Shubrick Point in 1977 and in late June and July of that year puffins (presumably young non-breeders) inspected most of the guillemot crevices I was studying. Guillemots with nests containing chicks gave alarm calls, mobbed, and chased Tufted Puffins that approached their nests (Nelson 1985). Aerial chases of puffins often included body contact. No Tufted Puffins were ever observed at East Landing, but two or three pairs of Rhinoceros Auklets nested there and several pairs also nested near my Shubrick Point study plot. One guillemot crevice on Shubrick Point was taken over by Rhinoceros Auklets in 1979. Circumstantial evidence suggested that Rhinoceros Auklets were associated with crevice changes by guillemots in two other cases in 1979.

DISCUSSION

Pigeon Guillemots on SE Farallon exhibited high annual adult survivorship, retention of the nest-site and mate, and deferral of first breeding until about three or four years of age. These estimated demographic parameters resemble those of other auks, especially the congeneric Black Guillemot (*Cepphus grylle*) (Asbirk 1979, Hudson 1985). The annual survivorship of 80% is similar to that of the Black Guillemot, but lower than estimates for most other auks, which average 90–95%. An exception is the Ancient Murrelet, with annual survival of 77% (Gaston 1990). Speich and Manuwal (1974) estimated annual survival of Cassin's Auklet on SE Farallon to be 83%. This estimate was based on the frequency distribution of gular pouch lengths within the population, and should be confirmed with banding data. My estimate may be somewhat low, as sampling effort declined in later years (1 month in 1981 and 1982). This may be partly responsible for the apparent decline in survival rates. The year with the lowest survival (1980–1981) was also the year I visited the island only in April, when colony attendance is highly variable (Nelson 1987). Dispersal from my study sites is an unlikely cause of low estimates, as I never sighted a banded breeder away from my sites.

In common with most other seabirds, Pigeon Guillemots retained the same mate and crevice from year to year in this and previous studies. On Mandarte Island, Drent (1965) recorded six instances of nest-site tenacity of at least four years. On SE Farallon, Tenaza (1966) recorded two pairs at the same crevices in two successive years.

The timing of mate loss and the availability of replacement mates may have influenced whether or not a bird switched crevices. Guillemots were more likely to move between nests if their mate did not return at the beginning of the breeding season than if the mate died during the breeding season. Since clutch size and fledging success decline with time (Nelson 1987, Ainley et al. 1990), it may be advantageous for a bird widowed early in the season to move and form a pair bond immediately with an available bird. Later in the season, there are few unoccupied crevices and more birds available to serve as replacement mates and competitors for crevices. The best tactic then may be to hold onto one's crevice and wait until next year.

Average survival to age of first breeding can be estimated if we make several assumptions. If pairs fledge an average of 1.0 chicks per year (Ainley et al. 1990), and adult survival is 80%, then 40% of fledged chicks would need to survive to breeding age. Average expectation of life after entering the breeding population is about 4.5 years (Cormack 1964). Both of these estimates are very sensitive to the estimated adult survivorship (Hudson 1985).

The presence of nest-site competitors has implications for the SE Farallon guillemot population. If the populations of Tufted Puffins and Rhinoceros Auklets continue to grow, then the guillemot population might decline (Ainley and Boekelheide 1990). The degree of decrease would be limited by the number and distribution of crevices large enough for guillemots, but too small for the larger species. In Bering Sea colonies, size-related interference competition for nest crevices also occurs among hole-nesting auks (Bédard 1969, Divoky 1982, Knudtson and Byrd 1982, Piatt et al. 1990).

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SHORT-TERM VARIATIONS IN WATER-VAPOR PRESSURE IN NESTS OF COMMON CANARIES[1]

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Key words: Common Canary; nest humidity; water-vapor pressure; nesting behavior; Serinus canarius.

The discovery that eggs, regardless of their size, lose similar proportions of water during incubation (Ar and Rahn 1980) generated considerable interest among avian biologists in the water-vapor pressure of the nest (P_N) since it determines how much water is lost from the egg. As a result, P_N has been measured in numerous avian species (Walsberg 1980, Rahn and Paganelli 1990).

However, most of these measurements were made with egg hygrometers which provide only one value of P_N for periods of incubation typically spanning one or more days. Until recently, little information was available concerning variations in the moisture content of nests over short intervals of time. We now have descriptions of such changes, but only from nests of a few large birds, specifically those of (1) swans and geese, where P_N fluctuates as much as 9 torr during 24-hr periods (Howey et al. 1984); (2) ostriches, where it only varies about 4 torr each day (Swart et al. 1987); and (3) ptarmigans, where it scarcely changes at all (Andersen and Steen 1986). No comparable information appears to exist for other birds, particularly small ones. We attempt here to remedy this situation partially by describing short-term variations in the moisture content of Common Canary (*Serinus canarius*) nests.

MATERIALS AND METHODS

We measured P_N in 11 canary nests throughout days 1, 4, 7, and/or 10 of incubation. In all, we collected data for 28 separate days of incubation (Table 1). During 23 of these days, we measured P_N every 15 min; during the other 5 days, at hourly intervals. Our canary hens were experienced birds which had raised broods successfully in previous seasons. However, the data (see below) suggest that some of the males with which they were paired were inexperienced breeders.

Pairs were kept in standard double-brooder cages (23 × 36 × 28 cm) in an indoor aviary. They were exposed to a long daily photoperiod (16L:8D, lights on from 06:00 to 22:00 EDT), air temperatures of 20.3–25.0°C (22.8°C on average), and ambient vapor pressures (P_I) of 7.8–16.7 torr. Within any given day, P_I varied 1.4–6.5 torr (4.1 torr on average; Fig. 1). The birds had access to food and fresh water ad libitum, and received greens and vitamins once or twice a week.

Each cage contained a lined, plastic nest pan in which the hens laid and incubated clutches of 4–5 eggs. The bottom of the nest pan was fitted with a 2-cm diameter scintered bronze (dust) cap. This enabled us to plug a relative humidity probe (Solomat Model HC1) into a nest for 24-hr periods without disturbing the incubating canary. Parts of the cap other than the surface facing the eggs were taped, and the cap itself taped to the probe, so that the only air reaching the sensor came from the nest. When P_N was not being measured, we kept a plug covered with Saran Wrap® in the cap to prevent it from draining heat and moisture from the nest.

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