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When birds go bad: circumstantial evidence for infanticide in the communal South-American Guira Cuckoo

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The Guira Cuckoo (*Guira guira*) is a communal breeder (joint-nester) that experiences high rates of egg loss due to tossing behaviour of individuals in the group, as well as exceptionally high mortality among nestlings. Here, we report events leading to the complete loss of broods in nine nests, resulting in the death of 48 nestlings. Circumstantial evidence surrounding each episode is suggestive of infanticidal behaviour by adult group members. No evidence of predation was noted, and the occurrence of dead nestlings in the nest, or on the ground, suggests that group members may adopt infanticide as a reproductive tactic. Many groups renest at least twice during the extended rainy season, with renestings observed 18 times during 68 group-years. Hence, individuals may have repeated opportunities for breeding successfully. We predict that infanticidal behaviour should be executed by those individuals excluded from reproduction within their groups. A new nesting episode, initiated within a shorter time interval, would presumably benefit the excluded individual(s) by providing a new breeding opportunity. Direct evidence is needed to verify the infanticide hypothesis.

KEY WORDS: infanticide, parental effort, Guira Cuckoo, *Guira guira*, communal breeding, Brazil.

INTRODUCTION

The conventional definition of infanticide is any "behaviour that makes a direct and significant contribution to the immediate death of an embryo or newly hatched (or born) member of the performer's own species" (MOCK 1984). Infanti-

cide has been widely documented since the late 1970's, for species in natural conditions (Hrdy 1979). Hrdy & Hausfater (1984) proposed five functional categories for infanticide, four of which are adaptive for the killer, and include: (1) cannibalism (infant is considered a resource); (2) competition for resources, where the killer increases resources available for itself or its kin; (3) sexual selection, where mating opportunities for the killer will increase by removal of the progeny; (4) parental manipulation of the progeny, whereby the parents, by eliminating certain offspring, gain fitness benefits; and (5) social pathology, a non-adaptive explanation. Avian infanticide has been observed, to date, mostly in the context of brood-reduction, involving parental manipulation of the progeny to maximize parental reproductive success (see Mock 1984 for review). In group-breeding birds, there are some reports of group members destroying eggs and, occasionally, nestlings as well (e.g. Vehrencamp 1977, Trail et al. 1981). These behaviours are assumed to be adaptive for the killer, by decreasing the reproductive success of other individuals. Alternatively, if the killer is an immigrant, it may gain an opportunity for breeding within the group. Infanticide, viewed in this light, has been recorded mostly for primates (Mohnot 1971, Hrdy 1974, Angst & Thommen 1977) and lions (Packer & Pusey 1983). Records of infanticide in birds, in the context of sexual selection, are much fewer (Stephens 1982, Stacey & Edwards Jr 1983, Fujioka 1986). Here, we report observations indicating that infanticide may be a common occurrence in the communally-breeding Guira Cuckoo (*Guira guira*), and may fall within the scope of the sexual selection category proposed by Hrdy & Hausfater (1984).

Communal breeding has evolved in at least 222 bird species, and is characterized by more than two adults participating in the care of nestlings (Brown 1987). The ecological factors underlying the evolution of such systems have been examined by several researchers (Selander 1964; Brown 1974, 1978, 1987; Emlen & Vehrencamp 1983; Koenig & Stacey 1990; Walters et al. 1992; Burt & Peterson 1993). It appears that there is no single explanation for the evolution of communal breeding; instead, a variety of circumstances may be major determinants (Koenig et al. 1992). These systems usually involve a single breeding pair, assisted by others in raising the offspring; this is particularly the case for singular-breeding species, where there is only a single breeding female in a unit (Brown 1978, 1987; Emlen 1991). Helpers usually are offspring of the breeding pair from earlier nesting bouts, and are thus contributing toward the survival of their own siblings. Some communal birds, however, are plural breeders, with two or more females breeding in the unit (and sometimes in the same nest, known as joint-nesting; Brown 1987). This type of breeding has been documented in relatively few species.

Plural breeding occurs in species such as the Pukeko, *Porphyrula martinica* (Craig & Jamieson 1990); Groove-billed and Smooth-billed Anis, *Crotophaga sulcirostris* and *C. ani*, respectively (Vehrencamp 1977, 1978; Loflin 1983; Vehrencamp et al. 1986, 1988); and Acorn Woodpecker, *Melanerpes formicivorus* (Koenig & Mumme 1987, Koenig et al. 1995). Plural breeders may exhibit polygynous, polyandrous, and monogamous breeding patterns, and some species, such as the Guira Cuckoo, apparently adopt all of these strategies (Quinn et al. 1994).

Communally-breeding Guira Cuckoos (*Guira guira*) are little-known members of the Crotophaginae, as are the Anis. They occur from northern Brazil to Bolivia, Argentina, and Uruguay, inhabiting savanna vegetation, and not occurring in the Amazon Basin (Sick 1984). Given the many superficial similarities between Guira Cuckoos and Anis (see Vehrencamp 1977, 1978; Vehrencamp et al. 1986; and Koford et al. 1990 for details regarding the reproductive biology of Anis), we

expected little divergence in behavioural patterns, mating system, and ecological variables. However, the results of this long-term study have shown many unique characteristics. Guira Cuckoos are monomorphic, communal breeders (joint nesters), with groups of as many as 13 adults using the same nest. Communal clutch size ranges from four to 20 eggs, and is correlated to group size. However, many eggs are lost due to the tossing behaviour exhibited by group members. Egg loss may affect the whole clutch, or only part of the clutch. The egg-laying phase involves a high degree of conflict, raising the issue of the high energetic investment that is lost in the tossed eggs. Guira Cuckoo eggs are relatively large, weighing about 25 g, approximately 16% of the adult bird weight (MACEDO 1992), yet the loss of a large number of eggs is common. In some nests, as many as 15 are laid and tossed (MACEDO 1991).

Typically, adults differ markedly in how frequently they contribute food to the nestlings. QUINN et al. (1994) used DNA fingerprinting to evaluate the parentage and relatedness among nestlings for four nesting groups, finding that nestmates were offspring of different adults, and that some adults in the group were not parents of any of the young. The data, therefore, did not support the assumption of monogamy for this species. Additionally, a single female was not responsible for the majority of nestlings in the nest. Hence, several important differences led us to focus more carefully on the social system of the Guira Cuckoo.

Complex breeding strategies characterize plural breeding systems (KOENIG & MUMME 1987). This is true particularly because adults in the group may, or may not, be genetically related to other adults and offspring. Such breeding systems naturally induce rivalries and reproductive conflict among group members. In this paper, we report detailed histories of nine nests where complete brood loss occurred in such a manner as to suggest that, in addition to predation and other events, adult group members may be regularly committing infanticide.

STUDY AREA AND METHODS

The study was conducted on the central Brazilian plateau (at 15°47'S, 47°56'W; altitude 1158 m) in a semi-urban area near Brasilia. The vegetation includes fragments of the native savanna (known as "cerrado") interspersed with cultivated areas and residential gardens. The climate is highly seasonal, with a marked rainy season. Reproductive activity of the Guira Cuckoos largely coincides with peak rains.

Breeding was monitored from July 1987 to January 1988, August to November 1988, July to October 1990, and August 1994 to August 1995. In all, 98 breeding attempts by 39 groups were monitored during these periods to obtain data on group structure and reproductive behaviour. This includes 18 nests where we were unable to determine the outcome of the nesting attempts, but which furnished partial data for some variables. Active nests were checked daily during the egg laying period and less frequently during the incubation and nestling phases. These birds are highly territorial, and visiting the nest often resulted in the aggregation of the group, especially during the early hatching period. During each visit, we recorded the number of adults present to determine group size: at least three visits with the same number of adults present were needed to confirm group size. Eggs in the nest were numbered sequentially as they were laid, and the ground beneath the tree was searched for tossed eggs. During the study, 91 adult birds were captured and banded. Most nestlings were banded at about 5 days of age. To gather data on parent-offspring interactions, seven broods were monitored from 3 to 5 hr daily, usually starting immediately after hatching until the chicks fledged, at approximately 12 to 15 days after hatching.

RESULTS

All chicks in a brood usually hatch on the same day, although a span of up to 4 days was observed in one nest. Chicks are confined to the nest cup for the first 3 or 4 days post-hatching, after which they scramble around the tree when an adult arrives with food. The results of each nesting attempt were classified in the following manner: (1) abandoned (33 nests) where desertion occurred during egg-laying; (2) total brood loss (10 nests), where all chicks disappeared or were found dead, but no clear cause for the death could be established; (3) partial brood loss (21 nests), wherein some nestlings disappeared over a period of several days while at least one nestmate survived to fledge, and the cause of death could not be established; (4) no brood loss (13 nests) where all hatched chicks survived to at least 7 days of age; and (5) clearcut predation events (3 nests) where all eggs or chicks disappeared simultaneously and the nest showed some evidence of disturbance (broken twigs, scattered egg-shells, etc.).

Clearly, chick mortality was a predominant element influencing the degree of success of each group, and occurred in approximately 31 nests where both hatching and nestling disappearance dates were known. Total brood losses, where all nestlings died, occurred in 10 nests (Tables 1 and 2), nine of which were closely monitored. Below, we give detailed accounts of the histories of nests that suffered complete brood loss. These descriptive cases, and the mortality patterns depicted, are typical of almost all nesting events monitored to date, whether with partial or total loss of the broods. These examples illustrate some general patterns: (1) nestlings usually die within the first 5 days after hatching; (2) nestlings in a brood do not usually disappear simultaneously; rather, one or a few are lost each day; and (3) sometimes nestlings are found dead beneath the nesting tree, some exhibiting external wounds. In two nests (A2.2 and B7.2), egg-laying and egg-loss sequences are included because of the unusual circumstance of a chick hatching simultaneously with eggs being laid in the nest.

Table 1.

Reproductive and group characteristics (averages, with n and ranges in parentheses) according to outcomes of nesting attempt: abandoned during egg laying; total brood loss, when all hatched chicks vanished or were found dead; partial brood loss, when at least one chick survived for a minimum of 7 days; no brood loss, when all hatched chicks survived for at least 7 days.

	Nesting cycle results			
	Abandoned	Total brood loss	Partial brood loss	No brood loss
Group size	6.61 (18; 3-11)	6.71 (7; 5-8)	6.84 (19; 3-13)	6.00 (10; 2-10)
Eggs laid	7.03 (31; 2-15)	10.00 (9; 6-13)	10.37 (19; 5-18)	7.40 (10; 4-13)
Eggs tossed	5.10 (30; 1-15)	3.33 (9; 0-9)	2.89 (19; 0-9)	1.80 (10; 0-4)
Hatched	—	5.33 (9; 1-8)	5.85 (20; 3-10)	3.10 (10; 1-6)
Cycle length [a]	11.83 (18; 4-22)	20.00 (8; 18-24)	27.00 (13; 19-34) [b]	23.29 (7; 21-25) [b]

[a] Cycle length in days from laying of first egg until one of the following occurred: (1) abandoned during egg laying; (2) all hatched chicks vanished or dead; or (3) until last nest check of approximately 1-week-old nestlings. [b] In these categories, if chicks survive to fledging, parental care in feeding and defense extends for at least another 3 weeks.

Table 2.

Nesting variables for nine Guira Cuckoo nests that suffered total brood loss. Nestings occurred in 1987, 1988, 1990, 1994, and 1995.

Nest	Group size	Eggs laid	Eggs tossed	Nest cycle length [a]	Subsequent renesting
C2.1	7	9	0	20	yes
B5.1	5	6	2	24	no
A2.2 [b]	—	7	6	23	no
B7.1	8	13	3	18	no
B1.1	8	10	3	18	no
C10.1	5	10	5	20	yes
B7.2 [b]	8	10	1	20	no
A8.1	—	17	9	—	yes
B8.2 [b]	6	8	1	17	no

[a] From beginning of egg-laying (some dates estimated from clutch size) until last chick disappeared.
[b] Group's second nesting attempt.

Nest C2.1 (1987). This nest was found on September 10 and was located at a height of 8.15 m. Seven adults, two of which were banded, were present. The nest contained five eggs when found, and the clutch of nine eggs was completed in the following 2 days. After the clutch was completed, 4 days elapsed before incubation was initiated. Eight nestlings hatched on September 25. Four chicks disappeared the day after hatching, and three more on the 2nd day. The last chick was found dead beneath the tree on September 29. This group renested in the same territory, using a different nest tree, only 4 m from the first site. Renesting occurred on October 16, approximately 1 month after the first attempt. This attempt was also unsuccessful, with the nest being abandoned during egg-laying, after a clutch of nine eggs had been laid. During this attempt, only four active adults were seen at the nest.

Nest B5.1 (1987). This nest was found on November 5 and was located at a height of 11.5 m. The group consisted of five adults, of which three were banded. The nest was found when five eggs had already been laid, a sixth was laid subsequently and incubating was initiated immediately. All young hatched synchronously. Two unhatched eggs disappeared from the nest the day four young hatched on November 17. Chicks were marked individually (#1, #2, #3, #4). The day following hatching, chick #1 disappeared and chick #2 was found dead on the ground, exhibiting an abdominal wound. Chicks #3 and #4 were alive in the nest, the latter also exhibiting an abdominal wound. On November 20, the wounded chick (#4) was no longer in the nest, and the remaining chick (#3) exhibited the same type of wound. Five adults were observed in the vicinity of the nest, but only one continued feeding the chick. On November 27 chick #3 disappeared. The group did not renest within the study period.

Nest A2.2 (1987). This nest was found on November 11 and was the group's second nesting attempt of the season. Group size could not be determined. In the first attempt (August) the group consisted of five adults, and one chick survived to fledge. In the second attempt, seven eggs were laid, one of which appeared in the

nest when one chick hatched on December 18. The single chick disappeared 2 days after hatching, and all unhatched eggs disappeared or were tossed during the 4 days following hatching.

Nest B7.1 (1988). This nest (6.9 m off ground) was found on September 12, with 10 eggs in the nest cup, and one on the ground. The group consisted of at least eight adults. All eggs were laid within a 1-week period. A clutch of 13 eggs was laid, and incubation started 2 days after clutch completion. Three eggs disappeared on the same day that seven chicks hatched. On the following day, five of the chicks had vanished, and two were dead inside the nest. Three eggs remained in the nest, two of which contained well-developed embryos.

Nest B1.1 (1988). This nest was found on September 7, at the very beginning of the egg-laying sequence. Group size was of eight adults, three of which were banded (as adults) the previous year in the same territory. Ten eggs were laid within 1 week, with only a single egg tossed. One egg disappeared on September 22, when most of the eggs were pipping. On September 23 seven young had hatched. On September 25 five young had disappeared from the nest and could not be found in the vicinity, and two were found dead on the ground a few metres from the nest tree; one had its head severed.

Nest C10.1 (1990). This nest was found on August 19, with four eggs in the nest cup and four already tossed. Ten eggs were laid, of which five were tossed. The group consisted of five members, one of which had been captured, as an adult, in 1987, 1988 and 1990, in the same territory. On August 23 six young hatched and one egg was tossed; one chick had disappeared by the next day. On August 25, four young had disappeared, and one was found dead beneath the tree.

Nest B7.2 (1990). This group of eight adults had a complicated series of events leading up to the nesting presently described. Its first attempt occurred in early August, during which four eggs were laid and abandoned. A second nesting attempt within the territory occurred concurrently, at a site approximately 80 m from the first; all four eggs at this site disappeared and the nest was also deserted. Only 20 days later, a new nest was initiated at the second site. Seven eggs were laid and incubated initially, none of which was tossed, and a single chick hatched on September 20. By the following day, three new eggs had been laid, and one egg was tossed (it is unknown whether the tossed egg was an old or new one). The 2-day-old chick vanished on September 22, and eight eggs remained in the nest, which were incubated for 6 days, and deserted on September 29.

Nest A8.1 (1994). This nest was found on November 7, during the egg-laying period. Group size could not be determined. A total of 17 eggs were laid, six of which were tossed before incubation started, and three of which vanished during incubation and after the chicks started hatching; eight chicks hatched over 3 days, starting on November 21. Within the first 4 days after hatching initiated, five nestlings disappeared; on November 25, only three chicks remained. Two days later, one of these had disappeared, and two were dead inside the nest.

Nest B8.2 (1995). This group's first attempt had been initiated in late October 1994, with only three adults seen around the nest. Ten eggs were laid, two of which were tossed; of the five hatched chicks, three survived to fledging. The second nesting attempt (B8.2) initiated approximately 3 months later, 24 January 1995, with a larger group composed of six adults. However, only eight eggs were laid. One egg disappeared during the incubation period; six nestlings hatched on February 6, all of which survived until February 7. The following day one nestling was found dead on the ground approximately 25 m from the nesting tree, and two others had dis-

appeared. On February 10, one more nestling was found dead on the ground under the tree, and the two remaining nestlings survived until February 14, when one disappeared. The last chick disappeared on February 15. One egg remained in the nest.

DISCUSSION

In addition to the egg loss through tossing, the loss of part or all of the brood in the early nestling stage is a fairly common event for Guira Cuckoos in this population, occurring in 69% of nests that produced chicks. Potential causes for this mortality include starvation, predation, disease, and accidents. Cause of death for many nestlings could not be associated easily with these "usual" categories of mortality. In most cases, nestlings died within days of hatching, when energetic demands are low, and starvation is improbable if food is being delivered by the adults.

Predation could potentially account for some of the mortality, as LACK (1954) estimated that 75% of all eggs and nestlings lost from open nest cups are taken by predators, and RICKLEFS (1969) estimated that, for passerine species, 66% of nestling losses was due to predation. However, several details indicate that predation is not the most likely cause for the majority of chick disappearances. No evidence of a predator attack was visible, in the form of broken eggs, crushed leaves, scattered twigs, etc. Nests are located on the crowns of thorny *Araucaria* trees, discouraging for terrestrial predators. Obviously, some predators, such as snakes or small marsupials, may be responsible for some of the observed mortality. However, in the case histories presented, dead nestlings in the nest cup or mutilated on the ground leads to our considering predation unlikely as a general explanation.

Infanticide is the only explanation for our observations. The laying of eggs concurrently with the hatching of chicks indicate conflicting individual reproductive tactics and, possibly, group composition may be the key factor determining the fate of eggs and nestlings. Individual adults in the study population are differentially successful in terms of nestling production, creating asymmetries in relatedness between adults and nestlings; some adult group members do not reproduce successfully (QUINN et al. 1994). The variability in feeding of nestlings and nest attendance behaviour noted for some nests (MACEDO 1995) may be one consequence of intra-group dynamics that, possibly, allots breeding opportunities to some, but not all, group members. Additionally, because many groups renest at least twice during the rainy season, the length of interval between attempts may depend upon the outcome of each nesting bout. On average, renesting attempts have significantly shorter intervals for groups that are unsuccessful during their first attempts (average 34.9 days) than for renestings following successful first attempts (average 65.7 days; MACEDO 1995). Intra-group conflict, in the form of egg-tossing or infanticide, may result in the disruption of the nesting cycle or of pair bonds among group members, allowing establishment of a new group hierarchy, wherein individual(s) excluded during the first breeding attempt will have a renewed opportunity to reproduce successfully, within a shorter interval of time. Kinship to the young in the nest, or to other co-breeders in the joint nest, may play an important role in determining the behaviour of individuals. KOENIG (1990) experimentally removed some male co-breeders in an Acorn Woodpecker population during the egg-laying

phase, thereby decreasing their opportunities for parentage. The result showed that, when renesting was likely, the manipulated dominant woodpeckers, with the reduced chances of parentage, destroyed the active nest and forced a renest. This did not occur with experimentally manipulated subordinates.

MOCK (1984) suggested that the prevailing monogamous mating system of birds is a constraint for the evolution of infanticide, in general. He suggested that the study of other mating systems in birds could provide valuable clues regarding the evolution of infanticide. The Guira Cuckoo system provides a unique testing ground for this biologically significant behaviour. There are polygynous and polyandrous matings within groups, and various levels of relatedness among adults and chicks. Any adult that does not breed successfully during a nesting bout has to delay breeding until the group resumes reproduction, after a prolonged interval of caring for the group's offspring, none of whom are his (her) direct descendants. The individual could presumably attempt to enter another group, which most certainly involves some costs. In either of these scenarios, infanticide could be adopted as a strategy to increase opportunities for breeding.

Because infanticide is a brief event (HAUSFATER & HRDY 1984), it is infrequently observed. Direct evidence is needed to ascertain the exact nature of the high mortality found for Guira Cuckoo nestlings in this population. If, indeed, direct evidence for infanticide is found, we hypothesize that group members, excluded from breeding, will exhibit little parental behaviour (feeding of nestlings and nest attendance) and may indulge in infanticide as well.

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