GEOGRAPHIC VARIATION OF GROUP SIZE, ONTOGENY, RATTLE CALLS, AND BODY SIZE IN *APHELOCOMA ULTRAMARINA*

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ABSTRACT.—We estimated sizes of over 90 social groups of *Aphelocoma ultramarina* in various regions of Mexico and recorded the presence or absence of Rattle calls. Group size over most of Mexico was similar to that in Arizona, not to that in Texas. We found that geographic variation in mean group size was not correlated with ontogeny of bill color. Group size correlated positively with body size. Rattles were found only in *A. u. couchii* but not in all populations. We hypothesize that natural selection may not be the only factor responsible for the patterns observed. *Received 27 November 1987, accepted 16 September 1988.*

THE genus *Aphelocoma* (*A. unicolor, A. coerulescens,* and *A. ultramarina*) demonstrates intraspecific geographic variation in size, plumage, ontogeny of bill coloration (Pitelka 1951), sociality and vocalization (summarized in Brown 1963, 1985). Several hypotheses based on behavioral studies in the United States and on studies of museum specimens have been proposed that relate these variables to each other in *A. ultramarina* (Strahl and Brown 1987).

The first hypothesis is related to the delayed acquisition of adult coloration. In one type of communal rearing of young, the helpers are typically nonbreeding members of broods from the previous year or two (Skutch 1935, Brown 1987). In many such species the nonbreeders show visual "signals of immaturity" (see Brown 1978, 1985, 1987 for illustrations and examples). If such birds remain on their natal territory until breeding age, then average group size should be larger in species that delay breeding longer (Brown 1974). The specific prediction we tested was that average group size is larger in those populations of *A. ultramarina* in which adult bill coloration is delayed for at least a year than in populations in which the adult coloration is acquired around the time of fledging. This resembles the "sociality" hypothesis of Hardy (1961), which links persistence of subadult coloration with sociality.

A second hypothesis stems from a recent study of *A. u. couchii* in Texas where this subspecies differs from *A. u. arizonae* by having Rattle calls and smaller groups (Strahl and Brown 1987). *A. u. couchii* belongs to the subspecies group (*couchii* and *potosina*; Pitelka 1951, 1961) in which adult bill coloration (black) develops "soon after the young bird leaves the nest" (Van Tyne and Sutton 1937), while the attainment of adult bill coloration is delayed at least a year in the other subspecies. The young of these subspecies have bills that are variously blotched with black and a light pink or horn color. We tested the prediction that three characters will vary concordantly. These are the presence or absence of delayed attainment of adult bill color; presence or absence of the Rattle; and group sizes like *couchii* (small) or like *arizonae* (large).

A third hypothesis also stems from the study of the population in the Chisos Mountains. Rattles, which seem to be given only by females, were associated with singular breeding (only one female breeding in a group); Strahl and Brown (1987) observed only one bird Rattling in each flock. If this association were general, in other populations no more than one jay should Rattle in each group.

Finally, because Strahl and Brown (1987) found that group sizes in *couchii* (a small-bodied subspecies) were conspicuously smaller than in *arizonae* (a large-bodied subspecies), we examined this relationship in a larger data set.

STUDY AREAS AND METHODS

Group size.—Group size was estimated by methods employed previously in studies of *A. u. arizonae* (Brown and Brown 1985) and *A. u. couchii* (Strahl and Brown 1987). *A. u. arizonae* lives in groups that remain in their territories all year. Groups respond to detection of an intruding group by rushing together to meet it. To census a group, a tape recording of calls was played toward the group by one person while a second person counted the jays as they flew across a road or large clearing toward the loudspeaker. This process was repeated on three different days for each group. The highest of the three counts was used to represent the group. A recording of *A. u. gracilis* was played to *A. u. gracilis* because they would not respond to calls of *arizonae.* For all other populations we used a tape of *arizonae,* to which the jays responded strongly.

Tapes were played on a compact cassette recorder (Sanyo TRC1550), and amplified and broadcast through a Sony speaker system (APM-007AV).

Rattles.—To determine whether or not Rattles were given in a particular population, we used a technique developed by Strahl and Brown (1987). We repeatedly played to each group a tape containing many Rattles and other calls recorded in the Chisos Mountains, Texas. Two of these Rattles were illustrated by Strahl and Brown (1987). To determine if two or more birds in a group Rattled we counted the number of birds giving Rattles within each group. These counts indicate the minimum number of birds giving Rattles.

Body size.—Means of measurements of wing length were taken from Pitelka (1951). Of several indicators of body size, we chose wing length because it seemed the best available index of body size. We chose adult males because sample sizes for them are larger than for other age-sex categories (Fig. 1).

Study areas.—We collected data on group sizes and Rattles at five localities in Mexico from four different subspecies. The capital letters, A–G, represent these localities and two others from published sources (Fig. 1, Table 1): (A) *A. u. arizonae.* Chiricahua Mountains, Arizona (Brown and Brown 1985). (B) *A. u. gracilis* (22–25 February and 3–7 March 1987). We censused five flocks in the Sierra de Bolaños in northern Jalisco, 30 km south of Villa Guerrero on the road to Bolaños at 1,700 m. The vegetation was low, sparse oak woodland with very few pines. One common species of oak (*Quercus* sp) had extremely large leaves. No other species of jay was observed here. (C) *A. u. colimae* (2–17 February 1987). We censused 20 flocks north and northeast of Tapalpa, Jalisco, within 16 km of this town. Elevations ranged from 2,100 m to 2,200 m. The vegetation was dominated by tall pines (*Pinus* spp) but contained some oak trees. Oaks were notably scarce in some territories (ca. 5% of trees). There was little understory. No other species of jays was observed here. (D) *A. u. potosina* (6–23 November 1986). We censused 30 flocks near Zimapan, Hidalgo. These were located in three areas: along the road to La Pechuga, along a different road to Nicolas Flores, and along Route 85 between Zimapan and Jacala. Elevations ranged from 1,800 m to 2,500 m. The flocks were found in open woodland composed of oaks, junipers (*Juniperus* spp) and pinyon pines; the pinyon predom-

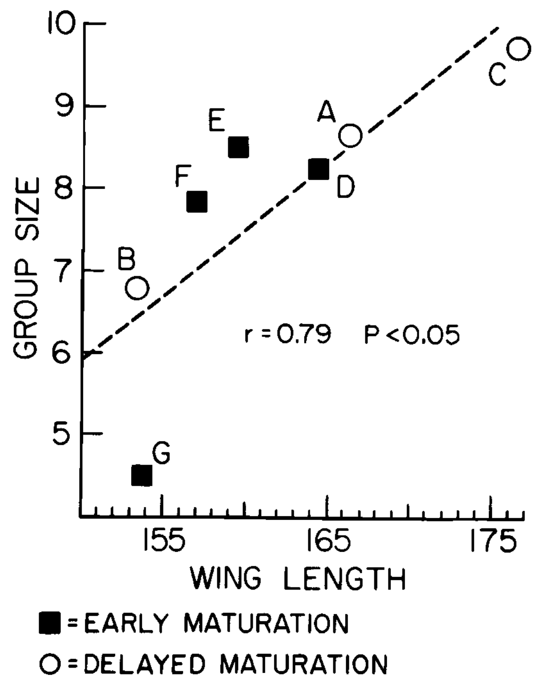

Fig. 1. Group size increases with body size in *Aphelocoma ultramarina.* Group sizes are the means from Table 1; body-size data are mean wing lengths of adult males. Localities are designated A–G as in Table 1. Data for wing length came from tables in Pitelka (1951): A, 40; B, 50; C, 57; D, 54; E, 53; F, 52; G, 51. The straight line is the linear regression of mean group size (G) on mean wing length (W): $G = 0.16W - 18.6$.

TABLE 1. Sizes of groups of *Aphelocoma ultramarina* in various localities (described in text). R = Rattle call present (+) or absent (−); *n* = number of groups sampled.

Subspecies	Locality	Group size 3	4	5	6	7	8	9	10	11	12	13	14	22	$\bar{x}$	SD	*n*	R
arizonae	A	—	—	4	2	6	5	3	1	10	1	1	—	—	8.67	2.33	33	−
gracilis	B	—	—	2	—	—	3	—	—	—	—	—	—	—	6.80	1.64	5	−
colimae	C	—	—	—	2	5	1	4	2	2	—	2	1	1	9.75	3.73	20	−
potosina	D	—	—	—	6	4	6	8	3	2	1	—	—	—	8.27	1.66	30	−
couchii	E	—	—	—	—	1	2	2	1	—	—	—	—	—	8.50	1.05	6	−
couchii	F	—	1	3	6	6	4	2	3	3	1	1	—	—	7.83	2.31	30	+
couchii	G	6	8	5	7	—	—	—	—	—	—	—	—	—	4.50	1.14	26	+

inated. Other species of jays were absent except for a single *Xanthoura yncas* at the lowest elevation (Route 85 near Jacala). (E) *A. u. couchii.* On 27-29 November 1986 we censused six groups in open woodland 23 km south of Ascension, Nuevo Leon, on Route 61 (2,000 m). The vegetation was similar to that at El Diamante, but large oaks were common. Neither *A. coerulescens* nor *C. stelleri* was observed. (F) *A. u. couchii* (30 November through 18 December 1986). We censused 30 groups in the valley of El Diamante, which lies just south of Saltillo in Coahuila. The flocks were along the dirt road leading west to El Diamante and Sierra Hermosa leaving Route 57 19 km south of its junction with Route 40 (2,150-2,400 m). Jays were found in open woodland composed of pines, junipers and a few scrub oaks on the slopes of the hills above the valley floor, which was used for agriculture. On the plateau above, trees were absent and desert conditions prevailed. *A. coerulescens* was uncommon and restricted mainly to the upper and lower borders of the pine-oak woodland. *Cyanocitta stelleri* was absent. (G) *A. u. couchii.* Chisos Mountains, Texas (Strahl and Brown 1987).

RESULTS

Group size.—All Mexican populations were composed of social groups of at least 4 birds (Table 1). Groups as small as 2 or 3 birds were encountered only in Texas (see also Ligon and Husar 1974). Means of group size in the various populations in Mexico ranged from 6.80 (*gracilis*) to 9.75 (*colimae*). Thus, the mean of the *arizonae* sample (8.67) is well within the normal range of the species in Mexico.

Only the one Mexican population of *gracilis* was smaller than average. The difference was not significant. Unfortunately, we were unable to sample more groups in this population, and the road to the other known populations of *gracilis* was impassable.

Our first hypothesis predicts that group sizes average larger in those populations in which attainment of adult bill coloration is delayed for at least a year. This prediction was not consistently upheld (Table 1). Although one nondelaying population (Chisos Mountains) had small groups, the other three did not (localities D, E, F in Table 1). The population means for these three range from 7.8 to 8.5 and fall within the range of the populations with delayed maturation of bill color (6.8-9.75). In the latter group the color of the immature bill is more conspicuous in the populations with large group sizes, such as *colimae* and *arizonae,* than in the one population that might have smaller groups, *gracilis* (Pitelka 1951: 371). The hypothesis can be rejected.

The second hypothesis posits that group size, bill color, and presence or absence of Rattle calls vary concordantly. Rattles were found only at localities F and G. Among the early maturing populations (D-G) Rattles may be present (F, G) or absent (D, E), and their presence is independent of group size. Therefore, the hypothesis of concordant variation can be rejected.

Our third hypothesis was that no more than one bird would give Rattles in each group. This can now be rejected. In the 1 Mexican population where Rattles were observed, El Diamante (F), at least 1 bird Rattled in every 1 of 30 groups. In 5 of these, 2 different birds were heard Rattling in succession. In 13 other groups Rattles were heard so close in time that it is extremely unlikely that they were given by a single female. Therefore, in at least 5 groups the hypothesis can be rejected and probably in at least 18 of the 30 groups.

We found a positive correlation ($r = 0.79$, Pearson correlation coefficient, $P < 0.05$, df = 5) between mean group size (Table 1) and mean wing length of adult males in the same population (Fig. 1), using the measurements of Pitelka (1951).

DISCUSSION

Group size and body size.—There was no obvious causal relationship between group size and body size. The correlation probably arose through causal relationships with other variables that affect both group and body size. One such variable is predation pressure. Both larger body size and larger group size are widely regarded as related to survival under conditions of severe predation. Correlated increases in body size and group size should also decrease the availability of unoccupied but suitable territories, thereby enhancing the effect of habitat saturation on delayed breeding and dispersal. It is conceivable that increased body size and flocking in these jays are both responses to predation by *Accipiter* hawks and that geographic variation in hawk predation pressure is ultimately responsible for the observed variation in flocking and body size.

Predation on *A. ultramarina arizonae* by both *Accipiter gentilis* and *A. cooperi* is intense in Arizona, where jays are an important food of *A. gentilis* in all seasons and of *A. cooperi* in summer

(N. Snyder pers. comm.). By contrast, in the Chisos Mountains neither species of *Accipiter* was recorded by Wauer (1971) as a regular occupant of any habitat in any season. The absence of *A. gentilis* in winter may be related to the rarity of forested breeding sites in the Great Plains to the north of the Chisos Mountains. Other explanations of geographic variation in body size and group size are also possible.

Group size in Arizona and Texas.—We sampled systematically group sizes of *A. ultramarina* in Mexico, where the vast majority of the range of the species occurs. The group sizes in Arizona, but not Texas, can now be accepted as fairly typical of the species over large parts of its range. Although the Texas and Arizona populations are geographically close, they lie at opposite ends of the U-shaped range and have many differences. The species can be separated into two groups with regard to ontogeny of bill coloration. In the eastern group of subspecies (*potosina,* and *couchii*), the adult coloration is acquired by the end of postjuvenile molt (Pitelka 1951); in the combined western and southern groups, the attainment of a solid black bill is delayed by at least a year. We wished to know whether these two ontogenetically defined groups also differed consistently in group size and Rattles. We found that these traits do not vary concordantly; the dividing lines for these traits fall in different areas.

South of Texas the first population with large group sizes and probable plural breeding occurred in Coahuila (locality F). The first population without Rattles occurred farther south in Nuevo Leon (locality E), and the last population with rapid maturation of bill color occurred even farther south in northern Hidalgo (locality D). From southern Hidalgo around the "U" and north to Arizona, all populations had large mean group sizes (except possibly *gracilis*), lacked Rattles, and had delayed maturation of bill coloration. Variation in group size was not well correlated with the ontogeny of bill color.

Heterochrony in Aphelocoma ultramarina.—The delay in acquisition of adult bill coloration in communally breeding birds, such as *A. u. arizonae,* has been suggested as a possible example of *neoteny* (Brown 1974: 76, Lawton and Lawton 1986), which Gould (1977) viewed as a special case of heterochrony. Individuals of *A. u. arizonae* with subadult (blotched) bills have been observed to breed (Brown 1963), although most do not (Brown 1985). In the breeding season individuals of *A. u. arizonae* in their first year almost never breed (Brown 1985). Yearling males show no interest in females. It is mainly a few two-year-old birds that breed with subadult bill color; and in them the bill is nearly black. Thus the case for neoteny is not strong for *A. u. arizonae.* Corresponding information for other subspecies that delay attainment of adult coloration is not available.

The juvenile bill coloration of one- and two-year-old jays might facilitate coexistence of dominant breeders and subordinate nonbreeders that are, nevertheless, capable of breeding (Hardy 1961; Brown 1974, 1978: 148; Lawton and Lawton 1986). Although this hypothesis finds some support from anecdotal observations in other species, it does not fit well with data on age and dominance in *A. ultramarina* (Barkan et al. 1986). In this species some individuals in their first winter commonly rank above the breeders, not below. Adults do not dominate these young birds but tend to avoid them at food sources in winter.

We reject for *ultramarina* the form of the hypothesis that requires yearlings to be subordinate, potential breeders. Instead, we suggest an alternative hypothesis. Because bills are used in sparring over food in winter when food is often scarce, yearlings profit from the attention that is drawn to their bills by their conspicuous coloration. Although yearlings weigh less than adults, their bills are approximately as long as those of older birds of either sex (unpubl. data; Pitelka 1951). Dominant yearlings might benefit from a visual signal that draws attention to them and allows them to win some interactions more easily, perhaps even uncontested. Subordinate yearlings might benefit from their resemblance to dominant yearlings in interactions with some adults. Our hypothesis shares with the rejected coexistence hypothesis stated above the consequence that the distinctive bill color facilitates staying in their natal units by individuals in their early years. The greater potential for visual recognition provided by the variegated bill coloration supports this result by enhancing individual recognition. The benefits of distinctive bill coloration of yearlings could be obtained with or without neoteny.

Historical and phylogenetic factors.—The populations of *A. u. ultramarina* that live in Texas (and a short distance into adjacent Mexico) possess a Rattle call and have smaller group sizes. The Texas population also differs from others morphologically and in coloration (Pitelka 1951). In most of these characters the Texas population differs from the remaining populations in the direction of *A. coerulescens* (Brown 1963, 1985). Here we briefly consider why the Texas population of *A. u. ultramarina* resembles *A. coerulescens* both behaviorally and morphologically. The *coerulescens*-like nature of *A. u. couchii* may not rest on strictly adaptationist principles. Historical events might have played some role and, therefore, deserve consideration.

Hybridization between *A. ultramarina* and *A. coerulescens* may have occurred frequently in the Chisos Mountains. It is noteworthy that *A. coerulescens* does not breed there now although it occurs nearby (Wauer 1973). Additionally or alternatively, *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. Either of these theories would explain the presence of so many *coerulescens* traits in *couchii* but not other subspecies of *A. ultramarina*. Both lead to the testable prediction that *A. coerulescens* is closer genetically to *A. u. couchii* than to the other subspecies of *A. ultramarina*.

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