the historic structures. To prevent disturbance to the colony, human access to the bat roosting areas should be restricted. The construction of bat gates over mine entrances that allow bats to enter, but preclude people, has resulted in the increase in bat numbers in both maternity and hibernation colonies of *Plecotus* (Pierson et al. 1991; Saugey 1991; G. Fellers 1994; C. Stihler 1994, pers. comm.; P. Brown pers. obs.). A similar barrier could be installed at the entrance to the "bakery."

Pallid bats (*Antrozous pallidus*) also roost in buildings on Santa Cruz Island, but they tend to hide in crevices between the bricks and are less conspicuous and accessible. Radio-telemetry studies of *Antrozous* on the island have shown a different foraging and roosting behavior than is reported in the present paper for *Plecotus* (Brown 1978–1991, unpubl. data). Female *Antrozous* form a maternity colony in spring and summer in the cow barn at the Stanton Ranch, while males roost alone in rock crevices. Both sexes forage among oak woodlands and nonnative grasslands for large beetles and Jerusalem crickets (*Stenopelmatus fuscus*) that are captured on or near the ground. The increase of grasslands after European man developed the island may have enhanced foraging habitat for this bat species. Most individual pallid bats gather after foraging at the night roost on the second floor of the horse barn. For some males, the barn is 5 km from their foraging area and day roost, and the nightly commute is apparently for socialization.

In contrast, *Plecotus* commute several kilometers from the day roost to forage among native vegetation, and then night roost near their foraging areas. The signals of the night-roosting *Plecotus* were in different areas, signifying that they either roosted alone or in the company of non-telemetered bats. Although lush vegetation has been planted near the ranch, the bats did not feed in this area during the radio-telemetry study. Other research has shown that *Plecotus* feed primarily on moths (Dalton and Brack 1986). During some periods in summer, large numbers of moths appear near the ranch buildings, and the residents there report the area littered with moth wings in the morning (D. Owens 1992, pers. comm.). Probably these are the result of *Plecotus* opportunistically feeding closer to their roost. Studies conducted at different seasons on Santa Cruz Island could show different foraging strategies for *Plecotus*. The results of this radio-telemetry study do implicate the importance of native vegetation to this species and may have relevance to conservation and management issues in other geographic locations.

Conclusions

Plecotus townsendii on East Santa Cruz Island prefer to day roost as a large colony in a cave-like building, but use shallow rock caves for night roosting and can use them as day roosts if necessary. The construction of buildings on Santa Cruz Island has altered the bats' roosting behavior. In midsummer, *Plecotus* forage primarily among native vegetation along north-facing slopes of mountains, sometimes at distances of more than 4 km from their day roost, by-passing the lush nonnative plantings near the day roost.

Acknowledgments. This research was supported by a contract from Channel Islands National Park. Assistance in the field was provided by Karen Pluff, Tim Coonan, Jim Rorabaugh, Pat Green and Ted Green. The authors wish to acknowledge the continued support of Dr. Lyndal Laughrin of the University of California Field Station, and Marla Daily and the Santa Cruz Island Foundation. We also thank Dr. Elizabeth Pierson for comments on this manuscript.

Literature Cited

Brown, P. E. 1980. Distribution of bats of the California Channel Islands. In: The California Islands: Proceedings of a Multi-disciplinary Symposium, (edited by D. M. Power), Santa Barbara Natural History Museum, Santa Barbara, California, p. 751–756.

Dalton, V. M., and V. Brack. 1986. Food habits of the big-eared bat, *P. townsendii virginianus*, in Virginia. Virginia Journal of Science 37(4):248–254.

Humphrey, S. R., and T. H. Kunz. 1976. Ecology of a Pleistocene relict, the western big-eared bat (*P. townsendii townsendii*) in the southern great plains. Journal of Mammalogy 57:470–494.

Pearson O. P., M. R. Koford, and A. K. Pearson. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33:273–320.

Pierson, E. D. Pierson, W. E. Rainey, and D. M. Koontz. 1991. Bats and mines: experimental mitigation for Townsend's big-eared bat at the McLaughlin Mine in California. In: Proceedings V: Issues and Technology in the Management of Impacted Wildlife, Thorne Ecological Institute, Snowmass, Colorado, April 8–10, 1991, p. 31–42.

Pierson, E. D. and W. E. Rainey. 1992. The distribution, status and management of Townsend's big-eared bat (*Plecotus townsendii*) in California. California Department of Fish and Game. 43 pp.

Saugey, D. A. 1991. U.S. National Forests: unsung home to America's bats. Bats 9(3):3–6.

Von Bloeker, J. C., Jr. 1967. The land mammals of the Southern California Islands. In: Proceedings of the Symposium on the Biology of the California Islands, (edited by R. N. Philbrick), Santa Barbara Botanic Garden, Santa Barbara, California, p. 245–264.

The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Delayed Breeding in the Santa Cruz Island Scrub Jay: Why Not Be Cooperative?

Charles T. Collins[1] and Kennon A. Corey[2]

[1]*Department of Biology, California State University, Long Beach, CA 90840*
Tel. (310) 985-4813; Fax (310) 985-2315
[2]*U.S. Fish and Wildlife Service, Carlsbad Field Office, 2730 Loker Avenue West, Carlsbad, CA 92008*
Tel. (619) 431-9440; Fax (619) 431-9624

Abstract. Passerine birds typically are reproductively competent and breed when they are 1 yr old. When suitable breeding habitat is saturated with breeding pairs, delayed reproduction and non-reproducing "floaters" can occur. In the endemic Santa Cruz Island scrub jay (*Aphelocoma coerulescens insularis*), 85% of young birds do not gain reproductive status until 3 yr of age or older. Unlike some other populations of this species, these jays do not exhibit cooperative breeding, and remain as long-term floaters until breeding status is achieved, forgoing any indirect component of inclusive fitness. The availability of marginal and undefended habitat facilitates this individualistic strategy.

Keywords: Santa Cruz Island; scrub jay; *Aphelocoma coerulescens*; *insularis*; cooperative breeding; survival; demography.

Introduction

Island populations offer unique opportunities to examine a number of evolutionary processes. Island bird populations have been previously shown to exhibit pronounced differences from their mainland counterparts in size and morphology (Murphy 1938; Grant 1965, 1967; Johnson 1972; Power 1980), reproductive behavior and demography (Blondel 1985), as well as population density and habitat utilization (MacArthur et al. 1972; Cox and Ricklefs 1977; Emlen 1979; Wright 1980; Blondel et al. 1989). Thus, study of the population biology and demography of the Santa Cruz Island scrub jay (*Aphelocoma coerulescens insularis*), a distinct population of the widespread North American scrub jay (A.O.U. 1983; Pitelka 1951), should be informative.

The Santa Cruz Island scrub jay is confined to Santa Cruz Island, the largest of the northern Channel Islands of coastal southern California (Philbrick 1967). It is the most highly differentiated element of the endemic Channel Islands avifauna, being distinctly brighter in coloration (Pitelka 1951) and larger (Pitelka 1951; Atwood 1978; Isitt 1989; pers. obs.) than adjacent mainland scrub jays. It has also been shown to be genetically distinct from other scrub jay populations (Peterson 1992).

Previous studies of the Santa Cruz Island scrub jay (Atwood 1978, 1980a, 1980b) have shown it to be sedentary, permanently territorial, monogamous and lacking the distinctive cooperative breeding system of the Florida scrub jay (*Aphelocoma coerulescens coerulescens*) (Woolfenden and Fitzpatrick 1984, 1990; Fitzpatrick and Woolfenden 1986). Annual survival of breeding adult Santa Cruz Island scrub jays is exceptionally high for a passerine bird (Atwood et al. 1990). Young birds show a delay of up to several years in the acquisition of territories and breeding status (Atwood 1980b; Atwood et al. 1990), which is not the case for mainland California scrub jays (Ritter 1972, 1983; Carmen 1988, M. J. Elpers 1993, pers. comm.) but which is typical of the cooperatively breeding Florida scrub jay (Woolfenden and Fitzpatrick 1984).

Herein we present additional data on the demography of the Santa Cruz Island scrub jay with special attention being given to the survival of pre-breeding individuals and the age of first breeding. The relation of these demographic parameters to the observed social system of the Santa Cruz Island scrub jay is also considered and comparisons made to both cooperative and non-cooperatively breeding mainland populations of scrub jays.

Methods

Santa Cruz Island, located 30 km off the coast of Santa Barbara, California, is the largest and most topographically diverse of the Channel Islands. It covers 249 km and rises to 753 m in elevation with 6 major vegetation zones (Philbrick 1967; Johnson et al. 1968; Minnich 1980). The study area, located in the island's dominant east-west oriented central valley, comprises approximately 250 ha of oak woodland, chaparral, *Eucalyptus* groves, *Baccarhis* thickets, and grassland surrounding the University of California's Santa Cruz Island Reserve field station (Atwood 1978).

Both breeding and non breeding jays are individually color-banded with 3 colored plastic bands and 1 U.S. Fish and Wildlife Service numbered aluminum band. Wire cages with drop doors propped up by a stick and baited with peanuts are used to selectively catch a targeted jay. Young jays are usually banded during their first fall; older birds are captured at all times of the year for initial banding or re-banding to replace worn or lost plastic bands. The color-banded population of Santa Cruz Island scrub jays followed in this study was expanded from approximately 19 pairs in 1975 to 61 pairs in 1992 and has been censused at least once in the fall and once in the spring during this period. All banded birds observed are recorded each trip. The age of unbanded birds was determined using the diagnostic shape and color of juvenal rectricies, alular coverts and quills (Pitelka 1945; Seel 1976). These feathers are retained until the late summer of their second year at which time they undergo their first complete pre-basic molt. In the field, sexes are distinguished by a sex-specific "rattle" call emitted by a territorial female. This normally occurs in the presence of her mate, when other jays intrude onto her territory (Atwood 1980a); this is homologous with the "burr" vocalization of the Florida scrub jay (Woolfenden and Fitzpatrick 1984).

Sighting a banded jay in the study area is normally not difficult as the birds are readily attracted to peanuts. Consequently, when censuses are taken, territorial breeders are rarely missed unless a death has occurred although females are particularly elusive during the spring when sitting on eggs. To avoid mistakenly scoring a bird as missing when it was not observed, breeding birds were only considered missing if not seen during 2 consecutive seasons (spring and fall). A breeding bird was considered dead if not observed for 3 trips in a row. Usually a replacement mate soon takes the place of a missing breeder, reinforcing the indirect evidence for death. In only 10 cases out of a total of nearly 800, have we, at a later date, sighted a jay that by the above criteria had been presumed dead. This was usually due to the rare cases of divorce, in which jays from nearby territories changed mates (Atwood 1980c; Woolfenden and Fitzpatrick 1984; Carmen 1988). In a few other cases, a jay was unable to hold onto a territory when its mate died, and was evicted or squeezed out to a new or peripheral location (pers. obs.). Both of these scenarios caused some dispersal among the otherwise permanently located breeders. However, this has been observed in only 4% of pairs in the study population and did not significantly impact the survival rates reported here.

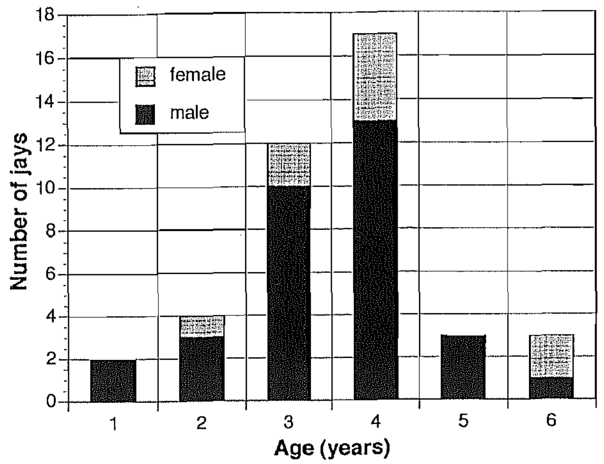

Figure 1. Age of first breeding for 41 known-age Santa Cruz Island scrub jays.

Results

Age of first breeding

Between 1980 and 1992, 147 jays were banded during their first year, both as hatching year (HY) and second year (SY) birds (U.S. Fish and Wildlife 1991), and hence were of known age. Of these, forty-one (27.9%) subsequently acquired breeding status on the study plot. The distribution of age of first breeding was similar in both sexes. The differences were not significant ($X^2 = 5.14$, $P < 0.01$), and data for both sexes were combined for further analysis. Most commonly the age of first breeding for both sexes was 3–4 yr (Fig. 1) with the average age of first breeding being 3.59 yr (± 0.04 SD). Santa Cruz Island scrub jays rarely breed at ages 1 and 2 (14.6%), although at least some birds are apparently physiologically capable of doing so during these early years. For other individuals (14.6%), first breeding did not occur until ages 5 and 6 (Fig. 1). The extreme sedentariness of breeders (Atwood 1980a; Atwood et al. 1990) makes it unlikely that any of these birds were breeding elsewhere at an earlier age and subsequently moved into the study plot.

The amount of dispersal of young jays and older nonbreeders is still unknown, even though attempts were made to locate dispersers of any age in the areas immediately surrounding the study plot. A total of 8 breeding pairs with at least 1 banded mate have been found in areas adjacent (< 0.4 km) to the main study plot. Five of these pairs involved known-age birds that were banded as HY/SY birds on the study site and dispersed to nearby areas. Only 2 banded birds have been observed at longer distances from the study plot. One was an older non-breeding bird banded on the plot and seen at Christie Ranch 13 km to the west in 1976, 55 dy later (Atwood 1978, 1980a). The second was banded as a known-age bird (HY/SY) on the study plot and observed in September 1991 on the slope above Pelican Bay 2 km north and over a 1,250-m ridge from the study site (W. Wehtje 1993, pers. comm.).

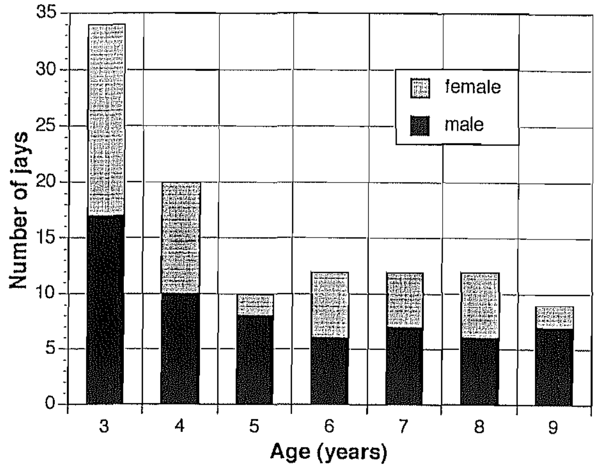

Figure 2. Age of first breeding for 110 unknown-age Santa Cruz Island scrub jays.

Table 1. Biannual survivorship of known age jays, 0.5–3.5 years.

Age (yr)	N	Sample surviving	Survival rate
0.5–1.0	91	47	0.5165
1.0–1.5	99	69	0.6969
1.5–2.0	70	60	0.8571
2.0–2.5	60	58	0.9666
2.5–3.0	58	52	0.8966
3.0–3.5	50	49	0.9800

The average estimated age of first breeding for jays banded as unknown-age pre-breeders was substantially higher than for known-age birds (Fig. 2). [With unknown-age birds, age of first breeding is assumed to be minimally 3 yr and determined by a combination of plumage characters and the average age of first breeding for known-age birds (Corey 1994).] However, this approach excludes the possibility of any 1- and 2-year-old breeders among the unknown-age category, the addition of which would slightly lower the average.

Some individuals appeared to take up to 9 yr to acquire breeding status on our study plot. However, most of the jays that were not detected as breeders until an age of 7 or greater were birds on territories adjacent to the original, smaller study plot. As a result, they were not initially recorded until these areas were subsequently included in the enlarged study plot. These birds may well have bred in these same areas in prior years. Thus, 6 yr seems to be the best documented maximum age of first breeding in Santa Cruz Island scrub jays.

Survival of Pre-breeders

Known-age (HY and SY) birds banded on the study plot were used to calculate pre-breeder survival. Since most young birds were not banded until their first fall, the analysis begins at age 0.5 yr. Additional young birds were added during the following spring (SY) when nearly 1 yr of age. Survival rates increase sharply from a low of 52% at 1 yr of age to 85% at 2.0 yr of age (Table 1), which is equivalent to the annual survival of all adult breeding birds and known-age adult breeder survival rates from 3 to 6 yr of age (Corey 1994). This is an exceptionally high survival rate for any passerine bird (Ricklefs 1983) and is attained by Santa Cruz Island scrub jays well before the average age of first breeding. Similarly, the proportion of the population of pre-breeders shows a sharp decline from 0.5 to 2 yr, at which point survivorship begins to level off and stabilize (Corey 1994). These values reflect minimum survivorship estimates, since no correction has been made for dispersal of pre-breeding birds. Such dispersers would be included among those banded jays that disappeared from the plot and were assumed to have died. Even so, survival of pre-breeding Santa Cruz Island scrub jays is high and inclusion of the few dispersers would not expectedly increase these values significantly.

Discussion

Among passerines, delayed breeding is an atypical phenomenon. The vast majority of these species first breed when they are about 1 yr old (Ricklefs 1973, 1983; Gill 1990). Included in this category are several populations of scrub jays in which acquiring a territory and breeding by yearling birds is commonly observed: *A. c. superciliosa* (Ritter 1972, 1983); *A. c. obscura* (M. J. Elpers, unpub. data). In the most thoroughly studied of these populations, 29% of territory vacancies of *A. c. californica* were filled by yearling males, and 50% by yearling females (Carmen 1988). All of these populations, as also true of Santa Cruz Island scrub jays, are not cooperative breeders. In the cooperatively breeding Florida scrub jay, the age of first breeding is commonly delayed for 2-3 yr and up to 5 yr in some males (Woolfenden and Fitzpatrick 1984, 1990).

Delayed reproduction is, in fact, typical of most cooperative breeding birds (Smith 1990). Florida scrub jays inhabit a unique habitat, Florida scrub, with sharp ecotonal boundaries. This habitat is restricted and contiguously filled with sharply delineated territories (Woolfenden and Fitzpatrick 1984, 1990). Prior to obtaining breeding status, young Florida scrub jays remain on the parental territory where they engage in a variety of cooperative behaviors including sentinel behavior (McGowen 1989) and assist with the rearing of subsequent broods (Woolfenden 1975;

Woolfenden and Fitzpatrick 1984). Young birds obtain a breeding territory by making occasional forays through other established territories in search of vacancies, which they then attempt to fill. If no vacancies are found, they return to the home territory between forays. On the home territory they are not pursued by resident territory holders and can accrue the benefits of group living (Woolfenden and Fitzpatrick 1984).

The evolution of cooperative breeding in Florida scrub jays has usually been linked to habitat saturation and limited opportunities for juvenile dispersal (Woolfenden and Fitzpatrick 1978, 1984; Koenig and Pitelka 1981; but see also Burt and Peterson 1993). However, cooperative breeding is a widespread phenomenon within New World jays (Pitelka 1951; Brown 1974; Woolfenden 1975; Peterson and Burt 1992; Burt and Peterson 1993) and "may be ancestral rather than a recently and repeatedly derived characteristic" (Atwood et al. 1990). Thus its absence in Santa Cruz Island scrub jays may in fact be a derived characteristic in this population. Alternatively, the absence of cooperative breeding in Santa Cruz Island scrub jays may result from the earlier loss of this behavior in western mainland populations ancestral to Santa Cruz Island scrub jays (Peterson 1992). In which case, the question of interest may not be "Why did cooperative breeding not evolve in Santa Cruz Island scrub jays" but "Why was it lost in ancestral mainland scrub jays and not secondarily reacquired in Santa Cruz Island scrub jays?" From either perspective, maintenance of the current pattern of Santa Cruz scrub jay demography and social behavior is rooted in the ecological conditions extant on Santa Cruz Island at present.

The pattern shown by the Santa Cruz Island scrub jay is, in some ways, intermediate between that of the cooperative breeding Florida scrub jay and western mainland populations of non-cooperative breeding scrub jays. Santa Cruz Island scrub jays have the delayed breeding pattern typical of the Florida scrub jay and other cooperative breeding birds but, like the western scrub jays, do not exhibit the complex cooperative breeding social system (Atwood 1978, 1980a). The principal difference may lie with the habitats these jays inhabit. Florida scrub jays are restricted to a single, distinct, patchy habitat that is usually saturated with strongly defended territories of breeding pairs. Thus the optimal strategy for young birds seems to be to remain on the parental territory, obtain the mutual benefits of cooperative breeding, and use it as a home base from which to explore for a breeding vacancy (Fitzpatrick and Woolfenden 1984; Woolfenden and Fitzpatrick 1984). Western scrub jay populations, including the Santa Cruz Island scrub jay, inhabit much more diverse habitats with mixtures of suitable and unsuitable, optimal and marginal areas for breeding (Atwood 1980b; Ritter 1983; Carmen 1988). Young birds can pursue a more clearly individual or "selfish" strategy by leaving the parental territory within 3 mo and wandering through available habitats in search of a place to set up a territory or the opportunity to replace an established breeder.

As documented by Carmen (1988), young mainland scrub jays leave the parental territory at an age of 2–3 mo post fledging and take up the role of a wanderer until becoming a breeder. They wander extensively through the territories of established pairs as well as marginal habitats. They are largely tolerated by the resident breeders, particularly during their distinctive brown-headed, juvenal plumage stage. During the following fall and winter the young jays wander over a somewhat prescribed home range area encompassing between 5 to 9 adult territories. They form semi-stable aggregations of similar-aged, pre-breeding individuals that are frequently encountered in the same general home range. The lack of aggression noted between any adults and these young birds suggests that the young are tolerated on the parental territory. Their departure and resultant status as wanderers is a matter of individual strategy rather than their having been excluded or chased off the parental territory as in the green jay (*Cyanocorax yncas*) (Gayou 1986).

Intense territorial defense, which excludes pre-breeding wanderers as well as other territorial adults, is limited to a brief period between late April and the beginning of July (Carmen 1988). This period starts well after the time of copulation and egg laying but starts before the end of fledging (Carmen 1988). During this period, the excluded pre-breeding jays are much less often encountered and presumably wander more extensively, making use of the seasonally increased abundance of insect food (Carmen 1988). Their more restricted wanderings during the fall and winter may represent a compromise between the advantage of exploring for breeding opportunities and the advantage of staying in an area where food, particularly acorns, can be stored and subsequently retrieved as part of the winter and early spring diet (Carmen 1988).

Our more limited data on young Santa Cruz Island scrub jays indicate a pattern of pre-breeder dispersal and wandering largely similar to that reported by Carmen (1988) for mainland scrub jays. Young Santa Cruz Island scrub jays leave the parental territory by the age of 3 mo (Atwood 1978, 1980a; pers. obs.) and are wanderers until breeding status is achieved, usually not until the age of 3 or 4 yr. Although they may, at times, form aggregations in marginal habitats (Atwood 1978, 1980a), they also wander extensively through and along the margins of adult territories (pers. obs.). Intense territoriality of breeding adults appears limited to the few months encompassing the peak of the breeding cycle. During this time pre-breeders may make even greater use of marginal habitats. At other times of the year the pre-breeding wanderers are found over areas encompassing several adult territories and seem to be utilizing an enlarged home range similar to that reported by Carmen (1988) for mainland scrub jays. During the period of peak acorn production in fall, large numbers of Santa Cruz Island scrub jays of all ages can at times be found concentrated at locations where a single oak tree or group of trees provides an abundant supply of acorns (Atwood 1978, 1980b; pers. obs.). These groups, which can reach 50–100 individuals (Atwood 1980b; pers. obs.), can include territory holding adults that have crossed 6–7 territories from up to 1.2 km away to reach the foraging site. Pre-breeding wanderers also make up a substantial portion of the jays foraging at these productive oak trees. The adult breeders tended to return to their home territories to cache their acorns (pers. obs.). Stored acorns are presumably an important component of winter and early spring diets of Santa Cruz Island scrub jays as they are for mainland scrub jays (Carmen 1988) and may similarly influence the more prescribed range of Santa Cruz Island scrub jay wanderers during the fall to spring time period (pers. obs.). Long distance dispersal data for Santa Cruz Island scrub jays is limited to observations of the 2 color-banded individuals, noted above, which were observed more than 1 km away from the study plot.

The greater delay in acquiring breeding territories by Santa Cruz Island scrub jays compared to mainland scrub jays (Carmen 1988; M. J. Elpers 1993, pers. com.) is quite likely related to the few vacancies available each year, which are in turn due to the high survival rate of breeding adults (Atwood et al. 1990; Corey 1994). This implies that most or all suitable breeding habitat is saturated within existing territories. Although detailed data are lacking, suboptimal or marginal areas that can sometimes be utilized, particularly by first time breeders, appear less common on Santa Cruz Island than on mainland areas.

Dispersal into less familiar surroundings has generally been considered to make the disperser or wanderer more vulnerable to predation (Metzgar 1967). In the Florida scrub jay, pre-breeding females that disperse earlier and further than males (Woolfenden and Fitzpatrick 1978, 1984) have been shown to have a higher mortality rate during the dispersal period (Woolfenden and Fitzpatrick 1984). In Santa Cruz Island scrub jays, pre-breeder mortality is highest during the first year of life as is typical of many species (Ricklefs 1973, 1983; Gill 1990). However, by the end of the first year, Santa Cruz Island scrub jay survival has reached a level (> 85%) equivalent to that of territorial adults, even though individuals may not become territory holders for up to 2–3 or more additional years.

Group breeding in which 1 to several non-breeding individuals help the breeding pair feed and care for their young is now known for a number of species (Rowley 1976; Stacey and Koenig 1990). Typically, helpers have a close genetic relatedness to the adults they are helping (Woolfenden and Fitzpatrick 1984; Koenig and Mumme 1987; Stacey and Koenig 1990; but see also Ligon and Ligon 1979; Brown and Brown 1980). This has suggested that the helpers may be able to increase their representation of their genes in the population by helping raise related young (Hamilton 1964; Mumme 1992) and that this indirect component of kin selection underlies the evolution of helping behavior (Brown 1974, 1987; Stacey and Koenig 1990). If this were in fact a significant influence on the evolution of cooperative breeding, Santa Cruz Island scrub jays would be expected to exhibit cooperative breeding, thereby increasing their inclusive fitness, during their prolonged pre-breeding period. The absence of cooperative breeding in Santa Cruz Island scrub jays and their abandonment of any indirect fitness strongly suggest that they are following a purely selfish individual strategy, one which is most likely to result in their obtaining reproductive status, as also suggested for the cooperatively breeding Florida scrub jay (Woolfenden and Fitzpatrick 1984).

Other suggestions concerning the evolution of cooperative breeding in birds have been presented by several authors (Koenig 1981; Koenig and Pitelka 1981; Emlen 1982, 1991; Woolfenden and Fitzpatrick 1984; Fitzpatrick and Woolfenden 1986; Brown 1987; Smith 1990). As previously noted, cooperative breeding usually occurs in ecologically unique settings where free access to successful breeding is in some way limited (Fitzpatrick and Woolfenden 1986). Heavy predation, localization of some critical resource (breeding habitat, nest site, concentrated food source) and unpredictable food supply are other ecological factors contributing to a limited access to successful breeding (Fitzpatrick and Woolfenden 1981; Koenig and Pitelka 1981).

Corresponding with these factors is often the presence of sharp ecotones between prime habitats (where survival and successful breeding can occur) and unusable habitats (Woolfenden and Fitzpatrick 1984). In the cooperatively breeding acorn woodpeckers (*Melanerpes formicivorous*), supurb blue wren (*Malurus cyaneus*), and white-fronted bee-eaters (*Merops bullockoides*), any opportunity for early dispersal and breeding is taken advantage of when habitat and food are available. This implies that these normally cooperative breeding birds will readily pursue a selfish individual strategy to become successful breeders on their own when possible (Rowley 1965; Emlen 1991). Where breeding is possible during the first year, even on marginal habitat, most passerine species disperse early, thereby forgoing any benefits of group living or indirect fitness (Gill 1990; Ricklefs 1973). When ecological factors prevent independent breeding as in the Florida scrub jay, the advantages of group living become important. These include increased individual fitness through increased predator detection and survival and a better chance of acquiring a territory in high quality habitat (Woolfenden and Fitzpatrick 1984, 1990; Stacey and Ligon 1987; Carmen 1988; Fitzpatrick and Woolfenden 1988). However, in at least one population of scrub jays in southern Mexico, cooperative breeding persists despite apparent absence of habitat limitation or habitat saturation (Burt and Peterson 1993).

In the Santa Cruz Island scrub jay, pre-breeding floaters are observed both in and out of the territories of breeding adults. This suggests refuges for pre-breeding jays do exist and are utilized until a breeding vacancy is found, a process that sometimes takes up to 6 yr (Atwood 1980a; this study). When given the opportunity, first year Santa Cruz Island scrub jays will attempt to breed and are physiologically competent at this time. This lends additional support to the view that delayed breeding, in itself, does not lead to cooperative breeding but is a secondary result of other ecological and demographic factors (Brown 1978, 1987; Lawton and Lawton 1986).

The individual strategy exhibited by Santa Cruz Island scrub jays entails early dispersal from the parental territory in search of suitable breeding habitat or the opportunity to replace a deceased breeding adult. This often prolonged dispersal strategy does not result in a decrease in survival as noted in the Florida scrub jay (Woolfenden and Fitzpatrick 1978). Given the long lifespan of Santa Cruz Island scrub jays of up to 18 yr (Corey 1994), lifetime reproductive fitness may still be high despite prolonged delays in acquiring breeding status.

The relative lack of predators on Santa Cruz Island has also undoubtedly helped in shaping the current social system (Atwood et al. 1990). The impact of avian predators appears to be minimal, and neither predator detection through sentinel behavior nor flock foraging to provide safety in numbers appears to be requisite. The occasionally observed groupings of Santa Cruz Island scrub jays may result in increased predator detection, but whether or not these groups are formed primarily for this purpose is unclear.

These observations strengthen the idea that the evolution and maintenance of cooperative breeding has complex ecological, evolutionary and demographic components. It is also not restricted to only the costs and benefits of helping behavior for both pre-breeding helpers and breeding adults (Stacey and Koenig 1990; Mumme 1992). Further study of all aspects of the biology of cooperative breeding birds and their non-cooperative breeding relatives will continue to be rewarding.

Acknowledgments. This study is an outgrowth of the initial studies of Santa Cruz Island scrub jays by Jon Atwood, who was also an active participant in many of these observations. We are indebted to him and the numerous observers who have spent time with us in pursuit of marked Santa Cruz Island scrub jays: D. Bradley, R. Bradley, P. Collins, M. Evans, B. Massey, P. Peters, W. Schew, D. Van de Water, and many other students and friends. We are also grateful to The Nature Conservancy and University of California Natural Reserve System for permission to work on Santa Cruz Island and use of the facilities of the Channel Islands Field Station. The U.S. Navy provided much appreciated transportation to the island. The Comments of J. L. Atwood and T. Coonan helped improve an earlier draft of this paper.

Literature Cited

American Ornithologists' Union. 1983. Checklist of North American birds. Sixth Edition, American Ornithologists' Union, Lawrence, Kansas.

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. Social interactions in the Santa Cruz Island scrub jay. Condor 82:440–448.

Atwood, J. L. 1980b. Breeding biology of the Santa Cruz Island scrub jay. In: The California Islands: Proceedings of a Multidisciplinary Symposium (edited by D.M. Power), Santa Barbara Natural History Museum, Santa Barbara, pp. 675–688.

Atwood, J. L. 1980c. Body weights of the Santa Cruz Island scrub jay. North American Bird-Bander 4:148–153.

Atwood, J. L., M. J. Elpers, and C. T. Collins. 1990. Survival of breeders in Santa Cruz Island and mainland California scrub jay populations. Condor 92:783–788.

Blondel, J. 1985. Breeding strategies of the Blue Tit and Coal Tit (*Parus*) in mainland and island Mediterranean habitats: a comparison. Journal of Animal Ecology 54:531–556.

Blondel, J, D. Chessel, and B. Frochot. 1989. Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats. Ecology 69:1899–1917.

Brown, J. L. 1974. Alternate routes to sociality in jays with a theory for the evolution of altruism and communal breeding. American Zoologist 14:63–80.

Brown, J. L. 1978. Avian communal breeding systems. Annual Review of Ecological Systems 9:123–155.

Brown, J. L. 1987. Helping and communal breeding in birds: ecology and evolution. Princeton University Press, Princeton. 354 pp.

Brown, J. L., and E. R. Brown. 1980. Extended family systems in a communal bird. Science 211:959–960.

Burt, D. B., and A. T. Peterson. 1993. Biology of cooperative-breeding scrub jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. Auk 110:207–214.

Carmen, W. J. 1988. Behavioral ecology of the California scrub jay (*Aphelocoma coerulescens californica*): noncooperative breeder with close cooperative relatives. Unpublished Ph.D. Dissertation, University of California, Berkeley. 333 pp.

Corey, K. A. 1994. Behavioral Biology and demography of the Santa Cruz Island scrub jay. M.S. Thesis. California State University, Long Beach.

Cox, G. W., and R. E. Ricklefs. 1977. Species diversity and ecological release in Caribbean land bird faunas. Oikos 28:113–122.

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

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. American Naturalist 119:29–39.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: Behavioral Ecology: An Evolutionary Approach (edited by J. R. Krebs and N. B. Davies), Blackwell Scientific Publications, Oxford, pp. 301–337.

Fitzpatrick, J. W., and G. E. Woolfenden. 1981. Demography is a cornerstone of sociobiology. Auk 98:406–7.

Fitzpatrick, J. W., and G. E. Woolfenden. 1984. The helpful shall inherit the scrub. Natural History 93:55–63.

Fitzpatrick, J. W., and G. E. Woolfenden. 1986. Demographic routes to cooperative breeding in some New World jays. In: Evolution of Animal Behavior (edited by M. Nitecki and J. Kitchell), University of Chicago Press, pp. 137–160.

Fitzpatrick, J. W., and G. E. Woolfenden. 1988. Components of lifetime reproductive success in the Florida scrub jay. In: Reproductive Success, Studies of Individual Variation in Contrasting Breeding Systems (edited by T. H. Clutton-Brock), University of Chicago Press, pp. 305–320.

Gayou, D. C. 1986. The social system of the Texas Green Jay. Auk 103:540–547.

Gill, Frank B. 1990. Ornithology. W. H. Freeman and Company, New York.

Grant, P. R. 1965. The adaptive significance of some size trends in island birds. Evolution 19:355–367.

Grant, P. R. 1967. Bill length variability in birds of the Tres Marias Islands, Mexico. Canadian Journal of Zoology 45:805–815.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I and II. Journal of Theoretical Biology 7:1–52.

Isitt, J. J. 1989. Evolution of the scrub jay (*Aphelocoma coerulescens*) in the western United States. M.S. Thesis. California State University, Long Beach.

Johnson, M. P., L. G. Mason, and P. H. Raven. 1968. Ecological parameters and plant species diversity. American Naturalist 102:297–306.

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

Koenig, W. D. 1981. Reproductive success, group size, and the evolution of cooperative breeding in the Acorn Woodpecker. American Naturalist 117:421–443.

Koenig, W. D., and F. A. Pitelka. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: Natural Selection and Social Behavior: Recent Research and New Theory (edited by R. D. Alexander, and D. Tinkle), Chiron Press, New York, pp. 261–280.

Koenig, W. D., and R. L. Mumme. 1987. Population Ecology of the Cooperatively Breeding Acorn Woodpecker. Princeton University Press. 435 pp.

Lawton, M. F., and R. O. Lawton 1986. Heterochrony, deferred breeding, and avian sociality. Current Ornithology 3:187–222.

Ligon, J. D., and S. H. Ligon. 1979. The communal social system of the Green Woodhoopoe in Kenya. The Living Bird 16:159–197.

MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. Ecology 53:330–342.

McGowen, K. J., and G. E. Woolfenden. 1989. A sentinel system in the Florida scrub jay. Animal Behavior 37:1000–1006.

Metzgar, L. H. 1967. An experimental comparison of Screech-Owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). Journal of Mammalogy 48:387–391.

Minnich, R. A. 1980. Vegetation of Santa Cruz and Santa Catalina Island. In: The California Islands: Proceedings of a Multidisciplinary Symposium (edited by D. M. Power), Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 123–137.

Mumme, R. L. 1992. Do helpers increase reproductive success? Behavioral Ecology and Sociobiology 31:319–378.

Murphy, R. C. 1938. The need of insular exploration as illustrated by birds. Science 88:533–539.

Peterson, T. A. 1992. Phylogeny and rates of molecular evolution in the *Aphelocoma* jays (Corvidae). The Auk 109(1):133–147.

Peterson, A. T., and D. B. Burt. 1992. A phylogenetic analysis of social evolution and habitat use in the *Aphelocoma* jays. Animal Behavior 44:859–866.

Philbrick, R. N. 1967. Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, California.

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 of American jays of the genus *Aphelocoma*. University of California Publications in Zoology 50:195–464.

Power, D. M. 1980. Evolution of land birds on the California Islands. In: The California Islands: Proceedings of a Multidisciplinary Symposium (edited by D. M. Power), Santa Barbara Museum of Natural History, pp. 613–643.

Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. In: Breeding Biology of Birds (edited by D. S. Farner), National Academy of Science, Washington D.C., pp. 366–435.

Ricklefs, R. E. 1983. Comparative avian demography. In: Current Ornithology (edited by R. F. Johnston), Plenum Press, London, pp. 1–32.

Ritter, L. V. 1972. The breeding biology of scrub jays. M.A. thesis, California State University, Chico.

Ritter, L. V. 1983. Nesting ecology of scrub jays in Chico, California. Western Birds 14:147–158.

Rowley, I. 1965. The life history of the Superb Blue Wren, *Malurus cyaneus*. Emu 64:251–297.

Rowley, I. 1976. Convener. Co-operative breeding in birds. In: Proceedings XVI International Ornithological Congress, pp. 655–684.

Seel, D. C. 1976. Moult in Corvidae. Ibis 118:494–520.

Smith, J. N. M. 1990. Summary. In: Cooperative Breeding in Birds (edited by P. B. Stacey and W. D. Koenig), Cambridge University Press, pp. 593–611.

Stacey, P. B., and J. D. Ligon. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat saturation model of cooperative breeding. American Naturalist 130:654–676.

Stacey, P. B., and W. D. Koenig. 1990. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press. 615 pp.

U.S. Fish and Wildlife Service. 1991. North American Bird Banding. Volume 1. Washington, D.C.

Woolfenden, G. E. 1975. Florida scrub jay helpers at the nest. Auk 92:1–15.

Woolfenden, G. E., and J. W. Fitzpatrick. 1978. The inheritance of territory in group living birds. Bioscience 78:104–108.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida scrub jay: demography of a cooperative breeding bird. Monographs in Population Biology number 20. Princeton University Press, Princeton. 406 pp.

Woolfenden, G. E., and J. W. Fitzpatrick 1990. Florida scrub jays: a synopsis after 18 years of study. In: Cooperative Breeding in Birds (edited by P. B. Stacey and W. D. Koenig), Cambridge University Press, pp. 241–266.

Wright, S. J. 1980. Density compensation in island avifaunas. Oecologia 45:385–389.

The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Conservation of the Island Spotted Skunk and Island Fox in a Recovering Island Ecosystem

Kevin R. Crooks[1] **and Dirk Van Vuren**[2]

[1]*Department of Biology, University of California, Santa Cruz, CA 95064*
Tel. (408) 335-1478; Fax (408) 459-3139
[2]*Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616*
Tel. (916) 752-4181; Fax (916) 752-4154

Abstract. We review available information on the ecology of island spotted skunks (*Spilogale gracilis amphiala*) and island foxes (*Urocyon littoralis santacruzae*) on Santa Cruz Island, with a focus on recent research, and present new information on distribution and abundance. Our objective is to evaluate the present and future status of skunks and foxes in the context of ongoing island recovery following removal of nonnative herbivores. Overall, foxes are abundant on Santa Cruz Island and display a wide range of resource use. They are habitat generalists, do not use permanent dens, are active both day and night, and have an omnivorous diet of mice, insects, and fruits. In comparison, spotted skunks are relatively rare and are resource specialists. They are more specialized in their habitat use, utilize excavated dens, are nocturnal, and have a carnivorous diet of primarily mice and insects. We suggest that island foxes, because they are more ecologically generalized than skunks, may initially benefit more from island recovery and are less susceptible to impacts of the rapidly expanding feral pig population on the island. The relatively specialized resource use of spotted skunks, coupled with their low population sizes and relatively narrow geographical range, increases both their susceptibility to environmental perturbations and their relative vulnerability of extinction.

Keywords: Santa Cruz Island; California Channel Islands; island spotted skunk; island fox; insular endemic carnivore; resource use; nonnative species; feral sheep; feral pigs.

Introduction

Species diversity on islands is typically lower than comparable areas of the mainland (MacArthur and Wilson 1967). Consistent with this pattern, Santa Cruz Island, largest of the California Channel Islands, possesses a depauperate and unbalanced vertebrate fauna (Wenner and Johnson 1980). Despite its relatively large size (25,000 ha), the island supports only 4 native species of non-volant, terrestrial mammals: the island spotted skunk (*Spilogale gracilis amphiala*), the island fox (*Urocyon littoralis santacruzae*), the deer mouse (*Peromyscus maniculatus santacruzae*), and the harvest mouse (*Reithrodontomys megalotis longicaudus*) (von Bloeker 1967; but see Collins and George 1990).

Little is known about the ecological relations of endemic mammalian carnivores on islands because they do not usually occur on islands (Williamson 1981; Brown and Gibson 1983). Santa Cruz Island is, therefore, unusual in that it supports not 1, but 2 species of similar-sized, endemic mammalian carnivores, the island spotted skunk and the island fox.

Insular ecosystems and the species they support are particularly sensitive to disturbance by nonnative species (Vitousek 1988; Coblentz 1990; Primack 1993). Detrimental effects of biological invasions on islands serve to increase extinction rates of insular endemics, rates already high due to small populations, narrow ranges, and low genetic diversity (Vitousek 1988). Unfortunately, Santa Cruz Island is no exception to the biological invasions so prevalent on islands. Long-term overgrazing by feral sheep, as well as domestic cattle, has resulted in severe environmental degradation on the island (Van Vuren and Coblentz 1987, 1989; Brumbaugh 1980; Hobbs 1980; Minnich 1980). Because of this damage, nearly 38,000 sheep were removed from the island in the early 1980s (Schuyler in press). Cattle were removed when the island's ranching operation was discontinued in 1988.

Removal of nonnative herbivores from islands is highly desirable because of the severe damage they cause to island ecosystems (Van Vuren and Coblentz 1987; Bratton 1988; Coblentz 1990); dramatic recovery of insular plant communities typically results (Hamann 1979; Meurk 1982; Scowcroft and Giffin 1983). Recovery, however, may not always lead to the full restoration of original communities. Release from grazing pressure may favor the spread of undesirable nonnative plants that can outcompete endemic species (Taylor 1968; Scowcroft 1987). Further, recovery of plant communities may improve habitat quality for nonnative animals, such as feral pigs (*Sus scrofa*), that themselves cause damage to island resources (Van Vuren 1981).