THE BREEDING BIOLOGY OF THE BROWN JAY IN MONTEVERDE, COSTA RICA

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ABSTRACT.—In an expanding population of Brown Jays (*Cyanocorax morio*) in the Cordillera de Tilaran of Costa Rica, flocks exhibit a broad range of breeding behavior involving the construction of one or more nests by two or more birds, egg-laying, incubation and brooding at one nest by one or more females, and nestling care by breeding and non-breeding birds. The form that breeding behavior takes may be related to the ages of flock members. Flocks vary considerably in age, and breeding success is correlated with the number of older birds. The variation in Brown Jay breeding behavior may provide some insight into the evolution of social organization in New World corvids.

Several authors have suggested that habitat change or release from saturation may induce enormous changes in social structure and behavior of cooperatively breeding birds (Brown and Balda 1977; Vehrencamp 1978; Stacey 1978, 1979a, b; Reyer 1980; Hardy et al. 1981). The most compelling arguments in favor of this hypothesis, however, have resulted from comparative studies of separate populations either in different environments (Cox, unpubl.; Stacey 1978, 1979a, b; Reyer 1980; Koenig 1981) or in populations where habitat quality varied conspicuously (at least to human eyes) over a small geographic area (Brown and Balda 1977, Vehrencamp 1978, Hardy et al. 1981).

To date, information on the demographic and behavioral effects of change in saturation within one population has been unavailable, in part because many researchers consider gross population manipulation (i.e., removing a significant portion of a population or destroying habitat) unethical. Moreover, because the study of complex social behavior necessitates long-term investigation, most field workers seek study populations in the protected environments of nature preserves. As a result, their study populations frequently exist under saturated conditions and do not fluctuate much from year to year.

One way to investigate the effects of saturation on social organization and behavior, however, is to study natural experiments by identifying and investigating populations that have recently been released from, or are rapidly approaching saturation. For instance, in 1978, one of the world's best studied populations of cooperative breeders (Woolfenden and Fitzpatrick 1984)—Florida Scrub Jays (*Aphelocoma coerulescens*) on the Archbold Biological Station in Florida—was decimated, probably by an epidemic (J. Fitzpatrick, pers. comm.). Because of the wealth of base line information available for this population, documenting changes in behavior and social organization as the population recovers represents an ideal natural experiment.

In this paper, we present the results of a two-year study of Brown Jays (*Cyanocorax morio*) in a population whose dynamics may also represent the naturally occurring experimental conditions necessary to test current notions of the relationship between habitat saturation and sociobiology. We designed a study to address a series of a priori hypotheses concerning the role of helpers at the nest (Lawton and Lawton 1980, Lawton and Guindon 1981, Lawton and Lawton, unpubl.). In the course of our work, we discovered that Brown Jay flocks in Monteverde are extraordinarily heterogeneous with respect to age-class composition. We think this heterogeneity may be attributed to the fact that the population is still expanding after original colonization about thirty years ago (W. Guindon, pers. comm.), shortly after the highland plateau of Monteverde was cleared for dairy farming.

Although Monteverde has experienced no significant clearing since our study began, the number of jays in our study area has increased twenty percent (Lawton, Lawton, Lewis, and Lowther, unpubl.). Population growth is not simply the result of increased flock size, but derives from an increased number of flocks in the study area (1978: $n = 14$; 1982: $n = 16$). Growth is also reflected by expansion into new habitat. Of two flocks formed since 1978, one has become established in the highest clearing in Monteverde, an area abutting a natural species border: the large, uninterrupted expanse of cloud forest.

Despite the availability of suitable habitat, however, new groups have not been formed by pairs dispersing to breed without helpers—a situation that would be expected if cooperative breeding were simply a reflection of crowding. Instead, each new flock has five to ten birds and has probably been formed by fissioning (Lawton, Lawton, Lewis, and Lowther, unpubl.).

We suspect that the peculiar pattern of flock composition occasioned by the fissioning of groups of young birds from their natal flocks may explain the wide range of breeding behaviors observed in Monteverde. We hypothesize that, as the population expands and new flocks are formed, competition for breeding status among inexperienced birds might be reflected in a wider range of breeding behavior. These phenomena might, in part, explain why Brown Jays in Monteverde display more variability than do conspecifics in other, more saturated populations.

The objectives of this paper, therefore, are four-fold. First, we will provide a more complete picture of Brown Jay breeding biology than Skutch's (1960) pioneering efforts have made available. Second, we will document the existence of geographic variation in social organization and behavior in this species by comparing our findings with those of Skutch. Third, we will examine our findings with respect to current ideas on the effects of saturation on cooperatively breeding birds. And fourth, we will suggest guidelines for future studies of these ideas.

STUDY AREA AND CLIMATE

We studied Brown Jays from August, 1976 until July, 1977, and from August, 1977 until December, 1978 in Monteverde, a 1,500-ha dairy farming community just below the Continental Divide at an elevation of 1,400–1,500 m on the Pacific slope of the Cordillera de Tilaran, Costa Rica (10°12′N, 84°42′W). The study tract is a mosaic of habitats in an area of rapid local change. Land recently cleared for pastures and cultivation of coffee and bananas alternates with forested windbreaks. Where hillsides are not too steep, selective logging has created clearings which are in various stages of regeneration. Some farms have recently been replanted with native trees, and, since 1976, saplings have begun to replace second growth. Where undisturbed, forest in the community is transitional between tropical lower montane moist and wet forest (*sensu* Holdridge 1967).

Throughout the year, the climate is dominated by the easterly trade winds. The area receives about 2,500 mm rainfall annually, most during the rainy season months of June through December. During the early dry season, Atlantic storms, called *temporales,* sweep across the mountains, often carrying a fine mist which makes the area suitable for grazing throughout the year (Fig. 1). These storms, with average windspeeds between 60 and 100 kph, are an important factor in Brown Jay nest-site selection and success (Lawton and Lawton 1980), and, although most common in December and January, may occur during any month (Fig. 1). Average windspeeds decline from January through May (Fig. 1), as hot air, rising off the Pacific slope, blocks the tradewinds (Lawton 1980). Thus, February through May is the calmest, driest period of the year.

METHODS

Brown Jays are well-suited to quantitative field investigation because they are large, noisy, and conspicuous (Sutton and Gilbert 1942), and can be individually identified without color-banding (Skutch 1960, Lawton and Guindon 1981). Soft-parts (eye ring, bill, legs, and feet) are yellow at birth and darken idiosyncratically over time. South of Mexico, where the white-tipped morph is found, adults have plumage differences that allow individual identification (Skutch 1978, and pers. observ.).

As in other *Cyanocorax* jays, soft-parts darken progressively with age (Hardy 1973). For the Brown Jay, we established three age classes, based on the percentage of soft-part darkening. A bird was classified as *Young* if it had yellow legs, feet, and eye rings, and if its bill was <50% black, as *Intermediate* if it had mottled legs, feet, and eye rings, and a 50% black bill, and as *Old* if it had fully black soft-parts. These categories refer strictly to morphological characters and mean nothing about sexual maturity or breeding status. Young birds may be sexually mature, and, in some flocks, are breeding members.

Observation began in August 1976, while flocks were still caring for dependent fledglings and before home ranges assumed non-breeding season size. Home ranges were mapped and home range use was observed until the beginning of the 1977 breeding season. All birds first identified as dependent fledglings remained as helpers in their natal flocks in 1977.

Our observations of 72 birds color-banded as nestlings in 1977 and 1978 suggested that the three age classes corresponded roughly to the age of 1–2 years (Young), 3 years (Intermediate), and four or more years (Old). When comparing behavior among flocks as a function of the age of their members, we calculated an Age Class Score. Although we knew the age of birds banded as nestlings, we did not know the exact age of Young birds observed in 1977.
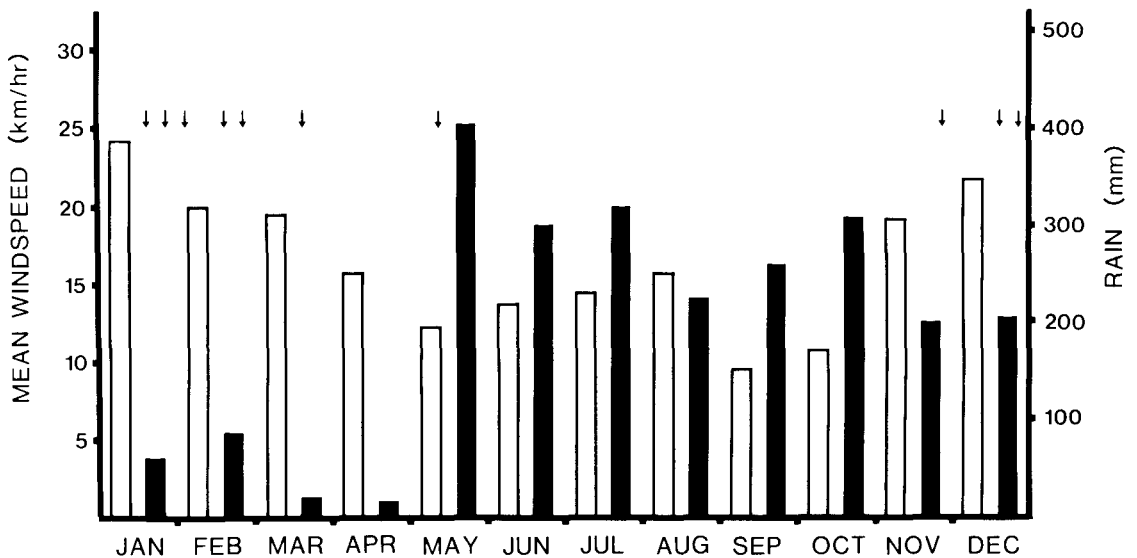
FIGURE 1.   Monthly rainfall in the Monteverde community and mean windspeed at the Continental Divide 2.5 km to the east for the year 1978. Vertical arrows indicate storms with sustained winds stronger than 45 km/h.

Therefore, the age of Young whose birthdays were unknown was figured as an average of 1.5 years. Intermediate birds were given an age of three years; although they may have been older, the age of Old birds was computed conservatively as four years. In 1977, we studied four flocks. In 1978, we monitored fourteen flocks, which included all the Brown Jays in Monteverde.

Brown Jays are noisy around their nests. When building, birds sit in the nest and give a distinctive whine call, loud enough to be heard 200 m away. Finding nests is a simple matter of tracking down the call.

Once a nest was located, we observed it daily (1977), every other day (1978), or weekly, depending on whether it belonged to a focal or to a non-focal flock (sensu Altmann 1974). In 1977, we sampled two focal flocks daily. Analysis of data gathered in 1977 indicated that observation hours could be reduced without losing statistical power. Consequently, in 1978, we doubled the number of focal nests, observing each every other day.

In March, 1978, an unusual storm destroyed ten of twelve broods under observation. The storm prolonged the breeding season; thus, it was possible for us to concentrate on additional flocks after two original focal flocks had fledged young. In all, in 1977, we observed two focal and two non-focal flocks for 420 h. In 1978, we watched six focal and six non-focal flocks for over 600 observation hours. Observations were made with 8 × 40 binoculars and a Bushnell spotting scope from distances ranging between 15 and 20 m from nests.

A day's monitoring of a focal flock consisted of three sample periods, each one hour long.

We divided the 12 daylight hours into three 4-h segments, and chose one sample hour at random from each segment. In this way, we could monitor more than one flock each day without risk that differences we observed among flocks resulted from different times of observation. We watched non-focal flocks at least once a week.

During each sample hour, we recorded all trips to the nest, noting the age class of the visitor, its activity, and, where possible, the identity of the individual. For focal flocks, we could recognize individuals over 94% of the time. At six randomly determined 1-min periods during each sample hour, we noted the number of whine calls, if any, given by a bird on the nest. During the next minute, we performed scan samples (Altmann 1974) of birds we could see or hear. Courtship and copulation were noted whenever they occurred.

RESULTS

STUDY POPULATION

Mean flock size before breeding for 14 flocks observed in 1978 was 7.2 (range 6–10, Table 1). Average fledging rate was 3.3 per year (range 0–6), giving a post-breeding flock size of 10.5 (range 6–15). On average, 2.3 Old flock members lived in each group, with a range from 0–3. Two flocks had no Old flock members. On average, flocks had 3 Intermediate birds (range 1–6), and 1.9 Young birds (range 0–5).

TIMING OF THE BREEDING SEASON

Brown Jays bred from February through May (Fig. 2). They were typically single-brooded, but the same female would lay up to four

TABLE 1. Age class composition, by number of individuals, of the Brown Jay flocks at Monteverde in 1978.

Flock	Old	Inter-mediate	Young	Young of the year
Lag	2	2	3	7*
Rf	3	5	2	5
Mr	2	6	1	6
Bt	0	1	5	1
Mig	3	3	0	4
Alon	3	2	1	—
Stl	1	4	1	2
Gaud	4	3	2	7
Rod	3	1	2	—
Varg	2	2	3	—
Est	2	2	2	—
Trsl	3	3	1	3
Arn	2	4	1	4
Ff	2	4	2	1

* From two clutches.

clutches to raise that brood. In 1978, however, one flock successfully raised two broods.

Of 28 clutches monitored in 1978, the earliest was begun on 2 February, the latest on 2 June. The last date probably is unusual since re-nesting after a catastrophic storm prolonged breeding well into the rainy season. In contrast, in 1977, breeding had ended throughout the study tract by the end of May when the rains began. In the Motagua Valley of Guatemala and in the Pejivalle Valley of Costa Rica, Brown Jays nested only in the dry season, from mid-February until May (Skutch 1960, and pers. comm.).

COURTSHIP AND PRE-NESTING BEHAVIOR

In the interims between *temporales*, beginning as early as November, we saw courtship feed-ing and heard the distinctive whine call of breeding females. On 1 March 1977, we saw the following interaction between members of a courting pair, which was typical of the eight occasions on which courtship was observed: while the flock foraged at a distance of 50–100 m away, the female perched in a tree, whining rapidly and intensely. She spread her wings, lifted her tail and looked over her shoulder at the male, perched behind her. When he approached with food, she flew into another tree, calling loudly and the male followed. The female continued to call, fanning her wings, raising her rump, and hopping in front of the male. He followed from branch to branch and from tree to tree until both birds flew out of sight.

On the three occasions when we saw copulation, the male mounted the female briefly as she perched in a tree. Twice, copulation occurred after a period of female solicitation and male pursuit. On the third occasion, however, when flocks were attending nestlings, a male mounted a female without these preliminaries.

During the period before nests were built and eggs were laid, we saw three types of behavior whose function was not clear. The first involved visiting between flocks. From November through February, Intermediate birds frequently flew from the flock with which they usually roosted, and in which they were subsequently nest attendants, to visit other flocks. On more than a dozen occasions, we watched one to three flock members leave their home flocks and spend from one hour to several days with other another flock.

These visits probably represented attempted dispersal and pair formation. For instance, for
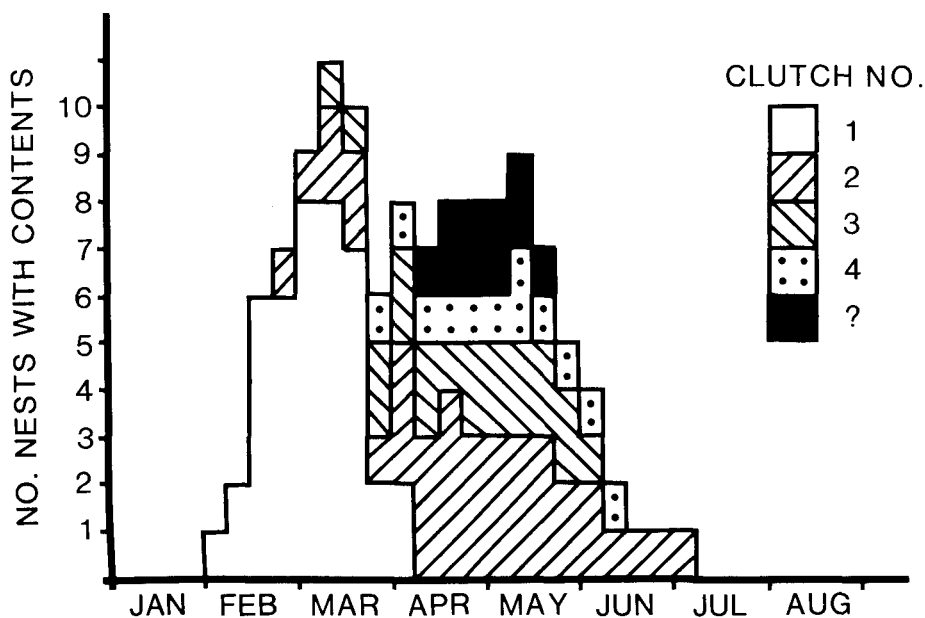

FIGURE 2. The nesting season of the Brown Jay at Monteverde during 1978, based on thirteen breeding flocks.

two weeks, one visitor (apparently a male) spent several hours a day foraging with and feeding a 2-year-old female at one focal flock. M. Lawton saw these birds copulate, and, although the male roosted with and helped feed nestlings at his roost flock, he also spent several hours daily throughout the breeding season in the focal flock he visited. He attended the focal nest and accounted for about 15% of the observed feeding at that nest.

A second behavior of uncertain function began to occur on calm days in late December when the jays gathered in groups of up to 25. These gatherings were characterized by remarkable aerial acrobatics, chasing, and calling. On more than a dozen occasions, we saw groups of over 20 birds gathered into two groups in adjacent canopy trees. While both groups called loudly, one bird flew out of each tree, flying directly at the other. Just before colliding, both birds seemed to stall in mid-air before pulling up abruptly and flying back to their respective trees.

On three occasions, we observed the following sequence of events: with a group of 8 to 10 birds gathered silently in one tree, suddenly all began to call, and then from one to three birds chased another across a clearing to another tree. Chasing was sometimes repeated for up to an hour, often accompanied by a harsh, chirring call by one or more of the birds giving chase. On two occasions, the chases occurred in the period before incubation, but in one group where a yearling female had displaced her mother as the breeding bird, chasing continued throughout the incubation and nestling periods.

Prior to nest-building, we saw a third type of interaction at least twenty times. The display, never seen between two Old birds, occurred when two birds perched on the same branch, either level with each other or with one bird slightly higher than the other. The birds stood side by side or faced one another at a distance of 0.3 to 0.5 m and performed two types of movement. First, one bird gave a head-bob, followed by a series of 5 to 7 head up-and-down movements. As the head moved, it seemed to undulate in a figure-eight motion. Next, the bird stretched its neck, either raising the head and bill skyward or giving the up-fluff display described by Hardy (1961) for a number of *Cyanocorax* jays. The display frequently led to bill-knocking, apparently similar to behavior described by Skutch (1960) in which both birds peck at each other's bills. Bill knocking was seen only in interactions involving Old birds, and was always followed by the younger bird flying away and being chased by

the Old bird. Twice, younger birds joined in the chase.

NESTS

Of 38 nests built over two years, 32 (84%) were built 8 to 12 m high in isolated trees, well away from windbreaks or woods. Predation accounted for the failure of only one of these nests. Nocturnal predators, however, destroyed all six nests built in trees whose crowns touched other trees. Brown Jays in other parts of their range also tend to build in isolated trees (Skutch 1960), which suggests that, throughout their range, Brown Jays choose isolated nest sites to reduce the likelihood of nest predation.

In Monteverde, the search for a suitably isolated tree was complicated by the probability of windstorms during the months when nest sites were selected (Fig. 1). All nests were built in relatively sheltered, but isolated, trees. Flocks that built in sites that were better protected from wind were more likely to fledge young than were flocks that built in more exposed sites (Lawton and Lawton 1980). For instance, the two nests unaffected by the late March, 1978 storm had been built in well-sheltered trees on leeward slopes.

Skutch (1960) described the cup-shaped nest and the process of nest building. In Monteverde, the jays appeared not to re-use materials to rebuild. On one occasion, however, a second clutch was laid in a nest whose contents had been removed by predators, and in 1978, one flock refurbished its 1977 nest.

The jays seemed not to prefer any one type of tree for nesting. We found nests in *Ficus tuerckheimii, Croton gossypifolius, Inga tonduzzii, Roupala montana, Alnus jorullensis, Xylosma* sp., and several species of Lauraceae.

In Guatemala, Skutch (1960) found that nest-building was almost exclusively the responsibility of one pair, although he once saw a third bird bring nesting materials. In contrast, in Monteverde, the number of individuals who built a nest varied enormously among flocks but in all 11 cases when nest building was observed, more than two jays contributed nesting material. In three instances, one pair did most of the nest building, while from one to three additional birds helped. In the other instances, up to six birds worked regularly on the nest.

Although flocks usually attended only one nest, on six occasions the beginning of the breeding season was characterized by different members of the same flock beginning two nests at once. In these cases, nest building was a protracted affair, with one or more females taking turns sitting in and calling from each
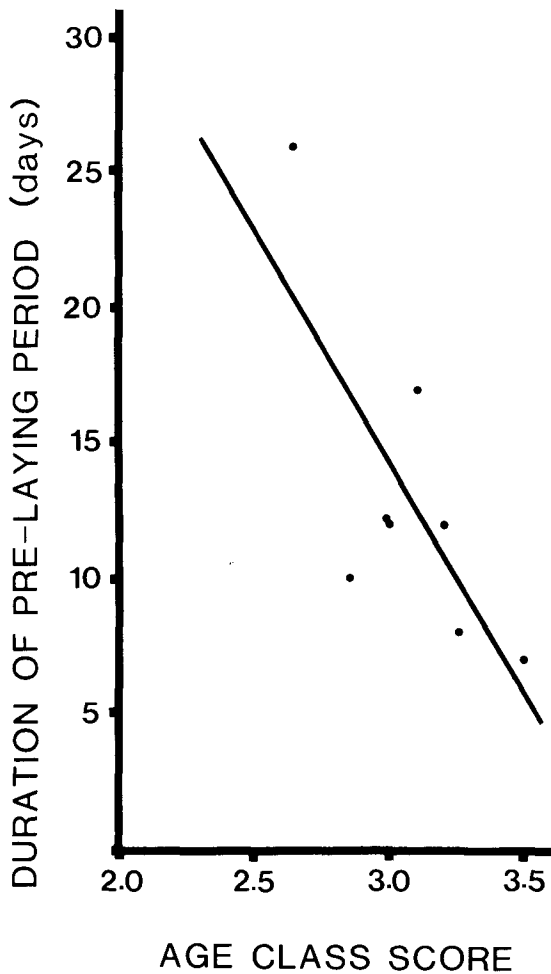
FIGURE 3. Time between initiation of nest building and the appearance of the first egg, as a function of the Age Class Score (see Methods) of the flock. The regression equation for the focal flocks at Monteverde in 1978 is: LENGTH OF PRE-LAYING PERIOD (DAYS) = -17.13(AGE CLASS SCORE) + 65.59; $S_b = -6.36$, $r = -0.747$; $P < 0.05$.

nest. On each occasion, one nest was abandoned in favor of the other.

After the catastrophic storm of 1978, two flocks, whose nests had been destroyed, each built two replacement nests. One flock used their two nests synchronously, with all flock members attending both nests, as do Gray-breasted Jays (*Aphelocoma ultramarina*; Brown 1963, 1970). In the other case, the nests were used sequentially, with all members attending nestlings first at one nest and later, after the first brood had fledged, at the second. Only once did we see a flock that had successfully-fledged young build a second nest. In 1978, members of this flock successfully fledged a brood of four in March and went on to build a second nest in May. The three young of this second brood fledged in July.

THE PRE-LAYING PERIOD

The pre-laying period, defined as the time from when the first sticks are placed in the nest site until the first egg is laid, lasted from one week to three months. Some of this variation may have been caused by the weather. If a *temporal* set in while the jays were building, they simply stopped building until the storm ended. Because some flocks used home ranges that were more exposed than others, weather had varying effects on the nesting behavior of different flocks.

Much of the variance in the pre-laying period seemed to be due to the presence or absence of experienced flock members. For instance, in 1977, one flock, which had no Old members, spent three months building and calling from its nest before laying eggs. By the time members of this flock did lay eggs, two of three other study flocks had fledged young, and the fourth was on its third, unsuccessful, attempt.

Although the Age Class Score (see Methods) is a crude measure, the duration of the pre-laying period decreased with the Age Class Score of the flock members (b = -17.13, S_b = -6.36, $P < 0.05$) for eight flocks in 1978 (Fig. 3).

The duration of the pre-laying period was not correlated with flock size or with the number of Old or Intermediate flock members, but increased significantly with the number of Young birds in the flock (b = 5.28, S_b = 1.64, $P < 0.025$; Fig. 4). The relationship with the number of Young flock members accounted for 57.3% of the observed differences between flocks in the length of the pre-laying period.

THE WHINE CALL

During the pre-laying period and throughout incubation, females spent increasing amounts of time calling from their nests. Observations of one female showed that she sat on the nest for 32.5% of 15 observation hours during the Pre-laying period, 61.9% of 15 observation hours during the Laying period, and 90.5% of 39 observation hours on the nest. During all observation hours, sitting females frequently uttered the loud whine call described by Skutch (1960). The behavior was curious, for, according to Lack (1968) and many others, the abundance of predators in the tropics causes most birds to be secretive around their nests.

The function of the whine call is unclear. The wide spacing (>200 m) between nests and our inability to hear whines of one nest from its nearest neighbor, made it unlikely that the whine call served in the establishment of
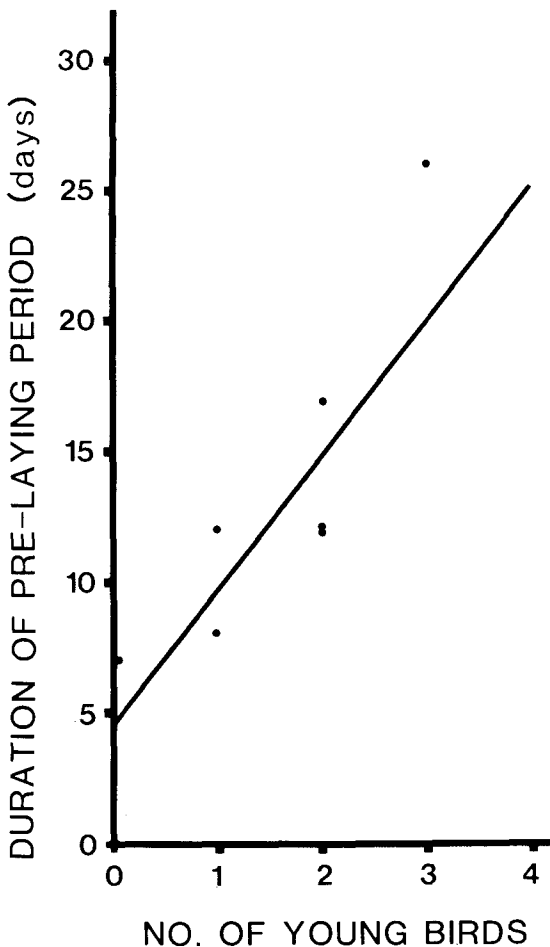
FIGURE 4. Time between initiation of nest building and the appearance of the first egg, as a function of the number of young birds in the flock. The regression equation for the focal flocks at Monteverde in 1978 is: LENGTH OF PRE-LAYING PERIOD (DAYS) = 5.28(NO. OF YOUNG BIRDS) + 4.45; $S_b = 1.64$, $r = 0.796$, $P < 0.025$.

TABLE 2. Variety in breeding among the focal flocks of Brown Jays at Monteverde. The observation year is given in parentheses after the flock designation.

Flock	Number of birds seen:				
	Courting	Copu-lating	Laying	Incu-bating	Brooding
Lag (77)	4	—	2	1	1
Lag (78)	4	4	—	1	1
Rf (77)	—	—	—	3	3
Rf (78)	—	—	5	3	3
Mr (78)	—	—	—	4	4
Bt (77)	—	—	3	—	—
Mig (78)	—	—	2	2	2
Arn (77 & 78)	5	—	—	1	1
Ff (77)	3	2	2	—	—
Ff (78)	3	—	3	3	3

breeding territories, but, rather, seemed to be involved in communication within flocks.

In order to test the latter idea, we examined the relationship between the frequency with which whine calls were given and the proximity of flock members (see Methods) at one flock during the pre-laying and incubation periods.

We found that the female was more likely to call when flock members were present than when they were absent. Calls were significantly more common when some birds were within 50 m of the nest than when no birds were within that distance ($\chi^2 = 46.85$, $P < 0.001$). The female whined in 82% of the observations when other flock members were present within 50 m of the nest. When no flock members were within our sight or hearing, the female was four times less likely to call, whining in only 27% of such cases.

Usually, within any given observation hour, the whining female was fed on the nest several times. Once, however, in a flock where one Old female did all incubation and brooding, we saw the following behavior: during the pre-laying period, we had already observed all flock members feeding the female on the nest. On this occasion, however, the female had spent 57 min on the nest, whining frequently. Although three Young flock members were in sight throughout the observation hour, neither these birds nor any other flock member had brought food to the whining female. Finally, she gave a loud whine and flew from the nest to where the Young birds were feeding. She returned, after less than a minute, followed by the three Young birds. After the Old bird had settled herself into the nest and whined twice, each Young bird presented her with food.

This incident seems to support Skutch's (1960) suggestion that females may give the whine call, which sounds like the begging call of nestlings and fledglings, in order to attract the attention of non-breeding flock members. Certainly, the female called when she could see or hear other flock members.

EGG-LAYING

Several lines of evidence suggest that in many flocks more than one bird contributed to the clutch.

Clutch size.—Clutch size in Monteverde ($\bar{x} = 4.5$, $n = 23$) was almost twice that reported in the Motagua Valley ($\bar{x} = 2.3$, $n = 6$; Skutch 1960, and unpubl.), a highly significant difference (Student's $t = 9.77$, $P < 0.001$).

Range in clutch size.—The range in clutch size in Monteverde was much broader (3–8) than that in other parts of the species range (1–3; Skutch 1960) or those of other jay species in which only one female lays.

Sequence of laying.—At three nests, two eggs were laid in one 24-h period.

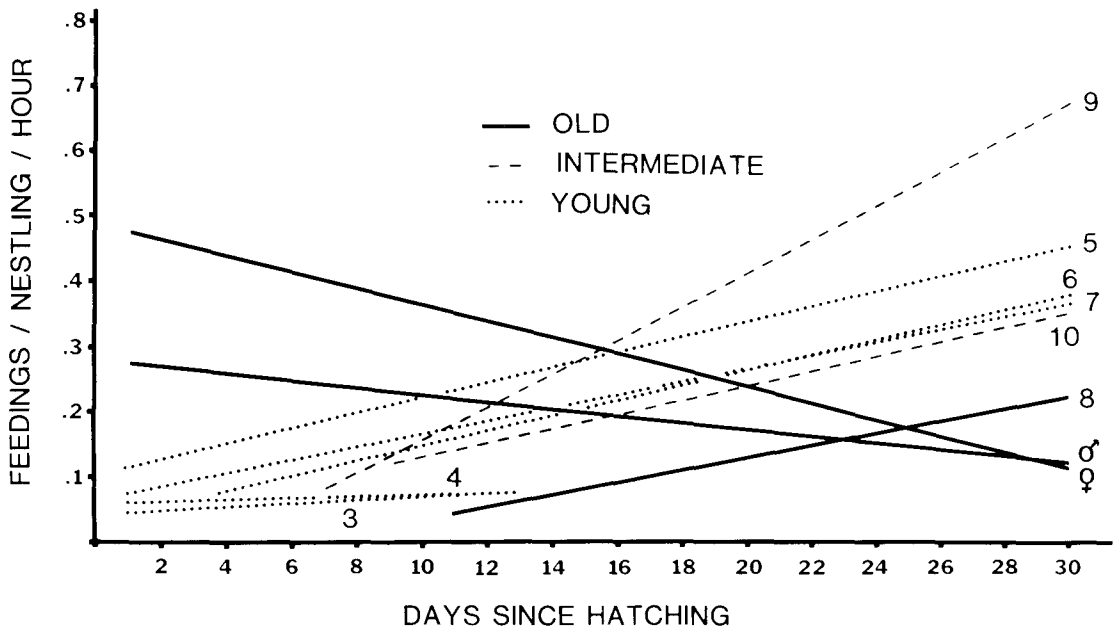*Behavior.*—At six nests, more than one bird sat on, called from, and was fed on the nests

FIGURE 5. Feedings/nestling/h delivered by each member of Lag Flock, as functions of the days since hatching in 1977. The regression equations with the $P(b = 0) < 0.1$, are: (δ) FEEDINGS $= -0.005$(DAYS) $+ 0.275$; $S_b = 0.003$, $P = 0.07$; ($\female$) FEEDINGS $= -0.013$(DAYS) $+ 0.504$; $S_b = 0.004$, $P = 0.005$; (9) FEEDINGS $= 0.024$(DAYS) $- 0.092$; $S_b = 0.007$, $P = 0.004$; (5) FEEDINGS $= 0.012$(DAYS) $+ 0.10$; $S_b = 0.003$, $P < 0.001$; (6) FEEDINGS $= 0.012$(DAYS) $+ 0.029$; $S_b = 0.003$, $P < 0.001$; (7) FEEDINGS $= 0.065$(DAYS) $+ 0.065$; $S_b = 0.002$, $P < 0.001$; (8) FEEDINGS $= 0.010$(DAYS) $- 0.070$; $S_b = 0.005$, $P = 0.04$.

during the egg-laying period (Table 2). In two cases in which Young birds sat on nests for long periods before the clutch was complete, two eggs appeared in each nest within one 24-h period. After the clutches were complete, however, we never again saw the Young birds sitting on the nests.

Our efforts to determine which of three Old birds were contributing to a clutch once caused the birds to abandon the nest with its three eggs. When these birds began to build another nest, two Young flock members began to sit in the abandoned nest and call from it. When the Old birds chased the Young off the abandoned nest, the Young began to sit in and call from the previous year's nest, which was located in the same pasture. In the next 24 h, two eggs appeared in this nest, but 48 h later we found them shattered beneath the tree.

INCUBATION, HATCHING, AND BROODING

Incubation, which began when the clutch was complete, lasted 19–20 days. All eggs hatched within 24 h. During incubation, females spent an average of 91% of each observation hour covering eggs ($n = 52$ h). The amount of time spent on the nest did not vary with time of day. At 3 of 8 focal nests, one bird did all incubating and brooding. In the five remaining cases, from 2 to 4 birds participated (Table 2).

We did not witness egg-tossing. At one nest,

however, where a clutch of three was originally seen in the nest, one egg disappeared the day after we saw it balanced on the branch supporting the nest.

Nestlings fledged about three weeks after they hatched, with fledging varying from 22 to 31 days. Nestlings were brooded until well-feathered at about 17 days. During the first week, females brooded for an average of 74.3% of each observation hour. During the second week, the average brooding time fell to 5%.

Much activity was associated with hatching, which usually occurred early in the morning, and was easily recognized by the excited behavior of flock members. Once, during the hatching of Lag Flock's first clutch of 1978, we saw nine flock members perched simultaneously on the nest. While they peered at the nestlings, six Young and Intermediate members from Arn Flock (Lag Flock's nearest neighbor) arrived. Members of Lag Flock moved away and the six non-flock members visited the nest. The activity continued for almost 20 min, accompanied by many soft vocalizations.

NESTLING CARE

Nestling care varied tremendously, but we emphasize three points here, which were illustrated by activities of birds feeding nestlings at the 1977 nests at Lag and Rf flocks (Figs.
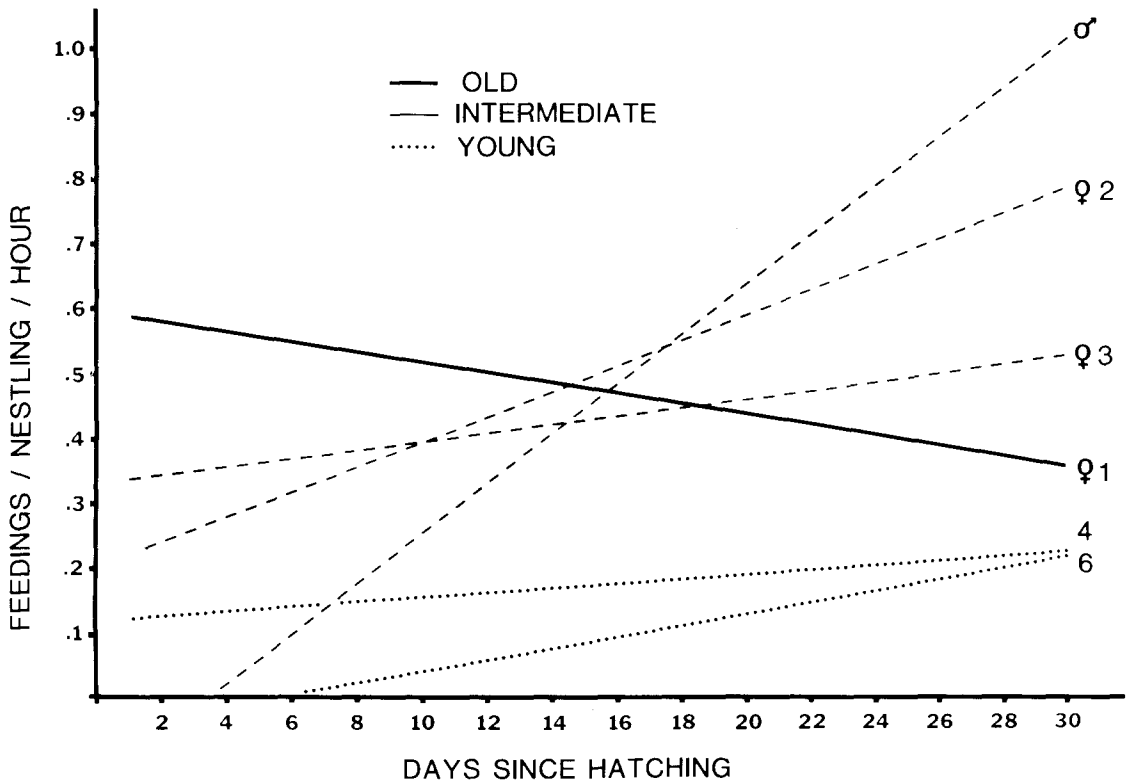
FIGURE 6. Feedings/nestling/h delivered by each member of Rf Flock, as functions of the days since hatching in 1977. The regression equations, with $P(b = 0) < 0.1$, are: (δ) FEEDINGS = 0.039(DAYS) − 0.103; $S_b = 0.011$, $P = 0.004$ ($\female 2$) FEEDINGS = 0.025(DAYS) + 0.19; $S_b = 0.012$, $P = 0.06$ (6) FEEDINGS = 0.009(DAYS) − 0.055; $S_b = 0.005$, $P = 0.09$.

5 and 6). As assessed by the number of feeding trips, variation in nest attendance was related to (1) age of the helpers, (2) breeding status of helpers, and (3) flock demography, i.e., what Brown (1978) called the "demographic environment."

All flock members fed the nestlings; yet individual contributions might vary significantly (Figs. 5 and 6). For instance, in 1978, Lag Flock's first brood was fed, not only by members of Lag Flock, but also by one Intermediate bird from Arn Flock. Judging from its behavior, this bird was a male who had established a pair bond with one of Lag Flock's two-year-old females. He accounted for 15% of the feeding visits made to the nestlings and was the only non-flock member ever seen to feed this brood.

During the first week, nest attendants passed food to the brooding female who then fed the nestlings. Later, helpers fed nestlings directly. The absolute number of feedings given to the nestlings increased as they grew; but the increased effort was not apportioned equally among flock members. In general, the contributions of Young and Intermediate jays increased significantly over time (Figs. 5 and 6). In the several instances when their contribu-

tions did not increase, special circumstances prevailed. For instance, at Lag Flock, some Young helpers died before we could assess changes in nest attendance. In another case, also at Lag Flock, an Intermediate bird, which joined the flock after nestlings hatched, showed no appreciable increase in feeding rate, although another Intermediate bird, which joined at the same time, did.

Although the contributions of Intermediate birds were generally similar in all flocks, the contributions of Young birds increased more slowly in some flocks than in others (Figs. 5 and 6). Indeed, at Rf Flock, one of the two Young birds did not show a significant increase at all. The differences in their behavior may, in part, be attributable to differences in absolute demand for food resulting from differences in clutch size. Lag Flock was caring for a brood of seven, Rf Flock for only a brood of three. Thus, both absolute demand for food and activity around the nest, which may serve as stimuli for the Young helpers, were lower in Rf Flock.

Observed differences in the rates at which the contributions of Young birds in the two flocks increased may have resulted from either lower demand or lower activity levels around

the nest. In either case, they may reflect real differences in the rates at which Young birds are learning to attend nestlings. Although all Young birds became more efficient nest attendants over time, their performance in flocks with Old, experienced birds improved more rapidly than that of Young birds in flocks composed largely or entirely of Young and Intermediate birds (Lawton and Guindon 1981). Young birds fed nestlings at consistently lower rates at Rf Flock than in Lag Flock, and only one Old jay lived in Rf Flock: the female that did most of the incubation and brooding. In contrast, both members of the nuclear pair at Lag Flock were Old birds, and, after hatching, a third Old bird joined the flock and attended nestlings at rates equal to or greater than those of the other Old birds. Even if Young birds did not receive active instruction, the activities of these Old members would have provided them with more opportunities for observational learning.

For instance, nine days after nestlings hatched at the 1977 nest of Lag Flock, we saw a Young bird approach the nest with a large katydid in its bill. Landing on the nest, it attempted unsuccessfully to feed the entire insect, which was almost the same size as the nestlings, to those uncooperative birds. After several moments, the Old female appeared, landed on the rim of the nest, called, and took the katydid from the Young helper. As the latter stood there, she removed the insect's wings, tore the body apart, and fed pieces to the nestlings. This incident suggests that active instruction may occur.

Skutch (1960) also saw Young helpers bring large, unrendered food items to nestlings. On one occasion, in a flock composed entirely of Young and Intermediate birds, he observed a Young helper bring an entire caterpillar to newly hatched nestlings. As the helper arrived at the nest, an Intermediate attendant took the prey, but flew away instead of feeding the nestlings.

The behavior of Old breeding birds differed markedly from that of Young and Intermediate flock members. The level of feeding behavior of Old birds did not increase, but remained constant or actually decreased over time (Figs. 5 and 6). Among other cooperatively breeding birds, e.g., Florida Scrub Jays (Stallcup and Woolfenden 1978), Green Wood-Hoopoes (*Phoeniculus purpureus*; Ligon and Ligon 1978), Gray-breasted Jays; Brown 1970, 1972), Common Babblers (*Turdoides caudatus*; Gaston 1978) and Grey-crowned Babblers (*Pomatostomus temporalis*; Brown et al. 1978), similar observations led Brown et al. (1978) and Emlen (1984) to suggest that the presence

of helpers allows breeders to decrease their work load.

On the other hand, Old, non-breeding birds behaved like helpers of other age classes. For instance, one Old bird, which joined the Lag Flock after the nestlings hatched, brought increasing amounts of food to the nestlings as they grew.

When the nestlings fledged, their first flights were accompanied by older flock members, usually Young and Intermediate birds, rather than Old breeding birds. After fledging, Young of the year continued to be fed regularly and frequently by all flock members for about three months. After this time, Young of the year might be fed if they pursued an older individual. This begging behavior sometimes persisted for as long as a year, but we never saw Yearlings being fed after the next breeding season began.

In addition to feeding, Young were protected by older members for up to a year after fledging. For instance, on one occasion a flock approached us as we sat in full view in an old field. The Young birds, then about three months old, approached to within 8 m. As they did so, older members scolded vigorously from a distance of 20 m and continued to scold until the Young flew to join them.

On three occasions while observing the post-fledging foraging behavior of the flock, we saw Young birds fall asleep and get left behind as the flock moved on. Twice, the Young birds awoke within 10 min of the flock's departure, flew to exposed perches, and called harshly while hopping and vigorously flicking their tails until an older flock member returned. On the third occasion when a Young bird slept in a guava tree after the flock departed, an Old bird returned and woke it by nudging it with its bill and calling softly.

BREEDING BEHAVIORS

The number of birds seen courting, copulating, or sitting on the nest during egg-laying, incubating, or brooding varied from flock to flock (Table 2). Thus, it is impossible to easily categorize the breeding behavior of this population. For the sake of simplicity and because we think their terminology is least likely to result in artificial reification or behavioral typology, we here adopt Emlen and Vehrencamp's (1983) broadly interpreted terms "helper-at-the-nest," "communal breeding," and "cooperative breeding" to describe the breeding behaviors we saw in Monteverde. "Cooperative breeding," which occurred in all flocks, refers to cases in which more than two birds cared for a brood. "Helping-at-the-nest," defined as birds contributing physically, but

not genetically to the rearing of young, was universal; however, "communal breeding," defined as shared percentage of any given brood, was not.

In five flocks, we suspect that broods were produced by more than one pair because we saw more than one pair courting and copulating, and because we saw more than one bird sitting on the nest during the laying, incubation, or brooding periods.

In contrast, another sort of communal breeding occurred in Lag Flock. In 1977, we saw two birds sit on the nest during the egg-laying period and two eggs were laid in one 24-h period. In this case, however, we only saw one bird incubate and brood. A similar situation may have existed for Lag Flock in 1978 and for Arn Flock in 1977 and 1978. Since we do not know, however, whether the brood was laid by more than one female, we cannot unambiguously categorize these cases as communal breeding.

On one occasion, members of Alon Flock built and attended two nests simultaneously. Although this may have represented the complex sort of cooperative breeding typical of Gray-breasted Jays, we do not know whether the broods were laid by one or more females, and we cannot rule out yet a third sort of communal breeding.

After its first nest failed, TRSL Flock split into two independent subgroups and built separate nests. Alvarez (1975) described a similar occurrence in Green Jays (*Cyanocorax yncas*), but in this case the new groups formed did not persist after the breeding season.

DISCUSSION

Recent field studies of the behavior of cooperative breeders have shown that breeding biology may vary with habitat saturation (Stacey 1978, 1979a), demography (Brown 1978), resource distribution (Verbeek 1973, Reyer 1980), or the disturbance regime (Hardy et al. 1981). Our observations of Brown Jays in Monteverde reveal behavioral differences of previously unreported magnitude within populations, and support the notion that habitat disturbance and demography affect the breeding behavior of these birds even more than has been generally appreciated.

In Monteverde, Brown Jays display the complete spectrum of cooperative breeding, from adult nuclear pairs assisted by young, non-breeding birds, to true communal breeding, similar to behavior observed in Groove-billed Anis (*Crotophaga sulcirostris*; Vehrencamp 1978). The range of behaviors in this population is broader than reported for any other population of cooperatively breeding species. In Monteverde, at any rate, Brown Jays cannot be said to have any one type of breeding system.

The most obvious way in which the breeding behavior of Brown Jays seems to be consistent with that of other cooperative breeders is nestling care; this, however, is the area in which other species are most variable. Brown Jays feed nestlings with the same degree of individuality reported for Green Jays (Alvarez 1975), Florida Scrub Jays (Stallcup and Woolfenden 1978, Woolfenden 1975), White-throated Magpie-Jays (*Calocitta formosa*; Winterstein, unpubl.) and Gray-breasted Jays (Brown 1970, 1972). In our population, as among Florida Scrub Jays, the rates at which helpers fed nestlings varied, not only among individuals, but also with age and breeding status of the helpers.

According to Skutch (1960, unpubl. and pers. comm.), individual, age, and breeding status variations in nestling care appear to obtain throughout the species range. Although he provided little quantitative information on nestling care, his published data reveal patterns similar to those we saw among Brown Jays in Monteverde. In general, the contributions of the nuclear pair remained constant or decreased over time, and, by the time nestlings were three weeks old, some helpers brought food twice as often as did the nuclear pair. Our observations are consistent with Skutch's, and suggest that, throughout their range, Brown Jays exhibit the same kind of individual variation in nestling care as that observed in other New World jays.

It is possible that, in other parts of the species range, other aspects of Brown Jay breeding behavior may more closely approach those of other New World jays. In the Motagua Valley of Guatemala and in the Pejivalle Valley of Costa Rica, for instance, the breeding behavior of these birds seems less diverse (Skutch 1960). According to Skutch (pers. comm.), in these areas, Brown Jays behave like Florida Scrub Jays, i.e., adult breeding pairs are assisted by non-breeding younger birds. Even here, however, there are hints that breeding behavior may be more variable than earlier reports suggest.

For instance, within the Motagua Valley population, Skutch (1960) saw three birds incubate or brood at one nest at different times, a situation not known to occur in Green Jays, Gray-breasted Jays, White-throated Magpie-Jays or Scrub Jays, but which we have frequently observed and which has been seen among some of the less well-studied *Cyanocorax* jays (Hardy, pers. comm.). On several occasions, Skutch has noted the disappearance

of eggs as a clutch was laid or has found broken eggs in the nest, behavior which led him to suspect that egg-tossing, common among communally breeding Groove-billed Anis (Vehrencamp 1978), was occurring. Skutch wondered whether Brown Jays might also be communal layers, but rejected the hypothesis because clutch size in his study population was small. Our observations of possible egg-tossing in the communally breeding flocks in Monteverde suggest that Skutch's original hypothesis may have been correct.

Flock composition by age class also varied more in Skutch's populations of Brown Jays than in other well-studied New World jays. For instance, of the two flocks whose behavior Skutch (1960) reported in detail, one had no Old birds, but was composed entirely of Young and Intermediate birds; this situation seems to have been the exception rather than the rule where Skutch worked, and it was unusual flock composition which led him to focus on the behavior of a second flock with only one Old member. It was in these two unusual flocks that Skutch observed several birds brooding or incubating, and in which eggs disappeared or were broken for unknown causes. Skutch's observations, augmented by our own, suggest that throughout their range, Brown Jays may vary in flock structure and breeding behavior more than do other cooperatively breeding New World jays.

Climatic factors also may influence breeding behavior. Along a population margin like that observed in Monteverde, there are density-independent catastrophes that can produce major setbacks in breeding. The greatest variety in breeding behavior followed the unseasonal *temporal* of 1978. As examples, it was at this time that one flock built and attended two nests simultaneously while another flock split up to build two independent nests. Thus, some variability in breeding behavior of the Brown Jays in Monteverde may be caused by storms, an idea that could be tested by comparing the behavior of other populations on species borders, for instance, of Brown Jays in Texas.

In Monteverde, the unusually broad spectrum of breeding behavior may reflect not only the peculiar history of a rapidly growing population in a harsh environment, but also a pattern of habitat occupation that may have been typical of this species for millennia and which may explain why Brown Jay breeding biology is more variable than that of close relatives. Although the large expanse of newly suitable habitat may make the situation in Monteverde unusual, such population expansion is not new to the Brown Jay.

Throughout Central America today, the species is associated with the human agricultural disturbance that has been widespread since the agricultural revolution which began some four to five thousand years ago. During that time, shifting agricultural patterns may well have created patchy and continually changing habitat, which has made it impossible for Brown Jays to saturate the colonizable area in most parts of their range.

Our observations of Brown Jays leave us with several questions. Do particular flocks tend to favor particular breeding behaviors over the years? If so, does a genetic component to breeding behavior exist or is it learned? If the observed variation in breeding behavior does represent genetically-based family traits, even in part, then the variation can provide the substrate for natural selection of social characters.

The fact that Brown Jays maintain a complex social organization and breed cooperatively even where suitable habitat for breeding pairs may exist, suggests that there are strong phylogenetic constraints on their social organization. Moreover, the persistence of a complex social life in expanding populations also suggests that the birds benefit either by learning or by enhanced survival, benefits which have been discussed extensively since Darwin's time (Darwin 1859, Allee et al. 1949, Wynne-Edwards 1962, Lack 1968). Indeed, our observations of age-specific patterns of behavior in several phases of the nesting cycle strongly suggest that learning is an important benefit of sociality in Brown Jays.

Flocks composed of Young and Intermediate birds are slower to begin building nests and, once begun, significantly slower to complete nests or to lay eggs. Although clutch size or egg viability are not significantly different between flocks composed of Young and Intermediate birds and flocks that have Old members, significant age-related fledging differences do exist. Specifically, fledging success increases as a function of flock age-class score and depends most heavily on the presence of Old, experienced flock members (Lawton and Guindon 1981).

Lawton and Guindon (1981) suggested that the age-specific differences in reproductive success observed in this species may stem from age-specific differences in behavior; the observations reported here augment their findings. For example, in flocks with Old, experienced members, the frequency with which Young helpers bring food to nestlings increases more rapidly than does that of Young birds in flocks of low age-class score. Moreover, on several occasions we have witnessed behavior suggesting that, in flocks with Old, experienced members, Young birds receive active instruc-

tion. These observations suggest that social learning is of great importance in this species and may explain, at least in part, why, in an area where suitable habitat is available, Young and Intermediate birds continue as helpers at the nest instead of dispersing to breed as pairs.

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