Breeding Biology of the Santa Cruz Island Scrub Jay

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INTRODUCTION

The Santa Cruz Island Scrub Jay, *Aphelocoma coerulescens insularis*, is a genetically isolated population limited in its geographic distribution to Santa Cruz Island, Santa Barbara County, California. This insular form is characterized by rather pronounced morphological differentiation from mainland populations of the same species; its uniqueness was quickly recognized by early observers, who described the jay as "the most interesting bird on the island" (Howell and van Rossem 1911) and "the most sharply differentiated of any of the island species" (Swarth 1918). Yet in spite of this early interest in the Santa Cruz Island Scrub Jay, remarkably little has been published concerning the details of its biology. Most of the recent references to *A. c. insularis* in the literature deal with its morphological characteristics (Pitelka 1951) or possible evolutionary history (Johnson 1972); Yeaton's (1974) ecological analysis of island and mainland bird communities included a cursory examination of the Santa Cruz Island Scrub Jay's foraging niche. Prior to the present study, however, no long-term, detailed field observations of the population had been made. This paper summarizes available data concerning the breeding biology of *A. c. insularis* and provides comparisons of this information with known mainland Scrub Jay populations. The results of an ongoing study of social interactions in the Santa Cruz Island Scrub Jay will be presented elsewhere (Atwood in prep.); brief analyses of the population's vocalizations, feeding ecology, and morphological characteristics are included in Atwood (1978, 1979).

The Santa Cruz Island Scrub Jay was initially described as a distinct species, *Aphelocoma insularis*, on the basis of strong morphological contrasts between the insular population and mainland Scrub Jay races (Henshaw 1886). More recently, the A.O.U. Check-list Committee (1957) considered the Santa Cruz Island Scrub Jay to be a well-marked subspecies of *A. coerulescens*. The question of what constitutes a biologically distinct species is frequently difficult to deal with and, in particular, the lack of sympatry of *A. c. insularis* with any mainland subspecies prevents any natural testing of isolating mechanisms. Pitelka (1951) concluded that "in the absence of natural or experimental proof of intersterility, specific segregation of the Santa Cruz Island form from its mainland relatives would seem to me to distort the facts of relationship which nomenclature attempts to convey."

Pitelka (1951) recognized eighteen subspecies of Scrub Jay which were divided into four major groupings. Numerically, the largest of these is the "*californica*" group, consisting of ten subspecies distributed in Oregon, California, and Baja California. *A. c. insularis* is clearly affiliated with the "*californica*" group (Pitelka 1951).

To appreciate the unique characteristics of the Santa Cruz Island Scrub Jay, it is necessary to briefly evaluate its history as an insular population. Henshaw's (1886) early postulation that vagrant Scrub Jays had become established on Santa Cruz Island probably represents the opinion held by most ornithologists at the turn of the century. Dawson (1920) later stated that

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since the wings of *A. c. insularis* are "too short and weak to permit of its attempting a sheer flight of twenty-five miles," the colonization of Santa Cruz Island "must have been assisted either by storm, or by drifting wreckage used as a refuge, or by human agency . . . or migration occurred at a time when the channel which separates the island from the mainland was much narrower than at present." The improbability of Scrub Jays successfully colonizing Santa Cruz Island via a direct over-water flight of at least eighteen miles (29 km) has been further suggested by more recent data. The low degree of vagility in *A. coerulescens* is evident in the failure of *A. c. insularis* to colonize the apparently suitable habitat of nearby Santa Rosa Island (Miller 1951). Also, recent intensive field work on the avifauna of the Channel Islands has failed to provide records of "vagrant" Scrub Jays from any of the islands (Jones 1975), and the species is unrecorded from Los Coronados Islands, located only eight miles (13 km) from the Mexican mainland (Jehl 1977). Similarly, Johnson (1972) considered the single individual of the species recorded for the Farallon Islands to have arrived probably via "accidental transport to the island, perhaps by ship." Pitelka (1951) described the movements of *A. coerulescens* as rarely involving any but relatively short flights and suggested that this characteristic is associated, at least in part, with a relatively weak humerus present in the species.

Based on the poor colonizing potential of *A. coerulescens*, as well as on early suggestions of possible land bridges between Santa Cruz Island and the mainland, Johnson (1972) concluded that the ancestors of *A. c. insularis* colonized overland "during the peninsular stage of the northern group of islands in the Pleistocene." More recent evidence, however, suggests the absence of such a land connection since at least early to mid-Pleistocene times (Vedder and Howell 1980, Wenner and Johnson 1980). The possibility of Scrub Jays arriving on the island by over-water colonization is increased by Wenner and Johnson's (1980) hypothesis that glacial lowering of the sea level between 70,000 and 10,000 years ago substantially reduced the width of the channel separating the mainland from the offshore land mass.

Regardless of how Scrub Jays reached Santa Cruz Island, the population's morphological divergence from mainland forms indicates an extensive period of genetic isolation (Johnson 1972). A detailed morphogical comparison of *A. c. insularis* with mainland subspecies has been provided by Pitelka (1951).

DESCRIPTION OF STUDY AREA AND METHODS

Santa Cruz Island, located approximately eighteen miles (29 km) from the nearest mainland point, is the largest and most topographically diverse of the Channel Islands. The climate is typically Mediterranean and is similar to that of the adjacent southern California mainland (Yeaton 1974). For the period 1904-72, mean annual rainfall on Santa Cruz Island was 20 inches (50.8 cm) and the mean annual temperature was 60°F (15.6°C) (Laughrin 1977). During the period of this study, rainfall patterns included approximately average conditions during the winter of 1974-75, drought conditions during the winters of 1975-76 and 1976-77, and greater than average precipitation during the winter of 1977-78.

The majority of my data were obtained within an approximately 500-acre area located in the central valley immediately west of the Stanton Ranch headquarters. This area includes typical examples of *A. c. insularis* breeding habitat—specifically, coast live oak woodland and chaparral occurring on both northern and southern slope exposures. Additionally, limited areas of marginal or unsuitable Scrub Jay breeding habitat are present, such as heavily grazed grassland, open *Baccharis* thickets, and groves of introduced *Eucalyptus* trees.

Within the principal study area, scrub oak (*Quercus dumosa*) was the dominant plant species of the chaparral, occurring on both north- and south-facing slopes. Other important plant species included California lilac (*Ceanothus megacarpus* and *C. arboreus*), chamise (*Adenostoma fasciculatum*), lemonadeberry (*Rhus integrifolia*), Catalina cherry (*Prunus lyonii*), toyon (*Heteromeles arbutifolia*), and mountain mahogany (*Cercocarpus betuloides*). Coast live oak (*Quercus agrifolia*) was present in deep canyons on both northern and southern slope exposures. The dense, arborescent, north-facing slope chaparral was nearly continuous in its overall distribution, while chaparral occurring on south-facing slopes was patchy in distribution, being restricted to gullies and shallowly sloped alluvial deposits.

Limited observations of Santa Cruz Island Scrub Jays were made in the insular pine forest located near the head of Christi Canyon. The dominant plant species in this habitat was Bishop pine (*Pinus muricata*); a dense understory composed of toyon, manzanita (*Arctostaphylos* sp.), summer-holly (*Comarostaphylis diversifolia*), and various oak species was usually present.

Santa Cruz Island was visited on a total of 129 days between November 1974 and November 1977. Observations were made during the following months: January (17 days), February (4), March (21), April (15), May (24), June (11), July (8), August (8), September (8), October (5), and November (8). Approximately 600 hours of field work were accomplished during these visits.

A total of 248 individual Santa Cruz Island Scrub Jays were marked with unique color band combinations between January 1975 and November 1977. This figure includes an estimated 80 to 90 per cent of the jay population within the principal study area. Captured birds were aged according to the criteria described by Pitelka (1945); in most cases, sex determination was possible only on the basis of behavioral and vocal characteristics.

To supplement field data on clutch size, nesting chronology, and nest placement, information was obtained from the Western Foundation of Vertebrate Zoology (WFVZ) oological collections. Additionally, L. Kiff (pers. comm.) provided information on similar data housed at the Santa Barbara Museum of Natural History, the San Bernardino County Museum of Natural History, the Museum of Vertebrate Zoology (University of California, Berkeley), the California Academy of Sciences, and the private collection of Nelson D. Hoy.

RESULTS AND DISCUSSION

Social Organization

Although details concerning social interactions in the Santa Cruz Island Scrub Jay will be presented elsewhere (Atwood in prep.), in general, *A. c. insularis* appears to be permanently monogamous in mating, with breeding pairs defending approximately four-acre territories throughout the year. No indication of cooperative breeding, such as has been described in the Florida Scrub Jay, *A. c. coerulescens* (Woolfenden 1975), was observed.

Chronology of Nesting

The primary references in the literature concerning the breeding schedule of the Santa Cruz Island Scrub Jay present variable dates for the peak of the nesting season. Willett (1912) claimed that the nesting season is in April and May, while Dawson (1923) stated that "the Santa Cruz Jay nests early. The last week in March is the height of the season." The extreme published dates for fresh eggs of *A. c. insularis* are 10 March (Dawson 1923) and 7 June (Willett 1912).

The following analysis of nesting chronology in the Santa Cruz Island Scrub Jay is based on the present study, as well as on the data of various egg collectors and ornithologists from 1897-1947 (Beck 1899, L. Kiff, pers. comm.). Two potential sources of error are immediately apparent. The pooled data may be biased by year-to-year variation in the onset of breeding, particularly since nearly 50 per cent of the nests for which specific collection data on the stage of incubation are available were taken during only three years (1906, 1916, and 1927). Annual differences in the initiation of breeding, correlated primarily with climatic variations, have been described for a number of bird species (Van Tyne and Berger 1959), including at least one corvid, the Piñon Jay (*Gymnorhinus cyanocephalus*) (Ligon 1971). In fact, the presence of "severe drought" conditions was suggested early as having a possible influence on the breeding of the Santa Cruz Island Scrub Jay (Mailliard 1899). Ritter (1972) suggested that in *A. c. superciliosa* the timing of egg laying was correlated with ambient temperature. However, based on a considerably greater sample size, Woolfenden (1974) stated that in *A. c. coerulescens* "variation in weather seems to have little effect on the breeding schedule. . . . Drought and warm winter temperatures broke long-term records during the field work, but I observed no changes in the timing of the laying of first clutches." In the absence of evidence to the contrary, I have assumed that, like the Florida Scrub Jay, the chronology of nesting for the Santa Cruz Island Scrub Jay is little affected by annual climatic variations and that the available data for the period 1897-1977 can therefore be combined for analysis.

A second potential source of error relates to the large number of ornithologists whose data have been incorporated into this analysis. Terms describing the stage of incubation undoubtedly vary in usage from one worker to another. Therefore, several arbitrary decisions have been made in determining for each clutch an approximate date for the initiation of incubation. Clutches designated "fresh" have been plotted on the date on which they were found. Based on an estimated incubation period of eighteen days (Woolfenden 1974, Ritter 1972), clutches described as "started," "begun," "⅓," or "commenced" have been plotted an arbitrary six days earlier than the date on which they were actually collected. Similarly, dates for the initiation of incubation for clutches termed "advanced," "½," "¾," "well begun," "well incubated," or "far along" have been defined arbitrarily as being 10 days prior to the actual date of collection. Based on an approximate 21-day nestling stage (Ritter 1972), nests containing young were defined as having begun incubation 30 days prior to the date on which they were actually located (except where more accurate adjustments were possible due to specific information on the age of the nestlings present). These data are presented in Figure 1.

An analysis of nesting chronology in the Santa Cruz Island Scrub Jay indicates that 91 per cent of the recorded incubation initiation dates fall between 15 March and 23 April. Furthermore, 60 per cent of the dates occur during the 15-day period between 19 March and 2 April; excluding the relatively uncertain dates extrapolated from nestlings of unknown age, 51 per cent of the total nest starts still fall between 19 March and 2 April. Figure 1 indicates an apparent peak in egg laying in early March; however, since these data points are composed almost entirely of dates extrapolated from nestlings of unknown age, I suspect that the early March peak in egg laying has no real significance.

The peak of nesting by the Santa Cruz Island Scrub Jay appears to occur during the last two weeks of March. Actually, the period of maximum nesting activity may average slightly earlier than indicated; undoubtedly some of the clutches recorded as "fresh" could have been described as "started," in which case there would have been additional backward projections for the date of incubation initiation. A more extensive computer analysis of Scrub Jay egg data indicates that *A. c. insularis* lays about eleven days earlier, on the average, than the adjacent mainland population (L. Kiff, pers. comm.); the significance of this difference is not yet clear.

I have been unable to obtain any evidence, either from my field study or from the available literature, that the Santa Cruz Island Scrub Jay regularly produces more than a single brood per season. Woolfenden (1974) reported only a single instance of a true second brood attempt from a large sample of Florida Scrub Jay nesting records. The smaller sample of Ritter (1972) included one instance of a true second brood in *A. c. superciliosa*. As with other Scrub Jay populations, *A. c. insularis* rapidly produces replacement clutches following nesting failures. Dawson (1923) mentioned that "in two cases we noted complete sets of five thirteen days after the first had been taken. The quick recovery was the more remarkable in one instance, because the first set had been near hatching." This rapid replacement rate is comparable to that which has been described for the Florida Scrub Jay (Woolfenden 1974) and *A. c. superciliosa* (Ritter

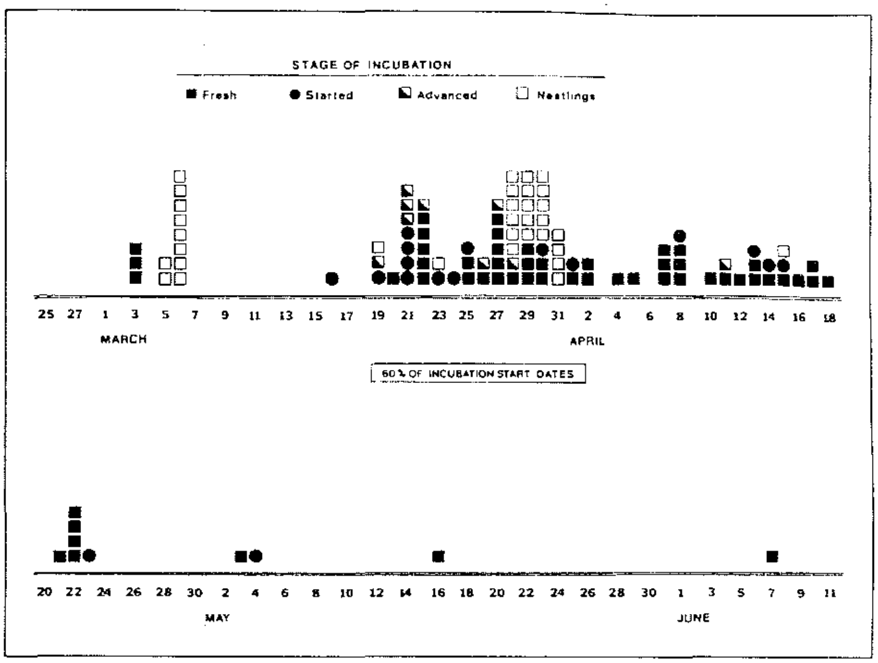

FIGURE 1. *Incubation initiation dates of Santa Cruz Island Scrub Jay nests. Clutches designated "fresh" have been plotted on the date when located; others have been projected backwards according to the stage of incubation (see text). Data for the period 1897-1977 are presented.*

1972). While 7 June is the latest date on which eggs have actually been seen, the observation of "adults feeding at least one well-grown fledgling" on 6 September (Pitelka 1950) probably indicates a nest which would have held eggs during late June or, possibly, early July. Such late dates for active nests probably represent renesting efforts.

As has been suggested for the Florida Scrub Jay (Woolfenden 1974), the timing of breeding in *A. c. insularis* appears to be closely correlated with the annual cycles of the local oak species. Although considered evergreen (Munz 1970), scrub oaks drop most of their leaves during January and February and then rapidly replace them with new foliage during mid-February and March. Leaf replacement in coast live oak is much more gradual; the species never appears largely devoid of leaves as does scrub oak in late winter. Both species flower mainly in March and April and acorns are present from August through November.

An observed increase in arthropods during March and April appears closely linked to the period of flowering and new foliage production in the chaparral plant species, as well as to the increase in ambient temperatures. The increased abundance of arthropods as a food resource is probably the primary factor influencing the breeding schedule of *A. c. insularis*. Similar correlations between the timing of spring production of flowers and new foliage, the period of maximum invertebrate abundance, and the peak of breeding in the Florida Scrub Jay have been suggested by Woolfenden (1974).

Woolfenden (1974) also commented that "if more Scrub Jays bred earlier, desertion of nests would increase because of exposure due to spring leaf fall." This may be true for the Santa Cruz Island Scrub Jay as well. Between late February and early March, much of the island chaparral, including the frequently dominant scrub oak, is decidedly lacking in dense foliage and suitably concealed Scrub Jay nest sites remain scarce until new foliage has been produced. The earliest recorded Santa Cruz Island Scrub Jay clutches are three on 3 March (L. Kiff, pers. comm.). The only one of these for which data concerning nest placement were available was located in the more truly evergreen coast live oak. Similarly, Woolfenden (1974) found that most of the unusually early nests of *A. c. coerulescens* were located in true evergreens rather than in those species subject to pronounced spring leaf fall.

Courtship Behavior

The only form of courtship behavior which I observed in the Santa Cruz Island Scrub Jay was courtship feeding, which was seen on 25 March 1975, 27 April 1975, 5 March 1977, 6 March 1977 (two instances involving different pairs), and 20 March 1977. Three of these cases involved pairs known to have been mated during at least the previous breeding season. I have never definitely observed the formation of a new pair, which may include additional courtship displays. Courtship feeding in *A. c. insularis* appears similar to that which has been described for *A. c. woodhouseii* (Hardy 1961), *A. c. superciliosa* (Ritter 1972), and *A. c. coerulescens* (G.E. Woolfenden, pers. comm.). Courtship feeding away from the nest reportedly is rare in the congeneric Mexican Jay (*Aphelocoma ultramarina*) (Brown 1963).

During courtship feeding, the female jay normally received food from the male without the use of vocalizations or pronounced postural displays. Occasionally I observed the female solicit courtship feeding by crouching slightly in front of the male while making nibbling or probing motions toward his bill. Whether food was actually passed from the male to the female was difficult to discern during most of these contacts. In one instance, the female dropped a small item which she had received from the male and did not retrieve it.

On 25 March 1975, I observed a prolonged example of courtship feeding which continued for approximately 90 minutes. During this period, the female followed the male as he foraged within an area of approximately 12 m radius and gave frequent short, wheezy, begging calls. These were repeated as frequently as every 5 seconds. The female maintained her head, tail, and body in the normal jay perching posture while giving this call, except that the vocalization was usually accompanied by rapid fluttering of her slightly drooped wings. Hardy (1961) stated that in *A. c. woodhouseii* courtship feeding during the nest building period involves "little display by either member of a pair. The feeding is accomplished quickly, with little or no fluttering of the wings by the female. Usually no vocalizations are given but occasionally a suppressed begging call is uttered by both birds or by the female."

Courtship feeding begins prior to egg laying and continues through incubation in both *A. c. californica* (Verbeek 1973) and *A. c. superciliosa* (Ritter 1972). At least two of my observations of courtship feeding away from the nest in the Santa Cruz Island Scrub Jay involved pairs which were known to be engaged in the process of nest construction; the stage of breeding in the remaining cases was unknown. The functions of courtship feeding in the Corvidae have been discussed by Hardy (1961), Brown (1963), and Goodwin (1976). In general, the behavior appears to solidify the pair bond and prepare the male for his future role in feeding the incubating and brooding female, as well as the nestlings.

Nest Construction

Santa Cruz Island Scrub Jays build a typical corvid nest—an open, bulky structure composed of coarse outer sticks and a firm lining of finer twigs and rootlets. The outer structure is usually approximately 30 cm in diameter and 15 cm high. However, these dimensions vary greatly according to the supportive characteristics of the site selected; one nest built in the relatively flexible portions of a *Baccharis* thicket was 45 cm at its greatest diameter. Of the nests which I observed, most of the sticks used in the outer shell were from oaks, although I also identified manzanita, mountain mahogany, chamise, *Baccharis*, and California lilac twigs in various nests. The outer shells of two nests which were dismantled contained 242 and 184 sticks or twigs. The lining cup of most *A. c. insularis* nests is approximately 10 cm in diameter and 7 cm deep; rootlets from a variety of plant species are used, with grasses sometimes being incorporated. Dawson (1923) reported that horsehair rarely was found in the nest lining of the Santa Cruz Island Scrub Jay. As has been found in the Florida Scrub Jay (Woolfenden 1974) and *A. c. superciliosa* (Ritter 1972), *A. c. insularis* does not use foreign materials or mud in the nest lining as do Blue Jays (*Cyanocitta cristata*) (Hardy 1961).

The actual nest building process in the Santa Cruz Island Scrub Jay appears to be similar to that which has been described in *A. c. coerulescens* (Woolfenden 1974), *A. c. superciliosa* (Ritter 1972), and *A. c. woodhouseii* (Hardy 1961) in that both members of a pair participate in the activity. During limited observations of actual nest building, I only saw nesting materials being broken from nearby trees and bushes, rather than being collected from the ground. Twigs which were dropped while flying to the nest site were not retrieved. Woolfenden (1974) reported similar observations for *A. c. coerulescens*. However, according to Ritter (1972) and Hardy (1961), *A. c. superciliosa* and *A. c. woodhouseii* regularly gathered nest building materials from the ground. I encountered no instances of *A. c. insularis* re-using old nests or the materials from old nests. On 30 April 1976, a male Santa Cruz Island Scrub Jay was observed vigorously pulling at several sticks in the outer shell of an old nest located in his territory, but no material was actually removed. Since this individual was clearly agitated by my presence, I suspect that his behavior at the old nest merely represented a displacement response.

Each of the five nests that I observed which were in the process of construction was carried to completion with no indication of incomplete or false nest building as has been described in the Blue Jay (Hardy 1961) and which was previously suggested for *A. c. insularis* (Howell 1917). Woolfenden (1974) stated that Florida Scrub Jays do not make incomplete nests, but Ritter (1972) found that "all pairs of Scrub Jays (*A. c. superciliosa*) observed prior to their building of a complete nest exhibited false nest-building."

Nest Placement

Santa Cruz Island Scrub Jays generally nest in dense bushes and trees where numerous twigs and small branches provide suitable support and concealment. Most nests are placed in terminal branches. In plant species such as mule fat (*Baccharis viminea*) and willow (*Salix* sp.), which lack an abundance of stiff, divergent twigs, nests usually are supported by major branches or by the trunk. All nests are remarkably well concealed and normally are visible only from below.

Santa Cruz Island Scrub Jay nests frequently persist for several years before disintegrating; of the 89 nests located between 1974 and 1977, 21 were found during the year in which they had been constructed and 68 had been built in previous years. The following list presents the number of Santa Cruz Island Scrub Jay nests that have been recorded in each of twelve plant species. The sample size of 172 nests includes those located during the present study, as well as 83 which were found during the period 1897-1947 (L. Kiff, pers. comm.):

Scrub oak (*Quercus dumosa*)—61, including 5 mixed with poison oak (*Toxicodendron diversilobum*) and one each with lemonadeberry (*Rhus integrifolia*), California sagebrush (*Artemesia californica*), and chamise (*Adenostoma fasciculatum*); coast live oak (*Quercus agrifolia*)—32; "oak" (*Quercus* spp., undoubtedly including mainly *Q. dumosa* and *Q. agrifolia*)—28; Catalina cherry (*Prunus lyonii*)—14; Catalina ironwood (*Lyonothamnus floribundus*)—12; lemonadeberry—7, including one mixed with poison

TABLE 1. Nest site preferences of Santa Cruz Island Scrub Jays in two habitats.

Plant species	Chaparral (southern slope exposure) % dominance	Chaparral (southern slope exposure) % of nests ($n=46$)	Chaparral (northern slope exposure) % dominance	Chaparral (northern slope exposure) % of nests ($n=36$)
Quercus dumosa	75	62	51	53
Quercus agrifolia	2	4	27	31
Adenostoma fasciculatum	1	-	8	-
Ceanothus megacarpus	7	2	-	-
Arctostaphylos insularis	-	-	4	3
Cercocarpus betuloides	2	-	3	3
Rhus integrifolia	3	11	1	5
Heteromeles arbutifolia	3	7	2	-
Prunus lyonii	3	7	1	5
Ceanothus arboreus	-	-	1	-
Salix sp.	1	7	-	-
Totals	97	100	98	100

oak; mule fat (*Baccharis viminea*)—5; willow (*Salix* sp.)—4; island manzanita (*Arctostaphylos insularis*)—3; toyon (*Heteromeles arbutifolia*)—3; California lilac (*Ceanothus insularis*)—1; mountain mahogany (*Cercocarpus betuloides*)—1; Bishop pine (*Pinus muricata*)—1.

Table 1 compares the percentage of nests which I found in given plant species with the dominance of those species in the study area; data are provided for the chaparral habitats occurring on both northern and southern slope exposures. The vegetation analysis of each habitat was based on ten randomly selected 25-m transects; the distance along the transect line covered by each plant species was measured and these values were used in calculating the percentage of the total area of woody vegetation occupied by each plant species in the habitat.

On both northern and southern slope exposures, scrub oak was clearly dominant; coast live oak occurred frequently on the northern slope exposures and in the adjacent canyon bottoms. Within the principal study area, Santa Cruz Island Scrub Jays nest primarily in these two oak species. The fact that relatively large numbers of nests were placed in the less frequently occurring lemonadeberry, toyon, Catalina cherry, and willow may indicate that these species are somewhat preferred as nest sites when available. However, in at least the cases of nests built in toyon and willow, these data are probably biased by the nesting preferences of particular pairs of jays. That is, all three nests found in toyon were present in a small, unusually thick stand of this species and are presumed to have been constructed by one pair of jays. Similarly, two of the three nests found in willow were present in a single tree and are known to have been built by a single pair of jays during successive years. Earlier authors have noted the tendency of *A. c. insularis* to nest within a relatively limited area during successive breeding seasons (Dawson 1923).

Few data are available for the nesting preferences of Santa Cruz Island Scrub Jays in the vicinity of the insular pine forests. Although earlier references state that nests are sometimes placed in the pines (Howell and van Rossem 1911, Dawson 1923), I know of only one specific nest which has been recorded in *Pinus*. The only nests which I was able to locate in the pine forest habitat were built in the chaparral understory; most of the pines do not seem to have numerous small, stiff, divergent branches which are necessary for nest support and concealment.

Nest placement for the Santa Cruz Island Scrub Jay has been stated as varying in height from 1.8 to 9.2 m (Blake 1887). Based on estimates made to the nearest 0.5 m, I have recorded nest heights ranging from 1.0 to 18.0 m. For the 89 nests located during the present study, the mean height was 4.0 m and the mode 2.5 m. Including data from 82 additional nests located between 1897 and 1947 (L. Kiff, pers. comm.), the mean for the total sample of 171 nests was 4.3 m and the mode 2.5 m.

Variation in the vegetation structure of different pairs' territories affected the height of nest placement. Nests found in dense thickets of *Baccharis* were at a mean height of 1.2 m (n = 5); suitable nesting sites in this vegetation type were available from ground level to approximately 1.3 m. In the south-facing slope chaparral, where the dense shrub layer extended from ground level to approximately 6.0 m, mean height for nest placement was 3.2 m (n = 45). Within the more arborescent, north-facing slope chaparral and the frequently associated coast live oak woodland, nests were at a mean height of 5.2 m (n = 36); in this habitat, suitable nesting sites were available from approximately 2.5 to 12.0 m.

Clutch Size

In addition to the present field study, data on clutch size for *A. c. insularis* were obtained from specimens housed at the WFVZ and from Beck (1899), Mailliard (1899), Howell and van Rossem (1911), and Kiff (pers. comm.). The mean clutch size for the total sample (n = 121) is 3.71 (*s.d.* = 0.70). Dawson (1923) reported that the Santa Cruz Island Scrub Jay lays "three or four, rarely five" eggs. From the overall sample, 7 nests held two eggs, 31 nests contained three eggs, 73 nests held four eggs, and 10 nests held five eggs. Of the nine active nests I observed in which egg laying progressed to completion, three nests contained three eggs and six nests held four eggs. I have included in this analysis clutch size values based on 10 nests that contained nestlings when found; exclusion of these values resulted in no statistically significant difference in mean clutch size. The fact that some early collectors of *A.c. insularis* eggs routinely selected only larger clutches (L. Kiff, pers. comm.) suggests that the true mean clutch size may be smaller than indicated by the collection data.

Table 2 presents clutch size data obtained primarily from the WFVZ oological collections for the following Scrub Jay populations: *A. c. superciliosa* (including data from Ritter 1972), *woodhouseii, oocleptica, obscura, immanis, californica, coerulescens* (including data from Woolfenden 1974), *cactophila, hypoleuca* (including data from Bancroft 1930 and Bryant 1899), and *insularis*. The mean clutch size of the Santa Cruz Island Scrub Jay is significantly smaller than the mean clutch sizes of both coastal southern California mainland subspecies (*californica* and *obscura*), as well as the more geographically distant populations of *superciliosa, woodhouseii, oocleptica,* and *immanis*. The Santa Cruz Island Scrub Jay is most similar in clutch size to the Florida Scrub Jay; these populations also resemble each other in the absence of six-egg clutches, which have been found in *superciliosa, woodhouseii, oocleptica, obscura, californica,* and *immanis*. Although the sample sizes are small, the two subspecies of Scrub Jay restricted to Baja California (*hypoleuca* and *cactophila*) have mean clutch sizes which are significantly smaller than those of any more northerly Scrub Jay populations for which adequate data were available.

In its reduction of clutch size, the Santa Cruz Island Scrub Jay appears to fit the model of a K-selected population as described by MacArthur and Wilson (1967) and Pianka (1970). Based on Cody's (1966) study of clutch size, MacArthur and Wilson (1967) summarized that "on the seasonal temperate mainland where r-selection is often more important, clutch size should be larger and feeding efficiency somewhat less. On the other hand, the effect should be reduced on

TABLE 2. Clutch size data for ten subspecific populations of *Aphelocoma coerulescens*.

Subspecies	Clutch size 2	3	4	5	6	Sample size	Mean	Standard deviation	95% confidence interval	Range	Mode
hypoleuca	11	9	-	-	-	20	2.45	0.51	2.68-2.22	2-3	2
cactophila	7	7	1	-	-	15	2.60	0.63	2.94-2.26	2-4	2/3
coerulescens	6	66	81	3	-	156	3.52	0.60	3.62-3.42	2-5	4
insularis	7	31	73	10	-	121	3.71	0.70	3.84-3.58	2-5	4
obscura	1	28	88	46	3	166	4.13	0.73	4.24-4.02	2-6	4
californica	-	19	93	50	14	176	4.34	0.77	4.46-4.22	3-6	4
oocleptica	-	7	127	88	16	238	4.47	0.67	4.56-4.38	3-6	4
superciliosa	-	4	18	31	3	56	4.59	0.71	4.78-4.40	3-6	5
woodhouseii	-	2	17	30	10	59	4.81	0.75	5.01-4.61	3-6	5
immanis	-	-	4	14	2	20	4.90	0.55	5.15-4.65	4-6	5

TABLE 3. Survival data for Santa Cruz Island Scrub Jays.

Banding date	Months after banding 0	1	2	3	4	5	6	7	8	9	10	11	12
Jan 1975	3*	3	3	3	1	1	1	1	1	1	1	1	1
Mar 1975	9	9	9	9	9	9	9	8	8	8	8	8	8
Apr 1975	14	14	14	14	14	14	14	14	14	14	14	14	14
Jun 1975	45	34	34	33	33	33	33	33	31	31	29	29	29
Aug 1975	8	7	5	5	5	5	4	4	4	4	4	4	4
Sep 1975	5	5	5	5	5	5	5	5	5	5	5	5	5
Jan 1976	26	20	20	20	20	18	18	16	16	14	14	14	14
Mar 1976	12	11	11	11	11	11	11	9	8	8	8	8	8
May 1976	8	6	6	5	5	5	5	5	5	5	5	4	4
Totals	130	109	107	105	103	101	100	95	92	90	88	87	87

* Numbers indicate minimum number of surviving jays at monthly time intervals.

offshore temperate islands, which enjoy a generally milder, less fluctuating climate." During the initial period of colonization and subsequent expansion by the ancestors of *A. c. insularis*, *r*-selection presumably was operative (MacArthur and Wilson 1967); however, the population's present-day saturation of the insular environment (Atwood in prep.) suggests that *K*-selection is now more important. While additional data concerning the relative climatic stabilities of island and mainland environments are essential for a conclusive analysis, the phenomenon of reduced clutch size in the Santa Cruz Island Scrub Jay is similar to that reported from a variety of other temperate, insular bird populations subject to *K*-selection (Cody 1966).

Reproductive Success and Survival

Although the data on reproductive success are very limited, it appears that nest predation, particularly egg loss, may be high in the Santa Cruz Island Scrub Jay. Of six nests containing eggs which were located during the study period, none successfully reached the nestling stage. Also, nine recently constructed nests located between 1 and 16 May 1976 were empty when found and were not used subsequently; it seems unlikely that all of these broods had successfully fledged prior to these relatively early dates of nest discovery. I suspect that at least several, if not most, of these clutches had been taken by predators. Three additional nests contained young when initially located; all of these successfully produced fledglings.

Potential nest predators are extremely few on Santa Cruz Island, being limited to two species of snake (Blue Racer, *Coluber constrictor*, and Gopher Snake, *Pituophis melanoleucus*), Western Spotted Skunk (*Spilogale gracilis*), Island Fox (*Urocyon littoralis*), Common Raven (*Corvus corax*), and *A. c. insularis* itself. Within my principal study area, snake populations appeared to be quite low; during three years of field work, I encountered only three small Gopher Snakes and one Blue Racer. Similarly, Spotted Skunks have been rare on Santa Cruz Island for at least the past ten years (Laughrin 1977). I never observed a Common Raven engaged in any activity which might be interpreted as searching for the well-concealed nests of small passerines. Therefore, I suspect that most nest predation in *A. c. insularis* results from Island Foxes and, possibly, other Santa Cruz Island Scrub Jays. Additional data concerning the extent and source of nest predation in *A. c. insularis* are currently being sought.

Beyond the fledgling stage, Santa Cruz Island Scrub Jays appear to be relatively long-lived with low adult mortality rates. Table 3 presents survival data for 130 jays that were banded between January 1975 and May 1976; no individuals less than eight months old are included in the sample. From this total sample, 87 individuals (67 per cent) were known to have been alive twelve months following their initial captures. The real survival rate of *A. c. insularis* undoubtedly is much higher. To compensate for unknown dispersal, as well as for birds which were attracted to the trapping station from territories distant from my principal study area, I have chosen to use for the initial population figure only those birds which were present two months following the date of their initial capture. These 107 individuals represent more accurately the resident population which could reasonably be expected to be re-encountered in the study area. On the basis of this analysis, Santa Cruz Island Scrub Jays have an annual survival rate of 81 per cent. Woolfenden (1974) found similarly high values in the Florida Scrub Jay (yearlings, 88 per cent; breeding adults at least two years of age, 80 per cent).

Based on a mortality rate of 19 per cent per year, the average life expectancy of a Santa Cruz Island Scrub Jay which survives the relatively dangerous early months of its fledgling existence (Woolfenden 1974) is 4.8 years.

SUMMARY

In its basic aspects of reproduction, the Santa Cruz Island Scrub Jay appears to resemble western mainland Scrub Jay populations. The peak of the breeding season for *A. c. insularis*

falls during the last two weeks of March. No true second brood attempts were encountered; late nesting records most likely involve replacement clutches.

Observed courtship behavior in the Santa Cruz Island Scrub Jay was limited to courtship feeding, which appeared similar in form and function to that which has been described for *A. c. superciliosa*, *A. c. woodhouseii*, and *A. c. coerulescens*. *A. c. insularis* constructs a typical corvid nest, with both members of the pair participating in the building activity. I observed no indication of false nest building such as has been described in *A. c. superciliosa*. Nests were placed in a wide variety of chaparral and oak woodland plant species, with scrub oak and coast live oak being the most frequently used. Recorded nest heights ranged from 1.0 to 18.0 m, with a mean value of 4.3 m and a mode of 2.5 m.

Mean clutch size for the Santa Cruz Island Scrub Jay is 3.71. Since both adjacent coastal mainland subspecies lay significantly larger clutches, the island population appears to fit MacArthur and Wilson's (1967) hypothesis that well-established, temperate insular forms are more subject to *K*-selection than their more *r*-selected mainland relatives.

Preliminary data suggest that nest predation, especially egg loss, may be high in *A. c. insularis*. Beyond the nest and early fledgling stages, however, Santa Cruz Island Scrub Jays have very low mortality (19 per cent per year); this figure closely resembles that which has been reported in the Florida Scrub Jay.

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Analysis of Avifaunal and Bat Remains from Midden Sites on San Miguel Island

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INTRODUCTION

Remains of birds were recovered from four sites on San Miguel Island excavated by Charles Rozaire for the Los Angeles County Museum of Natural History between 1964 and 1968. This paper reports on the information this excavated material provides on the past avifauna of San Miguel Island, as well as on the role of birds in the subsistence of the aboriginal inhabitants. Preliminary ages, based on artifacts and on information provided by Charles Rozaire, are also reported here. I also describe material from a cave deposit that includes bones referable to *Desmodus stocki*, an extinct species of vampire bat.

The four San Miguel Island deposits are:

SMI 1.—A large village site located on the bluffs overlooking Cuyler Harbor on the north coast of San Miguel. This site was subdivided on a grid and 68 random squares were excavated. Artifacts date occupation of this site from 4770 B.P. to no later than 1400 B.P.

SMI 525.—This excavation consisted of a 5 x 10-ft (1.5 x 3.0 m) test pit sunk along the face of a cliff where several midden and soil layers were exposed on the northwest shore of San Miguel. This site was occupied from 2000 to 400 B.P., with the major period of occupation from 2000 to 1200 B.P.

SMI 261.—This site is a cave at the base of a cliff near Bay Point on the northeast side of San Miguel. The whole interior of the cave was excavated and a trench dug perpendicular to the cave entrance, extending outward about 50 ft (15.2 m). Artifacts indicate that this site and 261A were occupied from 3150 B.P. to no later than 980 B.P.

SMI 261A.—Material from this locality is from a trench along the floor of a vertical fissure in the cliff near SMI 261. At its base, the fissure is about 5 ft (1.5 m) wide.

METHODS

All sites were excavated in 5-ft (1.5 m) squares, 6 inches (15.3 cm) at a time, and sieved with a quarter-inch (6.4 mm) mesh screen. Avian remains were identified with the aid of collections from the University of California at Los Angeles, the Los Angeles County Museum of Natural History, and the Joint Science Department of the Claremont Colleges. Minimum numbers of individuals (MNI) were calculated per level of excavation by summing the frequencies of the most commonly occurring unique skeletal element of each age class for each species. MNI values are biased upward, in that their calculation assumes no vertical scattering of faunal remains as might have occurred due to digging by pot hunters.

Skeletal completeness values (CSI) were calculated using the formula of Thomas (1971) where, for each species:

$$CSI = \frac{\text{number of bones found} \times 100}{\text{MNI} \times \text{estimated number of identifiable elements}}$$

The estimated number of identifiable elements for small birds, where vertebrae and phalanges are lost by sieving, was taken as 25. This is an overestimate for individual species of passerines and for this reason a CSI value is given for passerines as a group. For larger species, where