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INEQUITIES IN PARENTAL EFFORT AND COSTS OF COMMUNAL BREEDING IN THE GUIRA CUCKOO

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Abstract. I examined reproductive behavior and the parental roles of group members in the communal Guira Cuckoo (*Guira guira*) in central Brazil. Feeding of chicks was observed at seven focal nests and censuses were conducted on active nests in 886 breeding attempts. Adults in five focal groups did not share equally in the feeding of chicks or in nest attendance. Chicks in smaller broods tended to receive more nearly equal amounts of food, whereas a few chicks in large broods received disproportionately large shares. Most food was offered to chicks in a random manner, but some adults (6 of 33) fed particular chicks more frequently than expected by chance. Nestlings had a high mortality rate during the first week after hatching. Circumstantial evidence suggests that infanticide may be one important source of mortality in this population. Infanticide is hypothesized to function adaptively as a means by which nonbreeding group members sabotage a breeding cycle. Such truncation may result in a shorter interval between attempts, thus providing nonbreeders with a new reproductive opportunity. *Accepted 21 June 1994.*

Key words: Guira guira, *Cuculidae, communal breeding, cooperative breeding, kin recognition, Brazil.*

INTRODUCTION

Hypothesized benefits of living and breeding in groups include improved foraging, predator detection, territorial defense, and care of offspring (Alexander 1974; Brown 1978, 1987; Gaston 1978). For several species, sociality is also a natural context for the evolution of kin recognition, cooperation and discriminative nepotism (Sherman 1981, Hoogland 1983, Holmes 1984, Waldman 1988).

In cooperative breeding, where one pair of reproductive adults is assisted in caring for nestlings by nonbreeding individuals, many of these advantages have been confirmed. For example, nonbreeding group members may gain indirect fitness (Brown & Brown 1981), because they are usually related genetically to the chicks they help raise (Hamilton 1964, 1972; Brown 1974, 1980, 1983; West-Eberhard 1975; Rabenold 1985).

In communal breeding (as defined by Koenig & Pitelka 1981), several pairs share a single nest. Adult group members are not necessarily related, and within-group competition may occur (Vehrencamp 1983).

The competitive nature of communal reproduction has been documented for many species. These include: the Pukeko, *Porphyrula martinica* (Craig 1980); the Groove-billed and Smooth-billed Anis, *Crotophaga sulcirostris* and *C. ani*, respectively (Vehrencamp 1977, 1978; Loflin 1983; Vehrencamp *et al.* 1986, 1988); and the Acorn Woodpecker, *Melanerpes formicivorus* (Koenig & Mumme 1987).

One facet of reproductive competition, infanticide, occurs in various social mammals (Hrdy & Hausfater 1984). Documentation of infanticide in birds has been meager; however, it may be more widespread than previously believed (Stephens 1982, Crook & Shields 1985, Freed 1986, Fujioka 1986, Goldstein *et al.* 1986, Robertson & Stutchbury 1988, Emlen *et al.* 1989), and may take the form of brood reduction resulting from scramble competition or sibling aggression (siblicide), parental desertion of individuals or whole broods, or filial infanticide (*i. e.*, outright killing of certain young by parents; Hrdy & Hausfater 1984).

The social system of the Guira Cuckoo (*Guira guira*) provides an opportunity for examining several of the above issues. The Guira Cuckoo inhabits extensive areas in the savanna regions of south America (Sick 1984). This relatively unknown species has a complex social system in which groups of up to 13 birds share a single nest, with communal clutches of as

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many as 20 eggs. Egg tossing by group members is a prominent feature of reproduction in the Guira Cuckoo, and appears rather similar to that of the Groove-billed (*Crotophaga sulcirostris*) and Smooth-billed (*C. ani*) Anis (Vehrencamp 1977, 1978; Loflin 1983, Antas & Cavalcanti 1988, Cavalcanti *et al.* 1991).

The objectives of this research were threefold: (1) to describe parental care patterns in communal broods; (2) to assess the impact of group-living on the survival of chicks; and (3) to investigate the potential for parent-offspring recognition (through preferential treatment of young) in the context of a communal brood, where spatial or associational cues of relatedness (Holmes 1984, Sherman & Holmes 1985) are presumably lacking.

METHODS

Study site and population

The study was conducted in the central Brazilian savanna region, near Brasilia (15° 47' S, 47° 56' W; altitude = 1158 m), in 3000 ha of semi-urban habitat. The study monitored breeding from July 1987 to January 1988, August to November 1988, and July to October 1990. During these months, groups in the study area attempted breeding a total of 86 times. In 1987, the study population included at least 173 birds; in 1988, 125 birds; and in 1990, 130 birds (Macedo 1992).

At the start of each field season two nestlings were captured and hand-reared. They were used as lures to capture other individuals for color banding. A total of 91 adults and 65 nestlings were captured and banded over the three seasons.

Censuses on actively-breeding groups were conducted daily to collect data on egg laying, egg losses, group size, incubation, and hatching (details in Macedo 1991). Egg and chick disappearances were recorded during these visits.

Nest attendance

In 1987 I noticed that, after chicks hatched, it was common for one adult to perch on a tree near the nesting tree, in contrast to the usual absence of adults near the nest during laying. This perching behavior is hereafter labeled "nest-attendance". In 1988 I quantified nest-attendance during 67 h of observation at one nest (A3.1), and in 1990 during 63 h at another (Nest A7.1). Both of these groups consisted of six adults; in the first group, all six were individually recognizable, while in the latter group, five were banded.

After feeding a chick, adults had several alternatives: (1) to remain on the nesting tree; (2) to perch within 10 m of the nesting tree; (3) to travel >10 m from the nesting tree but remain within sight; or (4) to fly out of sight. Only the second option was quantified as attendance behavior because it excluded other possible activies, such as interactions with nestlings or nest maintenance activities while on the nesting tree, foraging within sight of the nesting tree, or other activities that could not be monitored when the bird flew out of sight.

Chick feeding

Data concerning the feeding of chicks were obtained from seven broods. The feeding of nestlings was observed from a blind atop a 6-m scaffold, roughly 10 m from the nest. Each group was observed for 3 to 5 h daily, usually starting immediately after hatching, until the chicks fledged (at 12 to 18 days). Observation times were as follows: Nest B1.1, 26 h; Nest C6.1, 33 h; Nest B4.1, 8 h; Nest D1.2, 27 h; Nest A3.1, 67 h; Nest D5.1, 77 h; Nest A7.1, 63 h.

During 1987, observations were scheduled for various periods of the day to evaluate possible time-related variations in feeding rate and relative contributions by individual adults (nests B4.1, B1.1, C6.1, D1.2). The objective was to determine whether adults, in general, tended to concentrate their feedings to chicks at a certain time period during the day. Although 3 of the 4 nests showed a variation in feeding frequency (significant *G* in total feedings), there was no overall pattern, each nest showing peaks of frequency at different times (Macedo 1991). Because no consistent and general pattern could be established for time-related variation in feeding, observations in 1988 were conducted generally during the afternoons, and in 1990, in the mornings.

Not all adults at each nest were color-banded; therefore, some analyses concern only those adults individually marked. It is probable that the majority of adults banded over the three study seasons were males. DNA fingerprinting was done only in 1988, and of the 41 adults caught in that year, only three turned out to be females (Quinn *et al.* 1994).

Upon hatching, all chicks were differentially dye-marked to allow identification until color bands could be applied. During observations, records were maintained on all feeding trips to the nest by group members. For each feeding trip, the identities of the adult bringing food and of the chick fed were recorded when those were known.

In three nests, food items were identified in a general manner and classified by size relative to the adult's bill length from measurements of the feather roots at the base to the tip (average bill length = 30.8 mm, SD = 2.47, n = 36). Food items were classified as multiples of bill length: (1) items smaller than one bill length (<31 mm); (2) 1 to 2 bill lengths (ca. 31 to 62 mm); (3) 2 to 3 bill lengths (ca. 62 to 92 mm); (4) 3 to 4 bill lengths (ca. 92 to 123 mm); and (5) 4 or more bill lengths (>123 mm).

RESULTS

A total of 2396 feeding trips by adults was recorded. Of these, 49 % (n = 1174) were cases where both adult and chick could be identified.

All chicks in a clutch usually hatched on the same day (75 % of 28 clutches), although hatching spans of one to four days sometimes occurred (Macedo 1992). During the first few days after hatching, chicks remained in the nest during feedings. They became ambulatory at about five days of age, and scrambled toward any adult landing on the tree, and vied for the food item. Because food items were swallowed whole, only one chick was fed per feeding trip. All chicks left the nest together, usually around the 15th day after hatching (average = 15.1 days, SD = 2.2, n = 13). They were fed by the parents for at least three weeks after fledging.

Food types and sizes

Food items brought to the chicks consisted mostly of invertebrates, with a few small vertebrates. Of 485 food items brought to three focal nests, 90.3% were invertebrates (large orthopterans mainly), 6.8% lizards, 2.3% toads, 0.4% snakes, and 0.2% unidentified. The proportions of 363 delivered food items in each of the five bill-length size categories were as follows: category (1) 71.7%; (2) 20.4%; (3) 4.2%; (4) 3.2%; and (5) 0.6%.

Chick food intake

Total food intake of broods among the six smaller groups (five having six members, one having five members) and one larger group of nine adults was compared in terms of the number of feeding trips by all adult group members per hour of observation per chick. Food item size was not a consideration in this analysis. Results indicated that individual marked adults in the smaller groups fed broods at the same rate ($\bar{x}$ = 2.52, SD = 1.02, n = 6) as did those in the larger group (x = 1.50 for the single observation; t = –0.93, P >0.40, df = 5; see Sokal & Rohlf 1981: comparison of a single observation with mean of a sample). Since food-delivery rates were corrected for brood size, this result suggests that, on a per-capita basis, broods of larger and smaller groups received approximately the same numbers of food items.

Adult food-delivery rates

In 5 of 7 groups adults differed significantly in how frequently they fed nestlings (Fig. 1). In Nest A3.1, for example, adults 4 and 6 each brought only one food item to nestlings out of 438 total feedings observed. Similarly, in Nest A7.1, adult 3 brought only five food items in a total of 478. In Nest B4.1 and Nest D1.2, group members shared the workload evenly.

In the two nests where food size and adult identify were known for a large number of feedings, the proportion of items in each size category was approximately the same for all adults (Macedo 1991). Only one adult, from Nest C6.1, differed significantly from others in bringing a greater proportion of food items in the largest size categories, 3—5 (G = 14.94, P <0.01, df = 3).

In nests with 2 offspring, there was no significant difference in the number of meals received by the two chicks (Nest B1.1: G = 0.39, P = 00.54, df = 1; Nest B4.1: G = 0.25, P = 0.62, df = 1; Nest C6.1: G = 0.36, P = 0.55, df = 1). However, in the four nests with larger numbers of chicks, the food was distributed unevenly (Nest D1.2, 4 chicks: G = 28.26, P <0.01, df = 3; Nest A3.1, 4 chicks: G = 14.52, P <0.01, df = 3; Nest A7.1, 5 chicks: G = 9.98, P = 0.04, df = 4; Nest D5.1, 6 chicks: G = 11.95, P = 0.04, df = 5).

The null hypothesis with respect to discrimination of young was that adults feed nestlings

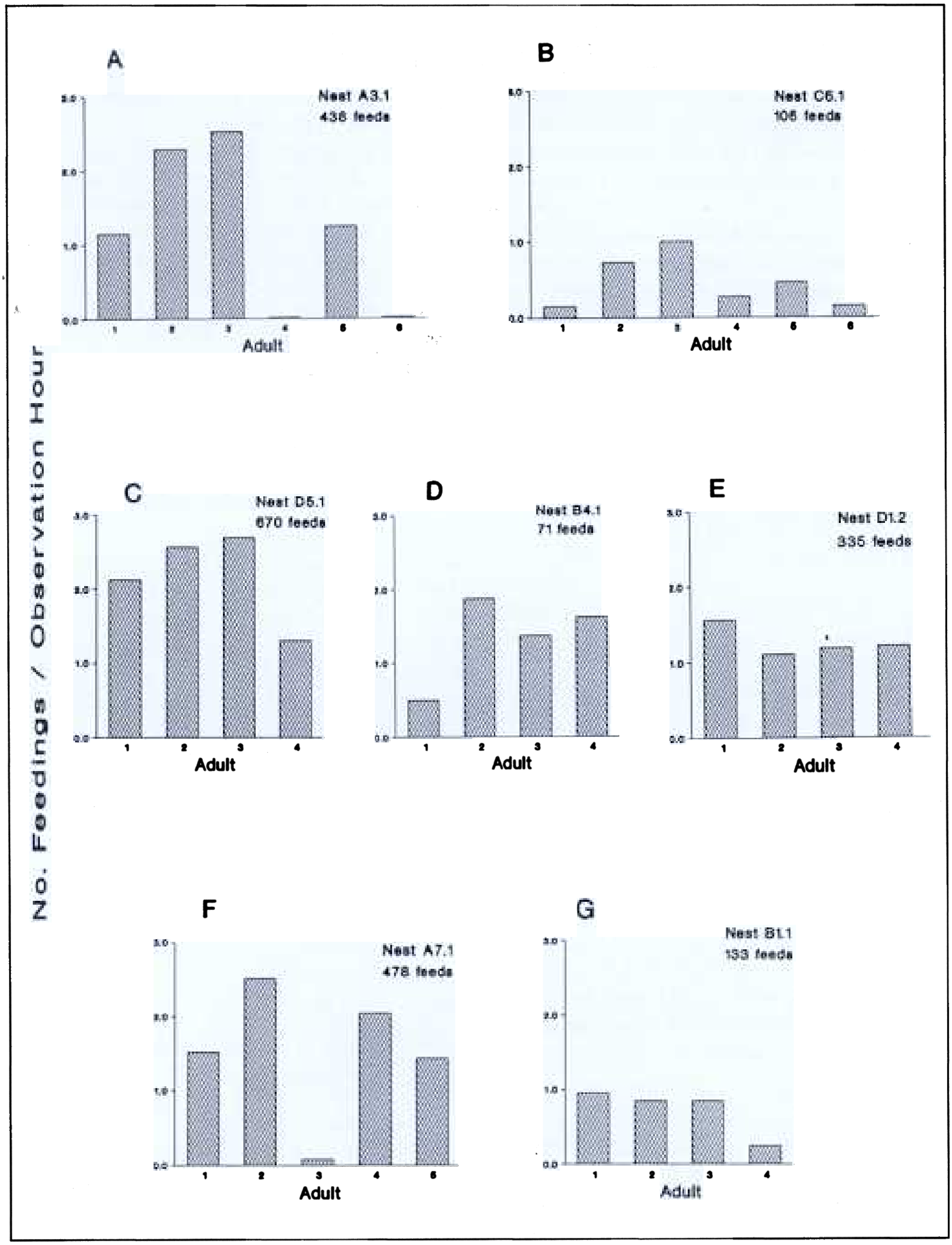

FIG. 1. Overall feeding contributions (number of feedings per hour of observation) by marked individuals in seven nests (adult numbering consistent in all figures). Heterogeneity in food delivery significant in five nests and close to significant in one nest (Nest A3.1, $G = 384.5$, $P < 0.01$, df = 5; Nest C6.1, $G = 32.5$, $P < 0.01$, df = 5; Nest D5.1, $G = 46.2$, $P < 0.01$, df = 3; Nest B4.1, $G = 7.5$, $P = 0.06$, df = 3; Nest D1.2, $G = 2.38$, $P = 0.50$, df = 3; Nest A7.1, $G = 196.5$, $P < 0.01$, df = 4; Nest B1.1, $G = 10.4$, $P < 0.05$, df = 3).

randomly. Deviations from a random pattern of feeding would lead to a rejection of discriminant feeding. Results of G-tests (Sokal & Rohlf 1981) on chick-feeding differences for each adult are presented in Table 1. Four nests had at least one adult feeding chicks nonrandomly, which resulted in significant heterogeneity in the feeding patterns at these nests. In the other three nests (C6.1, B4.1, and D5.1), none of the adults showed preferential treatment of the young, and the heterogeneity G for each of these nests was nonsignificant. Overall, of the 33 marked adults observed in these nests, 6 deviated from the random pattern predicted by the null hypothesis.

Nest-attendance behavior

In 1987 I noticed that individual participation in attendance was highly variable. In 1988 and 1990 I monitored the amount of time adults at two focal nests spent attending the nest. I tested the fit of the observed distribution of individual attendance times (Fig. 2) to an expected distribution of equal frequencies using the Kolmogorov-Smirnov test for goodness of fit. The observed distribution deviates significantly from the uniform frequency distribution in both nests (Nest A3.1: $D_{\max} = 0.50$, $n = 6$, $P < 0.01$; Nest A7.1: $D_{\max} = 0.40$, $n = 5$, $P < 0.01$). In Nest A3.1 four adults were responsible for almost all nest attendance. In contrast, adult 4 spent a negligible fraction of time attending the nest, while adult 6 never was observed perched near the nest. Birds that attended the nest for more total time also attended more frequently, and stayed longer (on average) during each attendance episode. The average times per attendance episode were significantly different among the four adults that attended the nest more than once (ANOVA: $F = 5.72$, $P < 0.002$; Fig. 2). In Nest A7.1, adults 1, 2, and 4 were mostly responsible for nest attendance, while adults 3 and 5 spent only a small fraction of time perched near the nest. The two birds (adults 1 and 2) with the highest total times in attendance had the highest numbers of attendance episodes. At this nest, the average times spent per attendance episode by adults were not significantly different (ANOVA: $F = 2.35$, $P = 0.0563$; Fig. 2). At both nests, individuals that had very low feeding rates also participated infrequently in nest attendance.

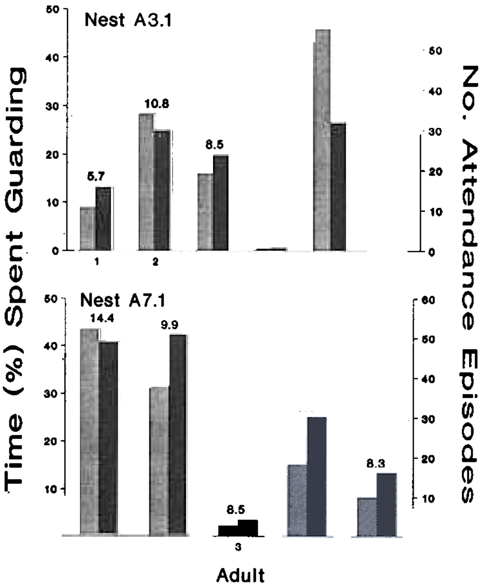

FIG. 2. Percent of time in attendance indicated by cross-hatched bars (100 x individual's time as attendant / group's total attendance time) and number of attendance episodes indicated by solid bars, for marked adults at Nests A3.1 and A7.1 (adult numbering consistent in all figures). Average number of minutes per attendance episode shown above bars (asterisks indicate that no means could be computed). Nest attended by group members for approximately 21 of 71 h at Nest A3.1, and 27 of 63 h at Nest A7.1 during observation periods.

Social conflict

Group members employ several apparently "uncooperative" behavioral tactics, such as egg tossing, that may be initiated as soon as laying starts (Table 2 and Macedo 1992). On four occasions I observed group members from four nests tossing a total of 12 eggs and, on seven other occasions, carrying eggs 10 m or more before dropping them (Macedo 1992).

Based on data from censuses, clutch size was positively correlated with group size, as was the number of lost eggs (Macedo 1992). The "hatchability" (no. eggs hatching/no. surviving until the end of incubation; Koenig 1982) for different group-size classes was unequal ($G = 16.37$, $P < 0.01$, df = 3; Table 3), but no pattern was found with relation to group-size class. Although larger broods fledged more chicks, there was no

TABLE 1. Adult Guira Cuckoo feeding frequencies relative to chicks in each nest (only feedings involving identified adult and chick are included). Significant probability levels (*P*) indicate deviation from expected pattern of random chick feeding (*G*-test).

Adult	Total no. feedings	G	P	DF
	Nest D1.2 (no. chicks = 4)			
1	21	10.3	*	3
2	13	15.5	**	3
3	17	3.5	NS	3
4	18	13.0	*	3
		Pooled G = 24.2, P <0.01, df = 3		
		Heterogeneity G = 42.3, P <0.01, df = 9		
	Nest B1.1 (no. chicks = 2)			
	6	0.7	NS	3
	4	0.0	NS	3
	9	12.5	**	3
4	5	0.2	NS	3
		Pooled = 1.5, P = 0.22, df = 1		
		Heterogeneity G = 13.4, P <0.01, df = 3		
	Nest C6.1 (no. chicks = 2)			
	6	0.7	NS	5
2	3	0.3	NS	5
3	5	1.9	NS	5
4	2	2.8	NS	5
5	12	1.4	NS	5
6	4	1.1	NS	5
		Pooled G = 0.1, P = 0.72, df = 1		
		Heterogeneity G = 8.1, P = 0.15, df = 5		
	Nest B4.1 (no. chicks = 2)			
1	12	1.4	NS	3
2	12	1.4	NS	3
3	10	1.7	NS	3
4	4	0.0	NS	3
		Pooled G = 0.4, P = 0.52, df = 1		
		Heterogeneity G = 4.4, P = 0.22, DF = 3		
	Nest A3.1 (no. chicks = 4)			
	39	1.4	NS	5
	103	1.7	NS	5
3	76	15.5	**	5
4	2	5.6	NS	5
5	41	3.3	NS	5
	2	5.6	NS	5
		Pooled G = 14.9, P <0.01, df = 3		
		Heterogeneity G = 33.0, P <0.01, df = 15		
	Nest D5.1 (no. chicks = 6)			
	113	6.9	NS	5
	148	5.2	NS	5
	144	3.8	NS	5
	70	4.1	NS	5
		Pooled G = 9.5, P = 0.09, df = 5		
		Heterogeneity G = 20.0, P = 0.15, df = 15		
	Nest A7.1 (no. chicks = 5)			
	62	3.8	NS	4
	108	4.6	NS	4
	3	5.8	NS	4
	88	21.5	**	4
	55	4.3	NS	4
		Pooled G = 13.4, P <0.05, df = 4		
		Heterogeneity G = 40.1, P <0.01, df = 16		

* P <0.05, ** P <0.01, NS P >0.05.

TABLE 2. Nest histories for seven focal nests. Clutch sizes include all eggs laid and, because of egg losses, none of the groups incubated all eggs. All lost eggs were found on the ground, except as noted. In Nest C6.1, nestlings disappeared within 6 days of hatching (one was found on the ground during pipping). In Nest D1.2, a nestling was carried away from nest by an adult on seventh day post-hatching.

Nest	Group size /no. marked	Clutch size	Lost eggs	Hatched eggs	Chicks disappeared	Fledged chicks
B1.1	6/4				0	
C6.1	9/6				7	
D1.2	6/4				2	
B4.1	6/4				0	
A3.1	6/6				0	
A7.1	6/5				4	
D5.1	5/4				0	

[a] Three of the four eggs disappeared.
[b] One of the three eggs disappeared.

significant correlation overall between group size and number of chicks fledging (Macedo 1992).

In four nests (C.1.2, C6.1, B4.1, C3.1), one or two eggs were lost just prior to hatching. In Nest C1.2, three marked adult group members were seen interacting aggressively around the nest when a pipping egg fell to the ground. The remaining nestlings in this particular nest started hatching the following day. In Nest B4.1, one egg was found on the ground below the nest, and another about 10 m from the nest, two days before chicks started hatching. Both eggs contained fully developed embryos. A pipping egg was found on the ground below each of the other two nests (C6.1 and C3.1) just before the hatching of the remaining eggs.

Chick mortality was classified in one of three categories. In those nests where all nestlings disappeared and the nest itself showed signs of disturbance (smashed eggs, broken twigs, leaf-lining in disarray), predation was designated as the probable cause of mortality. However, where no signs of disturbance were seen and nestling disappearances spanned several days, losses were classified simply as partial or complete brood losses (Table 4).

Over the three seasons, egg predation was obvious on only five occasions (5.8 % of the 86 nesting attempts), where the nest and contents were extensively damaged. Predation on nestlings was evident only once where, similarly, the nest and unhatched eggs were left in a disturbed state, and both nestlings disappeared (nest C10.1). In all remaining cases, chicks in the same brood disappeared over a prolonged period, and no damage to nests was observed. These chick deaths may have been due to predation (*e.g.*, avian and snake predators do not necessarily leave any evidence), infanticide, starvation, disease, or other agents.

Nestling mortality lacking obvious signs of terrestrial predation (designated partial or complete brood loss) took place in approximately 71 % of the 34 nests where I knew both hatching dates and dates of nestling disappearance. Partial brood losses occurred in 47 % of all nests, wherein some nestlings disappeared in a sequential manner, while other nestmates survived to fledge (Table 4). Complete brood loss, when all chicks died, involved fewer nests (24 %), but resulted in a similar total number of individual deaths (22 %) as partial brood loss.

TABLE 3. Egg hatchability according to group size for Guira Cuckoos.

Group size	No. nests	Eggs surviving to end of incubation	Eggs hatching	Percentage hatching
		10		40.0
		84		82.1
		106		63.2
		30		73.3

TABLE 4. Mortality for Guira Cuckoo chicks and nests. In this sample, 164 nestlings hatched in 34 nests.

Type of mortality	No. nestlings (% of total)	No. nests (% of total)
	2 (1.2)	1 (2.9)
	41 (25.0)	16 (47.1)
	36 (22.0)	8 (23.5)

[a] Losses where damaged nests indicated predation as the cause of mortality.
[b] Losses where no evidence indicated predation as the cause of mortality.

In all cases where partial brood loss occurred, nestlings disappeared within the first week after hatching (Table 5). Average mortality in these nests was 40 %.

Detailed case histories were obtained for seven nests where complete brood loss occurred. In five of these seven nests, some chicks were found dead on the ground or inside the nest; these had superficial abdominal wounds or were severely mangled. Chick disappearances ranged from one to seven offspring in each nest.

The lengthy rainy season in central Brazil enabled groups to attempt breeding more than once. Renesting attempts within the same season were observed 18 times during 68 group-years. For 14 of these groups, at least two members were banded during the first breeding attempt, and were seen during subsequent nestings in the same nesting site. Of these renesting attempts, six followed successful breedings, where groups had fledged some young. The average interval from one nesting attempt to the next (*i.e.*, between the first laying dates of successive cycles) was 65.7 days. In contrast, for the other 10 renesting attempts (*i.e.*, those following unsuccessful breeding efforts) the average interval before renesting was only 34.9 days. The two samples differ significantly in their distributions, with successful groups waiting for longer intervals before renesting (Mann-Whitney 2-sample: $U = 47.5$, $P < 0.05$).

DISCUSSION

Group size has been found to be correlated with the number of young that fledge in many cooperatively breeding species, where a pair of birds produces young and rears them with the assistance of one or more helpers. Among these are: Bicolored Wrens (*Campylorhynchus griseus*; Austad & Rabenold 1985), Stripe-backed Wrens

TABLE 5. Number and percent of nestlings that disappeared from 16 nests suffering partial brood loss, which occurred in 47.1 % (n = 34) of censused nests for which chick hatching and disappearing dates were known.

Nest	Group size	Chicks		Hatching time[a]	Percent mortality
		Hatched	Disappeared		
A2.1	5			1	75.0
C7.1	9			2	33.3
C1.2	6			1	50.0
C6.1	9			3	77.8
B1.2	5			1	25.0
D1.2	6			1	16.7
C2.1	6			1	33.3
C3.1	9			2	25.0
E2.1	9			—[b]	62.5
E4.1	13			1	40.0
A7.1	6			1	44.4
C13.1	—[b]			1	50.0
C10.2	5			1	33.3
B8.2	12			1	16.7
B1.1	8			1	42.9
A3.1	7			2	16.7

[a] Number of days over which hatching occurred.
[b] Unknown value.

(*C. nuchalis*; Rabenold 1985), Purple Gallinules (*Porphyrula martinica*; Hunter 1985), Superb Blue Wrens (*Malurus cyaneus*; Rowley 1965), Tasmanian Native Hens (*Tribonyx mortierii*; Ridpath 1972), and Florida Scrub Jays (*Aphelocoma ultramarina*; Woolfenden 1975, Woolfenden & Fitzpatrick 1984), among others (see Brown 1987).

When more than one female contributes eggs to the nest, however, the advantages of cooperation are less evident. Because birds in the group may or may not be related, individual interests may diverge.

For the Guira Cuckoo, group breeding involves conflict as well as cooperation. At least some individuals contribute to partial destruction of the communal clutch by tossing eggs. However, hatchability was not adversely affected by increasing group size.

Chick feeding was examined primarily to explore possible advantages associated with belonging to a larger group, whether through a reduced adult work load or more food being given per chick. This comparison revealed that a larger group did not yield an advantage of increased food per nestling. Adults in the larger group fed chicks at the same rate, on average, as adults in any of the smaller groups. Loflin (1983) found that food-delivery rates for Smooth-billed Anis were also independent of group size. He concluded that individual adults in larger groups either decreased the number of feeding trips or that some individuals participated little in caring for nestlings.

Skewed parental care was one of the patterns documented during the feeding of chicks. Substantial heterogeneity in feeding effort among adults was found in five of seven nests. This unequal sharing of parental duties also has been documented for two ani species. In the Groove-billed Ani, incubation duty and the amount of chick feeding performed by individuals are status-related (Vehrencamp 1976). Males invest in proportion to the number of eggs they probably fertilized; for females, effort is positively correlated with the number of eggs laid.

The inequalities in caring for chicks apparently extend to areas other than adult feeding effort. Group members may have increased chick survival by consistently attending the nest after chicks hatched. Group members apparently take turns perching close to the nest, and could be acting as "nest sentinels" (Macedo 1992). In two focal nests for which individual attendance time was recorded (A3.1 and A7.1), some adults spent little, if any, time perched within 10 m of the nest. It is clear from the data on these nests that the same adults invested little in caring for chicks, both in chick-feeding effort and in time attending the nest.

There was an inequality in food distribution among chicks in larger broods, as compared with those in smaller ones, where chicks received approximately equal shares. It may be advantageous for some chicks to have fewer nestmates. Because chicks compete for food, a large number of nestlings could result in smaller chicks being left out of the food distribution process.

The feeding data do not show evidence for preferential treatment of young by most adults. Although some adults deviated from random in their distribution of food to the brood, these were in the minority (18.2 % of 33 adults). The exclusion of one chick from feeding by adults could reflect that chick's poor competitive ability in obtaining food, rather than active discrimination by adults. However, six adults did deviate from a random feeding pattern, and there was no obvious explanation for this behavior. Falsification of the preferential-treatment hypothesis would require larger samples of nests and feedings per nest. What was evident in most nests was the relative lack of participation of some adults during feeding of chicks and, in two nests, during nest attendance (Nests A3.1 and A7.1).

Vehrencamp's (1983) game-theory model for cooperative breeding systems predicts that opposing forces of within-group conflict and competition eventually will produce stability, an optimum group size, as well as degree of skew in personal fitness that each group member will tolerate. In Guira Cuckoos, individual group members engage in several forms of uncooperative behavior (*e. g.*, egg tossing, possible infanticide, heterogeneity in chick-feeding effort and nest-guarding), while still retaining their status within the group.

In most instances of partial or complete brood loss in this population, chicks disappeared or were found dead within a week of hatching. Potential causes for this mortality could include predation, starvation, disease, infanticide, or accidental deaths. Starvation is an unlikely explanation for most of the observed chick mortality because chicks disappeared shortly after hatching, when energetic demands are low.

Because infanticide is commonly an event of short duration (Hausfater & Hrdy 1984), direct observations are rare. The presence of dead and mutilated nestlings on the ground or inside nests in five nests where complete brood loss occurred suggest infanticide. Although the evidence is largely circumstantial, details concerning complete brood loss and observations of egg-tossing during various stages of reproduction indicate that adults may often perform infanticide, perhaps largely accounting for the high mortality of newly-hatched Guira Cuckoos.

The possible function(s) of such infanticide remains unclear, and conclusions would be premature at this stage. I can, however, comment on the circumstances where infanticide could be beneficial to certain members of Guira Cuckoo groups. Participation in feeding and "guarding" of chicks is not uniform for all groups members. Some adults may participate little, or not at all, in caring for chicks. In Nest A3.1, both behavioral and genetic data were available (Quinn *et al.* 1994), showing that the two adults apparently related to some of the nestlings participated in parental duties, such as feeding the chicks and attending the nest. In contrast, the adult probably unrelated to any of the young participated very little in the feeding of young (0.01 % of all feedings) or in nest attendance (0.05 % of total attendance time). The DNA fingerprint data (Quinn *et al.* 1994) also suggest that some adult group members are closely related, while others are not. This produces marked degrees of asymmetries in relatedness between adults and nestlings, and among nestmates (which may be siblings, half-siblings, or unrelated). It would be of considerable interest to determine whether the adults with low relatedness to nestlings are the ones responsible for most egg tossing and/or infanticide.

Egg losses may result in nest desertion, leading to group-size changes before renesting attempts. Renestings may afford a new reproductive chance for nonbreeding individuals, esspecially if new birds join the group. Infanticide leading to nest failure might also result in a shorter time interval before renesting by the group takes place. Multi-generational data are needed to substantiate any one of these alternative explanations.

I found no increase in per-capita breeding success with larger group size (Macedo 1992), and no apparent advantage in the feeding of nestlings associated with group size in the Guira Cuckoos' communal breeding system. It remains to be shown what the long-term reproductive benefits might be for group members employing different behavioral tactics during nesting and feeding of chicks.

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