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FLOCK COMPOSITION, BREEDING SUCCESS, AND LEARNING IN THE BROWN JAY

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ABSTRACT.—Brown Jays are group breeders with helpers at the nest. In a montane population in Costa Rica, we found that flock composition by age class was highly variable. In this population the number of Old flock members predicted breeding success better than flock size. We suggest that experience may be important to the reproductive success of some cooperative breeders. This interpretation is supported by age-specific differences in nest attendance. Judged by the total number of feedings and the proportion of aborted feedings, the effectiveness of nest attendants increased with age. Further, Young birds improved significantly as nest attendants over one breeding season. To our knowledge, our findings offer the first quantitative support of Lack's hypotheses that young helpers are unlikely to breed successfully on their own and must learn to care for nestlings.

The selective advantages of cooperative breeding in birds are often unclear. The significant positive correlation between the number of helpers in a flock and fledging success reported for a growing number of species (Brown 1978) implies that cooperative breeding is advantageous to breeding birds. In some cooperative breeders, however, the correlation between the number of helpers and fledging success is not significant (Zahavi 1974, Brown 1975); and in others the relationship approaches an asymptote at a given flock size (Woolfenden and Fitzpatrick, unpubl.). Brown (1978) has suggested that studies of the benefit from helpers should include examining other correlates of flock size, e.g., territory quality and/or flock composition ("the demographic environment").

What are the advantages to non-breeding helpers? Lack (1968) suggested that helping at the nest could evolve by natural selection if young birds, unlikely to breed successfully on their own, help raise nestlings to whom they are closely related. Helpers could be raising their inclusive fitness and also, by learning to care for nestlings, could be serving an apprenticeship that would improve their breeding success later. Field studies have shown that, in many cases, helpers are young and closely related to those they help (c.f., Alvarez 1975, Brown 1963, 1970, 1972, Woolfenden 1973, 1975, Woolfenden and Fitzpatrick 1977, 1978, Stallcup and Woolfenden, 1978). Data on the breeding success of young inexperienced birds are sparse (Woolfenden 1975: Table 2), and we know of no quantitative demonstration that young helpers do learn to care for nestlings.

Testing hypotheses about learning and breeding success of young inexperienced birds in cooperatively breeding species is important for two reasons. First, if it can be shown that young birds are unlikely to breed successfully on their own and that they do learn to care for nestlings, then we may infer valid conclusions about the selective advantages of helping. Second, if it can be shown that the efficiency of helpers varies with age and sex, we can test Brown's hypothesis that the demographic environment, i.e., flock composition, is a better predictor than simple flock size of the effect of helping on breeding success.

As part of a field investigation into the behavior of the Brown Jay (*Psilorhinus morio*), a cooperatively breeding species, we addressed the following questions: 1) To what extent do differences in breeding success between flocks reflect differences in age structure and/or flock size? We predicted that if experience is an important component of breeding success, then flocks with older members should produce more nestlings than flocks composed of young birds. 2) Do young flock members make more unsuccessful or aborted feeding trips than older birds? If so, does the frequency of aborted feeding trips change over the nestling period? If young birds are learning, they should make more unsuccessful or aborted feeding trips, which we called mistakes, than older birds, and these mistakes should decrease over time.

STUDY ANIMAL

Brown Jays are well-suited to quantitative field investigation because they are large, noisy, conspicuous (Sutton and Gilbert 1942) and can be individually identified without color banding (Skutch 1960). Soft parts (eye-ring, bill, legs and feet) are yellow at birth and darken idiosyncratically with age. This makes it possible to estimate age and to identify individuals by field observation. In Costa Rica, where the morph with white-tipped outer rectrices is found, adults have plumage differences that allow individuals to be distinguished (Skutch 1978, and pers. observ.).

During nest-building and incubation, female Brown Jays vocalize, making their nests easy to find (Skutch 1960). Nests, generally built in isolated pasture trees, are easily observed. Brown Jays are accustomed to humans and tolerant of observers. Females return to incubate as soon as an observer leaves the nest tree. Counting eggs and weighing or banding nestlings does not seem to upset the birds or lead to increased nest predation, a problem of many field investigations (Lennington 1979).

Brown Jays live in flocks of six to ten, apparently with highly stable membership. Flocks use overlapping home ranges of 10 to 20 ha but defend smaller territories while breeding. A flock generally builds one nest that is attended by both breeding and nonbreeding members. At many nests we could not ascertain how many birds were breeders. Our observations of courtship behavior, feeding of incubating females, the sequence and timing of egg laying, and an average clutch twice that reported by Skutch (1960) suggested that more than a single pair bred at most nests (Lawton, unpubl.).

STUDY AREA AND METHODS

We studied Brown Jays 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. Annual rainfall is about 2,500 mm and falls mostly during the months of June to December. Throughout the year the climate is dominated by the Atlantic Trade Winds. During the early dry season, Atlantic storms sweep across the Continental Divide, carrying fine mist.

The study area 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 topography permits, selective logging has created clearings, which are in various stages of regeneration. Some farms have recently been replanted with native trees, and in the past five years saplings have begun to replace second growth.

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 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.

As in *Cyanocorax* jays (Hardy 1973), soft parts darken with age. For the Brown Jay we established three age classes, based on the percentage of soft part darkening. A bird was classified Young if it had yellow legs, feet and eye-rings, and if its bill was ≤50% black. An Intermediate bird had mottled legs, feet and eye-rings, and a bill ≥50% black. An Old bird was one with fully black soft parts. These categories refer strictly to morphological characters and are not meant to imply anything about sexual maturity or breeding status. Young birds are often sexually mature, and, in some flocks, are breeding members. Our observations of nestlings banded since 1977 suggest that the three age-classes correspond roughly to one to two years old (Young), three years (Intermediate), and four or more years (Old).

For the focal flocks, two in 1977 and six in 1978, assessing membership was straightforward. Because all flock members feed the young, membership was determined from daily observations of feeding. Membership of non-focal flocks, two in 1977 and four in 1978, was evaluated on a weekly basis. Each non-focal flock was followed for several hours, usually as the birds came from or went to roost. The flock was counted and followed until age-class composition was established. At this time, we also checked nests to learn the stage of the breeding cycle. In all, we followed four flocks in 1977 and 10 in 1978 to fledging or failure. In 1977 Lawton observed flocks for 420 h. In 1978, both authors observed flocks for over 800 h.

In 1977 Lawton observed two focal flocks, chosen for accessibility. The 12 daylight hours were divided into three 4-h segments. Focal nests were observed daily for one hour in each of the morning, midday and afternoon segments. In 1978, using the same daily sampling regime, the number of focal nests was increased. Early in the breeding season, four nests were observed for three hours each, every other day, until fledging or failure. Later, two additional flocks were observed for three hours each on alternate days. During each sample period Lawton recorded, by age-class and individual, which flock members fed young.

RESULTS

Table 1 summarizes the data on flock size, composition and fledging success. Two flocks observed in 1978 are excluded because they divided after nest failure and the composition of the sub-groups attending new nests is uncertain. Flock size varied from six to 10 individuals ($\bar{x}$ = 7.2) and the average number of Old members was 1.75 (range = 0–3). One-third of the study flocks did not have a nuclear pair of Old birds; two had no Old birds, and two only one. The number of Intermediate age members ($\bar{x}$ = 3.4, range = 1–6) was not correlated with the number of Old birds, but was negatively

TABLE 1. Flock composition and fledging success.

Flock	Size	No. Old	No. Int.	No. Young	Clutch	No. fledged	Proportion fledged
LAG77	7	2	2	3	7	4	.571
RF77	6	1	3	2	3	2	.667
BL77	6	0	1	5	*	1	*
FF77	6	0	4	2	*	0	*
LAG78a	7	2	2	3	5	4	.800
LAG78b	7	2	2	3	4	3	.750
RF78	10	3	5	2	5	5	1.000
FF78	8	2	4	2	5	1	.200
MR78	9	2	6	1	6	6	1.000
ARN78	8	2	4	2	6	4	.667
MIG78	6	3	3	0	*	4	*
TS78	7	3	3	1	5	3	.600
KEN78	6	1	4	1	4	2	.500
$\bar{x}$	7.2	1.75	3.4	2.1	5.0	3	.644

* Indicates inaccessible nest.

correlated with the number of Young birds ($r = -.641$, $P = .018$, Pearson Product Moment Correlation). Flocks had an average of 2.1 Young members (range = 0–5).

REPRODUCTIVE SUCCESS

Identifying an appropriate variable. Earlier investigations of the effect of helpers on reproductive success have not generally used comparable measures of reproductive success (Brown 1978). The most common measure used to compare flocks has been the numbers of fledglings raised. However, since clutch size in this population varied from two to eight (Lawton, unpubl.), we wanted to distinguish between flocks that fledged the same number of nestlings by raising a high proportion of a small clutch from those raising a small proportion of a large one. We did so by examining the correlations between three components of reproductive success (clutch size, proportion of the clutch fledged, and number of fledglings) with the four components of flock composition (flock size, number of Old members, number of Intermediate members, and number of Young members). The correlation matrix (Table 2) indicates that neither clutch size nor proportion fledged is significantly correlated with any component of flock composition. This enabled us to eliminate these variables and to use the number of fledglings in the following analysis of differential reproductive success among the study flocks.

Comparison among flocks. Reproductive success, measured in terms of number of fledglings, was significantly correlated with two components of flock composition: flock size ($r = .638$, $P = .02$) and number of Old members ($r = .713$, $P = .006$). Since these factors are themselves correlated ($r = .544$, $P = .05$), we had to determine whether the important factor affecting reproductive success was simply flock size, i.e., the number of nest attendants, or the number of Old, experienced nest attendants.

The first variable to enter a stepwise multiple regression was the number of Old flock members (number of fledglings = .843 + 1.22 number of Old members, $F = 11.35$, $P = .006$). The addition of flock size to the regression (number of fledglings = −2.01 + .890 number of Old members = .48 flock size, $F_{reg} = 7.42$, $P = .01$) marginally improved the proportion of the variance accounted for; R^2 rose from .51 to .60. However, in this regression the probability of the flock size effect occurring by chance was relatively high ($P = .17$). No other variables entered the regression. Therefore, we conclude that reproductive success was affected most by the number of Old members in a flock, and that the effect of flock size is largely accounted for by its relationship to flock composition.

TABLE 2. Pearson Product Moment Correlation matrix of three measures of reproductive success and flock composition. The probability of the observed correlation occurring by chance is given in parentheses.

	Clutch size	Proportion fledged	# Fledglings
No. Old flock members	.433 (.21)	.304 (.39)	.713 (.006)
No. Intermediate flock members	.142 (.69)	.300 (.39)	.349 (.24)
No. Young flock members	.117 (.75)	.012 (.97)	−.306 (.31)
Flock size	.455 (.18)	.488 (.15)	.638 (.02)

NEST ATTENDANCE

We observed 1,275 feeding trips by birds of known age-class in two flocks in 1977 and five in 1978. In 1978 the nestlings of the sixth focal flock were killed by predators when less than a week old. The feeding data from that flock are too sparse for inclusion in this analysis. Feeding trips were divided into successful and unsuccessful (mistakes). Three kinds of mistakes were distinguished; but since these forms of behavior were relatively rare, they were lumped for the statistical analysis.

Types of mistakes. Young birds made three types of mistakes. First, at the beginning of the nestling period Young birds presented inappropriate food items to nestlings. For instance, they occasionally brought an entire katydid to very small nestlings. Young birds tried repeatedly to feed such items whole to the nestlings before giving up and eating the food. It is possible either that Young birds were unable to distinguish food appropriate for the hatchlings, or that they had difficulty in catching small prey. As the nestling period progressed, Young birds brought fewer inappropriate items. However, in most cases, when Young birds brought large items, e.g., lizards, later in the nestling period, they tore them up before presenting them.

Second, early after hatching, when a Young bird approached the nest with live food, it sometimes landed in a nearby tree, and, after beating the prey against a branch, ate it. The Young bird would nonetheless approach the nest, land on its rim and utter the feeding note. When the nestlings responded by begging, the Young bird looked at them for a few moments and flew off, generally returning within five minutes with food. By the third week after hatching, Young birds rarely made this type of mistake.

Third, a Young bird might arrive at the nest with food and give the feeding call. Before passing food to the nestlings, it might be distracted by a disturbance nearby, e.g., other jays mobbing a hawk, and then might fly off without feeding the nestlings. More rarely, Young birds might cease feeding to mob the observer. This behavior was always ignored by older flock members and decreased in Young birds over time.

Intermediate and Old birds never made the first two types of mistakes. Rather, when they aborted feedings it was almost always in order to mob a potential predator. Intermediate and Old birds did not abort feedings to mob the observer. Only once, and in unusual circumstances, was an Old bird seen to make a different, fourth, type of mistake.

TABLE 3. Feeding data, reported by age class, used to test the null hypothesis that birds of all age classes make mistakes at equal rates. $\chi^2 = 39.22$, $P \ll .005$).

Age class	No. birds	No. feeding trips	No. mistakes observed	No. mistakes expected
Old	14	450	4	19
Intermediate	26	543	21	24
Young	15	282	30	12

We observed the fourth type of mistake at a nest that had been built in a fig tree (*Ficus tuerkheimii*), which lost and replaced its leaves during the nestling period. A large fig leaf had blown into the nest, completely covering the nestlings prior to the arrival of an Old bird with food. The Old bird, a male, landed on the nest, deposited the food on the rim, and picked up the leaf. The nestlings stood and begged. The Old bird, holding the leaf in his bill, turned his head from side to side, peering at the nestlings. He dropped the leaf, which once again covered the nestlings, and turned to pick up the food. When he turned back, uttering the feeding note, he found, not begging nestlings, but the fig leaf. The bird repeated this performance twice before taking the leaf in its bill and flying away, leaving the food on the nest and the nestlings begging loudly. He did not return for an hour.

Frequency of mistakes. We used a Chi-square test of the null hypothesis that all birds made mistakes at equal rates (Table 3). The number of mistakes was calculated according to methods suggested by Altmann and Altmann (1977) on the basis of both the number of members in the age-class and the number of feeding trips observed for that class. The null hypothesis was strongly rejected ($\chi^2 = 39.22$, $P \ll .005$). Old birds made mistakes less frequently than expected. Intermediate birds made mistakes at the mean rate, and Young birds at double the mean flock rate.

When we compared the number of successful feeding trips we again found significant age-specific differences ($\chi^2 = 83.54$, $P \ll .005$). Young birds brought food least frequently. Intermediate birds fed nestlings more often, and Old birds made the most feeding trips. Caution must be exercised in interpreting this comparison. The amount of food delivered per feeding trip can vary significantly with age and sex of the nest attendant (Stallcup and Woolfenden 1978).

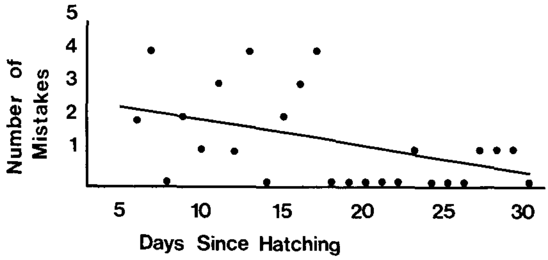

FIGURE 1. Regression of number of mistakes made by Young birds against days since hatching (b = −.085, $P < .05$).

Quantity of food delivered may, therefore, be a better unit of comparison than the number of feeding trips. We present the comparison here in terms of feeding trips because, calculated in comparable units, it emphasizes the pattern observed for unsuccessful feeding trips.

Rate of mistakes. We examined the change in the number of mistakes that Young birds made over the nestling period. Young birds did not begin to feed nestlings regularly until about a week after hatching, so the data begin on day six of the 30-day nestling period. Young birds made significantly fewer mistakes as the nestling period progressed ($b = -.085$, $P < .05$; Fig. 1). Similar regressions for Intermediate and Old birds showed no significant change over time (Intermediate birds: $P > .50$; Old birds: $P > .20$).

The wide scatter around the line and the relatively small proportion of the variance explained by the regression ($r^2 = .20$) reflect significant differences in the rates at which Young birds in different flocks made mistakes. Table 4 presents the number of mistakes made by Young birds, broken down by flock. Once again, a Chi-square test strongly rejected the null hypothesis that Young birds in all flocks made mistakes at equal rates ($\chi^2 = 18.21$, $P < .005$). These differences may be accounted for by many factors, such as the number of Old birds in a flock, the genetic or dominance relationships between flock members, the difference in stimuli presented to Young birds because of differences in brood size, or the sex of the Young birds. However, because the variance in the number of Old birds per flock and in clutch size was low, more observations will be needed in order to clarify the relationships between these variables and the mistakes of Young birds.

TABLE 4. Feeding behavior of Young birds, separated by flock, used to test null hypothesis that Young birds in all flocks make mistakes at equal rates ($\chi^2 = 83.54$, $P \ll .005$).

Flock	No. young birds	No. feedings observed	No. mistakes observed	No. mistakes expected
Lag78	3	33	2	3.5
FF78	2	17	4	1.8
Arn78	2	16	1	1.7
RF78	2	11	4	1.17
MR78	1	6	2	.638
RF77	2	31	6	3.29
Lag77	3	168	11	17.87

DISCUSSION

Among the Brown Jays of Monteverde, flock composition by age class was variable. Some flocks were composed entirely of morphologically sub-adult (Young and Intermediate) birds while others had one or more morphologically adult (Old) members. Interflock comparisons of breeding success, measured in terms of numbers of fledglings, reveal that reproductive success increased with flock size, but that this correlation was largely the result of the correlation between flock size and number of Old birds.

Brown (1978) predicted that the effect of helping at the nest could not be accurately gauged by looking for a simple positive correlation between flock size or number of helpers and reproductive success. Rather, this frequently observed correlation might be an artifact of the correlation between flock size and some other variable, e.g., flock composition. Our results support Brown's prediction. In the case of Brown Jays at Monteverde, flock composition, specifically, the number of Old flock members, was a better predictor than flock size of reproductive success.

Because morphologically adult (Old) birds are the oldest birds in any flock, we interpret our findings to suggest that the experience of these birds may be important in raising reproductive success. In some species that breed as pairs on territories (Lack 1968) and among numerous colonial breeders (Blus and Keahey 1978, Nelson 1978; for reviews see Lack 1968 and Cody 1971) young birds breeding for the first time are less successful than older, more experienced birds. Woolfenden (1975: Table 2) found similar success rates for inexperienced Florida Scrub Jays (*Aphelocoma coerulescens*) breeding for the first time. Separating novice pairs from pairs of experienced breeders, he learned that experienced birds bred successfully whereas novices fledged no young. Although his sample was small, his results suggested that experience is important to the breeding success of cooperative breeders as well. Our findings lend quantitative support to this suggestion and to the idea that young birds serve as helpers because they are less likely to breed successfully on their own.

Many factors could contribute to the reduced fledging success of flocks composed of young birds. Among these are initial differences in clutch size, and differences in egg viability. In other species, clutch size and viability are known to increase with the age of the laying female (Lack 1968 and Cody 1971). Our data do not allow us to determine the relative importance of differences in these two factors. Although we observed no significant differences in clutch size between flocks of different compositions, the number of accessible clutches produced by flocks composed of Young and Intermediate birds is small (n = 2). Mean clutch size for these flocks ($\bar{x}$ = 3.5) does appear smaller than the overall mean ($\bar{x}$ = 5, n = 10), suggesting that differences in reproductive success may in part be attributable to initial differences in clutch size. Our samples are likewise too small to distinguish whether flocks composed of young birds produce fewer viable eggs.

Post-hatching nestling care is a third factor that may affect the breeding success of flocks composed of young, inexperienced birds. Our data support the idea that observed differences in fledging success are due, at least in part, to age-specific behavioral differences. By two criteria, namely total number of feedings and proportion of aborted feedings, the effectiveness of nest attendants appears to increase with age. Young birds bring inappropriate food items and abort feedings more frequently than do Intermediate birds. In turn, Intermediate birds make more mistakes than Old birds. Similarly, we found that Old birds make more feeding visits than Intermediate birds, which deliver food more often than Young birds.

Other authors have presented data suggesting that not all helpers are equally helpful (Brown 1972, Alvarez 1975). Stallcup and Woolfenden (1978) reported age and sex differences in the feeding rates of helpers among Florida Scrub Jays. In general, they found that males feed nestlings more often than female helpers, and that old helpers bring food more often than young helpers. Our results, while not divided by sex, confirm this trend and support the idea that some helpers are better nest attendants than others. We suggest this is because the young helpers must learn to attend nestlings.

Several authors have reported that young helpers show apparent improvement in nest building (Rowley 1974) and nestling care (Brown 1972, Woolfenden 1975). Our observations provide the first quantitative demonstration of improvement by helpers over one breeding season. As the nestling period progresses Young birds show a progressively lower rate of unsuccessful feeding attempts.

A combination of factors may be responsible for the decline in the number of unsuccessful feeding trips. Over the nestling period, Young birds may learn to identify and process food suitable for nestlings. In addition, as the nestlings grow, they can eat larger prey whole, rendering appropriate food items that would have been inappropriate earlier. Third, as the nestlings develop, their begging calls become more audible; young helpers may respond more reliably to this stimulus as it becomes stronger.

An alternative "selfish gene" explanation for the unsuccessful feeding trips of young birds has been suggested (J. Pickering, pers. comm.). The mistakes of Young birds may actually be attempts to cheat. In order to maintain flock membership all birds may have to feed nestlings. If a Young bird, who is unlikely to be a breeder, makes "mistakes" it might retain membership while investing its foraging energies in feeding itself, rather than its siblings.

This argument has two weaknesses. First, cheating is a more complex behavior than making a mistake. One might therefore expect that Young birds would have to learn to cheat. If so, one would expect Young birds to make more mistakes over time, exactly the opposite of what, in fact, one sees. Second, if making mistakes were cheating, one would expect non-breeding Intermediate birds to make mistakes as frequently as do Young birds, an expectation not borne out by observation. The data are more parsimoniously explained by the conclusion that the Young birds are learning.

We found significant differences in the rates at which Young birds in different flocks make mistakes. This may be the result of several factors. For instance, if young flocks do produce smaller clutches or fewer viable eggs, then the stimulus level for young helpers will be lower throughout the nestling period. It would follow that Young birds in young flocks would learn more slowly than Young birds in flocks with older members. Also, if Young birds learn by observing the behavior of Old birds, which seems likely (Stallcup and Woolfenden, in press; Lawton unpubl.), then the absence of

Old birds might also affect Young helpers' rates of improvement. All these factors would combine to lower reproductive success.

CONCLUSIONS

Our findings have three principal implications. First, they represent the first quantitative support of Brown's (1978) prediction that the demographic environment is a critical factor in breeding success among cooperative breeders. For Brown Jays at Monteverde, breeding success increases largely as a function of the number of Old flock members, rather than as a simple function of flock size. Because morphologically adult (Old) birds are the oldest birds in any flock, we suggest that our findings support Lack's (1968) hypothesis that experience is important to breeding success among cooperative breeders, and that young birds are less likely to breed successfully on their own.

Second, we have demonstrated age-specific differences in the behavior of nest attendants. Judged by the total number of feeding trips and the proportion of aborted feeding trips, we have shown a hierarchy in helper efficiency. Old birds are the most efficient nest attendants, followed by Intermediate, and then Young helpers. It remains to be seen whether these behavioral differences obtain in other critical areas of breeding behavior, for instance, nest-site selection and defense, and whether there exist correlations between flock composition and territory quality.

Third, we have shown improvement in nestling care by Young birds over one nestling period. To our knowledge this represents the first such demonstration and provides the first quantitative support of Lack's (1968) idea that young helpers are serving an apprenticeship. We have also shown significant differences in the rates at which Young birds in different flocks learn to care for nestlings. Further investigation into the correlation between differences in the rates of learning and the demographic environment is indicated. Long-term observation of this population should reveal whether Young birds apprenticed in flocks of differing age structure show differences in breeding success in future years.

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