

## PHYLOGENY OF SOCIAL BEHAVIOR IN APHELOCOMA JAYS: A ROLE FOR HYBRIDIZATION?

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**ABSTRACT.**—The phylogeny of jays in the genus *Aphelocoma* describes the evolutionary appearance or disappearance of helping and other social behaviors that have been much studied in this genus. Using published allozyme data and new behavioral characters we reexamine the phylogeny of *Aphelocoma*. The best-fitting hypothesis is that the complex social system of the Mexican Jay (*Aphelocoma ultramarina*), including delayed maturation, helping, plural breeding, and loss of the rattle call, arose from a simpler state in a jay ancestor, perhaps one that already had occasional nonbreeding associates. The interpretation of phylogeny in eastern populations of the Mexican Jay may be complicated by hybridization with the Scrub Jay (*A. coerulescens*), suggesting the possibility of reticulate evolution in the genus. The Florida Scrub Jay (*A. c. coerulescens*) appears to be closely related to the population of Scrub Jays in southern Mexico, and together the two constitute a distinct clade within the Scrub Jay superspecies. Received 4 March 1994, accepted 28 January 1995.

ALTHOUGH BEHAVIOR was used as a tool to study phylogeny in birds in the 1940s and 1950s (e.g. Lorenz 1941), the tables have turned recently; now phylogeny has become a tool to study the evolution of behavior (Brooks and McLennan 1991, Harvey and Pagel 1991, Harvey and Purvis 1991, Price 1991, Lanyon 1992, Richman and Price 1992). The evolution of social behavior in general and of helping behavior in particular can be studied in this way (Edwards and Naeem 1993). The genus *Aphelocoma* is a promising subject for such research because it spans the gamut from a complex, plural-breeding system in the Mexican Jay (*Aphelocoma ultramarina*; Brown 1963), through a polyandrous system in the Unicolored Jay (*A. unicolor*; Webber and Brown 1994), to singular breeding in pairs with or without nonbreeding helpers in the Scrub Jay (*A. coerulescens*; Woolfenden 1975, Carmen 1989). The genus inhabits a wide range of habitats including Central American cloud forests (*A. unicolor*), pine-oak-juniper woodlands (*A. ultramarina*), and scrub vegetation (*A. coerulescens*).

Some of the behavioral, phylogenetic, and taxonomic problems in this genus concern the populations of *A. ultramarina* that inhabit the Sierra Madre Oriental of eastern Mexico. This chain of montane populations includes two subspecies and extends from the Mexican state of Hidalgo (*A. u. potosina*) north to the Chisos Mountains on the Texas border (*A. u. couchii*). The Mexican Jay has two other groups of sub-

species, a series of populations mainly in the mountains of western Mexico ranging from Arizona and New Mexico south through the Sierra Madre Occidental to Jalisco (*arizonae*, *wollweberi*, *gracilis*), and the populations crossing central Mexico in the Transvolcanic region (*A. u. ultramarina*, *A. u. colimae*). We refer to these geographic groups of subspecies as Orientalis, Occidentalis and Transvolcanic, respectively (Fig. 1). In this paper we survey the genus *Aphelocoma* with special reference to Orientalis.

The Orientalis group may have been critical in the origin or loss of helping behavior in the genus (Brown and Horvath 1989, Peterson 1992b). Orientalis also has attracted the attention of behavioral ecologists because of the presence of certain Scrub-Jay-like behaviors and developmental patterns that are absent or weakly developed in other populations of the Mexican Jay. Three decades ago it was noticed that *couchii*, the population of *Aphelocoma ultramarina* in the border mountains of Texas and Coahuila, was in many respects somewhat intermediate between the Occidentalis group and the Scrub Jay (Brown 1963). Later, Orientalis was found to resemble the Scrub Jay in additional aspects of its social behavior (Brown and Horvath 1989). Northern populations of Orientalis possess a rattle call that is not found in the other groups (Strahl and Brown 1987 and earlier authors). In addition, sizes of territorial flocks in these populations are smaller, and the flocks appear to have only one breeding female each (singular

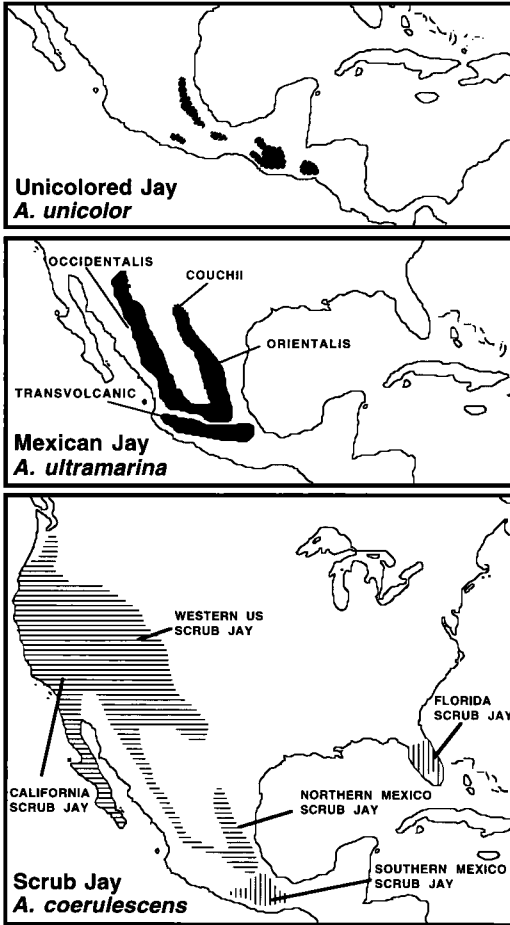


Fig. 1. Geographic distribution of populations of three species of *Aphelocoma* (after Peterson 1992b).

breeding), whereas the other subspecies usually have large flocks and two or more breeding females (plural breeding). *Orientalis* also is distinguished from most populations of *Occidentalis* and the Transvolcanic region by the absence of delayed maturation of the black bill coloration; *Orientalis* does not have the light blotches on the bill in the first year of life that characterize the other subspecies groups (with some mild qualification for *A. u. gracilis* [Peterson 1992a] and certain intergrading populations).

What is the significance of these linkages between the Scrub Jay and this particular population of the Mexican Jay? Brown and Horvath (1989) provided two alternative but not mutually exclusive phylogenetic hypotheses. We evaluate these hypotheses.

Hypothesis 1. Phylogenetic proximity. "*A. coerulescens* might have evolved from a *couchii*-like ancestor, with the Florida population retaining the degree of sociality found in the Chisos Mountains and other populations losing their sociality" (Brown and Horvath 1989:128).

Hypothesis 2. Introgressive hybridization. The Scrub-Jay-like features of northern *Orientalis* may have been caused by infusion of genes from the Scrub Jay through occasional past hybridization and backcrossing in that region, perhaps swamping and absorbing some local populations of the Scrub Jay entirely.

As part of a phylogenetic analysis of *Aphelocoma* jays from 35 locations throughout most of the range of the genus, Peterson (1990, 1992b) has reported data that may be used to test the two hypotheses. His results, which are based on 38 potentially informative electrophoretic alleles from 29 allozyme loci, appeared to confirm the closeness of *Orientalis* to the Scrub Jay, but he did not attempt to discriminate between the two hypotheses to explain it. Instead, Peterson chose the first hypothesis without any mention of the second. Here we consider both hypotheses using Peterson's data and new information.

In general, Peterson's results do not agree with expectations based on the established taxonomy (Pitelka 1951). In his published trees, populations from the three species of *Aphelocoma* did not fall into three clades representing the three species. Instead, the *Orientalis* population (his ULPOT) tended to group consistently with populations of the Scrub Jay, whereas other populations of the Mexican Jay grouped with each other (Peterson 1992b:fig. 7). In Peterson's (1992b:143) words, "On the whole it appears that the Gray-breasted Jay is a relatively old lineage that has been in the mountains of northern Mexico for a long period of time, and that Scrub Jays . . . were derived independently from . . . the Gray-breasted Jay complex", as in hypothesis 1 of Brown and Horvath (1989). (Note that the name Gray-breasted Jay has been changed to Mexican Jay.)

In this paper we have two objectives. First, we present a new phylogeny of the genus and relate it to the evolution of behavior. Second, we present data and arguments that hybridization may have played an important role in this genus, possibly affecting several aspects of behavior.

TABLE 1. Some behavioral and developmental character states for genus *Aphelocoma*.

Population	Rattle call	Delayed maturation	Breeding system	Helping at nest regular
California	Yes	No	Singular	No
Western U.S.	Yes	No	Singular	No
Northern Mexico	Yes	No	Singular	No
Southern Mexico	Yes	No	Singular	Fledglings*
Florida	Yes	No	Singular	Yes
Orientalis	Yes	No	Singular	Yes
Occidentalis	No	Yes	Plural	Yes
Transvolcanic	No	Yes	Plural	Yes
Unicolor	Yes	Yes	Singular	Yes
Outgroup	Yes	No	Singular	No

\* No regular helping at nest, but helping with fledglings. Coded as intermediate condition.

#### METHODS

Difficulties arise from the use of allozymes. As Peterson (1992b:145) observed, "My results serve to illustrate some of the difficulties of using electrophoretic characters in phylogenetic analyses." Because of the polymorphic condition of many allozyme loci, Peterson (1992b) chose to code each allele as an independent character. As he acknowledged, this violates one of the most important assumptions of phylogenetic analysis, namely the independence of characters (Swofford and Olsen 1990); the frequencies of two alleles at the same locus cannot be independent of each other. The presence-absence coding of alleles has been rigorously criticized by Murphy (1993).

We began our analysis with the allozyme data in Peterson's (1992b) more detailed table 2, accepting provisionally the limitations named above. To obtain a record for each subspecies group we combined populations exactly as Peterson (1992b) said that he had done. Using PAUP 3.1 (Swofford 1993), we first constructed trees based on the data from Peterson's (1992b) table 2. We then supplemented the allozyme data with behavioral data in our Table 1 to generate new phylogenetic trees.

Peterson (1992b) used a composite outgroup based on 17 species of jays from five genera. We feel that alternative assumptions on this matter are informative, and we show that they lead to different interpretations of the allozyme data. The composite outgroup might influence any tree rooted on it by increasing the probability of apparent homoplasy.

#### RESULTS AND DISCUSSION

*Allozyme data.*—Our allozyme-based tree (Fig. 2A) may be compared to the corresponding tree of Peterson (1992b:fig. 6). We used the same data, but in this particular tree Peterson omitted the Florida Scrub Jay (*A. c. coerulescens*). In our tree the populations of Mexican Jay arise from

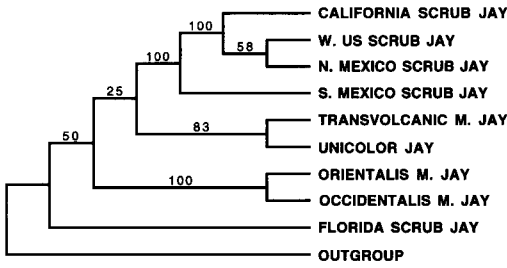
a Scrub Jay base because the Florida Scrub Jay is the most basal branch. The effect of leaving out the Florida Scrub Jay is to reverse this relationship; the most basal branches are then Mexican Jays and Unicolored Jays, causing the Scrub Jay to appear as arising from the Mexican Jay.

To illustrate changes in character states, Peterson and Burt (1992) chose the tree in Peterson's (1992b) figure 7A. It is not clear why this tree was chosen, since it required more steps than other trees, although it is said to be based on other trees in the same paper and on geography. The position of *Orientalis* differs among these three trees. In our trees in Figures 2A and 2B and that in Peterson's (1992b) figure 6, *Orientalis* groups most closely with *Occidentalis*; however, in Peterson's (1992b) figure 7A, which was used by Peterson and Burt (1992) for their character reconstructions, *Orientalis* groups most closely with the Scrub Jay clade. Because *Orientalis* intergrades geographically with *Occidentalis* in central Mexico, it is more logical for *Orientalis* to group with *Occidentalis* than with the Scrub Jay.

*New behavioral characters.*—Trees that are based upon few characters tend to be overly sensitive to single characters. Although 33 allozyme characters were used in Peterson's (1992b) analysis, the resulting trees were not robust. We now add and discuss the four behavioral and developmental characters shown in Table 1.

The rattle call is present in all studied populations of the Scrub Jay (New Mexico [Hardy 1961], Florida [Amadon 1944], and California, where J. L. Brown made numerous observations on color-banded birds) and is found in the Unicolored Jay (tape recordings by T. Webber and

**A. Allozyme data only**



**B. Allozyme and behavioral data**

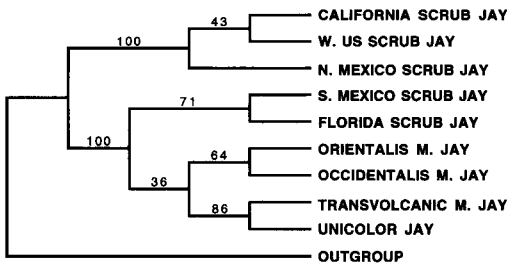


Fig. 2. Majority-rule (50%) consensus trees based on: (A) 12 most-parsimonious trees for allozyme data alone (tree length = 68; confidence index = 0.559; 38 characters); and (B) 14 most-parsimonious trees for combined allozyme and behavioral data (tree length = 78; confidence index = 0.564; 42 characters). Numbers above nodes show percentage of trees. When combined data set was used to construct tree with same topology as in A, the resulting tree was one step longer than the most-parsimonious trees.

heard by J. L. Brown). It is absent in the Mexican Jay except for the northern portion of Orientalis (for full details and sonograms, see Strahl and Brown 1987, Brown and Horvath 1989). The rattle also is widespread in the outgroup, being found in *Cyanocitta* spp. (Hardy 1961, Brown 1964), *Cyanocorax* (Hardy 1969), and other genera (Goodwin 1976). The absence of rattle calling in most populations of the Mexican Jay appears to be derived or apomorphic (Fig. 3). If Peterson's clade composed of the Scrub Jay and Orientalis was derived from Mexican Jay stock (as in fig. 7A of Peterson 1992b), it would have to reacquire the rattle call (homoplasy).

Could the rattle call be simply a learned dialect with zero heritability? There is no evidence for vocal learning of any sort in *Aphelocoma*. Other species in the range of these populations possess the rattle call (Scrub Jays and Steller's Jays [*Cyanocitta stelleri*]), so the absence is not due to lack of a model from which to learn.

Delayed maturation of the bill causes jays in their first year or two of age to retain light patches from the juvenile state. These patches typically are associated with delayed breeding in Arizona populations of the Mexican Jay (Brown 1963) and probably in other populations too. Delayed maturation of bill coloration is characteristic of Occidentalis, the Transvol-

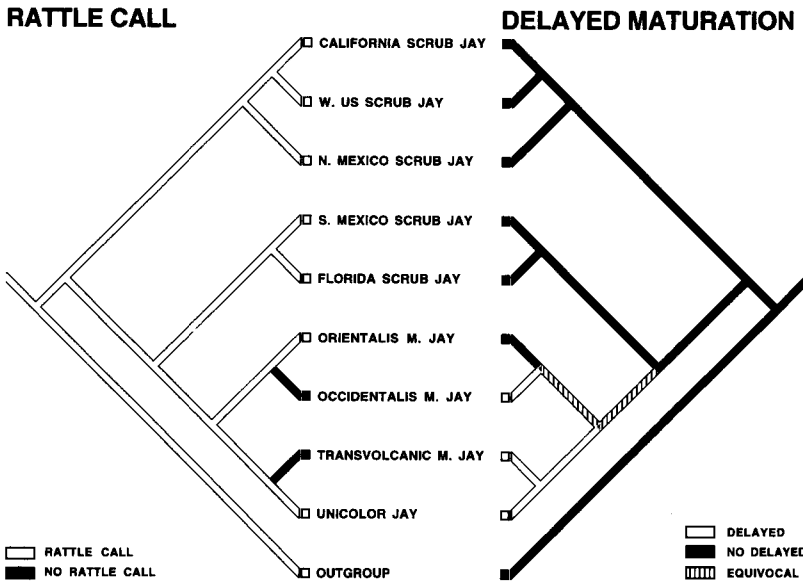


Fig. 3. State changes of Rattle call and delayed maturation of bill coloration on consensus tree based on allozyme and behavioral characters.

TABLE 2. Pairwise mean distance matrices for allozyme data without (above diagonal) and with (below diagonal) additional behavioral characters from Table 1. Each number is percentage of total number of characters that differ between the two groups.

Population	1	2	3	4	5	6	7	8	9
1 California	—	47	45	55	63	61	66	61	61
2 Western U.S.	43	—	34	55	53	55	55	55	55
3 Northern Mexico	41	31	—	47	50	63	53	53	53
4 Southern Mexico	55	55	48	—	24	32	21	21	26
5 Florida	62	52	55	24	—	34	18	24	24
6 Orientalis	60	55	62	31	31	—	16	26	26
7 Occidentalis	69	60	57	29	24	21	—	16	16
8 Transvolcanic	64	60	57	29	29	31	14	—	5
9 Unicolor	62	57	55	29	24	31	19	10	—

canic region (Peterson 1992a), and the Unicolored Jay, but not Orientalis and Scrub Jays (Pitelka 1951). The closest outgroup genera, including *Cyanocitta*, *Gymnorhynchus*, and *Cyanolyca*, do not have delayed maturation of bill color.

Plural breeding is the breeding of two or more females in the same territorial group (Brown 1978). It occurs in Occidentalis (Brown 1963, Brown and Brown 1990) and is presumed on the basis of field observations of group size (Brown and Horvath 1989) to occur in the Transvolcanic region. Plural breeding is rare in the broader context of New World jays and is probably a derived condition (Peterson 1991).

In the taxa we consider, helping is found in the Mexican Jay (Brown 1970), Unicolored Jay (Webber and Brown 1994), and Florida Scrub Jay (Woolfenden and Fitzpatrick 1984). In southern Mexico, nonbreeders feed fledglings, but typically do not feed nestlings (Burt and Peterson 1993). Therefore, we coded the feeding of fledglings as an intermediate condition.

*Trees based on allozymes and behavior.*—The main difference that resulted from adding the new characters to those coding allozymes was to group the Florida Scrub Jay with the population of Scrub Jays in southern Mexico (Fig. 2B). These two populations share an allozyme synapomorphy (Peterson 1992b), are similar in their breeding system, and have helpers.

Is Orientalis the closest group of Mexican Jay populations to the Scrub Jay, as depicted by Peterson (1992b)? The phyletic distances between the taxa with and without our new behavioral characters are shown in Table 2. These distances were estimated as the percentage of analyzed traits that differ between the two taxa. Using only allozyme data, the minimum percentages between the Mexican Jay and Scrub Jay are 21 for the Transvolcanic group, 18 for

Occidentalis, and 32 for Orientalis. The corresponding percentages based on both allozyme and behavioral characters (lower left half of Table 2) are 29 for the Transvolcanic group, 24 for Occidentalis, and 31 for Orientalis. Using allozymes alone or both types of data (neither data set is influenced by a composite outgroup), Orientalis is not closer to Scrub Jay stock than are the other groups, although Orientalis was closer in most of Peterson's (1992b) trees using his 17-species outgroup. Thus, in this comparison and contrary to Peterson's (1992b) cladistic results (using his data set or the combined data), Orientalis is not closer to the Scrub Jay than are the other Mexican Jay subspecies groups.

Judging from the phyletic distances shown in Table 2, the Scrub Jay is a much more geographically differentiated species than is the Mexican Jay. Phyletic distances among Scrub Jay populations range from 24 to 63 using allozyme data (24–62 using allozyme and behavioral data combined); in contrast, distances between Mexican Jay populations range only from 16 to 26 (14 to 31). Unless evolutionary rates are considerably faster in Scrub Jays generally than in Mexican Jays (see below), differentiation in the Scrub Jay appears to have started much earlier than in the other species. If true, the Mexican Jay would have to be derived from the Scrub Jay and not vice versa. Thus, our consensus tree fails to support Peterson's (1992b) contention that Scrub Jays were derived from the Mexican Jay complex.

*Character-state reconstructions.*—We have mapped the phylogenetic distribution of helping behavior and breeding system in Figure 4 using the combined data. Our analysis suggests that the larger group sizes required for plural breeding evolved from smaller ones in this genus, and that helping evolved from nonhelping

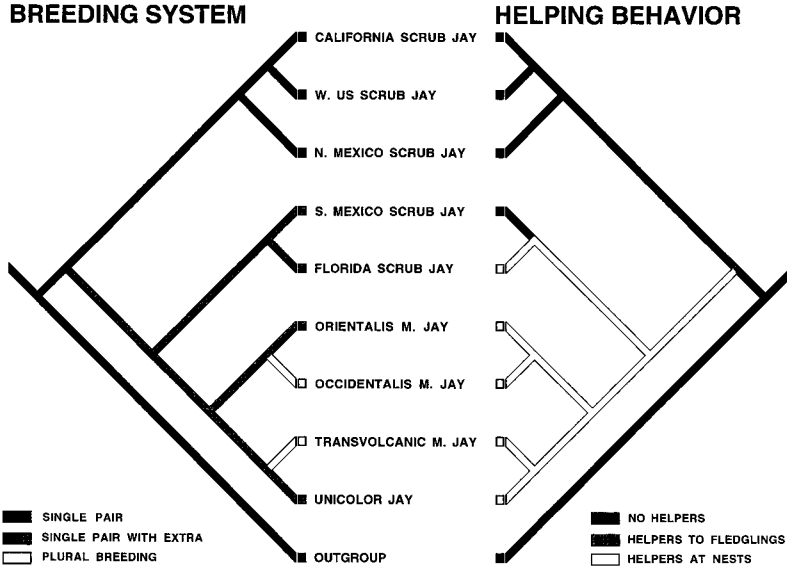


Fig. 4. State changes of breeding system and helping behavior on consensus tree based on allozyme and behavioral characters.

in a Scrub-Jay-like ancestor. In contrast, Peterson (1992b) and Peterson and Burt (1992) claimed that large group sizes and helping had been lost as the Scrub Jay evolved from the Mexican Jay.

Phylogenetic reconstruction of the rattle call in the genus is shown in Figure 3. The rattle call is nearly universal, but has been lost in two populations, namely in Occidentalis and the population of the Transvolcanic region, which are the only two groups in which plural breeding occurs (Figs. 3 and 4).

The phyletic distribution of delayed maturation of bill color is shown in Figure 3. This condition is characteristic of the Unicolored Jay and Mexican Jay with the exception of Orientalis. The latter population could have lost this trait through hybridization with the Scrub Jay, but more work is needed to test this hypothesis.

*Hybridization.*—Before considering the hybridization hypothesis, it is useful to review the characters in which *A. u. couchii* resembles a Scrub Jay to greater or lesser degree (for more details and most references, see Brown 1963, Brown and Horvath 1989). In addition to the characters discussed in the introduction, other characters also suggest hybridization. In molt, body size (wing chord of adult males), and some plumage characters, *couchii* differs from Occidentalis and the Transvolcanic populations in the direction of the Scrub Jay. These are the

facts that led to the prediction of genetic resemblance, but can they help us discriminate between the hypotheses? If the resemblance of *couchii* to the Scrub Jay was caused by convergent evolution of Scrub Jay stock to resemble a Mexican Jay or by origin of the Scrub Jay from Orientalis Mexican Jays, we should expect that the resemblance would affect some characters—the convergent ones—but not all. However, if the resemblance was due to hybridization, all or many characters should be affected (Wilson 1992)—as they are.

Additional evidence, not used originally by Brown and Horvath to derive the hypotheses, is now available. The eggs of Occidentalis and the Transvolcanic populations are unspotted. However, the eggs of *couchii* are polymorphic; some are spotted like the Scrub Jay and some are unspotted like the other subspecies groups of the Mexican Jay (Ligon and Husar 1974). Polymorphism is consistent with a hybrid origin, but is not predicted by the phylogenetic hypothesis. Furthermore, a population that has experienced introgressive hybridization should show enhanced genetic variability. In agreement with this prediction, the heterozygosities for the four Orientalis populations shown in Peterson's (1990) table 3 are all higher than any other population of the same species (*A. ultramarina*). Similarly, the number of alleles per polymorphic locus in Orientalis is as high as or

higher than any non-Orientalis population of *A. ultramarina*. The above data collectively are consistent with the hybridization hypothesis, but not explained by the phylogenetic hypothesis.

A peculiarity of the geographic range of the Scrub Jay also is consistent with the hybridization hypothesis and is otherwise unexplained. As shown in Figure 1, there is a gap in the range of the Scrub Jay just where evidence of hybridization is strongest, namely in the range of *A. ultramarina couchii* (Wauer 1973), which, according to the hypothesis, has genetically "swamped" the Scrub Jay in this area. If this area were the locus of hybridization, it would explain why the resemblance of the Mexican Jay to the Scrub Jay diminishes to the south within the Sierra Madre Orientalis (rattle call drops out; body size and flock size increase).

How plausible is hybridization in these jays? Hybridization between species of birds is widespread; 9.2% of the 9,672 species of birds and 8.2% of 5,712 species of passerines have bred with another species (Grant and Grant 1992). Hybridization between Blue Jays (*Cyanocitta cristata*) and the congeneric Steller's Jay is not uncommon (Williams and Wheat 1971). Hybridization between genera of jays has been reported both in nature (Pitelka et al. 1956) and in captivity (Pulich and Dellinger 1981).

The Scrub Jay is known to wander widely (Westcott 1969), and could easily have found itself in a population of Mexican Jays with no Scrub Jays of the opposite sex. The Mexican Jay wanders only rarely, and it is by far the more sedentary of the two species. Therefore, immigration by Scrub Jays into a population of Mexican Jays seems the more likely scenario for introgressive hybridization. Because of plural breeding in the Mexican Jay, females are tolerant of rivals breeding in the same flock. Consequently, a female Scrub Jay might be able to find a mate and nest successfully in a flock of Mexican Jays. A male Scrub Jay, being smaller, would have difficulty competing for females with Mexican Jays.

Care must be taken when constructing phylogenies from taxa that have hybridized (Cavalli-Sforza et al. 1988). "The evolutionary history of hybrids involves reticulation between lineages, whereas the cladistic method produces only divergent branching patterns. Cladistics can, therefore, never give the correct phylogeny for a group that includes taxa of hybrid

origin" (McDade 1990). Hybridization among animals actually is rather common; yet, its importance in causing diversity is often underestimated for vertebrates (e.g. Dowling and DeMarais 1993, Parsons et al. 1993, Grant and Grant 1994) and invertebrates (Sperling and Harrison 1994).

Has the Scrub Jay evolved from the Mexican Jay or vice versa? In other words, has helping in *Aphelocoma* evolved from a condition with no helping, or vice versa? If Peterson's (1992b) trees (his fig. 7A) and Brown and Horvath's (1989) hypothesis 1 were correct, then the Scrub Jay group would be derived from an already well differentiated Orientalis-like population of the Mexican Jay. An alternative way to describe the tree in Peterson's (1992b) figure 7 would be to say that Orientalis is a member of the Scrub Jay clade that has converged to appear like a Mexican Jay, or at least retained plumage of the Mexican Jay (Peterson's [1992b] paraphyly hypothesis). This scenario was interesting because it required a reduction and even loss of helping behavior (Peterson and Burt 1992). Our results, however, agree with the established taxonomy of the genus. Similarly, our results (Fig. 4) agree with earlier scenarios for the evolution of helping based on behavioral observations (Brown 1974, Woolfenden and Fitzpatrick 1984) in which helping evolves from nonhelping.

Hybridization may be more important for explaining similarities among jays than has been appreciated. Some of Peterson's (1992b) findings raise the question of hybridization for other cases that we have not analyzed. Hybridization involving *A. u. gracilis* and the Scrub Jay in western Mexico is suggested by the small size of *gracilis*, its unusual vocalizations (Horvath pers. com.), and its allozymic closeness to the Scrub Jay of Baja California. This hypothesis also would explain the allozymic closeness of *gracilis* to *couchii*, since both might have hybridized with Scrub Jays (see AUGRA, ACHY3 and AUCO2 in fig. 2 of Peterson 1992b).

The Unicolored Jay presents a similar problem. Although the eastern and western populations appear outwardly similar, the western population is highly differentiated while the eastern population is allozymically very similar to the local population of the Mexican Jay (see AUULT, ANCON and ANGUE in fig. 2 of Peterson 1992b). Has this similarity been caused by past introgressive hybridization between Unicolored and Mexican jays where their rang-

es now overlap in northeastern Mexico? Or, are the allozymes in these two species under similar selection pressures because they live in similar areas?

Our finding that the Florida Scrub Jay groups with the Scrub Jay of southern Mexico instead of on a long branch by itself reveals the lack of robustness of Peterson's (1992b) allozyme-based trees. Perhaps the Florida Scrub Jay is not so different genetically (as is suggested by the allozyme data alone). One of Peterson's (1992b) most interesting findings was that two other populations were distant from the rest (Scrub Jays on Santa Cruz Island and the Unicolored Jay in Guerrero). Sampling of populations of the Unicolored Jay in Central America may help to resolve the current uncertainty about these highly divergent populations.

Present data are consistent with two hypotheses: (1) The Mexican Jay has differentiated from a Scrub-Jay-like ancestor in which most populations lacked helping-at-the-nest but had non-breeding associates with some delayed dispersal, perhaps one like *A. c. sumichrasti* in southern Mexico. (2) Hybridization explains the genetic and phenetic diversity in *orientalis*, especially the acquisition of some Scrub-Jay-like character states, such as the rattle call and the spotted egg pattern. More characters, especially those based on sequence data for mitochondrial DNA, are needed to evaluate these hypotheses.

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