NESTING ECOLOGY OF SCRUB JAYS IN CHICO, CALIFORNIA

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Twelve races of the Scrub Jay (*Aphelocoma coerulescens*) occupy a geographic range extending from southern Mexico northward over most of western North America to southern Washington and Idaho. Another race is isolated in central Florida (American Ornithologists' Union 1957). Good quantitative information on nesting ecology is available only for the Florida race (*A. c. coerulescens;* Woolfenden 1973, 1975, Stallcup and Woolfenden 1978). Atwood (1978, 1980b) described the breeding biology of the Santa Cruz Island Scrub Jay (*A. c. insularis*), an insular population, but presented few quantitative data on nesting success. Anecdotal information on nesting by other races can be found in Bent (1946), Hardy (1961), Brown (1963), Stewart et al. (1972) and Verbeek (1973). This paper documents basic reproductive parameters of Scrub Jays (*A. c. superciliosa*) in the Sacramento Valley of northern California.

STUDY AREA AND METHODS

I conducted the study along upper Lindo Channel and Big Chico Creek, partly within Bidwell Park in the northeastern section of Chico, Butte County, California. Valley Oak woodland typified the habitat, with an overstory of Valley Oak (*Quercus lobata*), California Sycamore (*Platanus racemosa*), Black Walnut (*Juglans hindsii*), Box Elder (*Acer negundo*), Interior Live Oak (*Quercus wislizenii*) and California Laurel (*Umbellularia californica*). The understory consisted of California Wild Grape (*Vitis californica*), Blue Elderberry (*Sambucus mexicana*), Poison Oak (*Toxicodendron diversiloba*) and California Blackberry (*Rubus vitifolius*). Valley Oak woodlands are characteristically heterogeneous, with oaks dispersed in groves with intervening openings. Data were also collected from other nesting sites in the suburbs of Chico. All study locations were at an elevation of about 70 m (230 ft).

Jays were captured during the autumn and early winter months in ground traps baited with acorns from Valley Oaks. Each captured jay was weighed, aged (Pitelka 1945), banded, and marked with patagial flags to facilitate individual recognition (see Hester 1963).

The sizes of the territory and home range were determined by plotting locations on a field map and connecting the outermost points, to form the largest polygon possible, as described by Odum and Kuenzler (1955). Areas within the polygons were measured with a planimeter. The locations plotted while determining the size of territories were sites of boundary disputes during the breeding season. In the case of home range measurements, the pair's locations throughout the year were plotted.

Observations were made on 119 nests from January 1971 through June 1974. Nests were located by searching likely spots and by observing nest-building or food-carrying behavior. Nest height and nesting substrate were recorded at each active nest. I also recorded the date of initiation of each

clutch, clutch size, incubation period, numbers of eggs hatched and young fledged, and fledging period or cause of failure of a clutch. To obtain these data, I visited each nest at 3- to 5-day intervals and watched selected nests from blinds. Incubation periods were determined only for nests whose histories were carefully observed from beginning to end. Nest visits were kept brief to minimize altering the normal nesting activity or nest predation.

Nesting success was calculated using "egg-day" and "nestling-day" as units of exposure (Mayfield 1975). Calculations of nesting success assumed a 5-day egg-laying period, an 18-day incubation period and a 16-day nestling period. When calculating "egg-day" and "nestling-day," losses were assumed to have occurred midway through the interval between visits to the nest. Johnson's (1979) method was used to develop standard errors of daily mortality rates of eggs and nestlings. Furthermore, his ratio test was used to statistically compare mortality rates between stages of the nesting cycle, between initial and renest attempts, and between years. Hatching success was determined for nests that were found before hatching and that remained undisturbed through this phase of the incubation period. Nest failure was generally classified as caused by either predation or weather, depending on the appearance of the nest and its contents.

RESULTS AND DISCUSSION

SOCIAL INTERACTIONS AND TERRITORIALITY

Thirty-six adult jays and 66 birds of the year were banded and marked, mostly in 1970-1972. Trapping and field observations of social interactions were concentrated along upper Lindo Channel, where one or both members of six adjacent pairs of territory holders were marked. Breeding Scrub Jays in Chico appear to be resident, monogamous for life, and to recognize discrete territorial boundaries only during the breeding season. All activity during the breeding period was confined to the defended area, meeting criteria of the type "A" territory of Hinde (1956). Three pairs of Scrub Jays, which were marked in the fall of 1970 and observed regularly until June 1974, occupied the general vicinity of their capture locations throughout that period. Two of those pairs held territories with almost identical boundaries through four breeding seasons.

Other studies have suggested that Scrub Jays in the West maintain permanent pair bonds and year-round territories, although "territory" is not defined in these studies (Pitelka 1951; Hardy 1961; Brown 1963; Verbeek 1973; Atwood 1978, 1980a, 1980b). Florida Scrub Jays exhibit cooperative breeding and have year-round territories, with size depending on the number in the family unit (Stallcup and Woolfenden 1978, Woolfenden and Fitzpatrick 1978). The intensity of territorial disputes during the nonbreeding period seems to differ among localities. Verbeek (1973) found intense territorial defense throughout the year in Scrub Jays (*A. c. californica*) in Monterey County, California. Atwood (1980a, 1980b) noted a relaxation in territory defense during the nonbreeding season among Santa Cruz Island Scrub Jays. And among Scrub Jays (*A. c. oocleptica*) in Berkeley, California, Brown (1963) described a dominance hierarchy in which, during the nonbreeding

season, territory holders were dominant over all other jays that occurred in the area of their breeding territory.

During autumn and winter, Scrub Jays in Chico sometimes form loose aggregations of up to 10 birds, which may be partly familial. For example, three nestlings from the same nest that were banded during the spring of 1971 were recaptured within 100 m of the nest the following October to December. First-year birds seemed to make up a large proportion of flock members. Aggregations of jays often were observed in old territories of known breeders and were loosely associated with the resident pair. The nonbreeding ranges of adjacent territory holders, where one or both birds of the resident pairs were marked, often overlapped, but rarely were they observed to aggregate longer than about 15 minutes. Flocks of jays, as noted by Atwood (1980a), were not observed during the breeding season.

Aggressive encounters were frequent during the nonbreeding season, usually over food. It was common to see a jay chase and supplant another that was carrying food. Such supplanting flights typically followed circular paths, rather than linear flights typical of most territorial disputes.

Approximate territory size in western mainland and Santa Cruz Island Scrub Jay populations was 2 to 3 ha (Atwood 1980b). Florida Scrub Jays unassisted by helpers had territories of approximately 8 ha. Five territories of Scrub Jays in Chico averaged 2.2 ha (s.d. = 0.84, range = 1.0 to 3.1). During the nonbreeding period, marked pairs were seen most often in the area defended during the breeding season. However, considerable extension of their movements occurred during the nonbreeding season. The home ranges of two pairs throughout a 24-month period covered 4.9 ha and 5.4 ha.

NEST-SITE PREFERENCE

Four plant species, California Wild Grape, Blue Elderberry, Interior Live Oak and Coffeeberry, provided nest cover for 84% of all nests. Use of these cover species suggests that concealment of the nest was a primary factor in selection of plant species for nest placement. Nest-building typically occurred before most species of deciduous shrubs and trees had renewed their foliage. More nests were built in California Wild Grape vines than in any other cover species, and although this is a deciduous species, branch tangles provided protection from possible predation before new foliage provided concealment (but see section on nesting success). Blue Elderberry is among the first of the deciduous plants to renew its foliage in the spring, and it was typically in full leaf by the time jays built nests in it. Interior Live Oak and Coffeeberry are evergreen. All 19 nests found in suburban habitat were placed in evergreen shrubs and trees.

Variation among nesting sites was great. Nests were placed in terminal branches, the forks of branches, the forks of tree trunks, on lateral branches, and in vines.

Figure 1 shows the percentages of nests in various height intervals above the ground. Taking the 4 years together, just over 50% of the nests were placed from 2 to 4 m above the ground. The relatively large percentage of nests found above 6 m in 1972 may be due to the sampling variation present with small sample sizes. The height of 119 nests ranged from 0.6 to 15.2 m, with a

mean of 3.4 m (s.d. = 1.94 m). The mean nest heights were not significantly different between years (ANOVA). I found no significant difference in nest height of first ($\bar{x}$ = 2.8 m, s.d. = 1.14) and second ($\bar{x}$ = 3.6 m, s.d. = 1.82) nesting attempts. The sampled nest heights were similar to those of the Santa Cruz Island Scrub Jay ($\bar{x}$ = 4.0 m, n = 89; Atwood 1980a, 1980b) but higher than those of the Florida Scrub Jay ($\bar{x}$ = 1.2 m, n = 123; Woolfenden 1973) and Scrub Jays in Monterey County ($\bar{x}$ = 1.6 m, n = 25; Verbeek 1973).

NEST CONSTRUCTION

Jays were first observed building false nests in late February and early March. All pairs of jays observed prior to their building a complete, functional nest exhibited false nest-building. The false nest involved the arranging of one to several dozen sticks at a site (Ritter 1972). Among four pairs for which the onset of false nest-building was determined, an average of 12.8 days (s.d. = 5.2) was spent carrying materials to various false nests before starting a functional nest. An average of 12.7 days (n = 7, s.d. = 4.84) was required to complete a functional nest. No quantitative data are available on duration of nest-building by other subspecies of Scrub Jays. During favorable weather, nest building by Pinyon Jays (*Gymnorhinus cyanocephalus*) averaged 7.3 days (n = 21) and ranged from 5 to 9 days (Balda and Bateman 1972).

Nest-building by Scrub Jays in Chico was completed an average of 7.9 days (s.d. = 2.85, range = 5 to 12 days, n = 7) before initial oviposition. Woolfenden (1973) found the interval between building and egg-laying to be approximately 15, 16 and 17 days in three nests of Florida Scrub Jays. Pinyon Jays seem to have a much shorter transition period than Scrub Jays, averaging 2.3 days (range 1 to 5 days, n = 21; Balda and Bateman 1972).

EGG-LAYING AND INCUBATION

The earliest record I have of egg-laying in known first clutches was on 10 March 1972, and the latest was on 20 April 1973. Approximately 92% of all egg-laying occurred during the last week in March and the first week in April (Figure 2). Davis (1953) observed egg-laying from late March to late April in Butte County. Breeding chronology was similar for the Santa Cruz Island Scrub Jay (Atwood 1978, 1980b) and Scrub Jays in Monterey County (Verbeek 1973).

Mean, biweekly air temperatures are also presented in Figure 2. These data suggest that higher temperatures during nest-building in 1972 and 1974 than in 1971 or 1973 may have stimulated earlier oviposition. Earlier laying dates were correlated with higher air temperatures in the period prior to egg-laying in the Rook (*Corvus frugilegus*; Owen 1959) and the Black-billed Magpie (*Pica pica*; Erpino 1968). The chronology of nesting in the Santa Cruz Island Scrub Jay seemed little affected by annual climatic variations (Atwood 1978, 1980b).

Sixty-four completed clutches were examined. One egg was deposited daily until a clutch was completed, conforming to a general pattern found among corvids (Holyoak 1967). Clutch size ranged from four to six ($\bar{x}$ = 4.8,

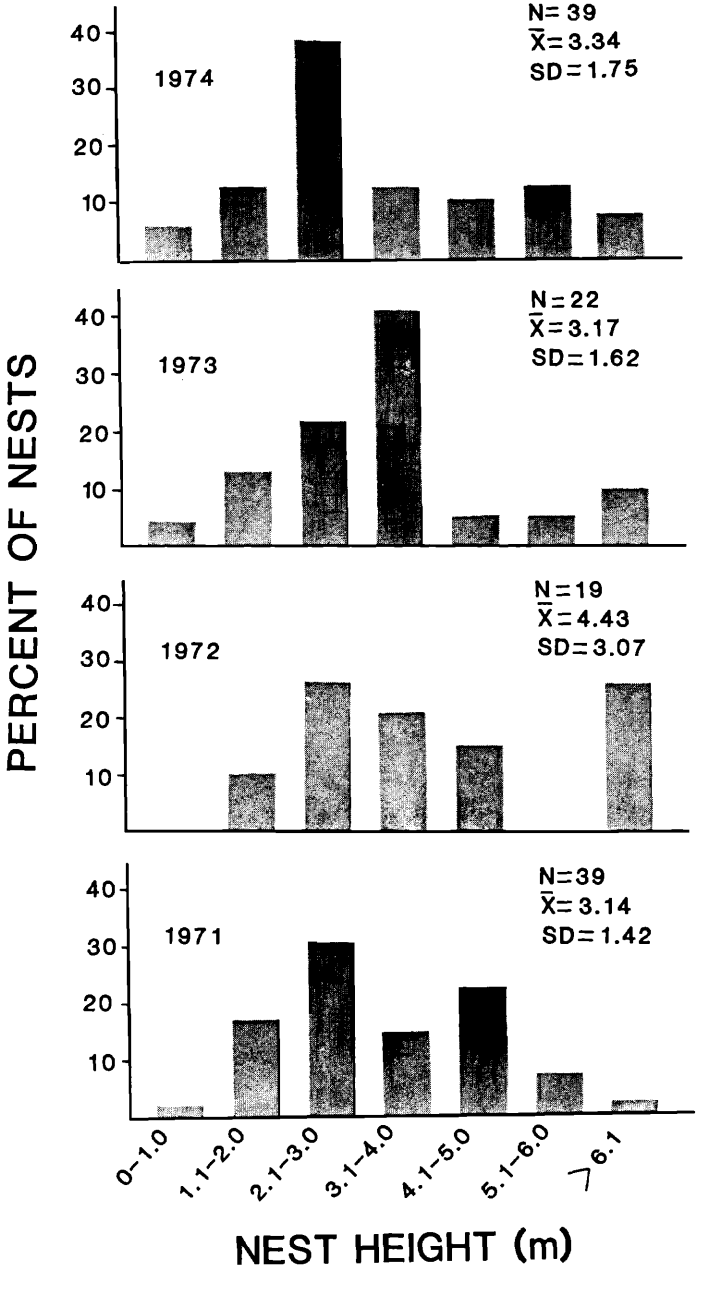

Figure 1. Height intervals of Scrub Jay nests in Chico, Butte County, California.

s.d. = 0.62). The modal clutch contained five eggs and comprised 57.8% of my sample. The differences in mean clutch size between years were not significant (ANOVA). For many bird species, including the Florida Scrub Jay (Woolfenden 1973), clutch size decreases as the nesting season progresses, with renesting attempts producing fewer eggs (Davis 1955, Klomp 1970).

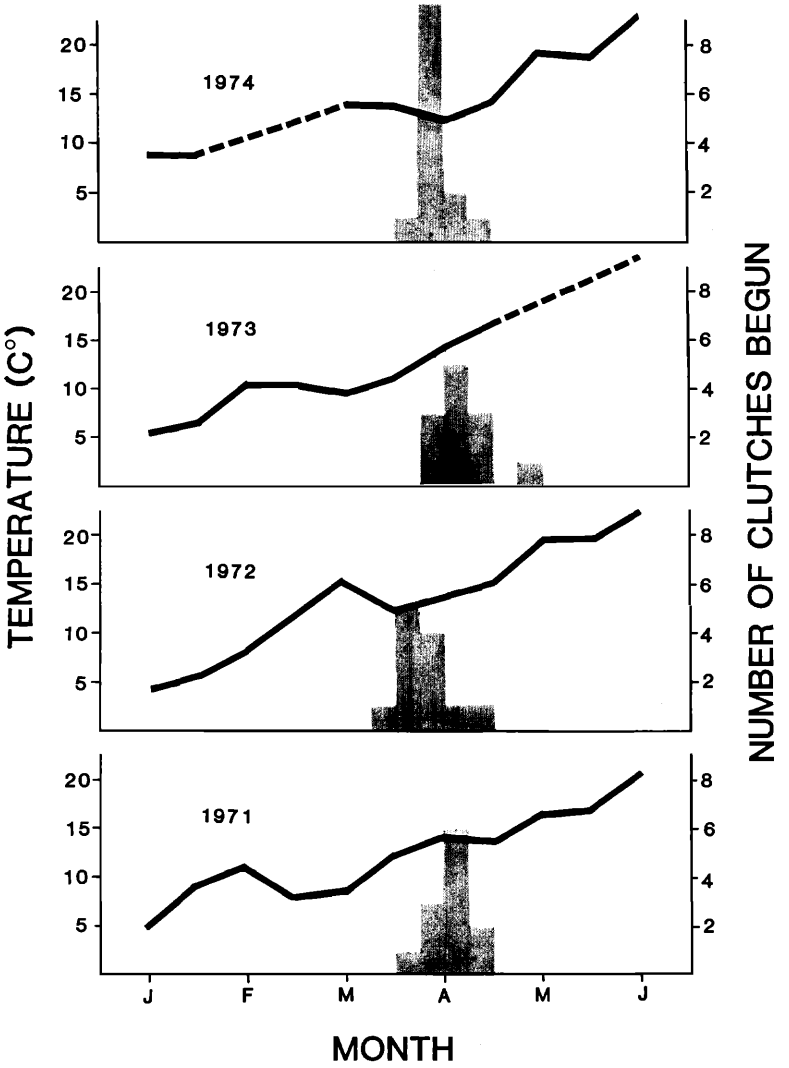

Figure 2. Scrub Jay egg-laying dates plotted at weekly intervals (shaded), and mean, biweekly air temperatures.

However, mean size of initial clutches in this study ($\bar{x}$ = 4.8, s.d. = 0.62, n = 48) was not significantly different from that of renesting efforts ($\bar{x}$ = 4.8, s.d. = 0.65, n = 16). Some marked jays of both sexes were found to nest successfully in their first year, but insufficient data were obtained to analyze properly the relationship among age of the bird, clutch size, date of clutch initiation or nesting success. Of 32 nesting jays of known-age, eight (25%) were first-year birds.

Clutch sizes found in this study were apparently larger than those reported in other races of Scrub Jays: Monterey County—$\bar{x}$ = 3.9, n = 29, range = 2 to 5 (Verbeek 1973); Santa Cruz Island—$\bar{x}$ = 3.7, s.d. = 0.70, n = 121, range = 2 to 5 (Atwood 1980b); and Florida—$\bar{x}$ = 3.4, s.d. = 0.60, n = 101, range = 2 to 5 (Woolfenden 1973). Atwood (1980a) suggests that reduced clutch size in the Santa Cruz Island and Florida Scrub Jays may have resulted from intense K-selection.

"Incubation period" in this study refers to the time between the laying and hatching of the last egg (Kendeigh 1963). Hatching of all eggs in a clutch required from 1 to 2 days. No attempt was made to study the relationship between the orders of laying and hatching. The average incubation period was 18.2 days (s.d. = 0.45, range = 18 to 19, n = 15). Incubation persisted for 28 days and 29 days at two nests in which the eggs failed to hatch. In a Scrub Jay nest in Marin County, California, incubation lasted 18 days and the young hatched one at a time during a 2-day period (Stewart et al. 1972). Verbeek (1973) found an incubation period of 17 to 18 days for Scrub Jays in Monterey County, and Stallcup and Woolfenden (1978) reported an incubation period of 16 to 19 days in the Florida Scrub Jay.

NESTING SUCCESS

Mayfield (1961, 1975) suggested that data on nesting mortality are most meaningful when reported as a mortality rate rather than as percentages of the nests observed and the total eggs laid that hatched or fledged, and that mortality and survival are best reported as probabilities. He further suggested that data be reduced to units of exposure that reflect not only the number of nests but the length of time each nest was observed. This method places all nests on a comparable basis by using only information from the period during which a nest was under observation, regardless of the developmental stage and knowledge of outcome. This method reduces the bias inherent in nesting success rates calculated by the traditional method (Johnson 1979).

Nest success based on Mayfield's (1961, 1975) exposure method is summarized in Table 1. Egg-laying apparently did not occur in 28% of the nests found completed and lined. Virtually all nests begun by Florida Scrub Jays receive eggs (Woolfenden pers. comm.). Considering only those nests in this study in which egg-laying occurred, success ranged from 21% in 1974 to 47% in 1972. Egg-laying in some nests may have been undetected, because of possible predation between visits and the subsequent abandonment of the nest. Nests in which egg-laying did not occur may reflect breeding inexperience of the territorial pair. However, a pair of marked adult jays established territories, constructed nests, and performed courtship feeding in 1971 and 1972, but failed to lay eggs or build a second nest either year.

Table 1. Success of Scrub Jay nests according to stage of the nesting cycle.

Year	Number nests[1]	Percent active nests[2]	Percent successful				
			Laying[3]	Incub.[3]	Hatching[4]	Nestling[3]	Overall success[5]
1971	32	72 (23)[6]	91	70	78	75	27
1972	19	69 (13)	80	100	75	79	33
1973	21	67 (14)	81	81	87	63	24
1974	33	79 (26)	72	51	83	68	16
Combined	105	72 (76)	82	72	81	71	24

[1]Number of accessible nests found.
[2]Nests in which egg-laying occurred.
[3]Percent successful based on "egg-days" or "nestling-days" (Mayfield 1975).
[4]Number of eggs hatched divided by the number of eggs in the nest at the time of hatching.
[5]Percentage of nests found prior to egg-laying from which at least one young fledged (percent active nests × laying success × incubation success × hatching success × nestling success = overall success).
[6]Number of active nests.

Except during the incubation period, factors affecting nesting outcome seemed to be consistent from year to year (Table 1). Results of ratio tests (Johnson 1979:657) indicated no significant difference between years during laying and nestling periods. Similarly, no significant difference was found between stages during any year (laying vs. incubation, laying vs. nestling, and incubation vs. nestling), suggesting a constant daily mortality rate throughout the nesting period. Only between the 1972 and 1974 incubation periods was a significant difference found (Johnson's ratio test, $P < 0.05$). The difference in mortality rates during the two incubation periods was attributed to higher predation in 1974, particularly during first nesting attempts. The lack of observed egg mortality during the 1972 incubation stage was probably due to a small sample size.

Woolfenden (1973) reported a hatching success of 92% and an overall nesting success of 43% in the Florida Scrub Jay. However, he calculated nesting success as the percentage of nests with eggs fledging at least one young. On a comparable basis, Scrub Jays near Chico had an overall nesting success of 54%. In general Scrub Jays have higher breeding success than other above-ground, open-nesting, altricial birds reported by Ricklefs (1969) and Nolan (1963), and most such species recorded by Best and Stauffer (1980).

Ricklefs (1969) indicates that predation is the main cause of nesting mortality among birds in general, and Woolfenden (1978) concluded that predation accounted for 80% of all nestling losses in Florida Scrub Jays. Similarly, predation was the greatest single cause of egg and nestling loss among Scrub Jays in this study. Predation accounted for 56 and 73% of egg and nestling mortality, respectively. I believe that Gray Squirrels (*Sciurus griseus*) and

Common Crows (*Corvus brachyrhynchos*) were the main predators involved. Intense scolding by jays towards those species was common during the breeding season. Holyoak (1967) found European Gray Squirrels (*S. carolinensis*) to be the main mammalian predator on British corvids. Likewise, Abert's Tassel-eared Squirrels (*S. aberti*) were the chief predators on Pinyon Jay eggs and nestlings (Balda and Bateman 1972). Destruction of eggs and young by corvids is well-documented (Jones and Hungerford 1972, Mulder et al. 1978).

One case of nest predation was likely the work of a Great Horned Owl (*Bubo virginianus*), as its feathers were found in and near the nest after it was found depredated. Three nestlings were missing from that nest, and remains of a fourth young and the adult female were in the nest.

Of 54 nests examined shortly after hatching, four clutches apparently failed to hatch because of infertility or early embryo death. One pair of jays was involved in two such nesting attempts. No attempt was made to examine all unhatched eggs, but some that were examined showed embryo death. Thirty-four percent of egg losses were attributed to hatching failure. Weather-caused nest destruction accounted for 5% of egg losses. Death by starvation of nestlings was limited to runts, but accounted for 18% of the nestling losses, and several nestlings were found strangled in nest fibers.

Seventeen eggs from five nests were taken during laying. Although eggs were removed throughout the incubation period, heaviest losses occurred during the first 12 days. Likewise, Best (1978) found predation to be lower late in the incubation period for Field Sparrows (*Spizella pusilla*). No trend was seen in the rate of nestling loss with age of the nestlings. Although greater nest mortality occurred during the incubation period than the nestling period, the difference was not significant.

Woolfenden (1973) reported renesting to be less successful than first nesting attempts among Florida Scrub Jays, but I found renesting attempts to be more successful (Johnson's ratio test, $P < 0.05$). Possible factors contributing to this difference were increased availability of nesting sites resulting from foliage development, the freeing of time for closer nest attentiveness, because less time was spent in territorial duties following the establishment of territory boundaries (Ritter 1972), and milder weather.

Differences in choice of nesting vegetation forms were not associated with differences in nesting success. Ten of 21 nests (48%) found in trees were successful; 14 of 28 (50%) found in shrubs were successful; and 13 of 25 (52%) found in vines were successful. These differences are not significant ($\chi^2 = 0.08$, 2 df, $P > 0.99$). Similarly, differences in success as related to nest heights were not statistically significant. Three of 6 nests (50%) placed from 0 to 1.5 m above the ground were successful; 21 of 38 (55%) in the 1.6- to 3.0-m interval were successful; 13 of 23 (56%) in the 3.1- to 4.5-m interval were successful; and 6 of 11 (54%) above 4.6 m were successful ($\chi^2 \doteq 0.11$, df = 3, $P > 0.99$).

NESTLING AND FLEDGLING PERIOD

The period from hatching to fledging averaged 20.0 days (s.d. = 2.61, range = 16 to 26 days, n = 27). The mean nestling period likely would have

been longer, but the young at three nests left the nest during my visits late in this period (16+ days). The nesting period for Florida Scrub Jays ranged from 12 to 21 days but seemed to vary with the amount of human handling (Woolfenden 1978). Nestling periods among Scrub Jays in Monterey County ranged from 20 to 24 days (Verbeek 1973).

The average number of young fledged per breeding effort (mean clutch size × probability of success) was 1.1 for all nests found and 1.5 considering only active nests. Florida Scrub Jays raised an average of 1.1 fledglings per completed nest (Woolfenden 1973). On a comparable basis, Scrub Jays in this study raised 1.4 fledglings per completed nest.

Parents of four broods continued to feed their young an average of 34.3 days (s.d. = 2.87, range = 32 to 38) after they had fledged. This corresponds approximately to the time when young are reported to begin their postjuvenal molt (about 5 weeks post-fledging—Pitelka 1945). Young in this study were first noticed actively foraging 20 days after fledging, but I did not determine at what age the young became self-sufficient. Atwood (1978) found evidence of Santa Cruz Island Scrub Jays feeding young 60 days after fledging. Adult Pinyon Jays continued to feed their young even after they were proficient at foraging (Balda and Bateman 1971).

RENESTING AND SECOND NESTING

Renesting always involved the construction of a new nest from new materials, with building continuing up to the time of egg-laying. Renesting occurred even among pairs whose initial attempts failed as late as the late nestling stage. The period from loss of eggs or young to egg-laying in a renesting attempt averaged 8.8 days (s.d. = 1.98, n = 8, range = 7 to 12 days). The renesting interval in Florida Scrub Jays was between 8 days and 2 weeks (Woolfenden 1973).

Among 31 pairs successful with their first nesting attempt, only one (3%) attempted a second nesting. In late May 1971, that pair was observed building a new nest while still involved in territorial defense and the feeding of fledglings from their first nest. The fledglings were estimated to be about 31 days old, from hatching, when building of the second nest began. Construction of the second nest took 5 or 6 days. Five eggs were laid in the second clutch, beginning 5 days after the second nest was complete. Feeding of the fledglings from the first nest continued into the incubation period at the second nest. Late in the incubation period however, feeding of the fledglings ceased, and they were driven from the nest tree by the adults but were tolerated elsewhere in the territory. Shortly after the hatching of the second clutch, the fledglings from the first nest were no longer observed in their parents' territory.

Woolfenden (pers. comm.) found a 13% frequency of true second nesting attempts among Florida Scrub Jays. Clutch overlap as a reproductive tactic (Burley 1980) may be more common in the Chico Scrub Jay population than indicated by my results, because of the increasing difficulty of following pairs through time and space when foliage development is complete.

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