

COMPARATIVE BREEDING BEHAVIOR AND ECOLOGY OF THE BUSHY-CRESTED AND NELSON SAN BLAS JAYS

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The Bushy-crested Jay (*Cyanocorax melanocyanea*) is a resident of open, mesic highland forests of Central America from Guatemala to Nicaragua. The Nelson San Blas Jay (*C. sanblasiana nelsoni*) occupies tropical deciduous woods and open palm wood plantations of foothills and lowlands of the Pacific slope of Mexico from Nayarit to Guerrero. Each species occurs in flocks throughout the year and is communal in reproductive habits. I have previously written of their systematic and phylogenetic relationships (Hardy 1961, 1969), their habits in following army ant swarms (Hardy 1974a), the ontogeny of plumage and softpart color change as well as sexual differences (Hardy 1973), and their displays and postures (1974b).

Communal breeding strategies are not rare in neotropical jays and this level of sociality may be primitive in the ornate line (Hardy 1974b). The studies reported here show that *C. melanocyanea* and *C. sanblasiana nelsoni* are socially reproductive, with helpers at the nest ranging from juveniles to adults, more than one adult incubating a single clutch, and mutual assistance in *C. s. nelsoni* by breeding pairs of the same social groups.

STUDY AREAS AND METHODS

Field study of the Bushy-crested Jay took place from 12 to 30 June 1969 on the grounds of the Hotel Santa Maria de Ostuma, 10 km north of Matagalpa, Nicaragua. I studied the Nelson San Blas Jay from 12 June to 1 July 1970 in lowlands near Las Varas, Nayarit, Mexico.

Nests were located and activity patterns studied at both sites. Birds were caught in mist nets and marked with paint for individual recognition. Some were recaptured later in the study for retention in captivity; the captives in an aviary provided information on reproductive roles not clearly revealed in the wild. Some young birds were also captured for examination. Specimens were collected for examination of stomach contents, reproductive status, sex, and for preservation as skins, skeletons, and in liquid. All specimens preserved are in the Moore Laboratory of Zoology, Occidental College. Besides direct observation, I made still and motion pictures of the birds' activities and recorded their voices. After mapping the physiographic and vegetational features of the study plots, I studied ranges of the flocks within them.

Bushy-crested Jay study area and habitat.—Santa Maria de Ostuma lies at 1200 m elevation on the Pacific complex at the western confluence of the Cordilleras Isabella and Dariense on the slopes of the mountain. Luxuriant cloud forest cloaks the Caribbean exposure and spills over the crest about 3 km up the mountain trail from the hotel, losing its tree fern component in the process and merging in ecotonal fashion with the mountain tropical evergreen forests at just below 1200 m. This is at the lower edge of the study area. Much of the study site has the large trees of the cloud forest, but the

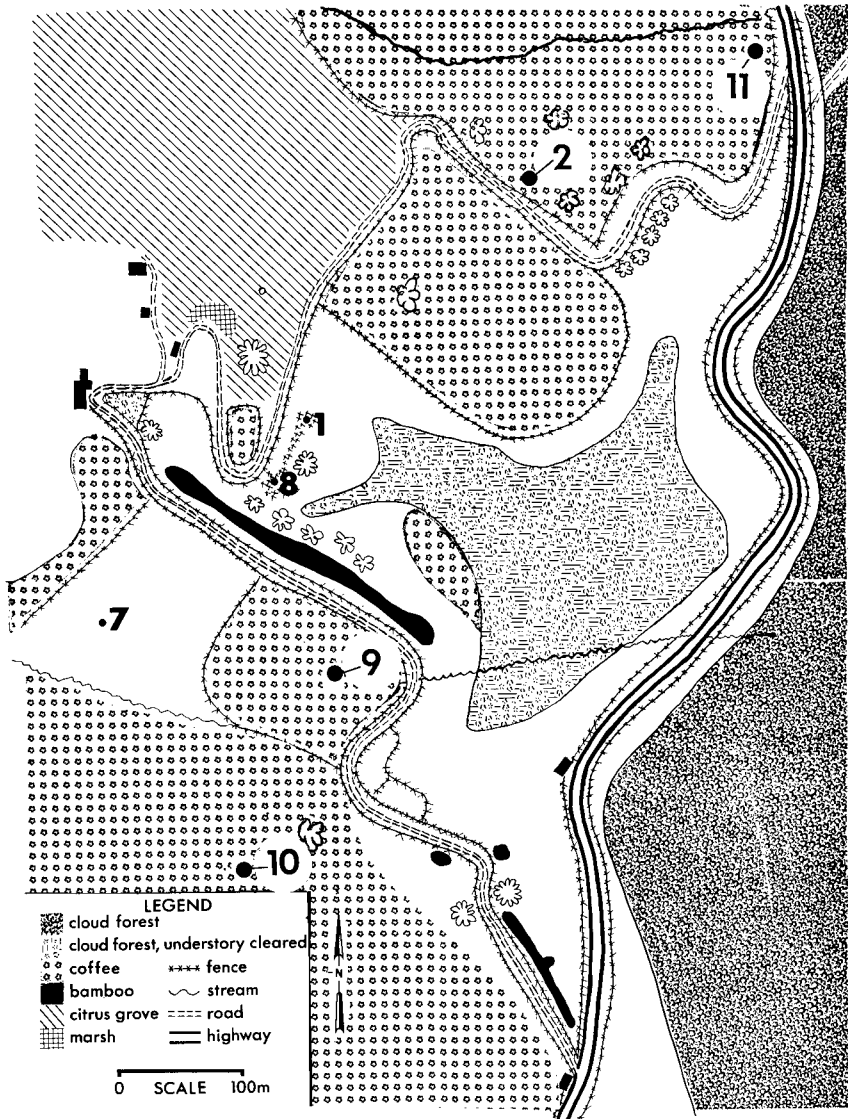


FIG. 1. Map of the Bushy-crested Jay study site at Santa Maria de Ostuma, Nicaragua.

subcanopy layers of vegetation have been removed and largely replaced by coffee trees (Fig. 1). I made no attempt to identify the tree species of the native forest.

The study site vegetation is evergreen and although there may be little rain from November through May, it can rain anytime and there is never a period that one could

classify as a dry season (Vivo 1964:210-211). During this study the temperature was remarkably constant, between 19.5° and 22°C day and night. Rain fell almost daily, mainly as brief heavy showers in the afternoon or at night.

The Bushy-crested Jay was abundant in the disturbed forest and could be found less commonly at times around old clearings made for growing corn or along open cattle trails in the relatively undisturbed cloud forest, especially when flocks were feeding young. This jay did not occur in the undisturbed forest or, during the breeding season at least, in the tropical forest at lower elevations.

San Blas Jay study area and habitat.—Las Varas, Nayarit, is near sea level at the boundary between coastal lowlands and the low hills. The former area originally supported a luxurious tropical deciduous to semi-evergreen forest. Now the native palms, *Acrocomia mexicana* and *Orbignya cohune*, grow not only wild but are extensively planted and grow in partially wild stands reproducing themselves. There is also other cultivation, mostly corn and grazing land. Nuts of *O. cohune* are harvested for their oil. I estimated that more than half the lowland in the vicinity of the study area was in palm growth; the remainder was about half small, partially disturbed plots of forest (second growth, even here with some palms) and half corn fields and pasture. Small sluggish streams and bayous are scattered through the land. Fig. 2 shows the habitat at the same site.

The tropical deciduous woodland on the foothills may have a species composition much the same as that of the adjacent lowlands, but in the foothills the growth form is more tortuous and the trees shorter. Thorns characterize many species.

A distinct wet season runs from mid-June to November or December, and a dry season from January to June (Shelford 1963:445). In the dry season the native forest almost completely loses its leaves, except for larger trees in the lowlands, especially along water courses, and some trees along the arroyos in the foothills.

Until 22 July temperature rose daily to the low and mid-30s C in early afternoon and fell to the low 20's C at night. Thereafter cloud cover and rain narrowed the range from high to mid-20's. Prior to 22 June relative humidity always rose to above 90% at night and remained above 80% except for a short midday period when it fell to between 40 and 60%. Thereafter daily minima seldom went below 70% in midday. These fluctuations were great compared to those at the highland study locality. From 12 to 23 June no rain fell at the study area. From then on to the end of the study period rains fell almost daily as heavy afternoon and evening thundershowers. Shelford (1963:445) gives the summer maximum temperature as 39°C in this zone and the period February through April and November as the driest periods.

The Nelson San Blas Jay was common in the vicinity of Las Varas in the breeding season in the palm groves, especially where the groves were contiguous with open pasture and cultivation, and in thicket mixtures of cutover forest and palms. The birds were rare or absent in the heavier forest; at least near Las Varas my impression was that they occurred in the foothill woodland only as nonbreeding flocks; therefore they were uncommon there at the time of this study.

Vegetational composition of home ranges.—Bushy-crested Jay home ranges spanned virtually all available habitats except completely undisturbed cloud forest (Figs. 1 and 3). Coffee plantation composes from approximately 20 to over 50%. Open habitats such as citrus groves, roadside clearings, and ecotonal areas between them (clear zones on Fig. 1) are all represented. The least frequented habitat was cloud forest with understory completely cleared (not planted in coffee, probably grazed heavily). Even where group 2 ranged into otherwise undisturbed cloud forest this was only near the edge and along



FIG. 2. Representative woodland of the San Blas Jay study area.

open trails into the forest. Bushy-crested Jays simply did not inhabit completely undisturbed cloud forest.

Nelson San Blas Jay groups 1 and 2 remained almost entirely within the mixed palm-native broadleaf woodland. Group 1's nest was on the thicket edge adjacent to an open corn field. The birds frequently flew out into the field to forage and also retired into the woodland, keeping higher in the trees. The woodland habitat of group 1 was dense, with canopy of native trees. That of group 2 was open in the area most frequented, palms being the tallest trees and other trees comprising the young second growth (Fig. 2). Group 3 inhabited severely disturbed acacia thicket with scattered palms mingled with small plots of pasture and roadside thicket. A summary characterization of the preferred situation based on these 3 groups suggests either variety by contiguity of different habitats or by internal disturbance of open palm-native broadleaf woodland. Accentuating this, our patrols of undisturbed foothill woodland revealed only occasional small groups of clearly nonbreeding jays, while patrols in lowlands several km away from our study sites, in situations having the variety of several artificial habitats plus roadsides, revealed other breeding jays. As with the areas of occurrence of the Bushy-crested Jay, the patches of undisturbed native forest had no Nelson San Blas Jays.

The native woodland in the foothills is virtually leafless in the dry season while the lowland forests provide the evergreen palms and generally more mesic aspect of the native woodland. Although the lowland broadleaved forest had adequate cover, it apparently lacked sufficient diversity and edge for these jays.

Field determination of age, sex, and individual identity.—The nature of ontogeny (Hardy 1973) in these jays makes it possible to distinguish age and sometimes sex and individual identity in the field—a boon to accurate study even when birds cannot all be captured and marked. In *C. melanocyanea*, juveniles have a dull grayish cast to the plumage, horn-colored bills, and dark irides. Yearlings have black bills and dark brown irides. Two-year-olds and older birds have black bills and yellow irides. In the hand, 2-year-olds can probably always be distinguished from older birds by the presence of a particolored bill interiorly. Older birds have solid black bills inside and out. Juvenile *C. s. nelsoni* have a yellowish horn-colored bill, dark irides, a tall erect fronto-nasal crest, and the grayish cast to the plumage. Yearlings have a particolored bill, the tall crest, and dark irides. Three-year-olds seemingly still have dark irides but these begin to change and may be slightly lighter than iris color in 2-year-olds. Though the bill is black exteriorly, it is pale or particolored interiorly. Adults may have no crest or 1 or 2 wispy crest feathers (a highly variable feature often useful in distinguishing individuals in a communal group) and black bills inside and out. Adult females have pure yellow irides, while males have brownish or greenish-yellow irides. This difference is sometimes visible through a binocular and useful when one becomes acquainted with a group under study. Non-overlapping weight differences of adult males and females (males more than 117 g, females 92–113 g) facilitate sexing captured birds.

BREEDING BIOLOGY

General Pattern of Breeding Behavior

The Bushy-crested and Nelson San Blas jays exhibit communal social systems in reproduction. A nucleus pair presumed to be the functionally reproductive pair, was sometimes detectable with respect to a nest. In *C. melanocyanea*, the adult flock size of the best studied group seems to have been 11,

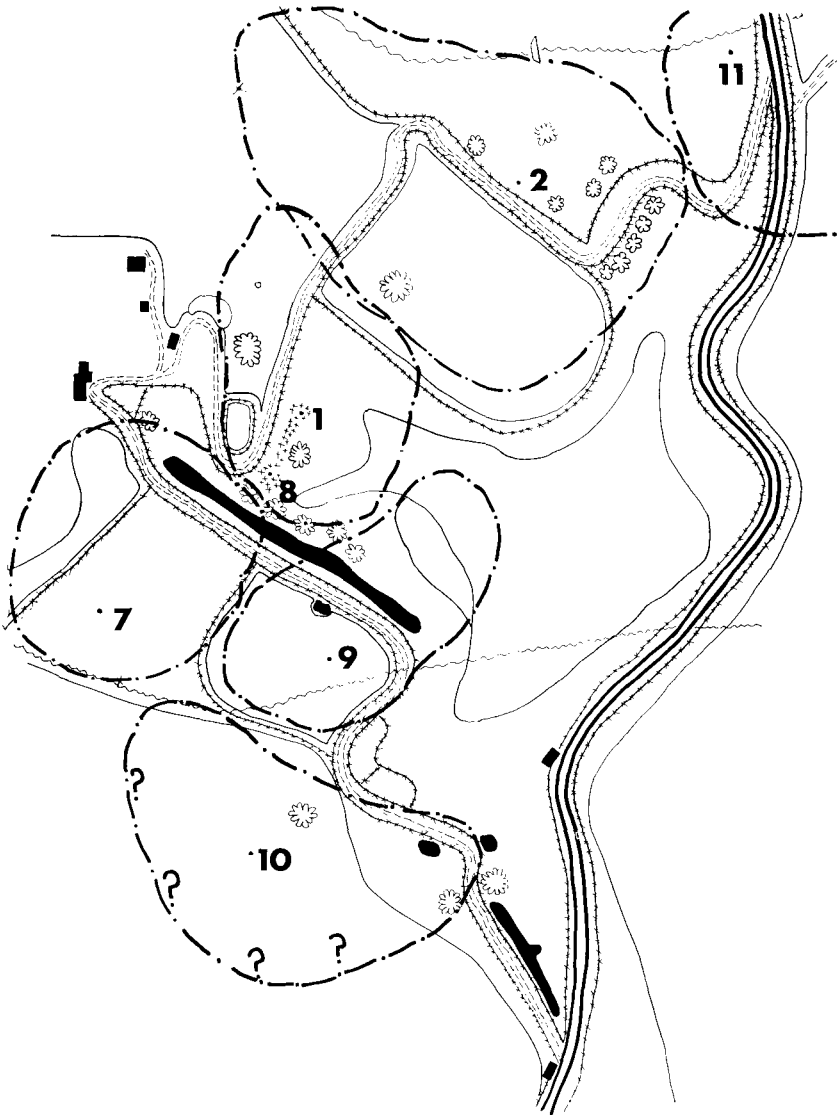


FIG. 3. Boundaries of communal group ranges of the Bushy-crested Jay.

based upon the estimated number of birds beyond juvenile age feeding young at nest 2. Other approximately equal numbers of adult and first year birds formed neighboring flocks, in the other areas shown on Fig. 3. At nest 2 of *C. s. nelsoni*, 4 or 5 adults (including at least 2 males and 2 females) formed

the main group, while at nest 3, 2 adult males and 2 adult females formed the basic communal group. Each group also had a yearling member. The fifth adult at nest 2 was rarely seen. It is probable that each of these groups had suffered some diminution by trapping, as I saw a trapper in the vicinity of number 2. Thus, at least 5 or 6 birds normally form these flocks.

Communal groups in both species have at least 2 partly overlapping nesting periods in the breeding season. I have no evidence for more than 2. I studied both species toward the end of the first period and while the second was well underway. At the beginning of each study period in early June, nestbuilding or incubation was underway, while nestlings or fledglings were being cared for by the same communal groups. The communal group seems to center its attention around one nest at a time but in the Bushy-crested Jay, nests 1 and 8 were simultaneous second-period nests of a flock caring for a single brood of fledglings. At nest 2 four grown fledglings were partially dependent on the communal group for food, and this group of 11 adults plus the 4 juveniles (or at least 3 of them) were attending a nest containing 4 young. At San Blas Jay nest 2, I suspected that the one adult female who rarely appeared at the nest was incubating at another nest nearby, but I was unable to verify this. At nest 3 the incubating female represented the second nesting of the group, for her attendants plus another adult female that occasionally replaced her on the nest were caring for fledglings in the immediate vicinity.

Nestbuilding.—In both species each nest was built mostly by the female that laid the eggs in it. In captivity at Occidental College females were closely accompanied by their presumed mates who also brought nest material to the nests but played lesser roles in actual construction. Indeed, it seemed that nucleus females may have been entirely responsible for nest construction most of the time. Other jays in the aviaries carried nest material around, visited the nests, and sometimes removed nest materials, but they contributed little if anything to nest construction. It seemed to me from this fact that the aviaries were creating artificial situations to a certain extent, by forcing individuals that would not have been normally involved in nestbuilding in the wild into proximity of the nests during their construction.

The nests of both species are simple accumulations of sticks with finer twigs composing the lining. The nests are very sparsely built and in the Bushy-crest may virtually disintegrate by the time the young fledge. The nest of the San Blas Jay is slightly sturdier than that of the Bushy-crest and composed of half again as much material.

Nest 2 (Fig. 4) of the Bushy-crested Jay was collected after the young fledged. It was typical of the ones we saw and measured as follows: total width, 17–20 cm; width of cup, 10 cm; maximum depth of cup, 5 cm (but probably slightly deeper when new); total nest depth, less than 10 cm but



FIG. 4. Nest of Bushy-crested Jay in a coffee tree.

nest 8 was much deeper, for nest situation determines this. This nest was constructed totally of twigs and coarse rootlets. There was no grass, moss, or plant fiber. The outer shell of coarse sticks was 2–5 mm in diameter and 10–30 cm in length. The rounded inner portion was composed of finer sticks 5–15 cm long and 1–3 mm in diameter and finer rootlets—but not so fine as to make a soft cup lining. The depth at center was approximately 2.5 cm. The nest generally appeared very flimsy and small for the bird. Except at center bottom of the cup where eggs rest, one could see through even the new nest.

Table 1 gives heights of nests of both species.

All active nests of the Bushy-crested Jay were in coffee trees within plantations. Nest 1 was in a young plantation where the trees were densely planted and from 2 to 4 m in height. Nests 2 and 8 were in a plantation where the trees were 3 to 6 m apart and from 3 to 6 m in height. Nest 10 was in an abandoned plantation being reclaimed by native understory vegetation. All but one of the inactive nests, none of which was definitely known to be a jay nest (although all were strongly believed to be), were at edges of clearings in the forest (3–7). Number 9 was near 10 in an overgrown coffee plantation.

TABLE 1
HEIGHTS OF NESTS (M) OF NELSON SAN BLAS AND BUSHY-CRESTED JAYS

Species	Nest Number									
	1	2	3	4	5	6*	7*	8*	9*	10*
San Blas	5.5	3.0	3.0							
Bushy-crested	3.8	2.4	4.0	5.5	4.0	4.0	3.8	4.3	1.5	5.9

* Inactive or unsuccessful nests.

Nest 1 of the San Blas Jay was in a tangle of vines near the top of a thicket-edge tree of the palm woodland within 1.5 m of a corn field. Nest 2 was in a crevice at the base of dead fronds of a palm standing in acacia thicket surrounded by second-growth woodland and pasture.

Egg-laying and the clutch.—The clutch in both species is produced by one female at each nest, judging from the small clutch size and observations of laying in one female of each species in captivity in aviaries containing other adult females. From data on captive birds, eggs seem to be laid partly on successive days or every other day, even within the same clutch. The shell colors of the 2 species (as well as of other species in the subgenus *Cissilopha*) are probably unique in New World jays. They are a pale pinkish buff base overlaid with irregular stippling and mottling of reddish-brown.

In the 2 nests of the Bushy-crested Jay (1 and 8) containing full clutches being incubated, the clutch sizes were 4 and 3, respectively. A third nest contained 4 nestlings. No nests containing eggs in the Nelson San Blas Jay were examined in the wild. The nest (1) where incubation behavior was watched at length could not be checked without chance of dislodging it. Nest 2 was discovered with 4 nestlings. Nest 3 was not checked until after the young hatched when it had 3 hatchlings.

Care of Eggs and Young in the Nelson San Blas Jay

Incubation and associated activities.—There are few data on length of incubation of the Nelson San Blas Jay. One female in captivity took 17 days to incubate 2 eggs successfully. Observations of Yucatan Jays, *C. yucatanica* (Raitt and Hardy, ms), suggest 17–18 days as a probable incubation period for that species.

I studied 2 nests of this species during incubation in the wild in 1970 (nests 1 and 3). At each of these the participating individuals were distinguishable by phenotypic features, so that our failure to capture and mark any but the nucleus female and a male at nest 3 was mitigated. Observation at nest 1

spanned the period 12–29 June from late nestbuilding phase, and at nest 3 the period 23 June–1 July, late incubation through hatching. At nest 1 the flock size had seemingly been greatly reduced by a bird trapper a few weeks before my study. (I personally verified his success by visiting his home to observe no fewer than 20 jays that he insisted came from near the location of my camp!) Thus our impressions of early incubation are probably distorted by the anomalous character of the group being studied. At this nest, there were only 3 birds, an adult female, her mate, probably a 2- or 3-year-old male, and a yearling. The female was discovered building the nest on 12 June and on 14 June completed it. She had begun to sit for short periods on 13 June and began prolonged nest-sitting on 14 June. I do not know when the eggs were laid, as the nest was situated in vines that precluded examination without severe disturbance. Presumably, eggs were laid in the first days after the last nest construction was seen (14 June). At this nest in a total of 1990 min of watch, only the female sat, for 1605 min (86.5% of total observation time). There were 17 exchanges, in which the male perched on the nest rim or very near the nest virtually the entire time the female was away (79.4% of total observation time). The nest was unattended in this period for only 79 min. The male made 41 visits to the nest and fed the female at or near the nest 28 times. The yearling bird often accompanied one or both of the adults, but did not participate in the nesting activities. It visited the nest 8 times, frequently begged food, and was fed by an adult.

Nest 3 was discovered about one week before hatching and incubation was observed from 23 to 27 June. The communal group at nest 3 had 4 consistently active participants. The facts that none of the attendant birds at nest 3 was marked until 29 June, and that variation in light and obstructions to our vision at the nest existed, precluded consistent identification of the attendants. The presumed female parent and the most frequent presumed male attendant were trapped on 30 June and verified as to sex by weight and iris color (see Hardy 1973). The few data gathered do not warrant tabular presentation or analysis. Data on participation in care of young at nest 2 where the 4 regular attendants were marked suggest that our general conclusions about attendance at nest 3 are valid. These tentative conclusions are as follows: There were 2 adults of each sex, plus a yearling. Most incubation was by an adult female distinguishable by 1 or 2 wispy crest feathers. Another female was her occasional replacement for periods of a few minutes as well as her occasional feeder. She had no discernible crest. The latter bird was the principal caretaker of 4 fledglings in the vicinity, 3 together and one alone. Presumably, she was their female parent. Two adult male attendants were distinguishable as males by “impure” yellow irides and in good light from each other by slightly different tint to iris color—brownish-yellow vs

greenish-yellow. These birds also visited the nest and fed the nest sitter and fledglings. Finally, a yearling bird with a tall stiff crest and some white on the bill frequented the vicinity and rarely visited the nest. It also fed the fledglings.

Hatching and early nestling care.—By the behavior of the adults, hatching was known to have occurred by 27 June. By 30 June the frequency of visits to the nest by attendants had increased greatly and seemingly involved the same birds in approximately the same proportions and roles: the presumed female parent adult performed most brooding, being occasionally spelled by the other adult female. On one occasion another adult, thought to be one of the presumed males, brooded the young for a few minutes. All 5 birds fed the young either directly or by delivering food to a female adult attendant.

Care of young to fledging.—On 15 June, nest 2 with half grown nestlings was discovered. Preliminary observations were made of unmarked attendants on 16 June. On 17 June the 4 principal adult attendants, by iris color and weight 2 females and 2 males, were captured and marked with paint in early morning hours. The remaining attendants seemed to be 1 additional adult female and a yearling and were distinguishable without being marked. On the day of fledging, 24 June, the color-marked birds were recaptured and their sexual identity verified by gonadal examination. They were prepared as study skins (JWH 765–768).

Number of attendants and their contribution.—Figure 5 summarizes the participation of these 6 birds in nestling care. Note that the 2 principal females were the only brooders, recalling nest 2 of the Bushy-crested Jay, and that they were the chief food-bringers as well. One male, L, made approximately twice as many visits as the other, J, and perhaps was the male parent. The 2 females, N and R, about half the time made prolonged visits in which they poked around the nest contents, examined the undersides of the nest and merely sat in apparent guard duty. Almost all times males visited the nest they were joined by one of the females or one of them was already there. The female then helped *distribute* the food and occasionally ate some of it herself. This habit persisted to fledging. The third female made 3 visits on 17 June and 3 on 18 June, but none later. The yearling visited the nest only the first day, 16 June. Neither of these birds was seen in the vicinity on succeeding days. No record was kept of fecal sac removal differences among the adults.

The attendants at nest 2 were remarkably tame; therefore, I think our observation without blind or other cover in no way altered frequency or character of attendance here. What happened to the unmarked adult and the yearling after 18 June? I speculate that it was the adult incubating at a nest that we failed to find, perhaps as at nest 1, being accompanied by the yearling. As there was no evidence that the marked adults were engaged in care of

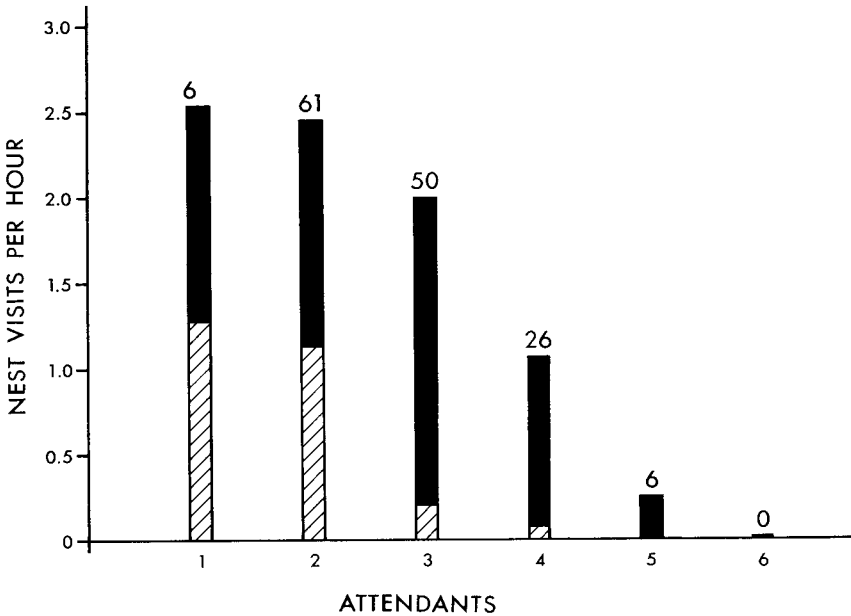


FIG. 5. Frequency of feeding visits to nest by 6 birds (5 adults, 1 yearling) at nest 2 of *C. sanblasiana nelsoni*. Numbers above each column = total visits. Cross-hatched areas of columns indicate frequency of nest visits more than 1 min long; solid areas less than 1 min. Letter symbols used in text (suggested by color markings, sex, or age in field studies) follow their figure number equivalents: 1 (N); 2 (C); 3 (L); 4 (J); 5 (third female); 6 (yearling). Birds 1, 4, and 5 were females, 2 and 3 males, and 6 was of unknown sex.

fledglings in the vicinity of nest 3, I presume that this was the first nesting of the year for this group.

I observed care of fledglings in the vicinity of nest 2. As previously stated, all birds attending the young in nest 3, except the presumed parent at the nest, were noted feeding these 4 fledglings. Three of these were together most of the time and the fourth was alone. They gave frequent location calls. These young were not over one week out of the nest when discovered on 24 June. I have no data on care or behavior of grown juveniles. Presumably their partial dependence on the adults for care is protracted, as the yearlings at both nests 1 and 3 begged and in the former case received food from an adult.

Care of Eggs and Young in the Bushy-crested Jay

Incubation and associated activities.—Incubation behavior in Bushy-crested Jays was studied at 2 nests, at which no birds were marked for individual

TABLE 2

SUMMARY OF ATTENTIVE BEHAVIOR DURING INCUBATION AT 2 NESTS OF THE BUSHY-CRESTED JAY

Nest	Total Time in min (no. periods)	% Time Eggs Covered	No. of Exchanges (with ceremony)	No. Times Sitter Fed (by juv.)	Minimum Total Adult Attendants (juvs.)
1	2050 (25)	98.3	15 (8)	16 (1)	4 (2)
8	756 (8)	87.5	3 (1)	1 (0)	4 (2)

identification (Table 2). At nest 1, 25 observation periods totaled 2050 min. At nest 8, 8 observation periods totaled 756 min. Observations at nest 1 began before the last of 4 eggs was laid, and continued past hatching. Observations at nest 8 were begun approximately half-way through incubation and continued past hatching. The total minutes and periods are for those times when only eggs were in the nest.

At nest 1, on 13 June, in an 87 min period, the sitting bird, presumably the nucleus female, was fed 4 times by adults and once by a juvenile with no begging or display. Because no birds were marked it was impossible to know how many attending adults there were. At one point on this day, however, 5 birds gathered at the nest; at least 2 of these were juveniles and 2 were adults. On 21 June, 1 bird fed the sitter, then replaced it on the nest. Immediately after the first sitter had departed, another adult flew to the nest and fed the new sitter. These activities verify that more than 2 adults visited the nest and suggest the possibility that more than 2 adults sit on the eggs.

Early in incubation exchanges at nest 8 were generally without ceremony whether accompanied by feeding of the sitter or not. But from 15 June onward, visits to the nest often were accompanied by wing-fluttering and vocal begging by the sitter, or sometimes just by slight fluttering. In the 5 observation periods within which 2 exchanges of adults at the nest occurred, one exchange involved begging ceremony while the other involved none or only slight wing fluttering. This suggests that a male and female were involved, full begging ceremony occurring when the female was relieved.

At nest 8, also, at least 2 adults sat on the eggs, and other birds, including juveniles, occasionally visited the nest. But there it seemed that one bird performed most of the sitting, although again, without marked birds, this cannot be certain. For the most part, as is suggested by the few exchanges of duties, the sitter merely left the nest unattended at times to feed and rest. This is also reflected in the smaller percentage of time the eggs were covered. The incubation period was not ascertained.

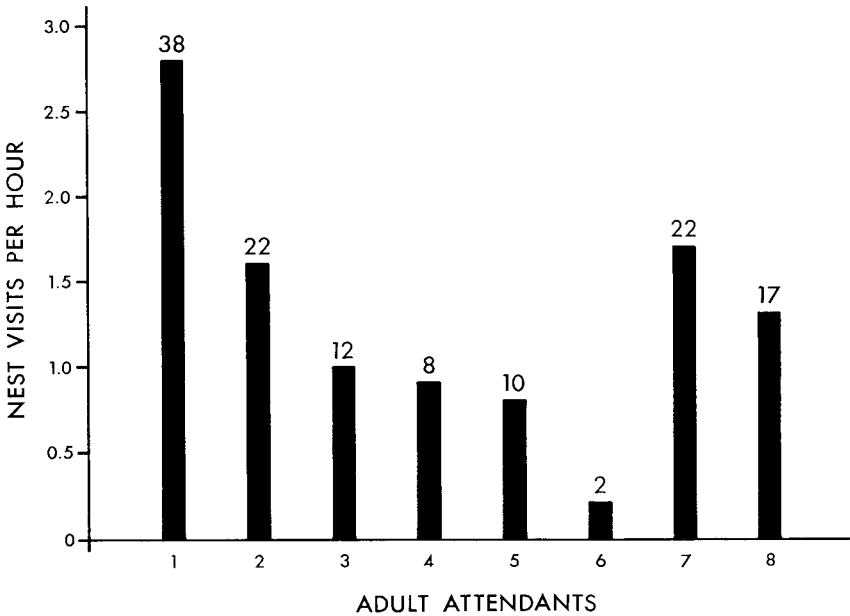


FIG. 6. Frequency of feeding visits to nest by adults at nest 2 of *C. melanocyanea*. Letter symbols used in the text (suggested by color markings employed in the field studies) follow their figure number equivalents: 1 (T); 2 (E); 3 (Y); 4; 5 (C); 6 (A); 7 (M); 8 (W). Birds 1-4 were males; 5-6, sex unknown; 7-8 females.

Hatching and early care of young.—I studied hatching and early care of young at nests 1 and 8. At least 2 birds continued to perform nest-sitting duties at each nest. Even before the clutches completely hatched, nest visitations by other birds increased. Hatching began first at nest 8 on 27 June. This was marked by the sitter getting up often, peering down into the nest and poking around, by increased begging by the sitter, and by the appearance of several juveniles near or at the nest. The juveniles begged and were fed by other adults. On 29 June when there were 2 young and one egg in nest 8 these juveniles begged the sitter and crouched beside it on the nest. Sometimes the sitter begged and at other times poked at these birds, but they were not intimidated and did not leave. At least 5 other adults were in the vicinity with the group of 3 or 4 juveniles. Four adults were seen simultaneously at or near nest 8. In the afternoon at one point when no adult was at the nest, 2 juveniles huddled on the nest rim and finally one of them actually brooded the young!

At nest 1 the group of 5 or 6 adults with 3 or 4 juveniles trouped past on

30 June when the eggs were beginning to hatch. One of these came out of the group and fed the adult on the nest. The juveniles were not seen at this nest during the hatching period.

On 30 June no birds were near nest 8 and it was empty. We made no further observations at either nest 1 or 8 after 1 July.

Later care of young.—We discovered nest 2 on 14 June when the 3 young were approximately 2 weeks old. We made almost daily morning and afternoon study of activities there and in the immediate vicinity. We color-marked 8 adults and 2 juveniles near the nest from 17–20 June and retrapped 5 of these adults plus one unmarked juvenile on 25 June as the young were leaving the nest. From 18 through 24 June, in a total of 1028 min, we gathered data on the contributions of these marked birds plus some unmarked ones. Figure 6 shows the nest visits of the 8 marked adults. No visits by the 2 marked juveniles were recorded, although they were seen in the vicinity. Unmarked juveniles did visit the nest 15 times in the period 14–25 June to feed the young. Four or 5 juveniles in the home range (Fig. 6) of the flock were involved in care of the young in nest 2.

Number of attending adults.—Probably 11 adults regularly visited nest 2; including the 8 marked birds. From 21–24 June, the 8 marked adults made 49 recorded visits (mean 6.1) and the unmarked adults made 20 visits. Assuming that unmarked adults averaged the same number of visits as marked ones, the suggestion is that 3 adults were involved, giving a mean of 6.7 visits per bird. We usually saw only one unmarked bird at a time at or near the nest, occasionally 2. Once I saw 3 such adults, one at the nest, one just leaving, and one just arriving. Therefore I believe that 3 unmarked adults were involved.

Differences in contribution by attendants.—Only one unmarked adult was significantly below the range of 1–3 visits/hr to the nest; this bird was very shy. It was frequently seen in the home range and made abortive approaches to the nest with food. Perhaps it had been frightened by capture, for we saw it feed the young only twice after being marked.

We watched this nest from a distance of approximately 20 m, without a blind or other cover. Although most of the time the birds seemed to pay only cursory attention to us, at irregular intervals individuals showed shyness by carrying food and not going to the nest. At these times, several jays scolded us briefly. These periods usually lasted only a few minutes. I concluded that our presence had some effect on the total attendance at the nest, but except for the one bird the proportionate attendance did not seem to be affected.

Frequency of visits to nest.—Total feeding visits per hour ranged from 5 to 28 (mean 13.3). Although the 2 busiest hours were recorded in “early”

TABLE 3
VISITS BY FEEDER ADULT AND JUVENILE BUSHY-CRESTED JAYS TO NEST 2

Dates in June	Time of observation in min	Length of observation (min)	Juvenile feedings	Adult feedings	Total feedings	Feedings per hour
14	09:20-09:45	25	1	4	5	12
15	09:25-10:25	60	0	5	5	5
16	08:10-09:25	75	3	9	12	9
17	06:05-06:55	50	0	3	3	3
18	11:10-12:00	50	4	5	9	11
18	15:00-16:05	65	0	13	13	12
19	08:05-10:15	130	0	14	14	7
19	17:05-18:05	60	0	25	25	25
20	05:15-06:50	95	2	21	23	15
20	16:20-16:55	35	0	9	9	15
20	08:43-10:43	120	2	30	32	17
21	16:02-17:02	60	0	16	16	16
22	09:00-10:00	60	2	11	13	13
24	08:15-09:15	60	0	28	28	28
		1028 min	15	207	222	

morning (28 feedings, 08:15-09:15, 24 June) and at dusk (25 feedings, 17:05-18:05, 19 June), I have no evidence otherwise for greater frequency early or late. Frequencies of 11 to 17 feedings/hr occurred after mid-afternoon; one evening when a light rain fell on 15 June, only 3 visits occurred in the final hour before brooding began near dark. Table 3 summarizes nest visitation data.

Division of nest visitation duties.—We tried to determine on behavioral grounds which birds were the nucleus pair. Two birds were the only ones seen to brood the young, mostly in late evening hours and presumably all night when the nestlings were young. Based upon our assumptions about the sexual identity of the principal attendants in incubation at nests 1 and 8, we predicted these 2 would prove to be male and female. Laparotomy later showed both to be females. This feature of breeding is also found in the San Blas Jay (see earlier description). Besides brooding, these 2 birds also performed nest “poking.” In nest poking, the bird perches below the nest and probes its interstices. At times the work seems to be directed toward slight nest repair, but at other times it is as if the birds were searching for something, perhaps ants, or other insects that we could not see. We have noted this behavior in the Yucatan and San Blas jays, and Jerram Brown (pers. comm.) has recorded it in Mexican Jays (*Aphelocoma ultramarina*) and believes the birds may be pecking at organisms such as ants or lice that infest the nest.

The most frequent feeder of the young was T by a wide margin. I collected this bird, having failed to recapture it, and it proved to be a male. In my view the putative nucleus pair was T and M, because of their prominent feeding and brooding duties, respectively.

Fecal sac removal was dominated by E (5 observed times), followed by M and T, (3 times each). Y and W each were seen to remove one fecal sac.

Prolonged nest rim sitting, as if guarding, was a special activity also observed for one bird. This was C, who averaged 3–4 min/hr from 18–24 June in this capacity, although he was the next to the least frequent feeder.

The data are few, of course, but the suggestion that there might be some division of activities in care of the young is one that should be pursued in further work on this and other communal species.

Role of juveniles in care of nestlings.—Contribution of the partially dependent juveniles to care of young is seemingly minor. We observed a juvenile brooding briefly at nest 8 and feeding nestlings at nest 2. Unmarked juveniles fed the young 15 times between 14 and 24 June and never interfered with the work of the adults or behaved in a way that might have been conspicuous to predators. At nest 10, however, where 4 juveniles frequented the vicinity of the nest, one of them stationed itself for approximately an hour near the nest and intercepted food being brought to the nest by adults. This would seem nonadaptive to the survival of the nestlings.

Sex ratio of adults in communal flocks.—The sex ratio of adult birds captured on the final day at nest 2 was 4 males, 2 females. C, A, and the 3 unmarked adults were not captured at this time. Unless females are more difficult to trap, for which there is no evidence, and unless 4 of the 5 adults uncaptured were females, there was an unbalanced sex ratio in the adult nest attendants at nest 2. Woolfenden (1975) discovered a similar and well-documented imbalance in the Scrub Jay (*A. coerulescens*) in Florida, with males favored by 15%. He attributed this to earlier mortality and greater dispersal of females.

Prevalence of helpers.—All evidence points to the likelihood that strongly communal habits in breeding are the rule in the Bushy-crested Jay. The adults at nest 10 were not marked, but our impression was that a number similar to that at nest 2 were involved in care of young. We estimated at first 6 adults at nest 10 which is the same number that seemed involved at nest 2 prior to marking of adults. The number of adults with juveniles frequenting the vicinity of and occasionally visiting nests 1 and 8 further support this estimate.

Summary of Participation of Flock Members in Incubation and Care of Young

In both the Bushy-crested and San Blas jays, more than 1 adult may incubate the eggs. In the Bushy-crested Jay evidence from brooding participa-

tion suggests that 2 females may incubate, but evidence directly from incubatory behavior is equivocal and leaves open the possibility that the nucleus male may participate. I have found no evidence that male New World jays incubate, outside of *Cissilopha*. I have seen an adult male captive Yucatan Jay incubate (Raitt and Hardy ms). Juveniles and other adults may visit the nest but their roles seem minor. In the San Blas Jay, the nucleus female was assisted in incubation on occasion by another adult female of the flock, and the sitting bird was fed by other flock members. In Bushy-crested Jays, 2 females may brood young, and other adults may show some emphasis in contribution such as fecal sac removal and guarding the nest or domination in bringing food. Seemingly the entire communal flock helps feed the brood. Even juveniles help sporadically in this way. In San Blas Jays, all members of the communal group may feed the young. At the 1 San Blas Jay nest studied in detail, 2 adult females brooded and also "supervised" the dispersal of food to the young by the contributing 2 male birds.

Group Dispersion

Communal home ranges.—Figure 3 shows the group home ranges of Bushy-crested Jays at Santa Maria de Ostuma. Their sizes in hectares were as follows: "1-8," 2.7; 2, 7.1; 7, 2.9; 9, 2.5; and 10, 3.8. Based on estimates of all ranges studied, some of which were uncertain, the mean size was 3.9 ha. If the area is determined using data only from ranges of groups 1-8, 2, 7, and 9, those ranges that I am most confident were measured correctly, the mean remains 3.9 ha. If data only from 1-8 and 2, in which the ranges were definitely known, are used, the mean size of group ranges is 4.9 ha.

Communal group home range in the Nelson San Blas Jay was measured only for the group at nest 2. The area where the birds foraged regularly measured approximately 3.1 ha, comparable to group range in the Bushy-crested Jay. Careful study revealed no instances of the birds foraging south of the home range. Most activity took place between the nest and the stream bed to the west, with limited activity immediately east and southeast of the nest. Our observation station was east of the nest, however, and this may have discouraged the birds from flying directly east and distorted our estimates of activity in that direction. Because of the smaller group size in the groups we studied, it might seem logical to predict a smaller group home range. The general low density of birds in the population could have resulted in the larger area of occupancy. The flock was seen to move out of the home range only once, when it flew north across the old field and into another woodlot chasing a Wood Owl (*Ciccaba virgata*). Except for the old field, immediately surrounding areas had scattered trees and cultivated fields in which the corn was

just sprouting or in which no crop had as yet appeared. Perhaps this discouraged the birds from moving outside the shown home range.

Territoriality.—I have deliberately used the term home range above. If territory is allowed in the broad sense of Kaufmann (1971) to include an exclusively occupied area maintained as such even by passive avoidance, then territory may be the better term for the areas occupied by the communal groups of both jays. In the Bushy-crested Jay I observed what I interpreted as a territorial skirmish at the boundary between the areas of groups 1–8 and 2. Here the group feeding grown juveniles of 2 was met by adults of 1–8. An adult of 1–8 briefly chased a juvenile. The 2 groups immediately departed from the “boundary” with no further chasing. Passive avoidance by my interpretation would almost necessitate rare reinforcement by such brief skirmishes. I think that typically such an event might involve (as this one did) an inexperienced juvenile bird.

Boundary skirmish is common in western Scrub Jays, *Aphelocoma coerulescens woodhouseii* (Hardy 1961). Certainly “passive avoidance” and spatial use that might be termed exclusive home range are typical of Blue Jays, *Cyanocitta cristata* (Hardy 1961) and Steller’s Jays, *C. stelleri* (Brown 1963). The latter species according to Brown has a territory that can be conceived of as a dominance phenomenon strongest at the nest site and decreasing in all directions from the nest, so that aggressiveness is least at the perimeter. This results in passive avoidance and little territorial behavior in the classic sense.

FOOD, FORAGING, AND CLIMATE

Stomach content analysis for specimens taken at the time of the studies (Table 4) bear out our field observations about the food of these species. We were impressed that foraging Bushy-crested Jays spent approximately one-half their time just above ground level in open places foraging for beetles in herbaceous growth. The remaining time spent feeding in the trees seemed to involve mostly foraging on the small figs (*Ficus* sp.) of the native forest. We did not see figs fed to young. It appeared to us that young were fed mostly beetles and grasshoppers. In contrast, we were surprised to find adult Nelson San Blas Jays bringing not only insects but parts of lizards and pieces of the orange fleshy pericarp of the cocoa-palm fruit to the nestlings. We verified the fruit delivery by netting adults on the way to the nest.

Insect populations useful to jays as food multiply with the onset of the rainy season in climates characterized by a wet and a dry season. The locality where we studied Bushy-crested Jays may technically have a wet and a dry season but the latter is moist in the cloud forest (see Vivo 1964:210–211). I see no reason to believe that there is significant fluctuation in the insect foods of the Bushy-crested Jay at Santa Maria de Ostuma. In Nayarit, however, the climate

TABLE 4
ANALYSIS OF STOMACH CONTENTS OF BUSHY-CRESTED AND NELSON SAN BLAS JAYS

Specimen	Date Collected	Beetle	Ant	Fly	Cockroach	Plant, Misc.
Bushy-crested						
JWH731 (yearling)	14 June 1969	60% (Tenebrionidae Scarabaeidae, et al.)	10%	10%		20% (detritus, incl. stones)
JWH732 (adult)	14 June 1969	80% (Carabidae, et al.)				20% (detritus)
JWH733 (juvenile)	15 June 1969	30%			60%	10% (detritus)
JWH734 (juvenile)	15 June 1969	70% (1 Tenebrionidae, darkling beetle, 1 Scarabaeidae, June beetle)				30% (22 fig seeds, 7 orange "banana-shaped" seeds, detritus)
JWH735 (adult)	26 June 1969	65% (Scarabaeidae, et al.)	10%			24% (detritus) 1% 2 small seeds (fig?)
JWH737 (nestling)	28 June 1969	100% (Scarabaeidae 30%; Weevil 70%)				
San Blas						
JWH766 (adult)	25 June 1970				"primarily"	
JWH643* (yearling)	27 April 1968	40% (Scarabaeidae)				40% kernels (corn?) 20% unidentified & misc., incl. feather

* This specimen collected 6 km SW Compostela, Nayarit.

is characterized by an almost totally dry season from November through early June and by a very wet season from mid-June to November (Vivo 1964:212). We made no quantitative studies of insect populations, but our general observations in the dry period immediately preceding the rainy season indicated few large insects or caterpillar larvae that the jays might eat or feed to young. That we found them bringing lizards and vegetable material to the nestlings suggests possible food shortages. The vegetation of the understory and ground level was almost leafless in the forage area near nest 2, and thus I feel our chances of seeing available insect prey were excellent.

In the San Blas Jays we studied it is probably adaptive for the over-lapping nestings to span the dry to wet season change. Young of the first nest were just requiring larger insects, and young of the second nesting at nest 3 (that we did not long observe) hatched just as the rains began. They too would have had the advantage of the first flush of insect abundance that occurs with the rains.

It seems likely that a marked dry-wet season character supports the communal habit as follows. Both nestings begin in the dry season when the adults need forage only for themselves and there is no loss of eggs by rain and storm. Young of the first nesting can have larger insects that appear with the first rains when they need them. Young of the second nesting, though having increased chance of mortality from rain, do not suffer from lack of food in any way, an advantage that may balance the rain mortality. Over-lapping of the 2 nesting attempts thus took maximum advantage of both wet and dry seasons and minimized negative factors of both.

PREDATION

In late incubation stage at nest 8 of the Bushy-crested Jay, the nest was abandoned and the eggs were missing. The egg predator here was not identified, but there are 3 prime candidates. The wren *Campylorhynchus zonatus* moved about in flocks in the canopy and subcanopy of the forest and was abundant. A small tree squirrel, *Sciurus* sp., was fairly common and the Emerald Toucanet, *Aulocorhynchus prasinus*, was common. All are known egg eaters.

While watching the communal group feed fledglings at nest 3 of the San Blas Jay, I suddenly heard one of the young give a squawk. I rushed to where it had been perched on a large limb in the subcanopy of a spreading tree in a pasture. At first I could not find the bird, but after about 5 min, I spied its legs hanging from the mouth of an iguana (*Iguana iguana*) about 70 cm long. I can find no published records of these arboreal lizards eating birds, their diet being principally vegetable matter. Alvarez del Toro (1972:61) discusses

the food of the iguana with no mention of avian prey, although he does state that the diet includes insects and frogs.

I saw no evidence of predation on adult jays of either species. We saw no hawks such as *Micrastur* spp. or *Accipiter* spp. at either study tract. The age composition of the communal groups seemed to suggest low mortality and predation pressure on adults. This is probably due to the buffering effect of group activity when lone individuals are more vulnerable to being taken by a hawk. When 4 to 12 birds are feeding in a loose flock the scene is constantly being monitored by at least one pair of eyes. One individual can then sound the predator alarm and all benefit.

Predator buffering effects of the communal group with regard to nest protection are uncertain from our studies. In home ranges we frequently saw the communal groups mob such animals as large tree lizards (*Iguana* sp., *Ctenosaurus* sp.), foxes (*Urocyon cinereoargenteus*), squirrels (*Sciurus* sp.), and predators invisible to us lodged in hollow cavities in trees. In other words, the jays were vigilant in patrolling and quick to come to terms with potential dangers to themselves. We saw no predators approach nests, but when we examined nest contents we were surprised, especially when they contained young, that we were not mobbed.

We found most of the study nests by their conspicuousness because of the presence of the communal group, and I expect that predators also find jay nests easily by the same means. Whether this effect is balanced by the increased efficiency of predator detection provided by so many adults is still a moot point.

THE BASIS OF COMMUNAL SOCIAL STRUCTURE

As I found both the Bushy-crested and San Blas jays breeding in edge situations provided by disturbed forest or woodland habitats, they do not support Brown's (1974) assertion, although I admit its logic, that "we should expect to find communal breeding among species inhabiting stable, climax vegetation forms more frequently than among species characteristic of transient environments." Moreover the Yucatan Jay (Raitt and Hardy ms) also is an edge and disturbed forest inhabitant. All evidence available to me suggests that these 3 jay species exist in groups of generally old age structure and are K-selected (little population fluctuation and existing at carrying capacity) as Brown believes is characteristic of species having communal kinship-based reproductive habits. Furthermore, it can be said that the disturbed transient nature of the lowland environments preferred by *C. yucatanica* and *C. sanblasi-ana* have prevailed since at least 1950 B.P. (Willey et al. 1964:446). Although the evidence is sparse and scattered, it seems reasonable to conclude that some kind of agricultural activity has been widespread throughout low-

land Middle America since at least 4000 and possibly 8950 B.P. (Mangelsdorf 1964:427-428). Moreover although agriculture doubtless involved some clearing of woodland, it seems probable that it capitalized in the beginning upon the existence of a savannah climate-vegetation regime that had evolved in the glaciation period between 20,000 and 10,000 years B.P. Tsukada (in Cowgill and Hutchinson 1966) certainly concludes this for the Petenxil area, Guatemala, where corn planting dates from about 4000 years ago. Thus Yucatan and San Blas jays have had available, and possibly have been inhabitants of, patchy and transient habitats throughout this period. We know less about the history of montane environments of Central America, where the Bushy-crested Jay lives. It seems probable that this species has faced more uniformly natural environments of forests and less disturbance of these by man. In short it is difficult to correlate persistence or origin of communal habits in Bushy-crested, Nelson San Blas, and Yucatan jays with the same factors. Millicent Ficken, one of the referees of this paper, points out that some workers early drew correlations between group size in certain primates and composition of habitat, but that when more data became available these correlations were weakened. I therefore decline to speculate further on the origin and ecological basis of communal social behavior in these jays until at least current studies by Raitt and myself on *C. s. sanblasiana* and *C. beecheii* are completed.

SUMMARY

Bushy-crested and Nelson San Blas jays were studied in captivity and in the field in montane Nicaragua and lowland Nayarit, Mexico, respectively. Bushy-crested Jays inhabit disturbed cloud forest and are especially common in coffee plantations. The species flocks at all seasons and is communal in breeding. The breeding season consisted of 2 overlapping nesting periods, with either one or 2 nests in each. Two or 3 birds attended nests during incubation and at least 2 birds incubated. Other flock members visited the nests toward time of hatching. Nests were mostly in coffee trees, in the understory of the forest. Care of young at one nest was probably by 11 adults plus juveniles of a first nesting of the year. Two adult females brooded the young.

Nelson San Blas Jays inhabit mixed palm and tropical deciduous forest in the breeding season in Nayarit and are communal in reproduction. Five adults plus a yearling attended one nest and 4 adults plus a yearling attended another nest. There are 2 overlapping nesting periods for a communal group. The presumed female parent of fledglings occasionally left her charges to incubate briefly at a second nest at which another adult female was the principal incubator. Two adult males and a yearling fed both the fledglings and the incubating birds.

Home ranges of the birds were mapped for both species; best data suggest these varied from 3 to 4 ha. These ranges may correspond to territories in the passive sense, but only one possible instance of territorial behavior was seen—in the Bushy-crested Jay.

Bushy-crested Jays fed on beetles, grasshoppers, and figs. Young were fed insects. San Blas Jays fed on insects and lizards, feeding the young these as well as fleshy portions of palm fruit. Food was seemingly not a limiting factor in nesting success of Bushy-crested Jays, which experience no marked dry/wet season. In Nelson San Blas Jays, the breeding

season began in the severe dry season when insects seemed to be in short supply (hence the presence of lizards and vegetable materials in the diet provided the young) and ended in the rainy season when insects were abundant.

Possible predators are listed for the Bushy-crested Jay; an arboreal iguana was recorded as a predator on fledglings in the Nelson San Blas Jay. The adaptive value of communal groups in predator detection and buffering is equivocal.

Communal reproductive habits in these jays do not seem correlated with the same basic historical and ecological factors and thus it is premature to speculate on the origin and basis for persistence of communal social behavior or on its temporal relationship to a lesser degree of sociality.

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REQUESTS FOR ASSISTANCE

Gyrfalcon.—Winter Gyrfalcon sightings are wanted. Information on the age and sex of clearly identified Gyrfalcons is needed in conjunction with research being done on nesting Yukon Gyrfalcons. Please send sightings along with date and general location to: Joseph B. Platt, Laboratory of Ornithology, Cornell University, Ithaca, NY 14853.

Shorebirds.—A cooperative International Shorebird Survey was started in 1975 to obtain information on shorebird migration and to identify and document areas of major importance. This scheme has been highly successful, with much very valuable information on shorebird distribution and migration coming from contributors throughout eastern Canada and the U.S., the Caribbean Islands, and Central and South America. In 1976 we are anxious to continue and extend the scheme in as many areas as possible. Any observer who may be able to participate in regular survey counts of shorebirds during spring and autumn migration periods, as well as during the winter in shorebird wintering areas, is asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome.

For areas in Canada: Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0H3.

For areas in the U.S., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, MA 02345.