BIOLOGY OF COOPERATIVE-BREEDING SCRUB JAYS (*APHELOCOMA COERULESCENS*) OF OAXACA, MEXICO

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ABSTRACT.—We studied a cooperative-breeding population of Scrub Jays (*Aphelocoma coerulescens*) in Oaxaca, Mexico. The jays occupied territories 1.5 ha in average size located in a wide range of habitats and were found in temporally stable groups of two to six adult individuals. No yearling was observed breeding. The jays nested at least from early April to late July. Clutch size was three, with subsequent brood reduction to two fledglings typical. Only breeding females incubated eggs. Breeding males fed nestlings more frequently than did breeding females. Ectoparasites were uncommon on adults, but nestlings commonly carried botfly larvae. Extra individuals commonly "helped" in predator defense, territorial defense, and feeding fledglings. Helpers attempted to assist in feeding nestlings, but usually were driven away by breeding adults. Singular breeding seems to be the rule, but plural breeding also may occur. Certain factors associated with the maintenance of cooperative breeding in the Florida Scrub Jay do not appear important in this Oaxacan population: usable habitats do not appear to be saturated with territories, and other jay species do not present an aggressive barrier to Scrub Jay habitat use. *Received 3 October 1991, accepted 6 September 1992.*

COMPARATIVE STUDIES of variation in social systems, ecology, and life-history traits have been very important in the development of current theory concerning the evolution of social systems in birds (Stacey and Koenig 1984, 1990, Woolfenden and Fitzpatrick 1984, Brown 1987). Such comparative studies require that information on the social system, demography, and ecology be available for all representatives of the groups under study, or at least that taxa included in the analyses be an unbiased sample of the study group (Krebs and Davies 1987). Hence, documentation of the diversity of social systems is important to advancing the understanding of social evolution in birds.

Most studies of cooperative-breeding birds have documented ecological limitations that apparently cause delayed dispersal and breeding (Brown 1987, Smith 1990). Opinions differ, however, on why these individuals display alloparental or helping behaviors (Woolfenden and Fitzpatrick 1984, 1990, Brown 1987, Jamie-

son 1989, 1991, Brown and Brown 1990, Emlen et al. 1991, Ligon and Stacey 1991, White et al. 1991).

The New World jays, and the genus *Aphelocoma* in particular, have served as a test group for many ideas on avian social evolution (Brown 1974, 1987, Atwood 1980, Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1986, Carmen 1988, Brown and Brown 1990, Woolfenden and Fitzpatrick 1990). Cooperative-breeding behavior is widespread but not universal in the genera *Aphelocoma*, *Calocitta*, and *Cyanocorax*, and absent or rare in the genera *Cyanocitta* and *Gymnorhinus* (Brown 1987). The breeding behavior of the genus *Cyanolyca* is little known; however, flocking behavior suggests that some form of cooperation takes place (Hardy 1964, Peterson pers. observ.). Within the genus *Aphelocoma*, the Unicolored Jay (*A. unicolor*; T. Webber pers. comm., Peterson pers. observ.), the Gray-breasted Jay (*A. ultramarina*; Brown and Brown 1981, 1990, Brown 1987), and the Florida populations of the Scrub Jay (*A. coerulescens*; Woolfenden and Fitzpatrick 1984, 1990) breed cooperatively.

Comparisons of the cooperative-breeding Florida populations with the noncooperative western North American populations of Scrub Jays have been particularly instructive. The
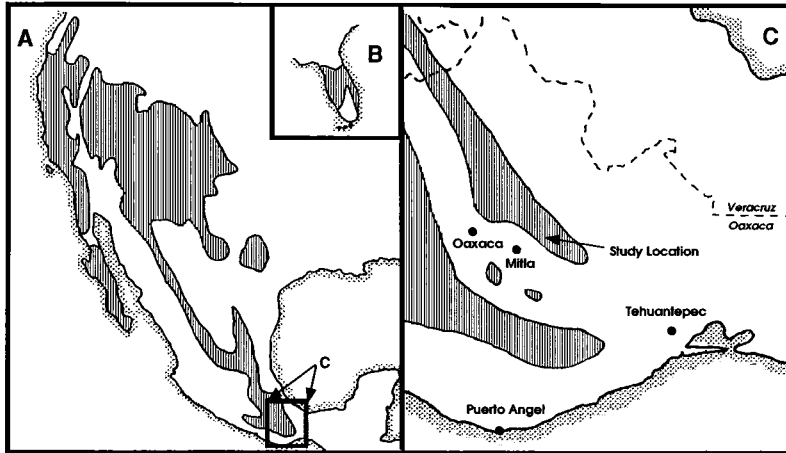
Fig. 1.   Map showing (A) western, (B) Florida, and (C) detailed southern Mexico distributions of Scrub Jays (Pitelka 1951, Peterson 1991).

Florida Scrub Jay lives in a rare, geographically restricted, relict oak–scrub habitat that is limited on all sides by either unusable habitat or habitat occupied by Blue Jays (*Cyanocitta cristata*; Woolfenden and Fitzpatrick 1984). Western Scrub Jays generally live in more continuous habitats, and probably can use a wider range of habitats (Pitelka 1951, Peterson and Vargas 1992). This ecological difference, particularly the absence of marginal habitats in a saturated environment in Florida, has been invoked to explain the diversity of social systems in Scrub Jay populations (Atwood 1980, Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1986).

Many Scrub Jay populations remain unstudied (e.g. Great Basin, all of Mexico). This study provides preliminary data on a cooperative-breeding population of Scrub Jays in southern Mexico and discusses its implications for understanding the evolution of social systems in *Aphelocoma* jays.

METHODS

This study was conducted in the Sierra de los Mixes (elevation 2,200 m), state of Oaxaca, Mexico, in a valley 4 km NW of Santa María de Albarradas on the road to Santo Domingo de Albarradas (Fig. 1). The original habitat in this area probably included both humid pine–oak and arid pine–oak forest (habitat terminology follows Binford 1989). Now, through centuries of human presence and greatly increased deforestation recently, the area contains a mosaic of habitats ranging from dense humid pine–oak forests and more open arid pine–oak forests and oak scrub to open, badly eroded grazed lands, cultivated fields, and bare rock.

We worked in the area on three occasions: (1) 7–13 May 1989, when Peterson made observations at sites throughout the Sierra de los Mixes; (2) 30 December 1989–13 January 1990, when we banded jays and surveyed habitat use and group sizes; and (3) 29 May–16 June 1990, when we banded additional individuals, mapped territories, and conducted intensive observations at two nests.

Working in pairs, we established survey points every 260 m (400 paces) along each of five trails leading out of camp, for a total of 34 points. At each point, we played a 3-min recording of an intense territorial interaction (*A. c. californica* vocalizations), recorded the number of individuals responding, and observed subsequent interactions to establish group memberships. Then, at each point, to measure aspects of habitat structure, we established 50-m transects in each of the four cardinal directions. We counted the number and estimated the average heights of pine, oak, and other tree species of greater than 5 cm dbh within 1 m of the transect. These figures were then averaged across the four transects. The maximum elevation change along the four transects also was estimated. Both observers independently assessed the percent coverage by woodland (to nearest 5%), as well as the abundance of acorns on the ground (0 = none, 1 = some, 2 = many), in the 100-m diameter circle; the estimates of the two observers were averaged. To avoid observer effects, the two observers (out of four total workers) and the trail to be surveyed were chosen at random each day. Statistical analysis of these data was performed using the SAS statistical package (SAS Institute 1988).

Jays were caught in mist nets and banded with unique four-band combinations of five colors of aluminum bands. For each jay captured, we recorded: age (based on plumage characters; Pitelka 1945), pres-

ence of brood patch (during breeding), mass (to near-
est 1 g), wing chord and tail length (to nearest 0.5
mm), tarsus length, exposed culmen length, and bill
length, width, and depth (the latter three at anterior
nostril edge; all five to nearest 0.1 mm).

The sex of individuals was determined by identi-
fication of a brood patch (breeding females only) for
captured birds and a female-specific vocalization (rattle
or hiccup call; Woolfenden and Fitzpatrick 1984). The
socially dominant male and female individuals were
assumed to be the breeding individuals, and the re-
maining subordinate individuals of a group were as-
sumed to be helpers.

Territorial boundaries were located by observing
territorial conflicts and individuals' home ranges.
Boundaries were plotted onto a map constructed from
surveys of the study area. Average territory size was
calculated by measuring the total area of usable land
(i.e. excluding areas of bare rock) with a planimeter
and dividing by the number of territorial groups.

We established blinds at two nests. The nest of
A-BYBm (m = male), B-AGAf (f = female), and two
unbanded helpers was observed for 53 h (6-11 June),
and that of BA-BYm and YA-RAf (without helpers)
for 24 h (11-13 June). Detailed notes on behavior and
the providing of food to nestlings were taken by sev-
en observers during 2-h shifts from 0600 to 1800 CST
each day as weather conditions permitted.

RESULTS

Habitat use.—Jays seemed to be most abun-
dant in cut-over, open oak woodland, using this
habitat for most foraging and territorial inter-
actions. They were rarely detected in tall, closed
forests. However, Mann-Whitney statistical tests
of the individual habitat characters showed no
significant differences among habitats in which
jays were present or absent. Only acorn abun-
dance had a probability value (0.07) that ap-
proached significance.

Using presence/absence of jays in each sam-
pling location as the dependent variable, we
attempted to develop a predictive model for
habitat use by logistic regression, and forward–
backward stepping and best-subsets methods of
selection for a multiple-linear-regression mod-
el. Residuals for each independent variable were
examined for any pattern, but none was de-
tected. No statistically significant model could
be developed that predicted the presence of jays
at sites. These results suggest that the Oaxaca
Scrub Jays use the available habitats as a gen-
eralist, particularly when compared with the
habitat use patterns of Florida Scrub Jays.

Groups.—Group size ranged from two to six
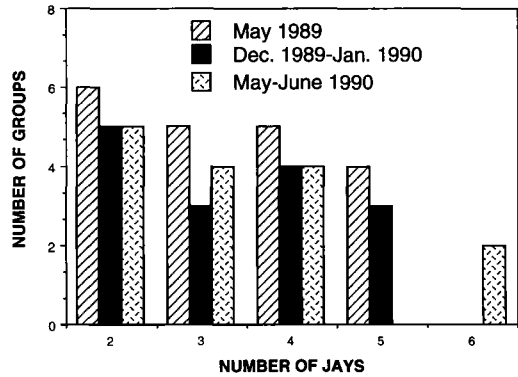individuals (Fig. 2). That these "groups" were

Fig. 2. Distributions of Scrub Jay group sizes en-
countered on three visits to study area.

not just pairs with newly fledged young or wan-
dering, nonterritorial floaters is indicated by
detailed observations of group composition and
temporal stability. We observed little fighting
within groups and nothing indicating spatial
separation within group territories. When re-
sponding to recordings of territorial vocaliza-
tions, all individuals usually arrived from and
departed in the same general direction. In nu-
merous revisits to territories on different days
or in different months, we found a high re-
peatability in group-size counts, indicating that
group membership was stable.

Our observations of individually marked birds
(Fig. 3) support these results. Four of six groups
with banded individuals included three to four
full-grown (based on plumage characters; Pi-
telka 1945) individuals. All members of each
group stayed within that group's territory and
could be found at almost any hour of the day.
The only examples of changes in group mem-
bership that we observed were in a group at
the northwestern end of the study area (not
shown in Fig. 3) in which a second-year indi-
vidual banded in January 1990 disappeared by
May 1990, and an unbanded individual took its
place. It is possible that the bird simply lost its
four bands, although loss of aluminum bands
is unusual in Scrub Jays (Burt unpubl. data, G.
E. Woolfenden pers. comm.).

Timing of breeding.—In May–June 1990 we en-
countered considerable variation in timing of
nest-cycle stages. In adjacent territories we si-
multaneously encountered a nest with a female
just beginning incubation and a pair with in-
dependent juveniles. For Oaxaca, Binford (1989)
reported a temporal range from a nest with three
eggs on 7 April to a nest with two small young
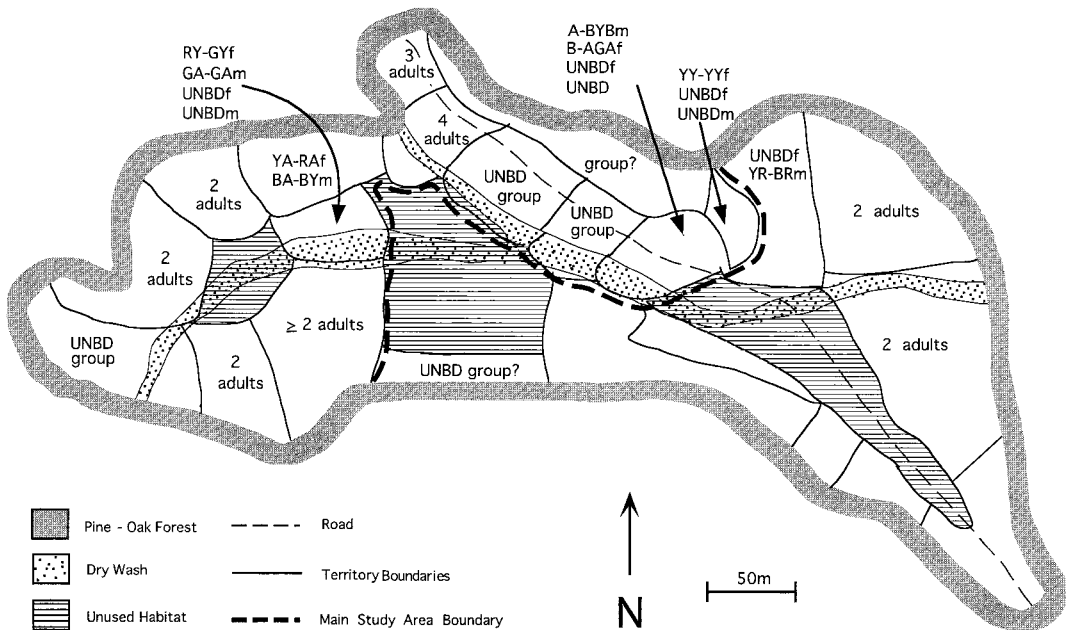and one egg on 21 July. Assuming an incubation

Fig. 3.   Map of Scrub Jay territories and group composition 4 km northwest of Santa María de Albarradas, Oaxaca, Mexico. UNBD = unbanded; other abbreviations refer to color-band combinations and sex (m = male; f = female).

period of 17 days and one egg laid per day, as in the Florida Scrub Jay (Woolfenden and Fitzpatrick 1984), clutch initiation dates should range at least from 5 April to 2 July.

Territories and nesting.—Each breeding territory contained both very open and relatively closed habitat types. Typical features that might be important for formation of territories included open areas for foraging, dense thickets, a tall tree or two which might be important in predator vigilance, and open arid pine–oak forest used for nesting. Average size of the 13 territories on the main portion of the study area (Fig. 3), excluding habitat that appeared unused, was 1.5 ha (density of 0.67 groups/ha).

An important demographic parameter is the age at which individuals first obtain breeding territories. Although firm conclusions are not possible without larger sample sizes and longitudinal data, we found no indication that these jays breed when one year old, as all breeders handled were in full adult plumage.

Eight nests were found at an average height of 2.8 m, all in oak trees averaging 5.1 m, generally within 1 m of the main trunk. Four nests were in dense tangles of mistletoe, and two were adjoining bromeliads.

Apparently, the normal clutch size is three. The two nests found with eggs each had three,

as did two nests reported by Binford (1989). We found no groups attending more than three young, either before or after fledging.

Incubation is apparently by the breeding female only. We observed two groups during the incubation stage, and at no point saw convincing evidence of more than one female incubating, even though both groups contained helper females. Females were fed on the nest frequently by the breeding male, although the capture of a second-year or older helper in a net close to the nest of an incubating female suggests this helper also may have been carrying food to the female.

Two nests were observed during the nestling stage. At both, the male fed the young more frequently than did the female (A-BYBm 58 feedings [55.8%] vs. B-AGAf 45 feedings [43.3%]; BA-BYm 31 feedings [77.5%] vs. YA-RAf 9 feedings [22.5%]). Only one of two helpers at the first nest fed nestlings and then only once during the total observation time. The second nest was that of a pair only (no helpers). On average, adults fed young 2.13 and 2.14 times/h at the two nests, respectively. The stomach of one dead nestling contained a section of a lizard torso, a 30-mm beetle larva, and numerous small insect parts.

At least five groups were observed with fledg-

lings of various ages, but never with more than two fledglings. As in other Scrub Jay populations, very young fledglings were quite sedentary, moving only to approach adults bringing food. Later, they were louder and more mobile, following the adults around the territory begging for food. Although detailed observations of groups at this stage were not possible, all members of at least one group (RR-BBm, GA-BYf and one unbanded helper) fed the fledglings. The stomachs of two full-grown juveniles found dead contained mostly fruit and seeds, and only a few insect parts.

Ectoparasites.—All jays handled were inspected for ectoparasites. In visual inspections of 30 adults (10 banded and 20 collected elsewhere in the same mountain range for genetic studies) and two full-grown juveniles, no ectoparasites were encountered (as is more or less normal in jays; Peterson unpubl. data), but mallophaga were collected by ethyl-acetate fumigation from 2 of the 20 collected adults. However, all five nestlings inspected carried at least four large botfly larvae (mean = 6.8 larvae/nestling). These were encountered mainly on the abdomen, throat, and wings, and at times on the face, where they appeared to impair vision. One dead 73.5-g nestling had eight larvae with a combined weight of 1.07 g, or 1.46% of the bird's body mass. That young jays can survive this parasite is demonstrated by the presence of healed botfly sores on one of the two full-grown juveniles inspected.

Brood mortality.—Although the normal clutch size is three, observations suggest that the jays usually are not able to rear that many young. The largest number of fledglings observed in any group was two, and of full-grown juveniles in any group only one (five groups observed). The stage at which this apparent mortality occurs and its causes are probably varied: in one case, an egg disappeared overnight from an actively incubated nest; in another, a large nestling of about 12 days age fell from its nest and died soon after.

Helping behavior.—Given that "extra" individuals were present in 10 of 17 (59%) breeding units on the study area, the obvious question is whether these individuals performed parent-like behavior to young that were not their own (Brown 1987). We examined this question at four stages in the breeding effort.

(1) Territorial defense: In response to both territorial challenges from other jays and to our recordings and vocal imitations, each extra individual normally participated in defending the territory at least as actively as the breeding female.

(2) Predator defense: Although we have no direct observations of extra individuals giving alarm calls to warn the group of the approach of a natural predator, alarm calls by all individuals in the group could be elicited by our presence in the general vicinity of the nest. In defending nest and young against potential predators such as ourselves, all members of the groups participated actively in mobbing.

(3) Feeding nestlings: At the nest of A-BYBm and B-AGAf, one or both extra individuals came to the nest tree an average of 0.189 times per hour (total of 10 times). On at least three (30%) of these occasions, the extra individual was carrying food in its beak or throat, but on only one occasion did an extra individual actually feed the nestlings. Although the extra individuals took an active interest in the nest and nestlings, on 5 out of 10 (50%) of their visits to the nest tree, they were chased from the immediate vicinity of the nest by one or both of the breeding adults. Hence, while the potential helpers attempted to provide food, their help usually was not accepted.

(4) Feeding fledglings: Our general impression from incidental observations of five different groups with both extra individuals and fledglings was that the fledglings begged food from whichever adult was closest, and that all adults actively provided food for the fledglings. On one occasion we witnessed a helper feeding a fledgling.

Therefore, given that the extra individuals present in this population actually help at least in three of four phases of the breeding effort, we feel justified in calling them "helpers."

DISCUSSION

Group living.—It is well established that Scrub Jay populations in the western United States breed exclusively in pairs (Atwood 1980, Carmen 1988, Burt unpubl. data). The behavior of Mexican populations, however, has long been a mystery (Hardy 1961, Woolfenden and Fitzpatrick 1984). We have visited all major sections of the Scrub Jay's range in Mexico, and have found them in groups only in Oaxaca and possibly in central Guerrero and eastern Puebla. It appears group living by Scrub Jays is limited to Florida and the southern extreme of the range.

Group sizes in the two populations are similar

(compare Fig. 2 with tables 5.1 and 6.2 in Wool-fenden and Fitzpatrick 1984) and, although be-haviors of both the Oaxaca and Florida popu-lations can be called helping, some intriguing differences exist. The Oaxaca Scrub Jays help in territory defense, antipredator behavior and feeding fledglings, but usually are chased away when attempting to feed nestlings. Helpers are not allowed access to the nest in at least one other cooperative breeding species, the Harris' Hawk (*Parabuteo unicinctus*). Dawson and Man-nan (1991) proposed social manipulation of sub-ordinates by breeders as one possible explana-tion for limited nest access to helpers in this species. Helpers were active in territorial de-fense, predator harassment and transporting captured prey to the nest, but typically were prevented from entering the nest. Occasional access to the nest was allowed to encourage these beneficial behaviors, but frequent access might induce full-breeding condition in helpers, caus-ing an increase in intragroup conflict. However, data on hormonal regulation of breeding status in the Florida Scrub Jay suggests this breeding-condition-induction explanation does not ap-ply to the Oaxaca population for the limiting of nest access to helpers (Schoech et al. 1991). Another possible explanation is that Oaxaca helpers were driven away by the breeding pair because of disturbance-related anxiety caused by our observation blind.

Even in the Florida population, helpers are not included in all stages of the breeding cycle. During nest building, incubation, and the first few days after hatching, helpers are driven from the nest by the breeders. Helpers are allowed to participate in all subsequent breeding activ-ities, including the provisioning of nestlings (Stallcup and Woolfenden 1978, Woolfenden and Fitzpatrick 1984). The proximate and evo-lutionary reasons for the rarity of alloparental feedings in the Oaxaca population require more study.

Plural breeding.—The wide range of clutch ini-tiation dates (April–July) suggests that Oaxaca Scrub Jays are able to renest frequently and, thereby, replace lost young. However, two in-complete observations suggest that more than just renesting might be occurring in the pop-ulation.

First, in the UNBDm/GA-GAf territory (UNBD = unbanded individual), the breeding pair had a nest with three eggs that GA-GAf was incubating almost continuously. Their two

helpers (RY-GYm, UNBDf) appeared during territorial battles, but were absent or not de-tected when all was quiet during four days of regular observation. Possibly, given their in-teractions (frequent rattle calls by the UNBDf in response to RY-GYm), these two individuals had an active nest elsewhere in the territory.

Second, in the RR-BBm/GA-BYf territory GA-BYf and an UNDB helper spent most of their time caring for a full-grown juvenile. RR-BBm, however, was strangely absent in three of five of our visits to the territory and, even when present, did not join the main group. Again, he may have had another active nest with a dif-ferent female. These observations are at best suggestive of the occurrence of plural breeding in the population.

Habitat limitation.—Woolfenden and Fitzpat-rick (1984) have argued convincingly that se-vere limitations in the availability of breeding and marginal habitats are responsible for de-layed dispersal by juvenile individuals in Flor-ida Scrub Jay populations. The presence of Blue Jays may limit the Scrub Jays' use of taller wood-lands and forests. Other surrounding habitats—open palmetto scrub, grasslands, and citrus groves—appear to be unsuitable for either breeding or floating. Hence, Florida Scrub Jays appear to be hemmed in on all sides.

We found no indication of strict habitat lim-itation. We present three lines of evidence:

(1) The Oaxaca Scrub Jays use a wide range of habitats. Although most frequently found in open oak woodlands, we also found them in closed humid and arid pine–oak forests, oak scrub, cultivated fields, grazed lands, and pop-ulated areas. Tall pine forest (height ca. 25 m) was used regularly during territorial interac-tions and predator vigilance, and treeless, grazed lands were used for foraging to a degree that neither of us has seen in other Scrub Jay pop-ulations.

(2) The habitats used by Scrub Jays in the Sierra de los Mixes are arranged in a complex, ever-changing mosaic. Although the more re-mote areas and steeper slopes are generally cov-ered with closed pine–oak forest, the remainder of the region is a patchwork of habitats, each of which the jays use to varying degrees. The important point is that the activities of the local people do not destroy the jays' habitat, but rath-er, open up the closed forest to make a contin-uum of habitats from completely unusable to very suitable. Increased pressure on the land in

the last few decades for more agricultural, forest, and domestic-animal production has led to vastly increased amounts of usable habitat in the region, so spatial limitations that might have been present probably are no longer in place.

(3) Other jay species are not common in adjacent habitats. Five jay species are found in the Sierra de los Mixes (Binford 1989), but none is common in habitats adjacent to those used by Scrub Jays. The White-throated Magpie-Jay (*Calocitta formosa*) is present in the tropical deciduous forest and arid tropical scrub at the base of the mountain range, but never ascends into the arid subtropical scrub (Binford 1989) that borders Scrub Jay habitat. The Unicolored and Azure-hooded jays (*Aphelocoma unicolor* and *Cyanolyca cucullata*, respectively) are restricted to cloud forest, while the Dwarf Jay (*Cyanolyca nana*) occurs in both cloud forest and humid pine–oak forest. None of these three species was found even in the darkest barrancas high in the hills above the study area. Steller's Jays (*Cyanocitta stelleri*) were found near the study area, but only regularly in the darkest, most closed barrancas. During our stays in the area, we saw them only three times, and they could not be lured out into more open forest. Thus, other jays do not present the aggressive barrier to Scrub Jay habitat use that they do in California, Florida, or northern Mexico (Peterson and Vargas 1992, Vargas in prep.).

For these reasons, we believe that ecological limitations, in the sense of the unavailability of habitats for dispersal as modeled in habitat-saturation and marginal-habitat models, are not important factors maintaining cooperative breeding in the Oaxaca Scrub Jay populations. Of course, other ecological factors not considered here (e.g. availability of food or nest sites) might exist that limit the jays' ability to disperse successfully and breed as yearlings. We simply argue that the factors identified as critical in limiting habitat use of the cooperative-breeding Florida Scrub Jays do not appear important in this case.

More detailed studies of variation in habitat quality and fitness payoffs in the Oaxaca Scrub Jay may support alternative explanations for the existence of cooperative breeding in this population. One possibility is that high variance in habitat quality among territories may make nondispersal the best choice for yearlings on high-quality territories (Stacey and Ligon 1987). Yearlings on "good" territories may optimize

lifetime fitness by delaying dispersal and serving as helpers until their natal territory or another of high quality is available. Another possibility is that cooperative breeding in this population is not adaptive under current conditions, instead reflecting selection in ancestral populations under very different ecological situations (Peterson and Burt 1992). More detailed field studies of the southern Mexican Scrub Jay populations are critical to resolve these possibilities.

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