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COOPERATIVE BREEDING IN THE FRUGIVOROUS TOUCAN BARBET (*SEMNORNIS RAMPHASTINUS*)

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ABSTRACT.—Cooperative breeding is rare in frugivorous birds, presumably because traits associated with frugivory do not favor permanent group living and helping behavior. We studied the Toucan Barbet (*Semnornis ramphastinus*) in southwestern Colombia to understand the possible benefits of group living and helping behavior in one of the few frugivorous birds exhibiting such behavior. Toucan Barbets lived in permanent groups, defended a territory year-round, roosted and nested in tree cavities built by themselves, and fed mostly on fruits. Toucan Barbet groups were composed of a breeding pair and their offspring; groups were significantly smaller during the breeding ($\bar{x}$ = 2.7 individuals) than during the nonbreeding season ($\bar{x}$ = 3.1 individuals). Sixty-two percent of pairs had helpers, which incubated eggs, brooded and fed nestlings, and defended nestlings against predators and cavity usurpers (mainly the Plate-billed Mountain-Toucan [*Andigena laminirostris*]). Pairs with helpers produced more fledglings ($\bar{x}$ = 1.3) than pairs without helpers ($\bar{x}$ = 0.5). We suggest that the increase in reproductive success of pairs with helpers explains why cooperative breeding is favored in this species. Furthermore, we suggest that frugivory by itself does not impede the evolution of delayed dispersal and helping behavior. *Received 23 September 1996, accepted 24 June 1997.*

COOPERATIVE BREEDING is particularly uncommon in frugivorous birds (Brown 1978, 1987). One postulated reason for the rarity of this behavior is that fruits, with their high depletion and low renewal rates, are costly to exploit and defend by groups (Brown 1982, 1987). Frugivorous birds often are seen in groups, however, and this behavior usually is linked to the exploitation of food resources rather than to breeding (McClure 1967, Leck 1971, Leighton 1982, Munn 1985, Powell 1985, Isler and Isler 1987). The question of why frugivores rarely live in permanent social units and breed cooperatively in spite of their tendency to form groups remains unanswered. We studied cooperatively breeding Toucan Barbets (*Semnornis ramphastinus*) to understand the circumstances under which delayed dispersal and helping behavior are favored in frugivores.

In cooperative breeding systems, offspring delay their dispersal (Koenig et al. 1992) and help defend their parents' territory and raise young (Brown 1974, Koenig and Pitelka 1981). Helpers seldom breed, even though they may be reproductively capable (Emlen 1978). Two sets of hypotheses have been proposed to explain such behavior. The first emphasizes the conditions that favor delayed dispersal of young (Koenig et al. 1992). The second emphasizes the conditions that favor helping by young once they remain in their parental territory and defer reproduction (Brown 1974, Emlen 1981). Food characteristics and availability of critical resources, such as roosting and nesting sites, may limit the opportunities for young to establish themselves independently and force them to remain in their parents' territory ("ecological limitation" or "extrinsic constraint" hypothesis; Emlen 1981; Koenig and Pitelka 1981; Brown 1982, 1987; Woolfenden and Fitzpatrick 1984; Ligon et al. 1988; du Plessis 1992; Komdeur et al. 1995). Alternatively, lack of skills, for example in foraging, may affect survival of young that try to establish independently and prevent them from dispersing ("skill limitation" or "intrinsic benefit" hypothesis; Alvarez 1976, Rowley 1978, Rabenold 1984, Brown 1987, Ford et al. 1988). Once young remain in their parental territory, they may help raise young as a way to increase their inclusive fitness through kin selection (Brown 1974, Ricklefs 1975, Brown and Brown 1981, Emlen and Vehrencamp 1985) or reci-

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procity (Emlen 1981, Ligon 1981, Rabenold 1984).

In this paper we: (1) examine some of the ecological factors that may favor delayed dispersal in the Toucan Barbet, (2) describe aspects of the Toucan Barbet breeding system that may explain why young that stay help, and (3) compare the Toucan Barbet with other members of the Ramphastidae to understand the evolution of cooperative breeding in this group of birds. We will show that frugivory per se does not necessarily constrain the evolution of cooperative breeding.

THE TOUCAN BARBET

Toucan Barbets are stout, medium-sized birds ($\bar{x} = 98 \pm$ SD of 15 g, $n = 8$) that occur in the mountains of southwestern Colombia and northwestern Ecuador between 1,000 and 2,400 m elevation (Hilty and Brown 1986). They are slightly sexually dimorphic, adult males having a black, glossy nuchal tuft that is absent in females (Meyer de Schauensee 1970). Toucan Barbets are well known for their duets, which are produced antiphonally by breeding pairs (Lehman 1957, Miller 1963, Restrepo and Mondragón unpubl. data). Toucan Barbets nest and roost in tree cavities that they build with their powerful beaks. Incubation lasts 15 days, and nestlings develop in 45 days (P. Shannon pers. comm., Restrepo and Mondragón unpubl. data). Fledglings resemble adults except that their plumage is dull, their irides are black instead of crimson, and their beaks lack the hook and notch characteristic of adults. Young remain in this stage for approximately two months, during which time their irides turn brown.

STUDY AREA AND METHODS

The study was carried out at the Reserva Natural La Planada, Municipality of Ricaurte, Department of Nariño, Colombia (78°00′W, 1°10′ N) between February 1987 and September 1989. La Planada is located at an elevation of 1,800 m and encompasses 3,000 ha of forest. Mean total annual precipitation is 4,900 mm, with one dry season from June to August; mean annual maximum and minimum temperatures are 25.6°C and 13.5°C, respectively (Restrepo 1990). Consequently, La Planada is classified as a transitional life zone between tropical premontane rainforest and wet forest (sensu Holdridge 1967). Our observations were concentrated in a 300-ha area in the northwestern portion of the reserve. This area is covered mostly by selectively logged forest (239 ha) with patches of second growth (26 ha) and pasture (35 ha; Restrepo 1990).

We set up a 4-km network of trails and located the trunks that were used by Toucan Barbets as roosting and/or nesting sites (Restrepo 1990). We used three different methods to record barbet activity: (1) observations along trails (2,143 h), (2) observations at active nests (1,637 h), and (3) observations at roosting sites (355 h). We walked portions of the trail network on a daily basis (ca. 18 days per month) from 0700 to 1200 and, when weather allowed, from 1400 to 1700. To detect the presence of barbets along the trails we used playback of their duets. Observation periods ran from 0630 to 1200 at active nests and began as early as 0530 and ended at 1900 at roosting sites. We located 23 Toucan Barbet groups and color-banded 30 individuals belonging to 16 groups. Barbets were captured using mist nets or traditional methods employed by hunters of these birds. The latter method allowed us to band all individuals within a group but was discarded because in some cases Toucan Barbets abandoned their roosting sites. In addition to the color bands, we used the black, glossy nuchal tuft found in males and body marks to recognize individuals attending nests during the breeding season. Two individuals were radio-tagged (Custom Telemetry and Consulting) and tracked using an LA 12 DS receiver (AVM, Inc.). We established the location of these individuals by intersecting two bearings taken from fixed points that usually were separated by 40 m (Cochram 1980).

Territorial behavior and territory characteristics.—Locations of Toucan Barbets that exhibited behaviors "in which rival intruders were excluded from a fixed area by some combination of advertisement, threat and attack" (Brown 1975) were used to define territory boundaries. Locations were plotted on a 1:2,000 map, and the most external points were joined to form the smallest possible convex polygon. We considered this to be the maximum territory size of any group (Odum and Kuenzler 1955). Territories were described by size and the types of vegetation (forest, second growth, and pastures) that they encompassed.

Trunk and cavity characteristics.—Three sets of characteristics were recorded: (1) trunk attributes (total height, diameter at breast height, species, and condition), (2) cavity attributes (cavity height from the ground), and (3) vegetation structure around trunks. Trunks were classified according to their condition into three categories: (1) snags (dead trees with a broken bole), (2) dead standing trees (dead trees with bole and limbs intact), and (3) live (trees with bole, limbs, and foliage intact). Preliminary observations indicated that Toucan Barbets were very active in an area of 0.11 ha around their nests. We used this information to sample the vegetation in a concentric area (0.28 ha, radius = 30 m) around the trunks (James 1971, Block et al. 1987). Each circular plot was divided by 20 transects rising from the trunk (radii), and six of them were chosen at random to sample the vegetation. We identified all plants >2 m tall whose crown projections were intercepted by any transect and estimated their height and diameter at breast height (dbh). For each plant we recorded the length of the crown projection and used these figures to estimate canopy cover (Canfield 1941). We derived seven variables to describe vegetation structure: (1) vegetation cover at 2 to 6.9 m, (2) vegetation cover at 7 to 11.9 m, (3) vegetation cover at 12 to 19.9 m, (4) vegetation cover at >20 m, (5) basal area, (6) *Chusquea* sp. cover, and (7) fruiting plant cover. The latter variable included only species that were used by Toucan Barbets. The cover of each vegetation stratum was estimated by adding the crown projection lengths of all plants found in the respective height categories.

We used a principal components analysis (PCA) to establish which trunk, cavity, and vegetation characteristics explained most of the variation among cavities used by Toucan Barbets as nesting sites. Data were analyzed using StatView 512+.

Diet.—We used the number of feeding records obtained along the trails and while making observations at nests to estimate the proportion of fruits and insects in the Toucan Barbet's diet per month per year. A fruit feeding record was defined as a foraging visit in which at least one fruit was ingested by a Toucan Barbet visiting one fruiting tree. An insect feeding record was defined as the capture and ingestion of a single insect. We classified fruiting plants according to growth form (trees, treelets, shrubs, and epiphytes or vines) and habitat (undisturbed, disturbed, and "unknown"). Species were assigned to the disturbed category if they were found primarily in or adjacent to treefall gaps, landslides, second growth, or forest edges. Species in undisturbed areas occurred most commonly under intact canopy.

Group characteristics.—Toucan Barbet groups were described by size and sex and age composition. To establish yearly changes in group size, we compared each group during the nonbreeding (one month before first breeding attempts occurred) and breeding (one week after first breeding attempt) seasons. We defined a breeding attempt as each clutch laid, irrespective of fate. The presence of an adult inside the nest for a prolonged period of time and its replacement by a second individual indicated that eggs were present. To establish a group's age composition, we classified individuals present during the middle of the breeding season (July) into one of three categories: (1) breeders; (2) old helpers, represented by individuals born during the previous breeding season that had fully adult plumage; and (3) young "helpers," represented by recently fledged individuals with dull-colored plumage, black irides, and beaks that were not fully developed. Breeders averaged 570 ± SD of 25 days ($n = 3$), old helpers 241 ± 50 days ($n = 6$), and young "helpers" 32 ± 13 days ($n = 6$) after fledging (Restrepo 1990).

Reproduction.—We found 28 nests at different stages of development and calculated approximate initiation dates by extrapolating based on the duration of the incubation and nestling periods (P. Shannon pers. comm., Restrepo and Mondragón unpubl. data). We expressed the contribution of an individual to nest attendance as the percentage of time spent in the nest incubating eggs and brooding nestlings or as the percentage of visits made to the nest to deliver food. We considered only those visits in which we could identify the individual, either by their color bands or sex. On average, we spent 58 h in front of each nest. Reproductive success is expressed as the number of fledglings produced per breeding attempt. We report means ± SD throughout the text.

RESULTS

Group territorial behavior.—Toucan Barbets lived in small groups that established their territories in forested areas. In the absence of any interference, groups occupied their territories year-round. Two groups remained for at least 2.5 years, one for at least 1.5 years, and two for at least 1 year. The remaining 18 groups stayed for less than one year, probably owing to loss of roosting sites and to human interference.

Upon sighting a neighboring group, Toucan Barbets rattled, shrieked, and made supplanting attacks. At the end of such encounters, mated pairs duetted. In the absence of visual contact, pairs counter-duetted after hearing neighboring pairs duetting. Duet production after group encounters and counter-duetting suggest that duets have a territorial function. Offspring, including 45-day-old young, sometimes joined duets produced by their parents. Young individuals produced harsh and out-of-tune notes. Duet production varied seasonally ($G = 127.9$, df = 11, $P < 0.001$; Fig. 1), increasing at the beginning of the year with a peak in April, and decreasing by the middle of the year when reproduction took place.

Territory characteristics.—Territories averaged 5.8 ± 1.8 ha in size (range 4.0 to 10.6 ha, $n = 12$) and included mostly mature forest (5.1 ± 1.2 ha, $n = 12$). Some territories included portions of second growth (0.5 ± 0.1 ha, $n = 2$) and pastures (2.0 ± 1.0 ha, $n = 3$). Each territory had at least one trunk in which Toucan

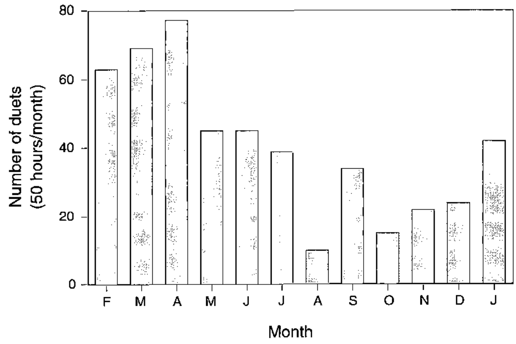

FIG. 1. Frequency of duet production by Toucan Barbets, February to December 1987 and January 1988.

TABLE 1. Correlation of principal components I and II with trunk, cavity, and vegetation variables at Toucan Barbet cavities. Vegetation variables measured within a 0.3-ha circle around each cavity. Amount of total variance explained was 29.4% (PC I) and 24.4% (PC II).

Variable	PC I	PC II
Vegetation cover at 2 to 6.9 m height	−0.67*	0.40
Vegetation cover at 7 to 11.9 m height	−0.29	0.65*
Vegetation cover at 12 to 19.9 m height	0.41	−0.07
Vegetation cover at ≥20 m height	0.54*	0.11
Basal area	0.57*	−0.06
Chusquea cover	−0.20	0.93*
Fruiting plants cover	0.55*	0.70*
Trunk height	0.79*	−0.11
Cavity height	0.71*	0.09
Trunk dbh	0.42	0.70*

*, $P < 0.05$.

Barbets excavated cavities that they used both as roosting and nesting sites.

Cavity characteristics and group size.—A total of 31 cavities was located, 23 were built in snags and 7 in dead standing trees; only one cavity was built in a dead branch of a living tree. Sixty-three percent of the trunks were in three species of the Lauraceae (two species of *Ocotea* and one species of *Nectandra*), and the remainder belonged to at least 11 other species. Trunk height and dbh were 19.0 ± 7.0 m (n = 15) and 0.38 ± 0.06 m (n = 13), respectively, and cavities were built 12.5 ± 5.9 m from the ground. Roosting sites of neighboring groups of Toucan Barbets were separated by 268 ± 96 m (n = 15).

The first two axes of the PCA explained 54% of the variation among cavities used as nesting sites (n = 27 cavities; Table 1). Cavities used by pairs without helpers were separated from those used by pairs with helpers along axis II (Fig. 2) The latter were found mostly in areas where vegetation cover at 7 to 11.9 m, cover of *Chusquea* and fruiting plants, and trunk dbh were low. In addition, most of the cavities used by pairs with helpers were found in areas where vegetation cover at 2 to 6.9 m was high (Fig. 2, Table 1). This suggests that pairs with helpers used trunks found in more open areas, such as recently created treefall gaps.

Interspecific interactions.—The presence of white-faced capuchins (*Cebus capucinus*), Neotropical dwarf squirrels (*Microsciurus* sp.), red squirrels (*Sciurus granatensis*), and Plate-billed Mountain-Toucans (*Andigena laminirostris*) around active nests elicited complex behaviors in Toucan Barbets (Table 2). First, Toucan Barbets knocked and/or pecked after they had rattled (n = 14). One member of the group would fly to the top of the trunk that contained the nest, or to a different cavity, and would knock the wood with its beak, peck at small pieces of moss, or tear and drop leaves. Second, Toucan Barbets mobbed potential predators and cavity usurpers (n = 15). After rattling, knocking, or pecking, members of the group made supplanting attacks against the intruders. Such behaviors were more frequent for pairs with helpers than for pairs alone ($\chi^2 = 6.8$, df = 1, $P < 0.01$, based on the combination of the knocking/pecking and mobbing categories in Table 2).

Plate-billed Mountain-Toucans represented a major threat. They usurped cavities built by Toucan Barbets and preyed upon their eggs and nestlings. Of 19 trunks lost during the study period, four were usurped permanently and five temporarily by Plate-billed Mountain-Toucans. One of the trunks lost temporarily was regained by barbets after they drove the toucans away. In the other four cases, Toucan Barbets returned and built a new cavity in the same trunk, breeding simultaneously with Plate-billed Mountain-Toucans.

Diet.—Of the total feeding records (n = 1,595), 73% were on fruit and 27% on insects. Once we observed Toucan Barbets feeding on flowers of *Cavendishia* sp. Fruits were important

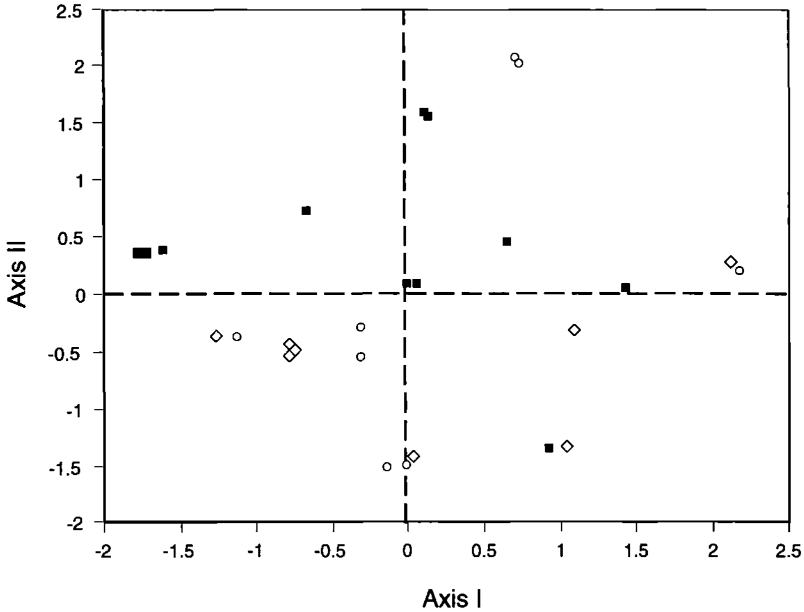

FIG. 2. Principal components ordination of 27 Toucan Barbet cavities. Cavities used by single pairs (filled squares), pairs with one helper (circles), and pairs with two helpers (diamonds). Trunk and cavity height, cover of vegetation at >20 m height, and basal area increase toward the positive side of axis I, whereas cover of vegetation at 2 to 7 m height increases toward the negative side of axis I. Cover of *Chusquea*, fruiting plants, trunk diameter at breast height, and cover of vegetation at 7 to 12 m increase toward the positive side of axis II.

during most of the year except in April (Fig. 3). Once in April 1988 and once in April 1989, we observed Toucan Barbets actively feeding on termites that flew above the canopy and settled onto leaves and branches. Toucan Barbets ingested fruits belonging to 62 plant species that were not distributed independently among the three habitats ($\chi^2 = 14.8$, df = 4, $P < 0.005$; Table 3). Tree species classified in the undisturbed and "unknown" habitat categories, and treelets and shrubs classified in the disturbed habitat category, were used more often than expected by chance.

Group characteristics.—Group size during the nonbreeding season (3.1 ± 0.9) was significantly larger than during the breeding season (2.7 ± 0.7; Wilcoxon signed-rank test, $n = 30$, $P = 0.008$). Reductions in group size started at the onset of the breeding season and continued

TABLE 2. Behavior of Toucan Barbets when potential predators and cavity usurpers were near active nests. Values are number of sightings.

Response	Pairs	Pairs with helpers
No apparent response	17	15
Rattling/knocking/pecking	4	10
Mobbing	2	13

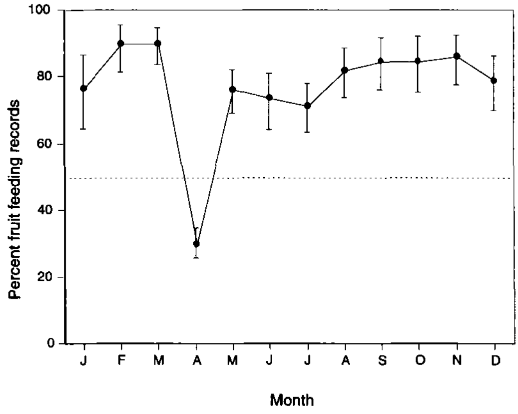

FIG. 3. Fruit component in the diet of Toucan Barbets. Points represent averages for the same month over the study period; bars are 90% confidence intervals. Changes from a fruit to an insect diet are indicated by the confidence intervals lying below the dashed line.

TABLE 3. Distribution of plant species in diet of Toucan Barbets categorized by growth form and habitat. A list of plant species consumed by Toucan Barbets is available upon request from the authors.

	Growth form		
Habitat	Trees	Treelets/ shrubs	Epiphytes/ vines
Disturbed	6	16	16
Undisturbed	7	3	1
Unknown[a]	7	1	5

[a] Includes most figs and some epiphytes that occupied a wide spectrum of habitats.

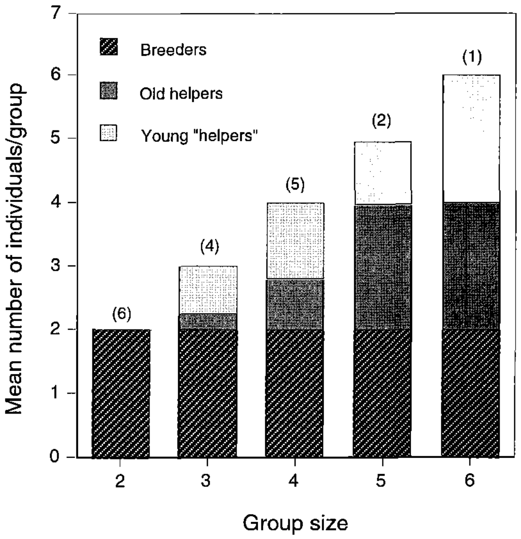

FIG. 4. Age composition of Toucan Barbet groups. Number of groups for which individuals were of known age are shown above bars.

until the first week of the nestling period when some individuals left their groups. In five occasions, individuals that left the groups were chased out by the other members before the breeding season. Chasing included supplanting attacks and shriek calls. Helpers were present in 16 breeding attempts; in 12 of these cases, the helpers were offspring that had been produced in the previous season by the breeding pair. In one breeding attempt, the helpers were the offspring of the male of the breeding pair. In the three remaining cases we could not determine the relationship between breeders and helpers. During the nonbreeding season unrelated individuals could join a mated pair. Group size increased initially by the addition of young helpers and later on by the accumulation of old helpers (Fig. 4). Nevertheless, the number of old helpers never exceeded two.

Reproduction.—Toucan Barbets had a defined breeding season that corresponded with La Planada's single dry season (Fig. 5). Compared with unaided pairs, pairs with helpers tended to lay first clutches earlier in the year (Kolmogorov-Smirnov test, $D = 0.57$, $n_1 = 9$, $n_2 = 10$, $P < 0.1$) and second clutches later in the year ($D = 1.49$, $n_1 = 7$, $n_2 = 2$, $P < 0.01$; Fig. 5).

Both males and females attended the nests. In pairs without helpers, males spent more time incubating (59 ± 15%) than females (41 ± 15%; Wilcoxon signed-rank test, $n = 9$, $P = 0.01$). Male and female contributions converged somewhat after egg hatching but males still spent more time brooding the nestlings than females (Wilcoxon signed-rank test, $n = 7$, $P = 0.05$; Table 4). The difference between males and females disappeared, however, when considering the number of feeding visits to nestlings (Wilcoxon signed-rank test, $n = 8$, $P > 0.05$). The overall contribution of males was even higher when male helpers were present (Table 4). Breeding females spent significantly less time brooding the nestlings in the presence of her mate plus two helpers (18.0 ± 1.7%, $n = 3$) than in the presence of her mate plus one helper (39.0 ± 13%, $n = 3$) or her mate and no helpers (45.0 ± 7.1%, $n = 7$; Kruskal-Wallis test, $H = 6.43$, $P < 0.05$). We found a similar trend regarding feeding visits, but the differences were not significant ($H = 5.2$, $P < 0.1$; Table 4).

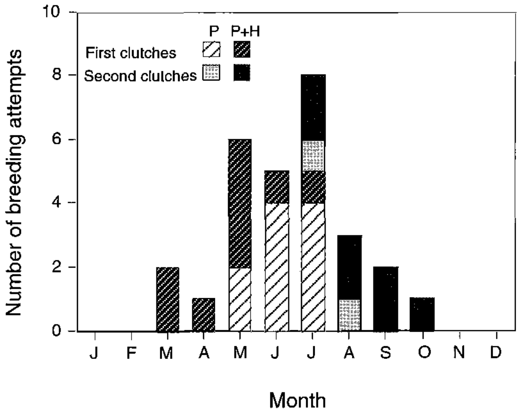

FIG. 5. Breeding season of Toucan Barbets. P = pairs without helpers; P + H = pairs with helpers.

TABLE 4. Contributions (%; $\bar{x}$ ± SD) by male and female Toucan Barbets by group size and composition. Number of breeding attempts in parentheses.

	Incubation[a]		Brooding[a]		Feeding visits[b]	
Group[c]	Male	Female	Male	Female	Male	Female
1 M, 1 F	59.2 ± 12.5 (9)	38.5 ± 13.6 (9)	55.1 ± 7.1 (7)	44.8 ± 7.1 (7)	48.7 ± 3.9 (8)	51.2 ± 3.9 (8)
2 M, 1 F	62 (1)	38 (1)	61.0 ± 13.0 (3)	39.0 ± 13.0 (3)	55.6 ± 12.6 (3)	44.3 ± 12.6 (3)
3 M, 1 F	88.0 ± 10.0 (2)	12.0 ± 10.0 (2)	82.0 ± 1.7 (3)	18.0 ± 1.7 (3)	65.6 ± 20.5 (3)	34.3 ± 20.5 (3)
2 M, 2 F	66 (1)	34 (1)	51 (1)	49 (1)	51 (1)	49 (1)
1 M, 2 F	72 (1)	28 (1)	45.0 ± 10.0 (2)	58.5 ± 4.9 (2)	48.8 ± 17.7 (3)	57.6 ± 21.4 (3)

[a] % of total time devoted to activity.
[b] % of total feeding visits.
[c] M = male, F = female.

Helpers were present in 57% of the breeding attempts (n = 28); they incubated eggs, brooded and fed nestlings, and defended nests. In four nests in which we identified helpers, they incubated eggs and brooded nestlings 43% (n = 1) and 33 ± 8% (n = 3) of the total time, respectively, and made 35 ± 16% of feeding visits (n = 4; Fig. 6). Helpers actively attended nests, but their presence did not increase attentiveness (i.e. the proportion of time eggs and nestlings were covered) or feeding visits per unit time significantly (Table 5). However, statistical power was low owing to small sample sizes, and all trends were in the expected direction of greater attentiveness with helpers.

Reproductive success.—Pairs with helpers produced significantly more fledglings per breeding attempt (1.1 ± 0.7, n = 15) than did pairs without helpers (0.5 ± 0.7, n = 13; Mann Whitney-U test, $P < 0.05$). When analyzing first and second breeding attempts separately, we found that the mean number of fledglings produced did not always increase with group size. In first breeding attempts, pairs with one helper produced significantly more fledglings per breeding attempt (1.2 ± 0.4, n = 5) than unaided pairs (0.5 ± 0.7, n = 11; Mann Whitney-U test, $P < 0.05$). However, pairs with two helpers did not produce significantly more fledglings (1.7 ± 0.6, n = 3) than did groups of three birds

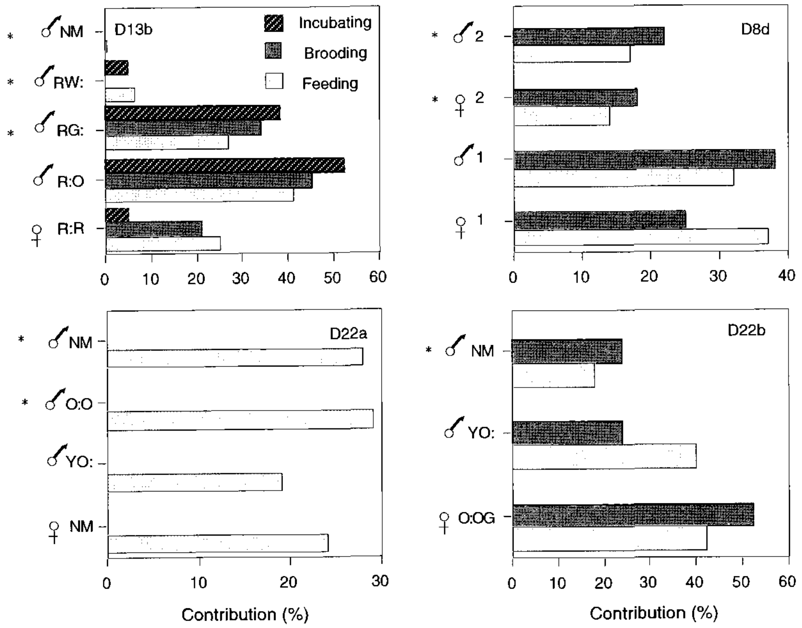

FIG. 6. Contribution of helpers at four Toucan Barbet nests. Helpers are denoted with an asterisk; other birds are breeders. Cavities were observed for 108 h (D13b), 106 h (D8d), 55 h (D22a), and 86 h (D22b).

TABLE 5. Nest attentiveness by Toucan Barbet pairs with and without helpers. Only clutches that produced one fledgling were included in analyses to eliminate clutch size as a source of variation. Values are $\bar{x} \pm$ SD, with number of breeding attempts in parentheses. In each case, differences between solo pairs and pairs with helpers were not significant.

Variable	Pairs	Pairs with helpers
Incubation (% of time)	79.7 ± 22.4 (3)	89.9 ± 1.9 (2)
Brooding (% of time)	55.5 ± 33.3 (3)	64.3 ± 3.7 (3)
Feeding visits (no. per h)	3.7 ± 1.2 (3)	4.5 ± 1.2 (4)

(Mann Whitney-U test, $P > 0.05$). In second clutches, groups of three produced on average 1.3 ± 0.6 fledglings ($n = 3$), whereas groups of two ($n = 2$) and four ($n = 3$) produced on average zero fledglings.

DISCUSSION

Toucan Barbets differ from most well-known frugivorous birds in that they are territorial, live in permanent groups, and the young help raise their parent's offspring. This challenges the idea that frugivory prevents the evolution of cooperative breeding (Brown 1987). We will discuss the Toucan Barbet's cooperative breeding system in terms of two questions that have been formulated to explain the evolution of this behavior: Why do offspring delay their dispersal, and why do offspring help? Our results suggest that frugivory does not increase the cost of group living and that helping is favored because it increases the reproductive success of breeding pairs.

DELAYED DISPERSAL

Food characteristics.—Variation in the diet of cooperative breeding birds led Brown (1982, 1987) to postulate that two characteristics of food availability, depletion and renewal rates, influence territory quality and thus the options available to dispersing individuals. According to his model, the benefits resulting from permanent defense of fruits by groups decrease due to high depletion and low renewal rates of fruits. At La Planada, Toucan Barbets seem to cope with changes in fruit abundance by exploiting a wide array of fruiting species that occur in a variety of habitats (Table 3; Restrepo 1990). Other frugivores reported to breed cooperatively (see Restrepo 1990) cope with possible changes in fruit abundance in various ways, e.g. feeding on a wide range of fruits (Skead 1950; Skutch 1954, 1958, 1961; Snow and Collins 1962; Snow 1971; Kemp 1978; Kemp and Kemp 1980; Isler and Isler 1982; Leighton 1982; Johns 1987, Short and Horne 1988; Witmer 1993), as do Toucan Barbets; ingesting other food items, such as nectar, sap, and flower petals (Hilty and Brown 1986, Kattan 1988, Winkler et al. 1995); or caching fruits (e.g. MacRoberts and MacRoberts 1976). Such responses are similar to those exhibited by generalist frugivores that do not breed cooperatively (e.g. Wheelwright et al. 1984). Moreover, among frugivorous cavity nesters, cooperative breeding occurs in species with generalist diets (Leighton 1982). Thus, frugivory by itself may not necessarily constrain the evolution of cooperative breeding because diet breadth and foraging plasticity may play a critical role. Ultimately, comparisons of cooperative and noncooperative frugivores can provide insight into what fruit characteristics may favor the cooperative defense and exploitation of fruits by groups.

Other limiting resources.—The dispersal of young and the opportunity for establishing independently may be prevented if resources other than food are limited (Koenig and Pitelka 1981). Under such circumstances, young are "forced" to remain in their parental territory and to delay their own reproduction (Brown 1969, Koenig 1981, Emlen 1982, Woolfenden and Fitzpatrick 1984, Ligon et al. 1988). Several lines of evidence suggest that trunks used by Toucan Barbets represent a limited resource that may prevent young from dispersing. First, of 31 trunks used as roosting and nesting sites, 19 were in the family Lauraceae. A plant inventory conducted in mature forest at La Planada showed that species in the Lauraceae with dbh >4 cm were not among the 10 most abundant trees (De Las Salas and Ballesteros 1986). If the abundance of snags and dead trees reflects that of living trees, then Lauraceae trunks may represent a limited resource for Toucan Barbets. Indeed, the availability of adequate substrates to build cavities often is limited for cavity-nesting birds (Nilsson 1984, Martin and Li 1992).

This idea is further supported by our observations that Toucan Barbet groups used the same trunk (but not the same cavity) multiple times, defended the trunks vigorously against Plate-billed Mountain-Toucans, nested simultaneously in the same trunk with the latter, and used the same trunks on a year-round basis. Second, the clustering of nesting cavities according to group size (Fig. 2) suggests that pairs with helpers favored cavities with certain characteristics that may have affected nesting success (Li and Martin 1991).

HELPING BEHAVIOR

One way to determine the benefits of helping is to compare the reproductive success between unaided pairs and pairs with helpers (e.g. Parry 1973, Rabenold 1984, Woolfenden and Fitzpatrick 1984). In Toucan Barbets, pairs with helpers had a two-fold increase in their reproductive success compared with unaided pairs. However, this seemed to result from the addition of a single helper. Groups of three produced the same number of fledglings as groups of four in first clutches and more fledglings than groups of either two or four in second clutches. Helper age may explain why, in second clutches, groups of four did not produce any fledglings. Three groups composed of four individuals each had one young "helper" (32 ± 13 days) that still begged for food and / or failed to chase predators. Some of these young "helpers" shared activities with an old helper. An optimal group size, represented by a breeding pair plus one old helper, seems to exist in which a maximum number of fledglings per group and per capita is produced. If this is true, then the presence of a second helper would not be advantageous for a breeding pair. This could help explain why in some instances old helpers were chased from the groups at the beginning of the breeding season, why groups remained small, and why the most common group size was three.

Breeding pairs do better with helpers, but it is unclear why this is so. Nest attentiveness did not differ between unaided pairs and pairs with helpers (Table 5). This suggests two explanations, which are not mutually exclusive, for the effect of helpers on the reproductive success of breeding pairs. First, helpers may reduce the amount of parental effort required to raise young, thereby increasing the breeders' lifetime reproductive success (Parry 1973, Brown et al. 1983, Rabenold 1984, Sydeman 1989). Toucan Barbets share with other frugivores an extended nesting period (Skead 1950, Skutch 1958, Bourne 1974, Kemp 1978). Adults devote 80 to 140 days attending the nest and fledglings, depending on whether they lay one or two clutches during each breeding season. Helpers may lessen the costs for the breeding pair, in particular for breeding females, especially when the helpers are males. Males contributed significantly more than females to incubation and brooding. Thus, the addition of male helpers may represent a substantial reduction in the female's share of parental investment. By saving energy, breeding pairs with helpers may produce successful second clutches. Second, helpers may detect and deter predators and cavity usurpers (Snow 1971, Woolfenden and Fitzpatrick 1984). Plate-billed Mountain-Toucans represent a serious threat for Toucan Barbets because they usurp cavities built by the barbets (Restrepo 1990, Beltrán 1994). Toucan Barbet pairs with helpers mobbed more frequently than did single pairs, suggesting that helpers are important in detecting and deterring intruders.

In Toucan Barbets, helping during the breeding season apparently is performed by the previous offspring of the breeding pair, and helpers do not remain for more than one breeding season. These factors determine to some extent the ways in which individuals may gain from helping and why helping has been favored. If staying and helping increases the survival of helpers and the probability of reaching the next breeding season (Restrepo 1990), then individual selection will favor such behavior. On the other hand, if Toucan Barbets have a low probability of establishing a territory and breeding successfully on their own during their first year, then helping to raise close kin may increase their inclusive fitness. During the breeding season following their birth, Toucan Barbets may: (1) disperse but not be able to breed, (2) breed but produce an average of 0.5 fledglings per breeding attempt, or (3) not disperse and help produce 1.1 fledglings per breeding attempt. In that breeding season, the greatest fitness gain will be obtained by helping (0.55), whereas breeding will represent only half that gain (0.25); not breeding and not helping will represent no gain. These estimates assume that helpers and new offspring are full siblings and that fledglings survive to reproduce. Based on these three outcomes and their underlying assumptions, we can understand why Toucan Barbets that remain in their parents' territory help raise their parents' offspring.

In summary, the presence of helpers in Toucan Barbets increases the reproductive success of breeding pairs two-fold. Two possible reasons exist: (1) deterrence of cavity competitors; and (2) reduced energy expenditure, especially for female breeders. Helpers benefit from this behavior because of an indirect gain in their fitness that probably could not be achieved otherwise during their first year. In addition, helpers gain by having access to resources that may not be abundant, or that may be exploited more efficiently by groups than by individuals.

BARBETS, TOUCANS, AND COOPERATIVE BREEDING

Among the Ramphastidae, cooperative breeding is found in two toucans (*Pteroglossus* spp.; Skutch 1958, Stiles and Skutch 1989) but apparently is absent in the remaining Neotropical barbets (Hilty and Brown 1986, Stiles and Skutch 1989), including the Prong-billed Barbet (*Semnornis frantzii*; Skutch 1944). Among the African barbets (family Lybiidae), cooperative breeding is found in at least 14 species belonging to five genera (Short and Horne 1988). Recent studies indicate that: (1) Neotropical barbets (Capitoninae) and toucans (Ramphastinae) are more closely related to each other than either is to the African barbets (Lybiidae) or the Asian barbets (Megalaimidae); (2) that as a group, they are more closely related to African than to Asian barbets; (3) and that *Semnornis* gave origin to the toucans (Burton 1984, Prum 1988, Sibley and Ahlquist 1990, Lanyon and Hall 1994). Based on this, two hypotheses can be postulated about the origin of cooperative breeding in the Toucan Barbet. First, cooperative breeding is an ancestral trait that has been retained by at least three groups of birds during the evolution of the barbet-toucan lineage. Second, cooperative breeding is a trait that has evolved independently at least three times during the evolution of the barbet-toucan lineage. The occurrence of cooperative breeding among ancestral species in the Capitoninae (*Semnornis*) and the Ramphastinae (*Pteroglossus*) supports the first hypothesis and raises the question of why this behavior has been lost through the evolution of the Ramphastidae.

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