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ECOLOGICAL CORRELATES OF GROUP SIZE IN A COMMUNALLY BREEDING JAY

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ABSTRACT.—We studied local variation in size of social units in the Gray-breasted (or Mexican) Jay (*Aphelocoma ultramarina*) throughout its elevation range in the Chiricahua Mountains, Arizona. At its lower limit (1,463 m), the ecological distribution of the species ended where oaks became rare, even though other large trees were present. The upper limit of distribution (2,103 m) coincided with the beginning of the area occupied by Steller's Jays (*Cyanocitta stelleri*), and not with a decrease in the number of species of *Quercus* or the availability of mast. Size among social units varied locally at all elevations. Unit size was not correlated with elevation.

We studied yearly variation in a small number of units over 15 years. Mean size of these groups varied from 6.7 to 17.5 individuals. Although group size was highly variable in space and time, our findings reaffirm reports from the Santa Rita Mountains that group size in the Arizona population of this species tends to be unusually large compared to that of other communally breeding birds. The number of juveniles per flock in August was positively correlated with group size in May. Along the canyon bottom, we estimated the linear density of the population in May at 1.7 flocks/km or 16.7 jays/km.

Social systems among communally breeding birds are known to vary geographically within some species, and this variation may provide insight into the environmental factors that influence social organization (Grimes 1976). Geographic variation in group size has long been known in *Aphelocoma* jays (Brown 1963, 1974, Woolfenden 1975). Such variation, however, can be confounded with temporal and local ecological variation. To assess the importance of these factors in a population of the Gray-breasted (or Mexican) Jay (*A. ultramarina*), we examined local variation among 33 social units in one year, and yearly variation of six units from 1969–1983. Related goals were to determine the influence, if any, of elevation on group size, and to consider the ecological correlates of the upper and lower limits of the species. In particular, since this jay relies heavily on acorns, we wished to test the oak-species-diversity hypothesis of Bock and Bock (1974).

STUDY AREA

Our study area lies mainly in Cave Creek Canyon, Chiricahua Mountains, Arizona. It covers the ecological range of the Gray-breasted Jay in these mountains and extends from desert at Portal (1,451 m) to ponderosa pine woodland at Rustler Park (2,560 m). We chose to study 33 flocks in this area. These flocks were distributed unevenly along an elevational gradient, with most flocks in middle and lower regions. At middle elevations (1,610–1,670 m) were six flocks that are the focus of a long-term, continuing study which began in 1969 (Brown 1970, in press). Most flocks were near the canyon bottom, roads, and permanent streams, but some were a kilometer or more from the nearest road and had no reliable water.

METHODS

CENSUSING

To study spatial variation, it was necessary to work with unbanded flocks, since banding 33 flocks would have been impractical. For this part of the study, we determined flock size by counting jays as they flew across valleys, roads, creeks, or other openings in the woodland. Although the jays sometimes flew across of their own accord, most were provoked either with

playbacks of jay calls or by herding the flock toward an opening. The tape was played on the opposite side of a canyon or clearing from the flock's location. Two or more observers worked as a team, with one playing the tape from a hillside or herding the flock, and the other strategically stationed to count jays as they flew past.

The same tape selection was used for all the playbacks. It had been recorded from the SW flock as it flew in to investigate some calls that had been played on another recorder. The calls on the tape were given in a context of territorial defense. In hundreds of trials, the calls were effective in inducing what we interpret as an aggressive response to a mock intruding flock. Flocks usually responded readily if they were within 50 m of the recorder, and sometimes from much farther. Since territories averaged 0.58 km in diameter (see Results), a playback from one spot often could not be heard in all parts of a territory.

We estimated total flock size, number of yearlings (spring only), and juveniles (August only). The field work was done during May, June, and August, 1975. Counts were usually made early in the morning, when the jays seemed most responsive and when most natural territorial encounters occurred. On a given morning, a team of two or three observers could census three or four flocks in about four hours. The highest of two or more counts for each flock in May–June was taken as the estimate of size for that flock; similarly, we estimated the numbers of yearlings or juveniles. In August, most, but not quite all, flocks were counted twice and the highest count was taken.

For the intensively studied, color-banded flocks in the long-term study, we used a tally method of counting. Records were kept of which individuals were seen regularly in each unit during the period 1 May through 30 June, and the number of individuals that were tallied was taken as an estimate of flock size. The tally method is less likely than field counts to miss individuals and tends to yield higher estimates.

We read elevations from U.S. Geological Survey topographic maps (scale 1:62,500, contour interval 80 ft). For each territory, the elevation was read from the map at a point along the creek-bed, half-way between neighboring territories up and down the creek.

AGING

In this paper, birds that were approximately one year old are referred to as "yearlings." They were recognized in May and June by the color of their bills. Adult Gray-breasted Jays have black bills. The bills of yearlings in Arizona have conspicuous patches of white or horn color, sometimes tinged with faint pink. The basal half of the lower mandible is commonly entirely pale. We have found that in known-age, banded two-year-olds, the white patches are much reduced and commonly are confined to the fleshy, external corners of the mouth. Three-year-old and older jays have bills that are black except, in some individuals, for a small, light gray patch on the ventral surface of the lower mandible, not seen in the field. In spring, yearlings can be distinguished in the field with near certainty, but two-year-olds were deemed too difficult to separate from adults. Representative pictures of bills may be seen in Hardy (1961) and Phillips et al. (1964). In August, jays were classified as either juveniles (1–3 months old) or post-juveniles (one or more years old). Juveniles were recognized by their juvenal plumage and/or extremely pale bills.

RESULTS

FLOCK SIZE

Flock sizes that we estimated by the playback method ranged from 5 to 22 birds, depending on location, year, and season (Fig. 1). These 33 flocks averaged 8.7 (SD = 2.3) members in May–June, and 11.2 (SD = 3.26) in August. The increase was due to the presence of juveniles in August. Large flocks were rarer than small ones. The estimate of the moment coefficient of skewness, g, was positive in all cases, but significantly different from zero only in August, 1975, when the flocks were augmented by many juveniles.

Because 1974 was an unsuccessful year for breeding, owing probably to the record drought and diminished insect populations in Cave Creek Canyon (unpubl. data of R. Ballinger), few 1974-year-class jays were present in 1975 (see Brown, in press). In 1975, there were actually more 1973-year-class jays than 1974 birds in the six flocks where this could be ascertained by color banding.

ALTITUDINAL LIMITS

In southern Arizona and northern Mexico, Gray-breasted Jays are permanent residents in pine-oak and oak (encinal) woodlands, from their lower borders with desert or grassland to their upper intergradation with ponderosa pine (*Pinus ponderosa*) forest (Marshall 1957).

The lower limits of altitudinal range along Silver Creek were determined by playing the flock calls at eight locations along the Silver Creek Road for 6.1 km from Portal (1,451 m) to Paradise (1,676 m). Scrub Jays (*Aphelocoma coerulescens*) were encountered at two sites along Silver Creek, where they had been seen regularly in other years, but Gray-breasted Jays

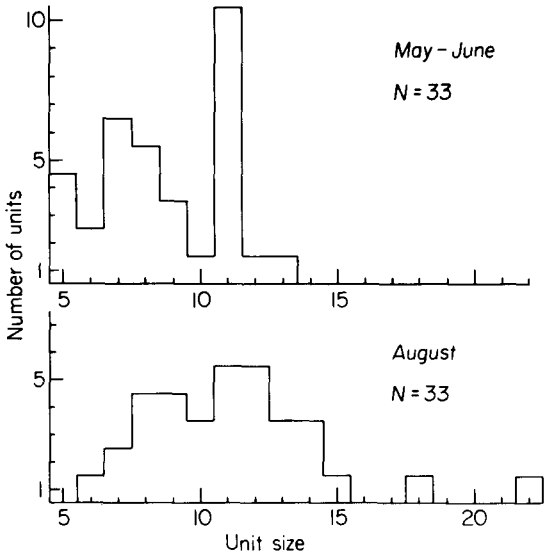

FIGURE 1. Frequency distributions of flock sizes in the Gray-breasted Jay in the Chiricahua Mountains, Arizona. The data for May and June include birds of all ages except young of the year. Young of the year are included in the August sample.

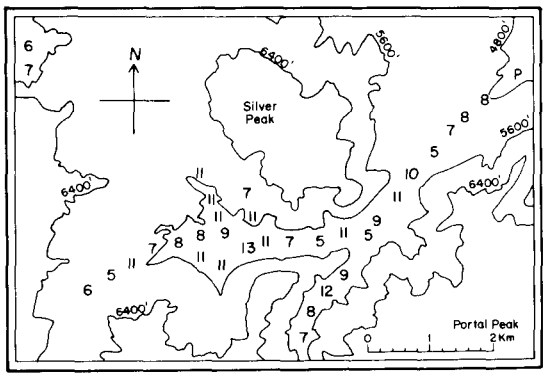

FIGURE 2. Map of the study area in Cave Creek Canyon showing locations and sizes in May–June, 1975, of the 33 flocks shown in Figure 1. Contour interval is 800 ft. P = town of Portal.

were not encountered until the cemetery in Paradise—the same spot where they were first encountered on the Christmas Count for Portal, Arizona, in December, 1974 (S. Spofford, pers. comm.). Paradise is the lowest place where pine-oak woodland occurs along Silver Creek Road. Scrub Jays in the Chiricahua Mountains are not restricted to low elevations. We did not see them on our other censuses, but during the breeding season they normally occur at high elevations (e.g., Silver Peak and Snowshed Peak) in scrubby vegetation.

Along Cave Creek, the lower limits of Gray-breasted Jays, as shown in Figure 2, were at 1,463 m, slightly above the village store at Portal (1,451 m). These jays are rarely seen in Portal (B. Bush [a resident of Portal] pers. comm., 1984).

In Arizona, Gray-breasted Jays occur in the fingers or corridors of woodland that extend along intermittent streams into the nearby treeless desert or grassland from the area of continuous woodland. In our study, the jays did not occur where these fingers were composed mainly of sycamores (*Platanus racemosa*) with few oaks. In the few areas where we found jays along these strips of riparian woodland, substantial patches of woodland, composed predominantly of oak, grew on adjacent north-facing side canyons.

The upper limits of these jays in the Chiricahua Mountains tended to coincide with the upper limits of continuous pine-oak woodland (mainly silverleaf oak, *Quercus hypoleucoides*, at the higher elevations) and the lower limits of ponderosa pine forest.

Since we have heard occasional oral reports of Gray-breasted Jays in ponderosa pine forest in the Chiricahuas and elsewhere in Arizona, we made a systematic effort to find flocks in this habitat. The playback method was used to detect jays at intervals along the road below and above Onion Saddle (2,316 m) to Rustler Park (2,560 m). We did not find any jays at six locations from Onion Saddle down to the highest flock of Mexican Jays that we observed, at 2,103 m, 2.7 km below Onion Saddle and 2.57 km above the intersection of the Paradise Road with Portal Road at Turkey Creek (the two most western units in Fig. 1). At this spot, the dominant tree was the silverleaf oak, and patches of ponderosa pine forest grew on nearby north-facing slopes. N. Hill (pers. comm.) determined independently that the highest flock of Gray-breasted Jays was found at this spot (5 April 1975). In many miles of hiking the higher altitudes of the Chiricahuas in spring and summer (1969–1984), we have only rarely found these jays above the pine-oak zone, and then not repeatably in the same locations.

CORRELATES OF ELEVATION

We examined elevation as a potential clue to the ecological correlates of flock size. Flock size varied widely at all elevations (Fig. 2). A simple linear regression of total flock size or number of young (the youngest year-class present, i.e., yearlings in May–June; juveniles in August) or older jays (post-yearlings in May–June; post-juveniles in August) on elevation was never significantly different than zero. In all cases, the moving average was highest at middle elevations, as were the highest counts. In all cases, a polynomial regression equation

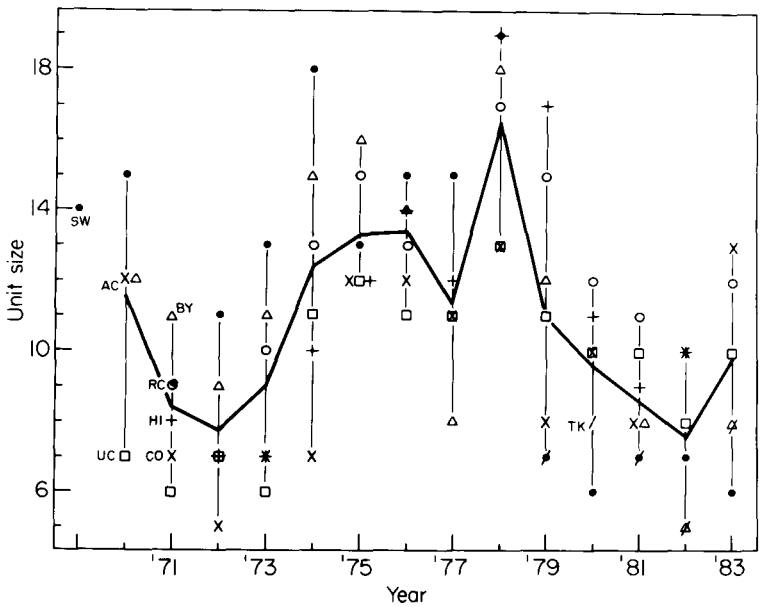

FIGURE 3. Yearly variation in flock size. Data are for color-banded units in May–June, excluding young of the year. The mean unit size is shown by the heavy line. Vertical lines show the range of sizes in individual flocks identified by symbol and letters (for comparison with other papers on this population).

with a peak at middle elevations provided a better fit to the data than a linear regression. All polynomials from the first to eleventh degree were tested for fit to each set of data. A coefficient of determination was computed for each data set and each polynomial degree. The best fits were invariably to quadratics or cubics with a peak at middle elevations; however, the fits were all poor (coefficient of determination = 0.13 for flock size), and elevation explained relatively little of the variation in flock size and age composition.

The number of yearlings per flock appeared to be higher at middle elevations than at lower or higher elevations; however, comparison of yearlings per flock at low (1,463–1,585 m, n = 11), middle (1,597–1,670 m, n = 11), and high (1,682–2,103 m, n = 11) elevations by a chi square test did not reject the null hypothesis of independence of elevation and yearlings. Shifting of the boundary between samples at middle and high elevations to 1,737 m did not alter the chi square value appreciably (χ^2 = 4.28; 6.00 needed for P = 0.05). Only 12 flocks contained any yearlings in May, 1975.

OAK SPECIES DIVERSITY

Bock and Bock (1974) suggested that the geographic range of the Acorn Woodpecker (*Melanerpes formicivorus*) might be limited at its northern boundary by oak species diversity, the idea being that years of total acorn crop failure become less likely as more species of oaks are added to the flora. We repeatedly observed that Gray-breasted Jays competed vigorously and aggressively with Acorn Woodpeckers for the harvesting of fresh acorns on the oaks in August and September. The jays then stored acorns, usually in the ground (Brown 1963). After the acorns were stored, we saw no evidence of one species raiding another's stores. The jays consumed acorns through the winters. We have found pieces of acorn in the stomachs of nestlings, although arthropods account for at least 90% of the nestling diet (unpubl. data). Gray-breasted Jays also avidly harvested and stored the nuts of the pinyon pine (*Pinus cembroides*). In short, we observed that acorns are an important food for these jays, as well as for Acorn Woodpeckers.

We, therefore, examined the following hypotheses for the limitation of elevational range in the Gray-breasted Jay: (H1) limitation by oak species number; (H2) limitation by oak abundance without regard to diversity; and, (H3) limitation by tree abundance without regard to species.

Oaks occurred throughout the elevational range of the jay in Cave Creek Canyon. At least two species of oaks whose acorns were eaten by Gray-breasted Jays were found from the lowest flock to the highest flock and far above the latter. The lowest two flocks' territories included large stands of *Quercus emoryi* and *Q. arizonica*. Below these territories were many Arizona sycamores (*Platanus wrightii*) along watercourses, and mesquite trees (*Prosopis juliflora*) in the drier areas, but no oaks or pinyon pine and no jays.

At middle elevations (c. 1,524 m), every ter-

ritory had at least two species of oak, mainly *Q. emoryi* and *Q. arizonica*. A few flocks, mainly those with north-facing slopes, had good stands of *Q. hyperleucoides*. In addition, nearly every flock had some pinyon pine.

On the highest territory (2,103 m) were three mast-bearing species, *Q. hyperleucoides, Q. arizonica,* and *Pinus cembroides*. Higher up, at Onion Saddle (2,316 m), were the same three mast-bearing species in good numbers but no Gray-breasted Jays. Still higher, at Barfoot Trail (2,652 m), were big trees of *Q. reticulata* and *Q. hyperleucoides,* plus a low, scrubby species of *Quercus* but no Gray-breasted Jays. Two or more species of oak grew at every locality where these birds occurred.

In short, Gray-breasted Jays appeared to be limited in some way by oaks at the birds' lower elevational limit, but not at their upper limit, where at least three species of oak plus the pinyon pine extended well beyond the upper limit. None of the three hypotheses that we considered above accounted for the upper limit. At the lower limit, we rejected H3 because sites with big trees were not occupied unless oaks were present. We know that as few as two species of oak were enough, but we do not know whether one species of oak would have been enough, because we did not find any areas with only one species of oak.

YEARLY VARIATION

Yearly variation in group size in May at the main study area from 1969 to 1983 was surprisingly large (Fig. 3). Mean group size in the population varied greatly among years, from a low of 6.7 to a high of 17.5. Among our 6–7 color-banded units, the largest group in some years (10 in 1982) was smaller than the smallest group in other years (e.g., 13 in 1978). Despite some interesting inconsistencies, individual groups tended to follow the population and usually, but not always, varied in roughly parallel fashion. The SW unit, the first to be studied, has varied between six and 19 birds over this 15-year period. The TK group was formed in 1979 and still exists (1985). The AC unit became extinct after 1970. The five other units shown in Figure 3 have persisted from 1970 or 1971 through 1985.

RECRUITMENT AND FLOCK SIZE

The number of juveniles in August was used as an estimate of recruitment. The number of juveniles per flock in August, 1975, was positively correlated with flock size in the preceding May–June ($r = 0.32$; $P = 0.034$, one-tailed). In order to examine the contribution by age, we separated individuals in May–June into yearlings and post-yearlings (two years old and older). The number of juveniles per flock was correlated with post-yearlings ($r = 0.46$; $P = 0.007$), but not with yearlings ($r = -0.12$; $P = 0.49$). Apparently, yearlings in 1975 made no detectable contribution to the correlation between group size and recruitment. This can also be seen by comparing the correlation of juveniles per flock with post-yearlings in flocks with and without yearlings. In the 21 flocks without yearlings, $r = 0.60$; in the 12 flocks with yearlings, $r = 0.38$. Although the two r-values are not significantly different from each other, they suggest, at least weakly, that yearlings had little or no effect on the number of juveniles per flock in 1975.

POPULATION DENSITY

We estimated linear density in Cave Creek Canyon to enable comparison with other populations when such data become available (Fig. 2). The territories of the flocks that we censused formed a continuous strip running 9.8 km along the bottom of the canyon from the lower edge of the population at the desert (1,463 m) to a point 1.4 km above the Southwestern Research Station on the North Fork of Cave Creek. In addition, we censused the flocks along the South Fork for 2.2 km and along the Middle Fork for 3.4 km. On this part of our census area, there were 26½ flock territories on a total of 15.4 km of linear transect, yielding an estimate of 1.72 flocks/km. The mean diameter of these territories was 0.58 km. Since most of these flocks nested in the lowlands along the creek and road, it is realistic to assume that the center of each territory transected by the creek and road lay near the road and, therefore, that the road distance across a territory was a reasonable estimate of its cross-section along the canyon bottom. Along this transect, we found 16.7 jays/km.

DISCUSSION

We had expected on theoretical grounds that flocks would be smaller at the upper and lower extremes of the elevational range than at middle elevations. The largest units did occur only at middle elevations, but the mean group size was only insignificantly larger there than at higher and lower elevations. The preponderance of large units at middle elevations may have been an artifact of sampling, since we censused more units in the middle elevations than in the extremes. The mid-elevation territories varied considerably in apparent quality. Casual observations give the impression that Gray-breasted Jays are restricted to riparian habitats along streams, but in the mid-elevations of the Chiricahua Mountains, this was not true. At lower elevations, where the

canyon is narrow and the walls are steep and high, these jays occurred in a single linear strip of territories along the creek (Fig. 2). At middle elevations, however, where the canyon broadens to form a basin, many territories were located on streambeds that were dry except when it rained. These territories appeared to be less productive of jays; and their flocks tended to be smaller, keeping the average low at middle elevations.

Bock and Bock's (1974) hypothesis that the geographic range of an acorn-harvesting species, the Acorn Woodpecker, is limited by oak species diversity is also relevant to the Gray-breasted Jay. Our observations suggest that, in the Chiricahua Mountains, the upper limit of these jays is not determined by the number of oak species, the density of oak trees, or by oak species diversity. Our preliminary counts of oak-tree density well above the highest territories of Gray-breasted Jays (Barfoot Lookout, 2,652 m) suggest that oak density was as high there as in the highest territories. Conceivably, extensive and precise measurements of acorn abundance might reveal that a threshold density of acorns is needed which coincides with the upper elevational limit of these jays in the Chiricahua Mountains. We regard this as unlikely, however, given our qualitative findings.

Other hypotheses for the upper limit exist. Low temperatures and heavy snowfall might impose greater energetic demands than Gray-breasted Jays can meet. These birds are permanent residents on their breeding territories and are not known to leave them, even in severe winters, except for forays by individuals into nearby territories.

Other species of acorn-harvesting jays may compete with Gray-breasted Jays. Steller's Jays (*Cyanocitta stelleri*) in the Chiracahua Mountains breed only at elevations above Gray-breasted Jays. They avoid severe winter conditions by descending to lower elevations where the two species often coexist. Referring to the Gray-breasted Jay in the Sierra del Carmen, Mexico, where Steller's and Scrub jays were absent, Miller (1955:159) wrote that it "completely takes over the habitats divided among the three jays in such regions as southern Arizona." Our observations and Miller's agree with the hypothesis that the upper limit of Gray-breasted Jays is determined in part by the occurrence of Steller's Jays. A role for climatic factors can also not be excluded.

Our finding of a positive correlation between number of juveniles per flock in August and flock size in spring should not be interpreted to mean that reproductive success has been augmented by helpers. We were unable to reject or confirm an effect of helpers because the number of females that are breeding varies among flocks (Brown, in press). The greater number of juveniles in larger flocks could be caused by a larger number of female breeders in those flocks.

The lack of a positive contribution to reproductive success per flock by yearlings is also ambiguous. This cannot be interpreted as a statement about helpers, since, in this species, most helpers are older than one year in most years, as was especially true in 1975.

We undertook the present study in order to gain a better perspective on variation in size of social unit in the Gray-breasted Jay. Our results indicate that size of social unit varies widely with season, locality, year, and, possibly, elevation. Nevertheless, our earlier finding of a relatively large unit size in the Santa Rita and Chiricahua mountains of Arizona is reaffirmed (Brown 1963, 1970). We did not find a unit smaller than five in our survey of 33 units in 1975, and the smallest mean unit size over a span of 14 years on the long-term study area was 7.6. Thus, social units of these jays in Arizona can safely be concluded to average larger than those in the congeneric Florida Scrub Jay, which commonly occurs in pairs and rarely in groups much larger than five (Woolfenden 1975).

Our second goal was to describe more accurately variability in unit size in one population, so that future studies of geographic variation in the Gray-breasted Jay can be interpreted more reliably. The generalization that has emerged is that unit size in Arizona varies widely in space and time, but is consistently large enough to allow two or more breeding pairs per territory for many if not most flocks. Studies of color-banded flocks in the Santa Rita Mountains (Brown 1963) and Chiricahua Mountains (Brown 1970, in press) have confirmed this feature.

By demonstrating considerable local and yearly variation in social structure of one species, our study suggests caution in reliance on small samples or brief studies when considering the social structure of other species.

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