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SURVIVAL OF BREEDERS IN SANTA CRUZ ISLAND AND MAINLAND CALIFORNIA SCRUB JAY POPULATIONS¹

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The Santa Cruz Island Scrub Jay (*Aphelocoma coerulescens insularis*) is the most morphologically differentiated member of the southern California Channel Islands' endemic avifauna (Johnson 1972). Furthermore, its isolation from mainland Scrub Jay populations provides an opportunity to examine various factors associated with the species' social evolution (Atwood 1980b, Woolfenden and Fitzpatrick 1984).

Although Scrub Jays in general are permanently monogamous throughout their breeding range (Woolfen-

den 1974, Atwood 1980b, Verbeek 1973), other aspects of their social behavior vary dramatically between populations. The Florida Scrub Jay, *A. c. coerulescens*, has a well-developed system of cooperative breeding, in which groups of related birds defend year-round territories and nonbreeders help raise offspring that are not their own (Woolfenden and Fitzpatrick 1984). The principal factor associated with the evolution of this social system is the lack of suitable breeding space within the population's rare, patchy, oak scrub habitat (Woolfenden and Fitzpatrick 1984). All suitable habitat always seems to be occupied by established breeders, which prevents young, subordinate individuals from acquiring nesting space. Consequently, breeding by 1-year-old Florida Scrub Jays is extremely rare (Woolfenden 1974, 1975; Woolfenden and Fitzpatrick 1978, 1984).

In contrast, western mainland Scrub Jay populations

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TABLE 1. Annual survival rates of breeding Santa Cruz Island Scrub Jays (1975–1985).

Year	Males			Females			Mean survival
	<i>n</i>	Deaths	Annual mortality ^a	<i>n</i>	Deaths	Annual mortality	
1975	9	0	0.00	7	1	0.14	0.938
1976	18	0	0.00	16	1	0.06	0.971
1977	19	1	0.05	19	1	0.05	0.947
1978	19	0	0.00	19	1	0.05	0.971
1979	19	1	0.05	21	1	0.05	0.950
1980	19	0	0.00	21	3	0.14	0.925
1981	23	2	0.09	28	3	0.11	0.902
1982	38	6	0.16	42	4	0.10	0.875
1983	40	1	0.03	42	1	0.02	0.976
1984	42	2	0.05	42	2	0.05	0.952
1985	36	3	0.08	35	6	0.17	0.873
Total	282	16	0.05	292	24	0.09	0.935 ± 0.04

^a Based on number of individuals present during indicated year that died prior to the following breeding season. Thus, of 23 males present in 1981, two (0.09) died prior to 1982. See text for further discussion.

do not breed cooperatively (Pitelka 1951, Atwood 1980b). Although few details have been published concerning their social behavior or demography, the presence of yearling breeders in western mainland Scrub Jays has been documented by several investigators (Ritter 1972; Verbeek 1973; Elpers, unpubl. data), suggesting that in these populations suitable nesting habitat frequently is available even to young individuals. Unlike the geographically and ecologically restricted Florida population, western mainland Scrub Jays occur in a wide range of habitats throughout western North America (Pitelka 1951).

Like western mainland forms, Santa Cruz Island Scrub Jays also lack cooperative breeding (Atwood 1980b, 1980c). However, this subspecies resembles the Florida Scrub Jay in that most first-year birds, as well as some older individuals, fail to occupy breeding space and thereby attain reproductive status (Atwood 1980c). Nonbreeding Santa Cruz Island Scrub Jays do not remain on their natal territories and act as helpers, but instead wander along the peripheries of established territories and in suboptimal habitats until breeding space can be acquired (Atwood 1980c).

The demography of these populations in relation to availability of breeding habitat is an important consideration. One index of the extent to which breeding

habitat is saturated is the frequency with which young individuals are able to acquire nesting territories. In relatively nonsaturated habitats, 1-year-old breeders would be predicted to occur more frequently than in saturated habitats where suitable space is occupied by established, older individuals. Data concerning this portion of our research will be presented elsewhere. Here we describe information concerning a second important and related aspect of Scrub Jay demography, namely, the frequency with which established breeders die, thereby creating vacancies in areas known to be suitable nesting habitat. These results are summarized from studies of Scrub Jays on Santa Cruz Island (Atwood and Collins), the southern California mainland (Elpers), and Florida (Woolfenden and Fitzpatrick 1984, unpubl. data).

STUDY AREAS AND METHODS

Santa Cruz Island, located approximately 30 km from the nearest mainland point, is the largest and topographically most diverse of the California Channel Islands, being approximately 249 km² in area and ranging elevationally from sea level to 753 m (Power 1980). It has been part of an island land mass since the early to mid-Pleistocene, although its degree of isolation during the lowered sea levels associated with glacial max-

TABLE 2. Annual survival rates of breeding California mainland Scrub Jays (1981–1985).

Year	Males			Females			Mean survival
	<i>n</i>	Deaths	Annual mortality ^a	<i>n</i>	Deaths	Annual mortality	
1981	6	0	0.00	8	3	0.38	0.786
1982	19	3	0.16	19	4	0.21	0.816
1983	25	5	0.20	26	5	0.19	0.804
1984	31	4	0.13	30	3	0.10	0.885
1985	30	5	0.17	33	3	0.09	0.873
Total	111	17	0.13	116	18	0.19	0.833 ± 0.04

^a Based on number of individuals present during indicated year that died prior to the following breeding season. See text and legend to Table 1 for further discussion.

ima was less than at the present time (Vedder and Howell 1980, Wenner and Johnson 1980). The substantial morphological divergence exhibited by the Santa Cruz Island Scrub Jay, in which linear measurements and body weights average approximately 20% larger than those of the adjacent mainland population (Pitelka 1951, Atwood 1980a), suggests an extended period of genetic isolation. No evidence exists for current interchange between the mainland and island Scrub Jay populations (Pitelka 1951, Jones 1975).

Principal vegetation types in the Santa Cruz Island study area, located near the University of California's Channel Islands Field Station, include (a) chaparral dominated by scrub oak (*Quercus dumosa*) and laurel sumac (*Malosma laurina*), (b) coast live oak (*Quercus agrifolia*) woodland, (c) variably open thickets of mulefat (*Baccharis glandulosa*), (d) introduced *Eucalyptus* groves, and (e) open grassland. Additional descriptions of the study area are provided in Yeaton (1974) and Atwood (1980b).

Mainland California Scrub Jays were studied at the Starr Ranch Wildlife Sanctuary of the National Audubon Society, located approximately 12 km northeast of San Juan Capistrano in the coastal foothills of the Santa Ana Mountains. The approximately 279-ha study area is situated in a major canyon featuring an intermittent stream. Southern oak woodland, dominated by coast live oak and California sycamore (*Platanus racemosa*) characterizes the canyon bottom. Other major vegetation types of the surrounding hillsides and ridges include (a) coastal sage scrub, dominated by California sagebrush (*Artemisia californica*), buckwheat (*Eriogonum fasciculatum*), and laurel sumac and (b) chaparral, dominated by scrub oak and toyon (*Heteromeles arbutifolia*).

Between 1975 and 1986 a total of 651 Santa Cruz Island Scrub Jays were uniquely color-banded; 439 mainland California Scrub Jays were similarly marked between 1980 and 1986. Determinations of sex and breeding status were based on behavior, including vocalizations (Atwood 1978).

Divorce occurs only rarely in known Scrub Jay populations (Woollfenden and Fitzpatrick 1984; Atwood 1980c; Elpers, unpubl. data). In the present analysis, when one member of a pair disappeared and was subsequently replaced by a new individual, the absent bird was assumed to have died. In cases where both members of a pair disappeared, it was usually impossible to distinguish between the scenarios of both birds dying more or less simultaneously and dispersal from the study area of a widowed bird which failed to maintain its territory following the death of its mate. Data from instances in which both members of a pair vanished were used, up to the year of disappearance, in calculating rates of annual mortality (Tables 1 and 2). However, birds belonging to "vanished pairs" were excluded from the regression analyses (Fig. 1).

Statistical analyses were performed using SAS (version 5.18) procedures NPAR1WAY, RANK, and GLM.

RESULTS

No significant difference in annual mortality between males and females were noted on Santa Cruz Island (Table 1; $P = 0.113$, $n = 11$) or in the mainland study population (Table 2; Wilcoxon's two-sample test, $P =$

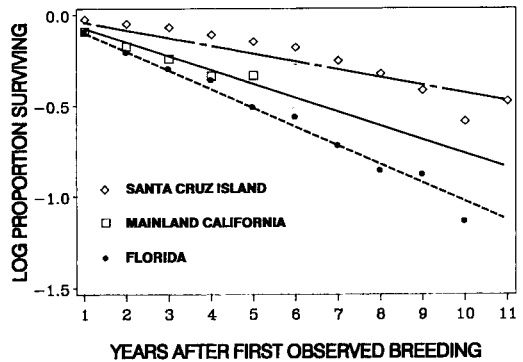


FIGURE 1. Survivorship rates of breeding Scrub Jays from three populations. Regression lines are weighted by sample sizes contributing to each year's survivorship estimate. See text for further discussion.

0.531, $n = 5$). Data presented by Fitzpatrick et al. (1988) also failed to indicate differential rates of mortality between breeding male and female Florida Scrub Jays. Consequently, in order to increase sample sizes for the following comparisons between populations, mortality data from both sexes were pooled.

A Kruskal-Wallis test obtained significant differences in annual mortality, calculated as the percentage of each year's breeders that died prior to the following nesting season, among the three study populations ($F = 11.56$, $P = 0.0004$). Santa Cruz Island Scrub Jays had higher mean survivorship rates ($\bar{x} = 0.94$, $SD = 0.04$, $n = 11$) than samples from either California ($\bar{x} = 0.83$, $SD = 0.04$, $n = 5$) or Florida ($\bar{x} = 0.82$, $SD = 0.09$, $n = 9$; Tukey's studentized range test, $P < 0.05$; $df = 22$; analysis based on ranked data due to small sample sizes). Annual survivorship rates of mainland California and Florida Scrub Jays did not differ significantly from one another ($P > 0.05$).

Linear regressions of survivorship during the years following first documentation of breeding are presented in Figure 1. Following the approach of Woollfenden and Fitzpatrick (1984), samples sizes for the Santa Cruz Island data varied from five individuals that were identified as breeders in 1975 and which could have potentially lived through 11 subsequent breeding seasons to 103 individuals (including those five birds first observed in 1975) that could have been followed for one breeding season. In the data set from mainland California, samples for each year cohort varied from six to 89 individuals. Because of these differences in sample sizes and resultant variation in the reliability of annual survivorship estimates, values were weighted by the number of birds contributing to each estimate. Since the proportion of survivors at year 0 (the initial year in which each bird was identified as a breeder) was by definition 1.00, the intercept of each line was fixed at the origin. In comparisons involving the California mainland sample, which included only 5 years of survivorship data, only the first 5 years of data from the longer-term studies in Florida and on Santa Cruz Island were used.

During the time periods included in this study, breeding Scrub Jays on both Santa Cruz Island and mainland California exhibited relatively constant rates of survivorship (Santa Cruz Island, $r^2 = 0.93$, $P = 0.0001$; mainland California, $r^2 = 0.99$, $P = 0.0001$). Similar results have been found in the Florida Scrub Jay (Woolfenden and Fitzpatrick 1984, Fitzpatrick et al. 1988).

In comparing the slopes of regression lines from each location (Fig. 1), the Santa Cruz Island population showed a significantly higher survivorship rate than both the mainland California Scrub Jay (based on data from years 1–5 only; $F = 35.83$; $P = 0.001$) and the Florida population (years 1–11; $F = 62.26$, $P = 0.0001$). The survivorship rate of the Florida Scrub Jay was lower, though not significantly so, than that of the mainland California population (years 1–5; $F = 4.29$, $P = 0.084$).

Using the slopes of these regression lines as estimates of mortality rates, we calculated annual survivorship with the equation

$$S_y = e^{-d}$$

where S_y represents the proportion of an original sample that survives y years after the first observed breeding season and d represents the instantaneous rate of mortality (Caughley 1977). Based on this approach, Woolfenden and Fitzpatrick (1984) and Fitzpatrick et al. (1988) calculated an annual survival rate of 82% for breeding Scrub Jays in Florida. Our calculations yield annual survivorship rates of 91% ($e^{-0.0945}$) for the Santa Cruz Island population and 83% ($e^{-0.1874}$) for the California mainland population.

DISCUSSION

Once reproductive status has been achieved, Scrub Jays are long lived in comparison with most passerine birds. In fact, the annual survivorship rates reported here, ranging from 91–94% in breeding Santa Cruz Island Scrub Jays, 83% in the mainland California population, and 82% in the Florida Scrub Jay (Woolfenden and Fitzpatrick 1984, Fitzpatrick et al. 1988), are among the highest that have been described for any passerine (Ricklefs 1973). Survivorship between males and females is comparable in all three populations.

The precise circumstances surrounding deaths of breeding jays in all three populations were generally unknown. However, we speculate that higher rates of adult survivorship in the Santa Cruz Island population reflect a relative absence of predators on the island when compared with mainland sites. On the adjacent California mainland and in Florida, opossums (*Didelphus marsupialis*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), longtail weasels (*Mustela frenata*), domestic cats (*Felis catus*), and (in western North America) coyotes (*Canis latrans*) are all potential or known predators on Scrub Jay eggs, nestlings, fledglings, or adults (Burt and Grossenheider 1964, Francis et al. 1989). On Santa Cruz Island, potential mammalian predators are limited to the island fox (*Urocyon littoralis*) and spotted skunk (von Bloeker 1967). Skunk densities on the island are so low as to be negligible as

an important source of avian mortality (von Bloeker 1967; Atwood, pers. observ.), and the diet of island foxes has been described as consisting primarily of insects and vegetable matter (Laughlin 1977).

Stebbins (1966) mentions at least seven species of snakes that prey occasionally on birds or bird eggs and which occur on the southern California mainland adjacent to Santa Cruz Island: gopher snake (*Pituophis melanoleucus*), racer (*Coluber constrictor*), coachwhip (*Masticophis flagellum*), striped racer (*M. lateralis*), rosy boa (*Lichanura trivirgata*), common kingsnake (*Lampropeltis getulus*), and western rattlesnake (*Crotalus viridis*). Of these, only gopher snakes and racers occur on Santa Cruz Island (Savage 1967), and their densities appear to be low compared to mainland sites. Francis et al. (1989) list nine species of snakes that are mobbed by Scrub Jays in Florida, including two species (coachwhip and indigo snake, *Drymarchon corais*) known to prey upon Scrub Jays. Florida Scrub Jays ignored or killed and ate snakes <60 cm in length (Francis et al. 1989); we have never seen snakes longer than approximately 45 cm on Santa Cruz Island.

Raptors are also less diverse on Santa Cruz Island than on the mainland sites; Red-shouldered Hawks (*Buteo lineatus*), Great Horned Owls (*Bubo virginianus*), and screech-owls (*Otus kennicottii* in California and *O. asio* in Florida) are absent from Santa Cruz Island (Jones 1975). The only potentially significant avian predators on volant Santa Cruz Island Scrub Jays are migrant and wintering Sharp-shinned (*Accipiter striatus*) and Cooper's (*A. cooperii*) hawks, both of which probably occur at lower densities on Santa Cruz Island than on the adjacent California mainland (H. Lee Jones, pers. comm.). The relative importance of these two species as predators of Scrub Jays on Santa Cruz Island compared with mainland California and Florida is unknown. However, we note that male Sharp-shinned Hawks are approximately 20% smaller in body mass than Santa Cruz Island Scrub Jays; although we have observed approximately 10 capture attempts by this species, we have never seen a Sharp-shinned Hawk successfully take a Santa Cruz Island Scrub Jay. On the California mainland and in Florida, Sharp-shinned Hawks are more evenly matched in body size with Scrub Jays, and may be a greater source of jay mortality.

Regardless of its cause, the lower rate of annual mortality in the Santa Cruz Island Scrub Jay, when compared with California mainland populations, contributes importantly to habitat saturation of the island subspecies (Atwood 1980b, 1980c). The opportunity for nonbreeding individuals to acquire suitable breeding space that has been left vacant through the death of an established territory holder occurs less frequently on the island than on the California mainland.

The absence of cooperative breeding in the Santa Cruz Island Scrub Jay is not yet fully explained. In both the Florida and Santa Cruz Island populations breeding space is in short supply, and young or subordinate individuals must delay reproduction for several years until they are able to acquire a suitable nesting territory. However, the social behavior of these two populations differs markedly, with Florida Scrub Jays having helpers at the nest, and Santa Cruz Island Scrub

Jays having "floaters" that are not associated with any established breeding territory. Two main hypotheses may be suggested to explain these contrasts.

First, as postulated by Atwood (1980c) and Woolfenden and Fitzpatrick (1984), nonbreeding Scrub Jays on Santa Cruz Island may be able to survive in areas that are unsuitable for breeding territories, whereas such "marginal" habitats are less available to the Florida population. Woolfenden (1974) characterized Florida Scrub Jays as having "extremely narrow habitat tolerances," and suggested that survivorship of nonbreeders in areas outside of suitable breeding habitat would be so low as to select for an alternative strategy, namely, juvenile birds remaining on their natal territories beyond the normal age of dispersal (Woolfenden and Fitzpatrick 1984). On Santa Cruz Island, nonbreeding individuals may be able to survive in marginal habitats or in limited areas of suitable habitat that are located in interstices between established territories without incurring the increased mortality rates postulated for such behavior in the Florida Scrub Jay (Woolfenden and Fitzpatrick 1984). By wandering through such unoccupied areas, nonbreeding Santa Cruz Island Scrub Jays may be better able to search for potential territory openings.

A related factor may be the relative scarcity of predators on Santa Cruz Island. Woolfenden and Fitzpatrick (1984) predicted that "Santa Cruz juveniles, while living and wandering through suboptimal habitat, experience higher survival than would analogous, juvenile dispersers in Florida." Because we have generally been unable to distinguish death from dispersal in nonbreeding Santa Cruz Island Scrub Jays, survivorship data for floaters is presently lacking. However, the lower levels of predation associated with the depauperate insular fauna may contribute to higher survivorship not only among breeding birds but also among nonbreeding individuals. Furthermore, reduced predation pressures on Santa Cruz Island may decrease the importance of one of the main benefits received by breeding pairs that allow auxiliary individuals to help. Woolfenden (1978) and Stallcup and Woolfenden (1978) suggested that predator dissuasion was the principal form of help given by Florida Scrub Jay helpers to the breeders with which they were associated, and Francis et al. (1989) showed that helpers contributed importantly to antipredator mobbing behavior. On Santa Cruz Island, where predation pressure on Scrub Jays is less than in mainland areas, there may simply be less opportunity for nonbreeding individuals to help.

An alternative explanation of the contrasting social structures of Santa Cruz Island and Florida Scrub Jays emphasizes the historical aspects of evolution of sociality in the genus *Aphelocoma*. Because cooperative breeding is a widespread phenomenon among the New World jay lineage, including all three species of *Aphelocoma* (Brown 1970, Pitelka 1951, Woolfenden 1975, Goodwin 1976), well-developed social behavior seems likely to be an ancestral rather than a recent, repeatedly derived characteristic. We concur with Woolfenden and Fitzpatrick (1984) that present-day ecology and demography are important in maintaining the social system of the Florida Scrub Jay, and that these factors probably reflect the 'ghost of selection

past' which led to the initial evolution of helping behavior within the New World jays. However, we do not know how quickly such social systems may evolve. Both Florida and Santa Cruz Island Scrub Jay populations probably became separated from western mainland forms during the Pleistocene (Pitelka 1951, Atwood 1980b, Woolfenden and Fitzpatrick 1984), but the timing of these two isolations relative to each other is unknown. Changes in ecology and population structure may have resulted in the disappearance of cooperative breeding from ancestral western Scrub Jays subsequent to isolation of the Florida population but prior to the establishment of the Santa Cruz Island deme. If true, derivation of the insular form from noncooperatively breeding ancestors, coupled with a relatively short period of genetic isolation, may be important in understanding its present social system. Even though Santa Cruz Island Scrub Jays are now characterized by habitat constraints and population demography similar to those of the cooperatively breeding Florida Scrub Jay, such selective pressures in and of themselves have failed thus far to result in evolution of a comparable social system.

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