SOCIAL INTERACTIONS IN THE SANTA CRUZ ISLAND SCRUB JAY

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ABSTRACT.—I studied social interactions in the genetically isolated Santa Cruz Island Scrub Jay (*Aphelocoma coerulescens insularis*) over a five-year period. A total of 254 individuals, representing most of the population within my approximately 225-ha study area, were color-banded.

This jay resembles known western mainland populations in its breeding biology and the general characteristics of its social system. Pairing is permanently monogamous, and breeders defend established territories throughout the year. This subspecies may include a higher percentage of non-breeding individuals, especially those older than one year of age, than poorly studied western mainland populations.

Populations of both the Santa Cruz Island Scrub Jay and Florida Scrub Jay (*A. c. coerulescens*) appear to saturate suitable nesting habitat. Mortality rates are low, and both populations produce individuals who delay breeding for up to several years. Unlike the ecologically restricted Florida Scrub Jay, the Santa Cruz Island Scrub Jay is ecologically broad, enabling non-breeders to maintain themselves in marginal habitats until such time as breeding space becomes available; cooperative breeding does not occur in *insularis*. Results of this study indicate that when dispersal from natal territories is ecologically feasible, selection does not favor the evolution of group-breeding behavior. The selective value of non-territorial, "floating" behavior by non-breeding Santa Cruz Island Scrub Jays presumably outweighs any possible benefits that might be derived through kin selection. At least in this species, the theory of habitat-forced cooperative breeding appears to explain most of the currently known range of social interactions.

The sociobiology of group-breeding birds has attracted attention, especially for those species characterized by the presence of non-breeding, helping individuals who participate in caring for the young of a breeding pair (Woolfenden 1976, Zahavi 1976, Fry 1977, Emlen 1978). Helpers at the nest have been reported in various taxa, including at least 12 of the 30 species of New World jays (Pitelka 1951, Skutch 1953, 1960, Crossin 1967, Hardy 1969, 1976, Brown 1970, Alvarez 1975, Woolfenden 1975, Raitt and Hardy 1976, 1979). Questions nevertheless remain concerning the evolution of group-breeding behavior, especially the relative importance of selection based on kinship vs. various ecological factors (Brown 1974, 1978, Wilson 1975, Koenig and Pitelka, in press).

Several authors have found an apparent correlation between group-breeding behavior and restricted ecologic distribution in certain New World jays. This suggests that intraspecific competition for breeding space or other limited resources may be an important factor in the evolution of social behavior in these species. Hardy (1961:55),

with reference to the Mexican Jay (*Aphelocoma ultramarina*), stated that "restriction to specific habitats may logically be correlated with highly social breeding habits." Crossin (1967) suggested a similar relationship between group-breeding behavior and ecological restriction in the Tufted Jay (*Cyanocorax dickeyi*). Woolfenden (1974:26) characterized group-breeding Florida Scrub Jays (*Aphelocoma c. coerulescens*) as having "extremely narrow habitat tolerances," and hypothesized that helping behavior in this population "represents a strategy used by nonbreeders to inherit the space necessary for breeding" (Woolfenden and Fitzpatrick 1978:104).

The Scrub Jay (*Aphelocoma coerulescens*) breeds in a wide variety of habitats in the western United States, Florida, and Mexico (Pitelka 1951). Social interactions within the species range from the group-breeding Florida subspecies (Woolfenden 1975) to non-social western mainland populations (Pitelka 1951, Hardy 1961, Brown 1963, Ritter 1972, Stewart et al. 1972, Verbeek 1973). Studies of different Scrub Jay populations could provide useful data con-

cerning the evolutionary basis of group-breeding systems within this and other New World jays.

The Santa Cruz Island Scrub Jay (*A. c. insularis*) is a completely isolated population limited in its geographic distribution to Santa Cruz Island, Santa Barbara County, California (Am. Ornithol. Union 1957). This subspecies shows pronounced morphological divergence from mainland Scrub Jay populations (Pitelka 1951). In several aspects of their breeding habits, such as phenology of nesting, courtship behavior, and nest construction, the island birds resemble those on the mainland (Atwood 1980b). The island population, however, has a very low adult mortality rate and, in comparison with the adjacent mainland subspecies, a reduced clutch size (Atwood 1980b). These attributes of a *K*-selected population, coupled with the physically restricted, insular habitat of the subspecies, suggest that intraspecific competition for breeding space or other resources could be an important selective force shaping the Santa Cruz Island Scrub Jay's social structure. I present here the results of a five-year investigation of these birds' social behavior, and compare them with available data about other Scrub Jay populations.

STUDY AREA

Santa Cruz Island lies directly south of Santa Barbara, California, and is about 29 km from the mainland. Approximately 250 km² in area, it is the largest and most topographically diverse of the California Channel Islands (Raven 1967). The climate is typically mediterranean, with most rainfall occurring during the cool winter months; the summer months are warm and dry.

Recent studies suggest that Santa Cruz Island has been separated from the southern California mainland by a water barrier since early- to mid-Pleistocene times (Vedder and Howell 1980, Wenner and Johnson 1980). The marked morphologic differentiation of island Scrub Jays from mainland forms suggests a considerable period of restricted gene flow between island and mainland populations (Johnson 1972).

Most of my observations were made within an approximately 225-ha study area in the central valley of Santa Cruz Island, immediately west of Stanton Ranch headquarters. Much of this area, as with much of the island, is typical Santa Cruz Island Scrub Jay breeding habitat: either coast live oak (*Quercus agrifolia*) woodland or chaparral dominated by scrub oak (*Quercus dumosa*). The chaparral is patchy on the southern slope exposures, especially on the higher, rocky ridges; by contrast, on north-facing slopes it is dense and continuous. The study area also includes habitats that are either marginal or unsuitable for Scrub Jay nesting activity, such as sparsely vegetated rocky slopes, heavily grazed grassland, open thickets of mulefat (*Baccharis viminea*), and groves of introduced *Eucalyptus* trees. Except for the eucalyptus groves, which are restricted to the island's central valley, the distribution of marginal Scrub Jay habitats in the study area

is comparable to that present on the remainder of Santa Cruz Island. Further description of the study area's climate and vegetation structure is in Yeaton (1974) and Atwood (1980b).

METHODS

I visited Santa Cruz Island on 134 days between November 1974 and June 1979, mostly in 1976–1977. Approximately 600 hours of field observations were completed during the following months: January (17 days), February (4), March (25), April (15), May (24), June (15), July (8), August (8), September (8), October (5), and November (8).

Between January 1975 and June 1979 I captured 254 Scrub Jays and marked them with unique leg band combinations consisting of a numbered U.S.F.W.S. band and three coiled celluloid color bands sealed with either Duco cement (1975) or acetone (1976–1979). Worn color bands were replaced during the study, and only a few color bands were lost.

I aged captured jays according to the shape and coloration of the greater primary coverts and the shape of the rectrices (Pitelka 1945). As most trapping was conducted during the fall and winter, I determined sexes largely on the basis of voice (Atwood 1978) and behavior (Atwood 1980b). The sex of a few individuals could be safely determined by body weight (Atwood 1980a).

Color-banded individuals made up an estimated 80–90% of the population present within the principal study area during the period of my observations. Territory boundaries and movements of marked jays were mapped in the field using a 30-m grid superimposed over an aerial photograph of the study area. Breeding status was determined by observing active nests, courtship feeding, joint participation in territorial defense, or consistent association during foraging activities.

RESULTS

MATING SYSTEM

Santa Cruz Island Scrub Jays appeared to be permanently monogamous in almost all cases. During the study, two pairs lasted together throughout five consecutive years, six pairs lasted throughout four consecutive years, five pairs throughout three consecutive years, and two pairs throughout two consecutive years. I found only five cases of broken pair-bonds from a total of 42 instances for which pair-bond information was available from consecutive breeding seasons. Of these dissolved pairs, one (BS-RG/YS-RW) was caused by the death of one member, and two (GS-GW/RS-GR; SB-YG/SY-WB) were suspected to have suffered this same fate. The remaining two broken pair-bonds (SR-GY/GS-RB; YR-SB/RW-BS) seemed to represent cases of "divorce," since the four individuals involved were alive after they separated.

The jays usually did not breed until their second year, and some individuals did not breed until later. Of 58 known breeding individuals (28 ♂♂, 30 ♀♀) only one, a female, was less than two years of age. Also, 12 of 13 yearlings whose status was known did

TABLE 1.   Formation of new pair-bonds in the Santa Cruz Island Scrub Jay.

Pair (male/female)	Date first observed as a pair	Previous history of male	Previous history of female
GS-GW/BR-SY	10 June 1979	Banded at 2+ years of age on 12 Apr. 1975. Breeder (GS-GW/RS-GR) during 1975–1978. Presumed widowed after 1978 breeding season.	Banded at 2+ years of age on 20 Mar. 1976. Non-breeder during 1976–1978.
BS-RG/BR-SG	9 June 1979	Banded at 2+ years of age on 26 Mar. 1975. Breeder (BS-RG/YS-RW) during 1975–1976. Widowed on 16 May 1976. Unknown breeding status during 1977–1978.	Banded as a fledgling on 14 Sep. 1975. Non-breeder during 1976–1978.
SB-YG/RY-SY	26 Jan. 1976	Banded at 2+ years of age on 27 Mar. 1975. Breeder (SB-YG/SY-WB) during 1975. Presumed widowed after 14 Sep. 1975.	Banded as a yearling on 13 Apr. 1975. Probable non-breeder during 1975.
SG-BG/GS-WB	10 June 1979	Banded as a yearling on 27 May 1976. Non-breeder during 1976–1978.	Banded as a yearling on 11 June 1979.
SR-GY/YB-RS	16 Apr. 1977	Banded at 2+ years of age on 25 Mar. 1975. Breeder (SR-GY/GS-RB) in 1975. Divorced between 13 Sep. 1975 and 20 Mar. 1976. Breeding status unknown during 1976.	Banded at unknown age on 13 Apr. 1975. Unknown breeding status during 1975–1976.
YR-SB/GS-RB	20 Mar. 1976.	Banded at 2+ years of age on 13 Apr. 1975. Breeder (YR-SB/RW-BS) in 1975. Divorced between 13 Sep. 1975 and 20 Mar. 1976.	Banded at 2+ years of age on 25 Mar. 1975. Breeder (SR-GY/GS-RB) in 1975. Divorced between 13 Sep. 1975 and 20 Mar. 1976.

not breed; at least seven of these non-breeders had not formed pair-bonds or begun nesting at two years of age, at least five still had not bred after three years, and at least two did not breed in their fourth year. Two additional individuals, of unknown age when originally banded, remained as non-breeders for at least three consecutive years.

The jays never bred in groups larger than pairs. I watched 20 known breeding pairs for a collective total of 58 breeding seasons, and never saw any "extra" or helping individuals participate in nesting activities or territorial defense. I obtained only limited data on the behavior of recently fledged jays; however, there was no evidence of prolonged family group associations. In the most closely monitored example, the two surviving young of a pair were fed by their parents for approximately 60 days following fledging. I never again saw these fledglings in association with either their parents or their natal territory. Similar data were obtained from several other pairs and their young.

Only female Santa Cruz Island Scrub Jays incubated eggs and brooded nestlings. Males regularly fed females on their nests during incubation. Both members of a pair fed the young and removed fecal sacs.

I was able to observe pair-bond formation on six occasions (Table 1). Of these newly formed pairs, one (YR-SB/GS-RB) included individuals both of which had had prior breeding experience, and one (SR-GY/YB-RS) was composed of a previously established breeder and an individual of unknown prior breeding status. Three cases (GS-GW/BR-SY; BS-RG/BR-SG; SB-YG/RY-SY) involved known breeders mating with birds who had been non-breeders for at least the previous year, with two individuals having been non-breeders for three preceding years. The remaining newly formed pair (SG-BG/GS-WB) included an individual that had been a non-breeder for three consecutive years and the only bird I ever found that bred as a yearling. These limited data indicate that at least some Santa Cruz Island Scrub Jays, even after prolonged periods of non-breeding status, are eventually successful in becoming breeding members of the population.

Santa Cruz Island Scrub Jays are long-lived, with mortality rates of individuals

eight months of age and older being approximately 19% per year (Atwood 1980b). This value is derived largely from observations and recaptures made at trapping stations, and includes both breeders and non-breeders in unknown proportions. Dissection of these data to permit survivorship analysis for individuals of known breeding status greatly reduces the sample sizes. Mortality of established breeders, however, appears to have been low (6% per year based on an initial sample of 22 individuals followed over three consecutive years; 9% per year based on a sample of 14 followed over four consecutive years). Comparable calculations cannot be made for non-breeders, since the disappearance of these non-territorial individuals (see below) could be the result of death or undetected dispersal away from the principal study area. The maximum mortality rate of non-breeders was approximately 25% per year, based on an initial sample of 14 individuals followed over a two-year period. The true mortality rate was probably lower than this. Based on admittedly sparse data, the annual mortality of non-breeding jays appears to have been greater than that of breeders, but failure to achieve breeding status did not result in especially low annual survivorship.

TERRITORIALITY AND FLOCKING

Established breeding pairs maintained year-round territories in which nesting and nearly all maintenance activities occurred. While agonistic behavior diminished following the fledging of young until November, I never saw a complete relaxation of territorial vigilance by breeders. During the actual nesting season I never observed known pairs away from their territories. On about six occasions during late summer and fall, I nevertheless found several pairs foraging briefly in unoccupied areas of marginal habitat that were not included in their defended territories; such areas were within 50 m of the pairs' established territorial boundaries. Even more rarely, concentrations of food attracted pairs considerable distances from their territories. For example, during five hours' observation on 12–13 November 1977 at least 52 individuals fed at a single coast live oak that was bearing a heavy crop of acorns; at least one pair present was approximately 650 m from its territory. Little intraspecific conflict occurred in this instance, not even from the pair whose territory included the tree.

Both sexes participated in territorial defense but males generally assumed more active roles. While agonistic behavior usually consisted only of vocalizations (Atwood 1978) or chases, on 1 May 1977 I observed a defending pair drive a trespassing jay to the ground where physical contact occurred for several seconds before the intruder escaped. I regularly saw jays, especially non-breeders, that were missing feathers on the nape or crown. I suspect that these "bare-headed" individuals had been involved in violent intraspecific interactions, since I observed dominant jays peck subordinate individuals on their heads during trapping operations. In one case, death of the female of a known pair (BS-RG/YS-RW) may have indirectly resulted from such a contact. This individual was found paralyzed on 16 May 1976 near the periphery of her territory, with a number of feathers missing from the nape; motor ability had not returned after four hours and the bird was salvaged as a specimen. It is unlikely that one of the adult jays' few potential predators at this time of year (island fox, *Urocyon littoralis*; American Kestrel, *Falco sparverius*; Saw-whet Owl, *Aegolius acadicus*) would have successfully paralyzed its prey yet allowed it to escape.

Territory boundaries of established pairs remained stable from year to year. Fourteen pairs observed over two years maintained essentially the same territories, as did eight pairs for which such data were available over four breeding seasons. Ten territories mapped during the 1977 breeding season averaged 1.5 ha in area (Fig. 1).

In marked contrast with established breeding pairs, non-breeding individuals were completely non-territorial throughout the year. Although I never witnessed flocking or social aggregation by known breeding pairs, non-breeders regularly occurred in loose groupings, which foraged over extensive areas not included in the defended territories of established pairs (Fig. 1). These areas either were completely unsuitable for Scrub Jay nesting (such as grassland) or were marginal due to limited habitat quality or extent (such as open *Baccharis* vegetation or small, isolated patches of chaparral). Aggression was low among members of non-breeding flocks, and I frequently saw individuals perching or foraging within 3 m of one another without any apparent interaction.

Flocks of non-breeders were usually, but not always, observed in the late afternoon and immediately prior to sunset. I found no evidence that such social behavior resulted
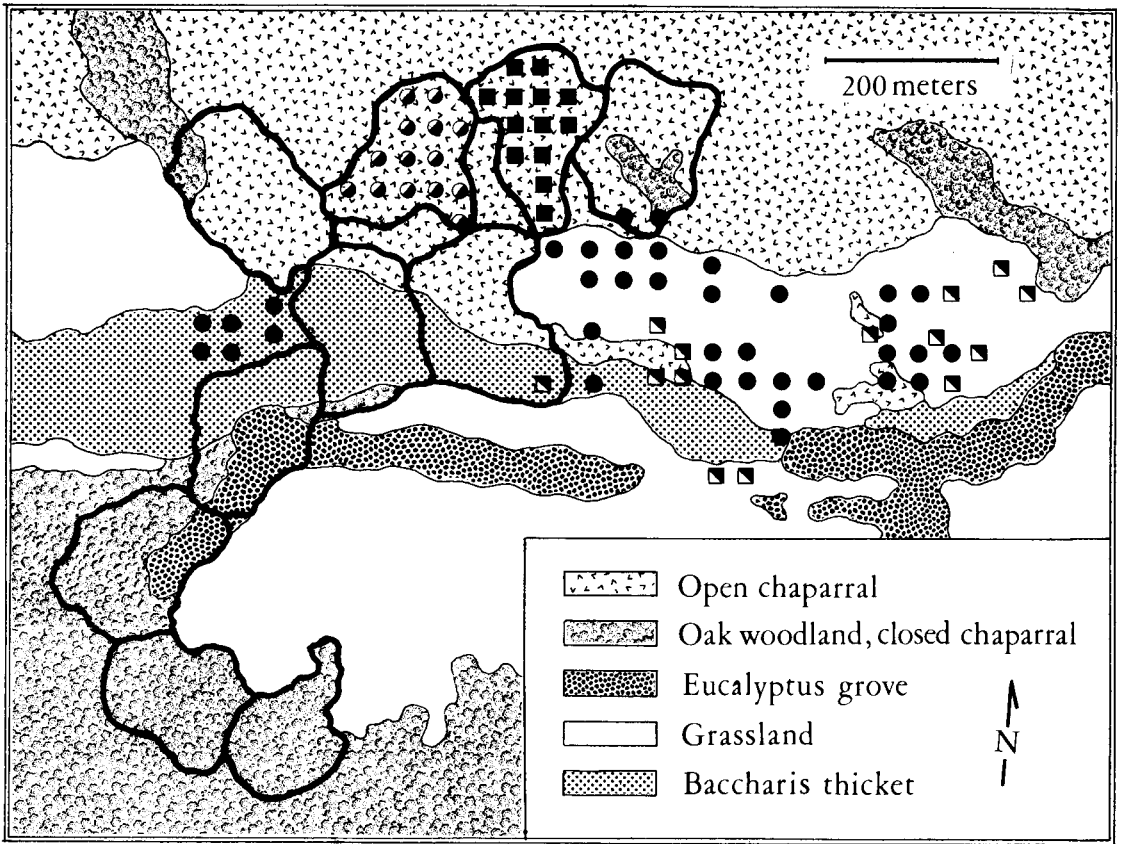
FIGURE 1. Comparative movements of breeding and non-breeding Santa Cruz Island Scrub Jays during the period 13 February–4 June 1977. Territory boundaries of ten breeding pairs are indicated. Movements of two breeding pairs (SR-GW/YB-YS = solid squares; GY-SR/BS-YG = half-shaded circles), one yearling non-breeder (RSR-B = half-shaded squares), and one three-year-old non-breeder (BS-YB = solid circles) are shown by the respective symbols.

from concentrations of food. However, non-breeding jays regularly flew directly from sunny, late afternoon social foraging areas to roosting locations in nearby eucalyptus groves, suggesting that this behavior may resemble the pre-roosting flocking of Clark's Nutcrackers (*Nucifraga columbiana*; Tomback 1978). Social tendencies of non-breeding Santa Cruz Island Scrub Jays may provide benefits associated with flocking such as greater foraging efficiency or predator detection (Moynihan 1962, Pulliam 1973).

Membership in groups of non-breeding jays was not apparently consistent. Although some non-breeders seemed to remain in a general area for up to four years, most individuals that were banded at localities being frequented by groups of non-breeders were never seen again and presumably were transients. For example, I often found numbers of unbanded, probably non-breeding jays during late summer and fall in areas where I had previously done much trapping; such influxes included not only recently fledged young but also many individuals one year of age and older. One such transient, banded on 26 July 1976, had moved about 13 km from the point of initial capture by 19 September 1976.

I could not accurately determine the age composition of these unstable groups of non-breeders. However, non-breeding individuals one to four years of age regularly occurred as members of non-breeding flocks, and I noted two fledglings with such a group within seven days after separation from their parents. Non-breeding flocks were at their maximum size of approximately 25 individuals immediately after the nesting period. They then dwindled, presumably either as a result of death and/or reduction of social tendencies, to small groups of three to five individuals immediately before the next breeding season.

Although non-breeders were most evident when foraging in small flocks in unoccupied areas of marginal habitat, on six occasions I saw solitary jays in suitable hab-
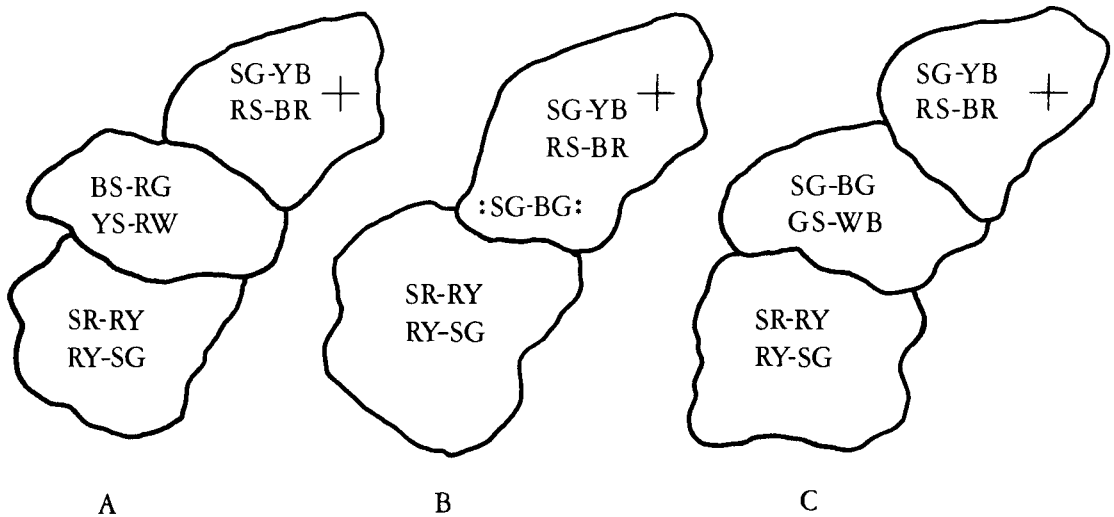
FIGURE 2.   Territory boundaries and non-breeder trespassing behavior in the Santa Cruz Island Scrub Jay. Approximate locations of territory boundaries are indicated for the following breeding seasons: (A) 1975–1976; (B) 1977–1978; and (C) 1979. The location where SG-BG was observed in 1978 as a trespassing non-breeder is also indicated in (B). Note the territorial expansions of SG-YB/RS-BR and SR-RY/RY-SG following the death of YS-RW on 16 May 1977, and the apparent inability of these pairs to defend these enlarged territories from intrusion and subsequent occupation by SG-BG/GS-WB in 1979.

itat included in the territories of breeding pairs. Such non-breeders behaved very secretively, usually perching quietly in dense foliage; if discovered by the resident pair, they were promptly chased from the territory. I rarely observed non-breeders trespassing in established territories, probably because of the activity's inconspicuous nature. However, trespassing may be an important means by which non-breeding Santa Cruz Island Scrub Jays find unoccupied or poorly defended territories and thereby acquire breeding space and status in the population. Two individuals that had been non-breeders during 1976–1978 successfully bred in 1979 in the very areas where I noted them as trespassers during the previous breeding season. In one of these cases, the territory of SG-BG/GS-WB was established around an area where SG-BG was observed trespassing on 19 March 1978; the history of territorial boundaries at this location suggests that the area annexed by this newly formed pair may have been poorly defended by the resident pairs SG-YB/RS-BR and SR-RY/RY-SG (Fig. 2). In a different sequence of events, female BR-SY mated in 1979 with the recently widowed male (GS-GW) on whose established territory I observed her trespassing as a non-breeder on 19 March 1978. Similar behavior has been described in non-breeding, helping Florida Scrub Jays (Woolfenden and Fitzpatrick 1978).

DISCUSSION

In the basic aspects of their breeding biology, mating system, and territorial behavior, Scrub Jays on Santa Cruz Island resemble those in western mainland populations (Table 2). Comparisons are difficult because few long-term detailed studies have been made of social interactions in western mainland forms. Santa Cruz Island Scrub Jays differ from those in Florida in the absence of any form of group-breeding behavior; they resemble each other, however, in the presence of non-breeding individuals up to four years of age (Table 2).

The jays on Santa Cruz Island have a permanently monogamous mating system identical to that described for those in Florida (Woolfenden 1974) and various western mainland subspecies (Hardy 1961, Brown 1963, Ritter 1972, Verbeek 1973). Established pairs of island jays defend discrete territories throughout the year, as do western mainland populations (Hardy 1961, Brown 1963, Verbeek 1973). Widely divergent habitats make statistical comparison of territory size in different western Scrub Jay populations meaningless. It is nonetheless surprising that territories of *insularis*, the largest subspecies, appear to be smaller than or approximately the same size as those of western mainland subspecies (Table 2). If indeed this is the case, the relatively compressed territories of the island birds suggest that the breeding habitat of this popu-

TABLE 2. Comparison of breeding biology and socioecology in populations of the Scrub Jay (*Aphelocoma coerulescens*).

	Western mainland populations[a]	Santa Cruz Island population[b]	Florida population[c]
Subspecies	(*woodhouseii, oocleptica, obscura, superciliosa, californica*)	(*insularis*)	(*coerulescens*)
Mating system	permanently monogamous	permanently monogamous	permanently monogamous
Approximate territory size	2–3 ha	2 ha	8 ha[d]
Adult mortality rate	unknown	19% per year	20% per year
Mean clutch size (sample size)	4.47 (SD = 0.13) (n = 695)	3.71 (SD = 0.70) (n = 121)	3.52 (SD = 0.60) (n = 156)
Clutch size (range)	3–6[e]	2–5	2–5
Occurrence of yearling breeders (frequency, sample size)	probably regular	occasional (0.08, n = 13)	rare (0.01, n = 81)
Ages of known non-breeders	1 year	1–4 years	1–5 years
Ecological tolerance	broad	broad	narrow
Cooperative breeding	absent	absent	present

[a] Based on data presented by Pitelka (1951), Hardy (1961), Brown (1963), Miller and Stebbins (1964), Ritter (1972), Verbeek (1973), Atwood (1980b), Pitelka (pers. comm.), Atwood (unpubl. data).
[b] Based on data presented by Pitelka (1951), Atwood (1980b), this study.
[c] Based on data presented by Woolfenden (1974), Stallcup and Woolfenden (1978), Woolfenden and Fitzpatrick (1978), Atwood (1980b).
[d] Approximate territory size of simple breeding pairs unassisted by helpers (from Woolfenden and Fitzpatrick 1978).
[e] Excluding a single, probably incomplete 2-egg clutch reported from *obscura* (Atwood 1980b).

lation may be saturated. Stable, year-round territories also exist in the Florida Scrub Jay, with territory sizes varying greatly depending on the size of the defending family unit (Stallcup and Woolfenden 1978, Woolfenden and Fitzpatrick 1978). Because single pairs unassisted by helpers have territories much larger than those reported from western subspecies (Table 2), Florida Scrub Jays apparently differ from other populations of the species in their requirements for breeding space.

Yearling Santa Cruz Island Scrub Jays usually did not breed although capable of doing so. Yearlings have been found to be sexually mature in Florida birds (Stallcup and Woolfenden 1978) and several western mainland populations (Ritter 1972, Verbeek 1973); however, there may be significant variation in the frequency with which they actually breed. In the Florida Scrub Jay, a sample of 81 yearlings included only one breeder (Stallcup and Woolfenden 1978), whereas yearling breeders have been frequently reported from limited studies of western mainland populations (Miller and Stebbins 1964, Ritter 1972, Verbeek 1973, Pitelka, pers. comm., Atwood, unpubl. data). Yearling breeding may occur more frequently in *insularis* than in *coerulescens*, but it probably is less common than in western mainland subspecies. Non-breeders older than one year of age occur in *insularis* and *coerulescens*, but have not been

reported from western mainland populations.

The apparently frequent breeding of first-year western mainland Scrub Jays suggests that breeding space often is available even to subordinate and/or inexperienced individuals. Relative to these western mainland forms, the Santa Cruz population exhibits various characteristics of *K*-selection, including reduced clutch size (Atwood 1980b) and greater frequency of non-breeding "floaters"; such characteristics may reflect the physical restriction or "fence-effect" (Krebs et al. 1969) imposed by the insular setting (Emlen 1979). The small clutch size, absence of unoccupied nesting habitat, and large non-breeding population of Florida Scrub Jays (Woolfenden 1974, Woolfenden and Fitzpatrick 1978) likewise suggest that they too experience relatively intense *K*-selection (Cody 1966, MacArthur and Wilson 1967, Pianka 1970). Suitable nesting habitat appears saturated on Santa Cruz Island and in Florida and individuals usually are forced to delay breeding for up to several years.

The most significant comparisons to be made between the Santa Cruz Island and other populations concern the behavior of non-breeders and the subspecies' ecological requirements. In Florida Scrub Jays, which are restricted to a specialized habitat of limited distribution (Hardy 1961, Woolfenden 1974), non-breeders always partici-

pate as helpers in the nesting and territorial defense of an established breeding pair (Woolfenden 1975). Despite the presence of at least some non-breeding individuals, group-breeding has not been found in any western Scrub Jay population, including *insularis*. In contrast to the ecologically narrow *coerulescens*, western populations have broad ecological tolerances as reflected by the variety of habitats they occupy (Pitelka 1951) and by the successful use by non-breeders of marginal habitats unsuitable for nesting.

Koenig and Pitelka (in press) proposed that "among cooperative species there is a lack of areas that are 'marginal' with regard to access to or amount of some limiting resource." Given a population in which annual recruitment exceeds mortality, this ecological setting would be expected to result in a "surplus of individuals effectively unable to disperse to unoccupied habitat and therefore ecologically 'forced' to remain on their natal territories for an indeterminate length of time, during which period they may defer reproduction and assist in the raising of subsequent group offspring" (Koenig and Pitelka, in press). These authors predicted that "the strategy of 'helping' should, in all cases where resource localization is the primary selective force behind it, be adopted by an independent offspring only as a last resort strategy." In other words, non-breeders would be expected to remain on their natal territories as helpers only when dispersal is restricted or prevented by the absence or scarcity of unoccupied marginal habitats in which such individuals are able to maintain themselves at relatively high rates of survivorship.

Comparisons of the Florida Scrub Jay with western jays, including *insularis*, seem consistent with the hypothesis that limited breeding habitat and the ecological inability to use marginal habitats are the primary factors in the evolution of sociality in *coerulescens*. My data indicate that cooperative breeding is *not* selected for when at least moderate survivorship of non-breeders in marginal habitats is ecologically possible. In the ecologically broad Santa Cruz Island Scrub Jay, non-breeders disperse from their natal territories into marginal habitats, which provide adequate resources for their maintenance. By allowing for increased mobility and reduced time spent in defense of a territory, the "floating" behavior of non-breeders presumably increases their chances of rapidly acquiring suitable nesting habitat. Such non-territorial behav-

ior apparently more than compensates for the sacrifice of any possible benefits derived from kin selection, even when several years as a non-breeder may result from the behavior. Although behaviorally quite different, social interactions in both the Santa Cruz Island and the Florida Scrub jays appear to be evolutionarily based mainly on directly "selfish" benefits being obtained by non-breeding individuals.

ACKNOWLEDGMENTS

LITERATURE CITED

ALVAREZ, H. 1975. The social system of the Green Jay in Colombia. Living Bird 14:5–44.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. 5th ed. Am. Ornithol. Union, Baltimore.

ATWOOD, J. L. 1978. The breeding biology of the Santa Cruz Island Scrub Jay, *Aphelocoma coerulescens insularis*. M.A. thesis, California State Univ., Long Beach.

ATWOOD, J. L. 1980a. Body weights of the Santa Cruz Island Scrub Jay. North Am. Bird-Bander 4:148–153.

ATWOOD, J. L. 1980b. Breeding biology of the Santa Cruz Island Scrub Jay, p. 675–688. *In* D. M. Power [ed.], The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Natural History Museum, Santa Barbara, CA.

BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. Condor 65:126–153.

BROWN, J. L. 1970. Cooperative breeding and altruistic behavior in the Mexican Jay, *Aphelocoma ultramarina*. Anim. Behav. 20:395–403.

BROWN, J. L. 1974. Alternate-routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63–80.

BROWN, J. L. 1978. Avian communal breeding systems. Annu. Rev. Ecol. Syst. 9:123–155.

CODY, M. L. 1966. A general theory of clutch size. Evolution 20:174–184.

CROSSIN, R. S. 1967. The breeding biology of the Tufted Jay. Proc. West. Found. Vertebr. Zool. 1:265–299.

EMLEN, J. T. 1979. Land bird densities on Baja California islands. Auk 96:152–167.

EMLEN, S. T. 1978. The evolution of cooperative breeding in birds, p. 245–281. *In* J. R. Krebs and N. B. Davies [eds.], Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford.

FRY, C. H. 1977. The evolutionary significance of co-operative breeding in birds, p. 127–135. *In* B. Stonehouse and C. M. Perrins [eds.], Evolutionary ecology. University Park Press, Baltimore.

HARDY, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kans. Sci. Bull. 42:13–149.

HARDY, J. W. 1969. A taxonomic revision of the New World jays. Condor 71:360–375.

HARDY, J. W. 1976. Comparative breeding behavior and ecology of the Bushy-crested and Nelson San Blas jays. Wilson Bull. 88:96–120.

JOHNSON, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. Condor 74:295–315.

KOENIG, W. D. AND F. A. PITELKA. In press. Ecological factors and kin selection in the evolution of cooperative breeding in birds. *In* R. D. Alexander and D. W. Tinkle [eds.], Natural selection and social behavior: recent research and new theory. Chiron Press, New York.

KREBS, C., B. KELLER, AND R. TAMARIN. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587–607.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Monogr. Popul. Biol. No. 1. Princeton Univ. Press, Princeton, NJ.

MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. of California Press, Berkeley.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithson. Misc. Collect. 143:1–140.

PIANKA, E. R. 1970. On *r*- and *K*-selection. Am. Nat. 104:592–597.

PITELKA, F. A. 1945. Pterylography, molt and age determination of American jays of the genus *Aphelocoma*. Condor 47:229–260.

PITELKA, F. A. 1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. Univ. Calif. Publ. Zool. 50:195–464.

PULLIAM, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38:419–422.

RAITT, R. J., AND J. W. HARDY. 1976. Behavioral ecology of the Yucatan Jay. Wilson Bull. 88:529–554.

RAITT, R. J., AND J. W. HARDY. 1979. Social behavior, habitat and food of the Beechey Jay. Wilson Bull. 91:1–15.

RAVEN, P. H. 1967. The floristics of the California Islands, pp. 57–67. *In* R. N. Philbrick [ed.], Proceedings of the symposium on the biology of the California Islands. Santa Barbara Botanic Gardens, Santa Barbara, CA.

RITTER, L. V. 1972. The breeding biology of Scrub Jays. Unpubl. M.A. thesis, California State Univ., Chico.

SKUTCH, A. F. 1953. The White-throated Magpie Jay. Wilson Bull. 65:68–74.

SKUTCH, A. F. 1960. Life histories of Central American birds, Vol. 2. Pac. Coast Avif. 34:7–593.

STALLCUP, J. A., AND G. E. WOOLFENDEN. 1978. Family status and contributions to breeding by Florida Scrub Jays. Anim. Behav. 26:1144–1156.

STEWART, R. M., S. M. LONG, AND M. STEWART. 1972. Observations on the nest behavior of the California Scrub Jay. Calif. Birds 3:93–95.

TOMBACK. D. F. 1978. Pre-roosting flight of the Clark's Nutcracker. Auk 95:554–562.

VEDDER, J. G., AND D. G. HOWELL. 1980. Topographic evolution of the southern California borderland during late Cenozoic time, p. 7–31. *In* D. M. Power [ed.], The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Natural History Museum, Santa Barbara, CA.

VERBEEK, N. A. M. 1973. The exploitation system of the Yellow-billed Magpie. Univ. Calif. Publ. Zool. 99:1–58.

WENNER, A. M., AND D. L. JOHNSON. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges?, p. 497–530. *In* D. M. Power [ed.], The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Natural History Museum, Santa Barbara, CA.

WILSON, E. O. 1975. Sociobiology: the new synthesis. Harvard Univ. Press, Cambridge, MA.

WOOLFENDEN, G. E. 1974. Nesting and survival in a population of Florida Scrub Jays. Living Bird 12:25–49.

WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. Auk 92:1–15.

WOOLFENDEN, G. E. 1976. Co-operative breeding in American birds. Proc. XVI Int. Ornithol. Congr. (1974):674–684.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. BioScience 28:104–108.

YEATON, R. I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55:959–973.

ZAHAVI, A. 1976. Co-operative nesting in Eurasian birds. Proc. XVI Int. Ornithol. Congr. (1974):685–693.

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