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3 October 1980; revised 15 December 1980

Extended Family System in a Communal Bird

Abstract. *The genealogical structure of an extended family system in a nonprimate species is described. In Mexican jays, social units are more complex genealogically than in most other communal birds and may contain grandparents, uncles, aunts, and cousins in addition to parents and older siblings. The average relatedness within the units varies greatly, and is lower than would be expected for a highly social bird.*

Anthropologists are turning increasingly to animal social systems for insights into the origins of human behavior (*1*). Considerable attention has focused on the ways in which natural selection might affect helping behavior in birds (*2*). It has been suggested that close relatedness within communal units of jays may enhance cooperative behavior and ameliorate competitive behavior—that is, may bias natural selection (*3, 4*). In many communal species, helpers are closely related to parent-recipients (*2*). Most of the relevant studies, however, have concerned species in which the commune is a nuclear family consisting of a single pair of parents and their nonbreeding offspring. We refer to these as singular breeding species (*2*). In contrast, the genealogical organization of communal species in which two or more females simultaneously breed within a social unit—referred to as plural-breeding species (*2*)—is poorly known. We describe here the genealogical basis of an extended family system in a nonprimate species and discuss implications for the evolution of social behavior.

Since 1971 we have studied six social units of the Mexican jay (*Aphelocoma ultramarina*) in Arizona, compiling the histories of over 500 banded birds. Mexican jays live all year in territorial, nonmigratory flocks. The composition of a unit is remarkably stable from day to day, and its members do not mix with those of neighboring units (*5*). Although individuals may scatter widely within their territory when foraging, they rally to defend the territory or nest. Most or all members of a unit feed the young within the unit (*6*). Thus in some respects this jays's communal system resembles that of some lions, primates, and canids (*7*).

We have compiled genealogies from records of the parents of banded nestlings (*8*). Most of the six units we studied were more genealogically complex than singular-breeding communal species (Fig. 1), and most had several simultaneously active nests. Helpers in a territorial communal species have the advantage of being able to breed near or within the communal territory (*9*); thus "the most productive territories of an area are handed down from generation to generation within the ownership of the same genetic lineages" (*4*). Our observations confirm that some former helpers of both sexes breed within the territory of their parents (Fig. 1). Some helpers breed successfully even in the presence of parents of the same or opposite sex. Because stay-at-home breeders often mate with immigrants, incestuous matings are uncommon.

Stay-at-home breeding may result in the presence of three generations in some units. In the CO unit, grandchildren (I, J, K) served as helpers for their grandfather's (C) nestlings. In the

Table 1. Relatedness in six social units of Mexican jays in 1979. The number of individuals in each unit with the indicated relatedness is given as a frequency distribution. Abbreviations: $\bar{r}_{\mathrm{HN}}$, average relatedness of helpers to nestlings, excluding parents of nestlings; $\bar{r}_{\mathrm{MN}}$, average relatedness of all unit members to nestlings; $\bar{r}_{\mathrm{MM}}$, average relatedness among members, excluding nestlings. For $\bar{r}_{\mathrm{MM}}$, the number of relationships is $N(N - 1)/2$, where N = number of unit members.

Unit and nest	Relatedness to nestlings					Relatedness to members				$\bar{r}_{\mathrm{HN}}$	$\bar{r}_{\mathrm{MN}}$	$\bar{r}_{\mathrm{MM}}$
	0	1/8	1/4	3/8	1/2	0	1/8	1/4	1/2			
HI-1	7	4	4	0	1	86	3	13	18	0.10	0.13	0.11
HI-3	11	0	4	0	1					0.07	0.09	
HI-4	7	1	6	0	2					0.12	0.16	
SW-3	1	0	1	3	2	8	3	3	7	0.28	0.34	0.22
CO-3	2	3	1	0	2	17	3	5	3	0.10	0.20	0.11
UC-3	2	0	6	0	2	29	0	0	16	0.19	0.25	0.18
UC-4	3	0	5	0	2					0.16	0.23	
UC-6	3	0	5	0	2					0.16	0.23	
BY-1	7	0	3	0	2	61	0	0	5	0.08	0.15	0.04
BY-2	8	0	2	0	2					0.05	0.13	
BY-3	10	0	0	0	2					0.00	0.08	
RC-2	11	0	2	0	2	101	0	0	4	0.06	0.14	0.02

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HI unit, grandchildren (L, M, N, O) were helpers for their grandfather's (B) nestlings as well as for their cousins and half-sibs. Other relationships not found in nuclear families were also found, such as cousins, aunts, uncles, nieces, and nephews (units HI, BY, and UC in Fig. 1).

In 1979 the average relatedness of unit members to the nestlings in their units was low compared to that of singular-breeding species (*10*). It varied from 0.08 to 0.34 (Table 1). When parents of the nestlings concerned are excluded, the relatedness values ranged from 0 to 0.28. The values are low for several reasons. We have mentioned the presence of third-generation relatives and others more distant than the nuclear family, but perhaps the main cause is the typical presence of immigrants as breeders. In the six units, across 6 years, about 30 of 41 male breeders and 30 of 39 female breeders were immigrants. A third factor is the rarity of yearling full-sibs because of the underrepresentation of the 1978 class in 1979.

Communal birds, in addition to serving as nest helpers, also benefit their unit by calling alarm and harrassing predators. Therefore, it is appropriate to consider the relatedness of unit members exclusive of nestlings (Table 1). Again, average relatedness is low, ranging from 0.02 in the RC unit to 0.22 in the SW unit. In this case there are many more full-sib and parent-offspring relationships (see columns for relatedness = 1/2 in Table 1) than with nestlings included, but their effect on the averages is reduced by the immigrants.

The variability in average intraunit relatedness is striking (*11*). The two extremes are the SW unit, with high relatedness, and the RC unit, with low relatedness. The principal origin of these differences is the frequency of immigration: there are many immigrants in the RC unit but few in the SW unit. Conversely, many of the members of the SW unit were hatched in the same unit, reflecting the generally higher rate of reproductive success in this unit over the years.

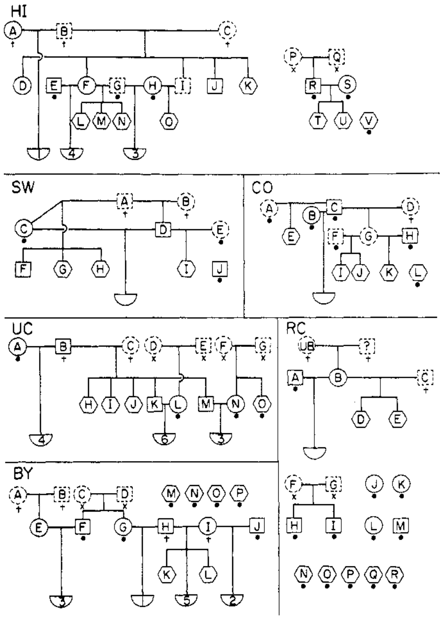

Fig. 1. Genealogies of the six social units of Mexican jays. All individuals present in May 1979 are indicated by symbols with solid lines. Selected ancestors no longer alive or in another unit are indicated by dashed symbols. Symbols: (□) male, (○) female, (○) sex unknown, (▽) nest with young, (●) immigrant, (+) present at start of study (1971), ancestry unknown, and (×) in neighboring unit.

The relatively low relatedness in social units of Mexican jays suggests that the indirect component (*12*) of inclusive fitness (*3*) might be less important in the evolution of communal breeding in jays than previously hypothesized (*4*). However, the low relatedness might be partially offset by three factors. First, individuals might choose to aid recipients that are more closely related than the average (*13*). Second, the number of related recipients in a unit is often larger than in nuclear families. In trait groups the intensity of selection for alarm-calling and territorial defense increases in direct proportion to the number of recipients carrying the gene in question (*14*). Third, reproductive success might be above average in units with higher relatedness (*13*).

Our estimates of relatedness do not take into account the general level of inbreeding in the population, which, in the absence of pure outbreeding, must be greater than zero. However, since we have not yet discovered any inbred offspring. we defer consideration of the effects of inbreeding. Another factor whose significance cannot yet be evaluated is the degree of relatedness between neighboring units. Some members of the BY, HI, and UC units came from the SW unit (Fig. 1) and were related to members of the SW unit in 1979.

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8. The mother of a brood of nestlings is the only individual to incubate eggs and brood the young at her nest. Identification of the father is slightly less certain. Typically the nest is begun by the male, who is later joined by a mate. Normally, only these two birds build (*5*). During the period of building, and especially for several days before laying, the two consort together and the male drives other males away. Paternity is established by observing which male builds and consorts with the female at a given nest. Copulations are rarely observed. Only once have two females been seen at a nest, and sexual sharing of a female by two or more males in the same year is rare.
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8 July 1980

Hemispheric Specialization for Language Processes

Although ". . . in studies of dichotic listening, the superior performance of the right ear has been explained as a reflection of the left cerebral hemisphere's subserving linguistic abilities" (*1*, p. 1380), shifts in the *degree* of right ear superiority, with variations in the acoustic structure of competing syllables, cannot be safely interpreted as reflecting shifts in the *degree* of left hemisphere engagement. This limitation exists because an ear advantage in dichotic listening is not a simple index of hemispheric specialization.

Two conditions are necessary for an ear advantage: (i) hemispheric specialization, and (ii) some degree of ipsilateral loss. Ipsilateral loss has been attributed either to suppression of the ipsilateral signal because of the greater number of contralateral fibers (*2*) or to attentional mechanisms associated with spatial orientation toward the side contralateral to the activated hemisphere (*3*).

Either or both of these mechanisms are compatible with repeated demonstrations that the magnitude of the right ear advantage (REA) for dichotically pre-