REPRODUCTIVE PATTERNS AND SOCIAL ORGANIZATION OF THE COMMUNAL GUIRA CUCKOO (*GUIRA GUIRA*) IN CENTRAL BRAZIL

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ABSTRACT.—The communal breeding system of the Guira Cuckoo (*Guira guira*) was studied near Brasilia, Brazil. Guiras occurred in groups of 2 to 13 adults (mode of 6) in the 86 nests observed. Communal clutch size was correlated with group size, an indirect indication that more birds contribute to the clutch in larger groups. Clutch size varied from 4 to 20 eggs, but usually fewer eggs were incubated than were laid, since egg tossing by the adults was common. The temporal patterns of egg laying and egg loss, while generally similar to those of other crotophagines, differed in some ways. Egg losses occur at any time after laying starts. Losses may occur after several eggs have accumulated in the nest, may affect only part of the clutch, and may happen close to, or during, the hatching of chicks. Only 26% of eggs developed into fledglings; high mortality rates for eggs and chicks are due to several causes. An individual may pay a price for group membership through a lowered short-term reproductive success; however, long-term data are needed to clarify individual lifetime benefits associated with communal breeding in this species. *Received 18 June 1991, accepted 20 February 1992.*

MUCH RESEARCH and speculation has been devoted to identifying common ecological factors that promote the evolution of communal and cooperative breeding systems (e.g. Selander 1964, Brown 1974, 1978, 1983, 1987, Koenig and Pitelka 1981, Emlen 1982a, b, 1984, Emlen and Vehrencamp 1983, Ford et al. 1988, Koenig and Mumme 1990, Koenig and Stacey 1990, Koford et al. 1990). In cooperative breeding, a single pair may raise young with the assistance of other individuals; less commonly, in communal breeding, three or more breeders raise young in the same nest (Koenig and Pitelka 1981). Although a number of explanations for these social systems has been proposed, the habitat-saturation hypothesis (Selander 1964) is cited most widely. According to this idea, when a habitat is "saturated," young birds do not have the option of dispersing to attempt independent breeding.

In this paper, I describe the social system of the Guira Cuckoo (*Guira guira*), which is evaluated with regard to the advantages and disadvantages of group living, and the available breeding options. Despite general information concerning its natural history, little has been published on the guira's breeding biology and behavior.

The crotophagine species (Cuculidae) are of interest because of their social nesting behavior. This group of Neotropical birds consists of the monotypic genus *Guira*, and three ani species in the genus *Crotophaga* (Groove-billed Ani, *C. sulcirostris*; Smooth-billed Ani, *C. ani*; and Greater Ani, *C. major*). Only Groove-billed and Smooth-billed anis have been studied in detail with respect to behavior and breeding ecology (Koster 1971, Vehrencamp 1977, 1978, Loflin 1983, Koford et al. 1986, Vehrencamp et al. 1986). These investigations revealed that anis breed either in isolated pairs or in groups, where up to four females lay eggs in a single nest. Female anis engage in several behaviors that increase the number of their own young that hatch within a clutch. For example, females that have not yet laid eggs repeatedly visit the nest and toss out eggs laid by other females (Vehrencamp 1977, Emlen and Vehrencamp 1983). This strategy results in the last-laying female contributing a greater proportion of eggs in the clutch than would be expected simply from her share of production.

METHODS

Study site.—I studied Guira Cuckoos on the central Brazilian Plateau (altitude 1,158 m) near Brasilia (15°47′S, 47°56′W) from: July 1987 to January 1988; August to November 1988; and July to October 1990. The climate of the central Brazilian Plateau is highly

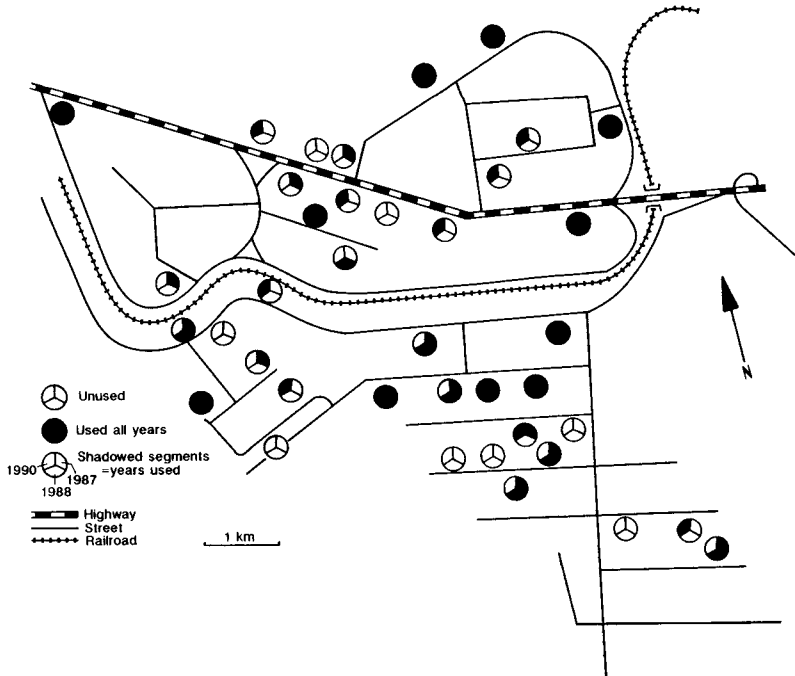[1] Present address: SQS 111, Bloco D, apto. 303 Brasilia, DF 70374-040, Brazil.

Fig. 1. Map of study area showing spatial distribution of Guira Cuckoo nest sites (circles) during 1987, 1988 and 1990 breeding seasons.

seasonal, with marked rainy and dry seasons. Most of the rain is concentrated in the hottest months of the year (October to March). The monthly precipitation levels during this time average about 192 mm; June, July, and August are dry months, averaging about 16 mm of rain (period 1982–1986). Mean annual temperature is about 21°C (data courtesy of Instituto Nacional de Meteorologia, Brasilia). The study site included approximately 3,000 ha, distributed over a suburban area near Brasilia.

Study population and banding.—General observations concerning flock behavior, foraging, and vocalizations were conducted before most nesting activity started. For descriptive purposes, I taped songs from two birds (one song type from each) and used Staicer's (1989) terminology to describe the sonograms obtained from these vocalizations. Repeated units in a song are called notes and are identified with a given letter. Songs are sequences of notes preceded and followed by relatively long quiet intervals in comparison to the intervals between notes. Songs are composed of one or more phrases, which are sequences of the same note. A phrase pattern is a specific sequence of phrases, coded numerically, which is used to characterize a song.

To obtain birds for banding, the only successful capturing method was the use of caged, hand-reared lure birds surrounded by entangling monofilament "noose mats." These traps were placed within a group's territory after incubation had started (see Vehren-

camp 1977). Some birds never came to the trap and, with repeated use of captive decoys on a single territory, the probability of catching birds was lowered. The adult population under study consisted of at least 173 birds in 1987 (approximately 21% banded), 125 birds in 1988 (approximately 34% banded), and 130 birds in 1990 (approximately 10% banded). Over the three years, 91 adult birds were captured and banded. Sexing of birds by laparotomy was attempted initially, but discontinued when three groups deserted their nests after this procedure was first employed.

Nest censusing.—Systematic searches revealed that almost all nests were placed in a single tree species, *Araucaria angustifolia* (an introduced, thorny tree in the Central Brazilian Plateau, but native to southern Brazil). A total of 177 Araucaria trees occurred within the area (Table 1). After the rains started each year, I searched the trees for active nests at weekly intervals.

The geographical distribution pattern of the groups in the area was analyzed by evaluating the number of potentially suitable but unoccupied breeding sites in the area. I defined a nesting site as an area of approximately 0.28 km² (i.e. a circular area with a 300-m radius), containing at least one Araucaria tree, with evidence of prior breeding in the form of old, but functional (i.e. not obviously deteriorated), guira nests. There were 39 such sites in the study area (Fig. 1). Of these, 20.5% were unoccupied in all years. For a more conservative approach in the analyses below, I restricted the definition of "potential nesting site"

TABLE 1. Study area characteristics and nest-site usage during 1987, 1988 and 1990 breeding seasons in central Brazil.

Variable	Total
No. Araucaria trees	177
Area (ha)	2,900
Araucaria trees/ha	0.06
Total nest sites available[a]	31
Sites used in 1987 (%)	22 (71.0)
Percent empty sites (300-m radius)	29.0
Percent empty sites (600-m radius)	16.1
Sites used in 1988 (%)	18 (58.1)
Percent empty sites (300-m radius)	41.9
Percent empty sites (600-m radius)	25.8
Sites used in 1990 (%)	20 (64.5)
Percent empty sites (300-m radius)	35.5
Percent empty sites (600-m radius)	9.7
Sites used only in 1987 (%)	4 (12.9)
Sites used only in 1988 (%)	1 (3.2)
Sites used only in 1990 (%)	8 (25.8)
Sites used all years (%)	11 (35.5)

[a] Nest site defined as including all Araucaria trees within 300 m².

to the 31 sites where breeding occurred at least once during the study. Additionally, for each year, values are also given (Table 1) for the percentage of empty nesting sites when the area around each active breeding site is calculated using a 600-m radius. This larger radius effectively quadruples the potentially defended area around an active nest site, providing a more restrained estimate of the number of empty sites available. Group members were rarely spotted more than 300 m away from the active nest.

Distances between the center of an active nesting site and the outer circumference of a neighboring site ranged from 200 m in one case (one exception to the above definition) to 2,700 m ($\bar{x}$ = 603 m). In most cases (94.0%, n = 31 sites), sites contained at least one other Araucaria tree, and sometimes a dozen or more.

In 1990 an experimental procedure was introduced to assess whether empty, but apparently suitable, breeding sites adjacent to active ones were, in fact, within the nesting group's territory. Seven groups nested in territories that had empty adjacent sites at various distances (range = 200 to 350 m; $\bar{x}$ = 299 ± SD of 43 m). Two caged guiras were left for 30 min at these unoccupied sites to test whether territorial defense took place (average distance between active nest and lure birds = 298 m). A control procedure was repeated on another day at an approximately equal distance from the nesting group, but in an area determined as unsuitable for breeding (i.e. no Araucaria trees; average distance between active nest and lure birds = 292 m).

During the study, I located breeding territories for 38 groups of Guira Cuckoos and monitored these groups during 86 breeding attempts. Once nest activity was observed at a given site, nest height was recorded, and the group was visited every third day until laying started. During laying, nest contents were checked daily.

Eggs were numbered in the sequence laid (if the nest was discovered early in laying), measured (length and breadth), and (in 1988) photographed for pattern analysis (eggs are mottled). These egg variables were evaluated in an effort to establish egg ownership among different females in the event that clutches of individual females differ in physical characteristics. A shape index was calculated using the ratio of maximum diameter to length (Kendeigh et al. 1956). Individual egg photographs from each clutch were compared to identify patterns in the shell marks. In addition, each egg's background color was rated through comparison with Munsell color chips.

A total of 197 eggs was lost from all nests. The ground and tree branches beneath nests were searched for egg remains. Eggs on the ground accounted for 76.7% of all eggs lost. Guira nests are deep and well built, and eggs cannot be rolled out by the wind. Eggs were lost either sequentially (one per day), or several at once. On six occasions I observed adults tossing eggs (dropping them directly over the nest's rim).

The remaining 23.3% of lost eggs simply disappeared from the nest. Their consumption by terrestrial predators was unlikely to have been the source of mortality for most of the eggs that disappeared because they vanished one per day. I assumed that most terrestrial predators would have consumed all eggs, left puncture marks on eggs, or broken egg shells inside the nest. Clearly, some eggs may have been taken by predators that left no sign of their activities (e.g. snakes or birds), but there is evidence suggesting that most of the eggs that disappeared were carried and tossed farther from the nest by adult guiras. On seven occasions I observed adults carrying eggs (in their bills) from nests and dropping them at a distance of several meters (in two of these cases the egg was dropped about 10 m from the nest, while in the other instances the birds flew out of sight with the eggs). In some analyses for this paper I have pooled tossed eggs (those found on the ground) and eggs that disappeared and refer to them simply as eggs lost.

Of the 134 nestlings from 40 nests that survived to fledging (i.e. those that were able to leave the nesting tree through sustained flight) in all years, 65 (49.0%) were banded. Groups were visited periodically to check on the progress of the nestlings, but observations were conducted at a distance to avoid nest disturbance. Once incubation started, the nest was not checked until some hatching was expected.

Group size.—Group size was determined by counting all birds around the nest at each visit. Because not all birds were present each time, several counts were necessary before a consistent number was

reached. Group size was not determined for 22 of the 86 census nests because consistent counts could not be obtained. This occurred when the birds were in dense cover, or when the nest was deserted before many group counts had been made.

Behavioral observations.—Seven focal groups were observed to collect data on adult participation in caring for chicks. Typically, observations were conducted from a vantage point about 10 m from the nest, using a blind placed on a 6-m scaffold.

Nest attendance (see below) was recorded at two nests after the chicks had hatched (A3.1 in 1988; A7.1 in 1990) during 67 and 63 h of observation, respectively. Nest attendance behavior generally followed a feeding trip, and only one adult at a time acted as attendant. I recorded the time each group member spent on exposed perches within 10 m of the nest after having fed a chick. Other behavioral options were possible after adults fed chicks, but were not considered attendance behavior. These included: adult remaining on nesting tree; perching within sight but >10 m from nest; foraging within sight of nest; and flying out of sight. Observations generally were conducted for 5 h each day, from just after chicks hatched until they fledged.

Because no among-year differences in breeding-success variables were found, data were pooled across years for several statistical analyses: clutch size ($F = 0.86, P = 0.57$); lost eggs ($F = 0.09, P = 0.91$); hatched eggs ($F = 0.09, P = 0.92$); and chicks that disappeared ($F = 1.38, P = 0.26$). All other breeding-success measures used were derived from the above variables.
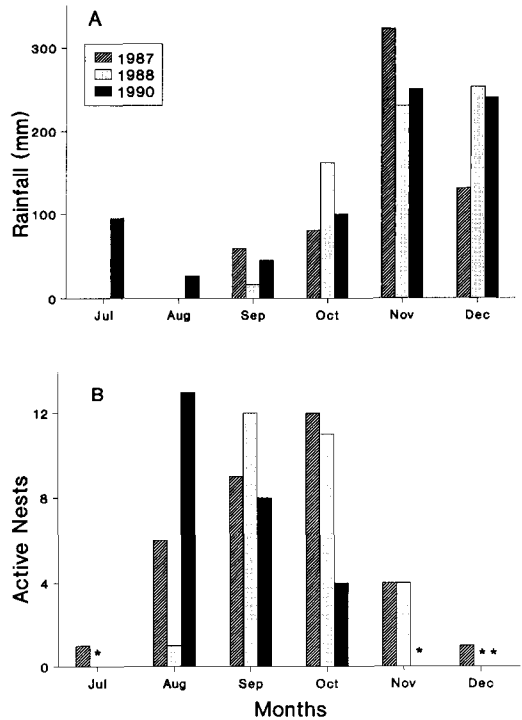

Fig. 2. (A) Rainfall levels for each month in Brasilia, Brazil (1987, 1988, 1990). (B) Number of active Guira Cuckoo nests found; asterisks indicate that no data were collected in July and December of 1988, and November and December of 1990.

RESULTS

Breeding activity and rainfall.—Guira groups in central Brazil may attempt to breed during the driest months (May through August; Antas and Cavalcanti 1988). However, breeding activity is most intense during the rainy season, and some groups have time to raise at least two broods (18 of 86 active nests were renesting attempts). In 1987 and 1988, no rain fell in July (Fig. 2), although in 1990 the rainy season started in July. In all three years, very little rain fell during August, but active nests were found. Finally, heavy rain started in September and October. The number of active nests was greatest during these two months in 1987 and 1988. In 1990, peak activity occurred in August, perhaps because the rainy season started earlier in that year.

In the central region of Brazil, there are at least 104 species of native cerrado trees (Ratter 1982). In spite of this species richness, guiras

nested overwhelmingly in the Araucaria (82 of 86 breeding attempts). Araucaria has prickly, stiff, triangular leaves over the entire trunk and branches.

For the 31 potential breeding sites identified (Fig. 1), the pattern of occupation was as follows: (1) 22.6% were occupied during two of the three years; (2) 41.9% were occupied in only one year; and (3) 35.5% were used during all years. For each year, nest site occupation was as follows: 71.0% in 1987; 58.1% in 1988; and 64.5% in 1990. For each nesting group, the nearest potential breeding site was checked for signs of occupation by another group. There were seven cases where sites were used every year, and for which the nearest potential breeding territory remained vacant in some years ($\bar{x}$ distance apart = 1,014 m). There were no sites occupied all years for which the nearest suitable site was always vacant. Finally, there were three breeding sites used every year, where the near-
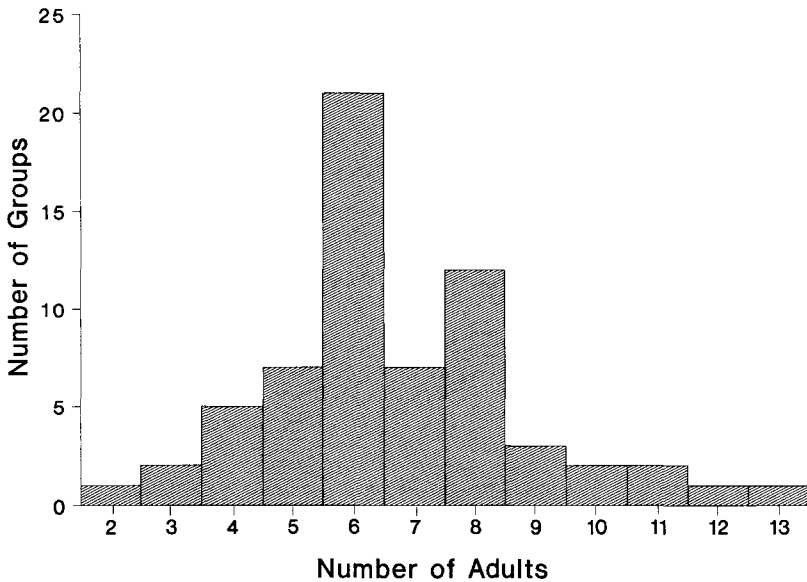
Fig. 3. Frequency distribution of breeding-group sizes of Guira Cuckoos in Brasilia, Brazil (1987, 1988, 1990).

est suitable breeding sites were always occupied ($\bar{x}$ distance apart = 683 m).

During the study, groups used the same territories for renesting within the same breeding season 18 times. For 14 of these groups, at least two adults were marked (either banded or marked with dye left inside the nest) during the first breeding attempt, and were recognizable during subsequent renestings. In 10 of these cases, the group used a different tree within the territory that was 3 to 100 m from the first nesting tree. The remaining groups used the same nest for renesting.

The 1990 experimental procedure to evaluate group defense of adjacent and suitable nesting sites was applied to seven active groups. In six cases, no guira was attracted to the lures (the minimum distance of lure birds to active nest was 300 m in these cases). In the seventh group, two guiras arrived at the site within 20 min and remained perched nearby for another 5 min before leaving; the distance between the lure birds and the active nest was 200 m in this case. The control procedure for the experiment only attracted neighboring birds once, when the distance between lure birds and the active nest was 200 m.

Social organization.—In my study population, guira breeding group sizes averaged 6.7 ± 2.1 individuals (n = 64; Fig. 3) and ranged from a pair to 13 birds. The most common group size

observed was six individuals (32.8%), with the next most common group size being eight birds (18.8%). Group size changed in six of the nine renesting attempts where group size could be determined for each nesting.

Vocalizations play a conspicuous role in the social organization of these birds. The three vocalizations most frequently heard were the glacis song, the staccato song, and the croak (sonograms for first two shown in Fig. 4). The glacis song (also described by Davis 1940) is given either in flight or from a perch, and may vary in duration from about 6 to 8 s ($\bar{x}$ = 7.29 ± 0.62 s, n = 7). It consists of a descending series of seven or eight piercing notes that can be divided into three phrases (phrase pattern *in-m-c*). The first phrase (*in*) is composed of two or three brief but widely spaced notes (average note duration = 0.38 ± 0.06 s, n = 16; average internote interval = 0.83 ± 0.24 s, n = 10). The second phrase (*m*) is not always present, but may contain one to three notes of longer duration than those of the first phrase, but spaced more closely (average note duration = 0.42 ± 0.05 s, n = 13; average internote interval = 0.74 ± 0.14 s, n = 7). The last phrase (*c*) is also variable and may range from two to five notes that are longer in duration than those of the first two phrases, but even more tightly bound (average note duration = 0.49 ± 0.11 s, n = 24; average internote interval = 0.39 ± 0.10 s, n = 16). When the group
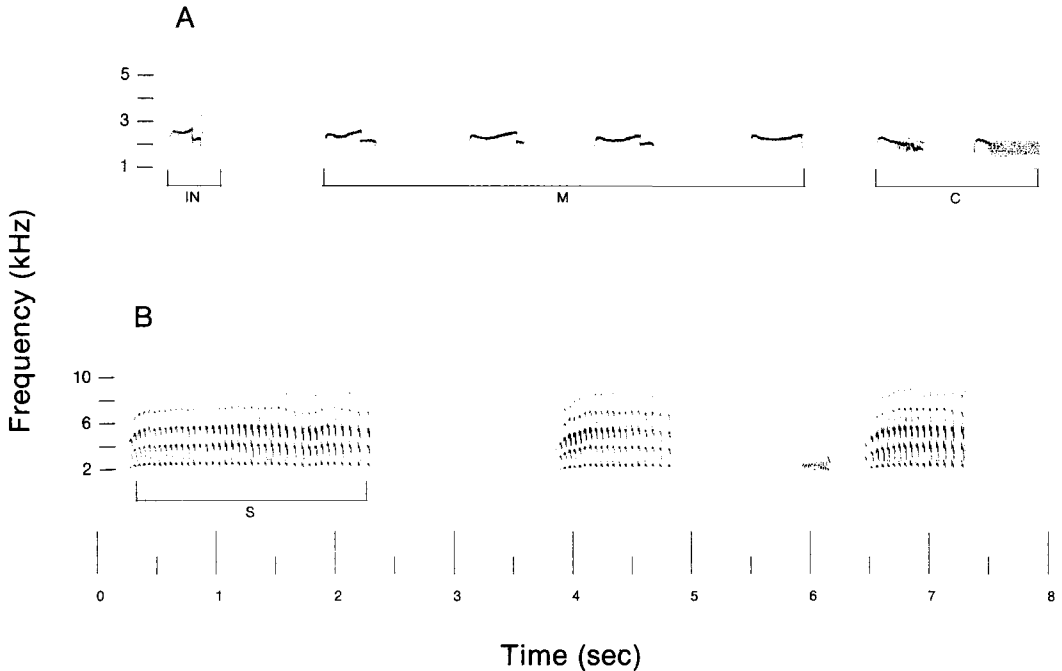
Fig. 4.   Sonograms of Guira Cuckoo vocalizations: (A) glacis song; (B) staccato song.

is scattered, birds call back and forth from different locations using the glacis song. This vocalization did not have the effect of bringing the group together.

The staccato song is a high-pitched series of notes. It is composed of only one phrase (*a*), and the single note is repeated a varying number of times. Notes are short and close together (average note duration = 0.02 ± 0.05 s, $n = 34$; average internote interval = 0.02 ± 0.01 s, $n = 32$). The staccato song duration is quite variable, and may range from 0.45 s to 2.4 s (average song duration = 1.08 ± 0.64 s, $n = 18$). Staccato calls are given under apparently threatening circumstances, usually when a potential predator approaches a foraging group or nest. The birds, if scattered, quickly gather and either confront the intruder or flee *en masse*.

A third conspicuous vocalization is a low, hoarse croaking, given at irregular intervals when a bird is perched and relaxed. This vocalization does not obviously characterize any specific situation and seems to be restricted to times when the caller is not stressed. In addition to these three common vocalizations, the guira employs several other shrill screeches, whines, and croaks, but none that was easily categorized.

Nesting and laying.—Nest building was observed only twice, as the birds in my area generally used old nests (97.7% of 86 breeding attempts). Typically, nests were reoccupied by the birds, then renovated through the addition of twigs. Guira Cuckoos nest as high as possible within the tree, usually at the crown. Nest heights ranged from 3.0 to 12.2 m ($\bar{x} = 7.5 \pm 2.2$ m; $n = 79$ nests).

Communal clutch sizes varied widely, with a small clutch of 4 eggs produced in one group of 6 individuals, and 20 eggs laid by a group having 11 adults. The mean communal clutch size over all years was 10.0 ± 3.7 eggs ($n = 33$ nests where clutches were incubated).

Guira eggs are large, averaging 25.3 ± 2.7 g ($n = 70$), approximately 16% of the adult bird weight ($\bar{x} = 156.7 \pm 12.1$ g, $n = 34$). Egg lengths ranged from 37.6 to 48.8 mm ($\bar{x} = 42.5 \pm 1.9$ mm, $n = 148$), and egg breadths from 27.8 to 37.6 mm ($\bar{x} = 31.8 \pm 1.4$ mm, $n = 148$). Eggs are turquoise, with a lacelike calcareous pattern of white splotches and streaks. The turquoise color for 83 fresh eggs from 14 nests was rated according to the Munsell color scale. The background shell color of fresh eggs was evaluated and nine shades of turquoise were found (for numerical codes in the Munsell Color Standard,

TABLE 2.   Guira Cuckoo egg-laying and egg-loss patterns for Nest A2.1 (five group members).

Egg no.	Date			
	Laid	Egg apparently tossed[a] (T) or disappeared (D)	Hatched	Chick fledged (F) or disappeared (D)
1	25 Aug	26 Aug (T)		
2	26 Aug	26 Aug (T)		
3	26 Aug		12 Sep	15 Sep (D)
4	31 Aug		12 Sep	15 Sep (D)
5	31 Aug		12 Sep	8 Oct (F)
6	1 Sep	15 Sep (D)		
7	1 Sep		12 Sep	15 Sep (D)

[a] Eggs found broken on ground.

see Macedo 1991). The egg variables evaluated (shape, shell pattern, and color) were not helpful in my identifying individual female clutches. In most clutches, these egg characteristics were broadly overlapping.

The egg-laying and egg-loss patterns for many groups are complicated. The "normal" sequence starts with one egg being laid each day (presumably by a single female), with other females gradually joining in until several are laying concurrently (multiple new eggs per day), usually after three or four days (see example in Table 2). Eggs laid at the beginning of the nesting cycle frequently disappeared or were found below the nest the following day. Groups where no eggs were lost (19% of 63 nests) ranged in size from two to nine individuals. In one large

TABLE 3.   Guira Cuckoo egg-laying and egg-loss patterns for Nest D2.1 (11 group members).[a] All eggs lost in this nest were presumably tossed (i.e. found broken on ground beneath nest).

Date	No. eggs		
	Laid	Lost	In nest
30 Sep	2	2	0
1 Oct	2	0	2
2 Oct	2	0	4
3 Oct	3	0	7
4 Oct	0	5	2
5–6 Oct	8	3	7
7 Oct	0	0	7
8 Oct	1	2	6
9 Oct	2	0	8

[a] On 20 October, two young hatched and six eggs in nest. On 23 October, two young and six eggs in nest. On 24 October, three young in nest. On 4 November, the young fledged.

group, up to 15 eggs were found on the ground before the nest was deserted. The average number of lost eggs was 3.2 ± 2.76 (range 0–12, n = 33; calculations based on nests where clutches had been completed and were incubated). Some of the eggs presumably could have been consumed by predators, as indicated above. Alternatively, but probably infrequently, a few eggs may have been tossed by nongroup members. Direct observation of marked group members tossing eggs occurred at four nests for a total of 12 eggs.

Egg laying and losses did not always follow the same pattern. Losses sometimes occurred after four or more eggs had accumulated in the nest and/or only part of the clutch was lost (Tables 2, 3 and 4). Of 33 nests where at least one chick hatched and where the total incubation period was monitored, some eggs were found on the ground after incubation was completed and, in four nests, as chicks were about to hatch.

The most common egg-loss pattern (66.1% of 56 nests) was sequential (one egg per day), typically before incubation started (Table 4). However, in 23% of the nests, multiple eggs were lost simultaneously, and this occurred before and after incubation had started. In one nest, the whole clutch was found on the ground (within a 24-h period) after incubation was initiated.

Average incubation time is 10.1 ± 1.42 days (n = 23 nests). In four groups (B1.1, B7.1, D5.1 and B8.2), where incubation was observed for a total of 14 h, I found that several group members contributed toward incubation of the clutch. Nest mates usually hatched within 24 h, but occasional asynchrony was also observed. Of 28 clutches where hatching dates for all chicks were known, 75% hatched all members synchronously (within 24 h). In four clutches (14.3%), a single egg took one day longer to hatch than those in the rest of the clutch, in two clutches (7.1%), three days elapsed before the last egg hatched and, in one clutch, the span was four days.

Guira Cuckoo chicks grow very rapidly and by the fifth or sixth day can leave the nest and move to the far side of the tree if approached. Fledging typically occurs around the 15th day after hatching, but occurred as early as the 12th day ($\bar{x}$ = 15.1 ± 2.2 days, n = 13).

Nesting success.—In 1987, 33 breeding cycles were monitored for all or part of the cycle. In-

TABLE 4. Number of nests classified according to type of egg losses observed (includes only eggs found on ground): (1) sequential = 1 egg per day; (2) partial = simultaneous loss of several eggs in one day; (3) whole = simultaneous loss of all eggs in one day. Includes both successful and failed nests. Nests classified in one category only (with less-common taking precedence over more-common behavior). For example, a nest classified in "whole clutch" may also have had eggs lost sequentially.

Type of loss	Nests where egg losses occurred				
	Prior to incubation	During incubation	During pipping	After hatching	Totals (%)
Sequential	25	—	4	8	37 (66.1)
Partial	5	7	—	—	13 (23.2)
Whole clutch	5	1	—	—	6 (10.7)
Total (%)	35 (62.5)	8 (14.3)	4 (7.1)	8 (16.1)	55

cluded are five groups that bred twice and one that bred three times within the first six months of the rainy season. Of these, three produced hatchlings both times, two did so in only one of the nesting attempts, and the group that attempted breeding three times was successful only in its first two nestings.

In 1988, 28 breeding cycles were monitored, of which five were second nestings. In these renesting groups, three were unsuccessful both times, and two groups produced chicks only once.

In 1990, 25 breeding cycles were monitored. Of these, five were renesting attempts in which just one group was unsuccessful both times. Of all nesting attempts recorded ($n = 86$), 35.0% resulted in nest desertion, either during laying or incubation. Some of the desertions during incubation probably resulted from disturbance to the nest from research-related activities.

Loss of eggs or young obviously due to predation apparently was not a major cause of mortality (5 of 86 nests). Predation was inferred whenever the whole clutch or brood disappeared simultaneously or the nest and/or contents were visibly damaged (other cases of predation may have gone undetected). Predation after the chicks had hatched was obvious in only one case; the other four cases involved full sets of eggs.

Nests classified as "failed" (8.1% of 86 breeding attempts) were those where some young hatched successfully, then all died within several days. Because nestlings did not all disappear simultaneously, and some were occasionally found dead and mutilated on the ground, I did not include these nests in the obvious-predation category. This "sequential disappearance" of nestlings also occurred in nests where several young managed to survive to fledging.

This type of mortality is discussed elsewhere (Macedo 1991). Finally, at least one nestling survived to fledging in 46.5% ($n = 86$) of the nests, which therefore were considered successful. Probit analysis indicated that the probability of nesting successfully (defined as fledging at least one young) did not change across group sizes ($X^2 = 15.46$, $P > 0.05$, $n = 62$ nests where group size was known).

Analysis of nesting success is restricted to the 33 nests where at least one chick hatched and where data for laying, losses and hatching were obtained (Table 5). The survival of eggs and chicks from laying to fledging depended on several events. Of the 331 eggs laid in the 33 clutches, 32.0% were found broken on the ground or disappeared. Of all eggs incubated, 69.8% eventually hatched. Of all chicks that hatched, approximately 45.0% did not fledge. Thus, only 26.0% of 331 eggs developed into fledged young.

Groups were classed as small (2 to 5 adults), medium (6 to 8), or large (9 to 13). The proportions of eggs lost were similar across these group-size categories (Table 6), roughly one-third of the total laid. Also, the proportions of chicks lost and chicks fledging did not differ significantly as a function of these group-size categories.

Two variables—clutch size and number of eggs lost (Table 7)—varied significantly with group size. A positive correlation was found between clutch and group sizes ($r = 0.66$). The other positive correlation was between group size and number of lost eggs ($r = 0.56$). However, there was no significant positive correlation between group size and the number of young that hatched or fledged. In fact, on a per capita basis, there was a significant negative relationship between group size and number of

TABLE 5. Nesting success of Guira Cuckoos in Brasilia, Brazil (1987, 1988 and 1990). Includes only nests with complete data where at least one chick hatched.

Number	Year			Total or average (SD)
	1987	1988	1990	
Successful nests	13	11	9	33
Total eggs laid	120	117	94	331
Eggs per nest	9.2	10.6	10.4	10.0 (3.7)
Eggs incubated per nest	6.0	7.6	7.1	6.8 (2.6)
Eggs apparently tossed[a] per nest	2.4	1.6	2.9	2.3 (2.5)
Eggs disappeared per nest	0.9	1.5	1.0	1.1 (1.2)
Hatched per nest	4.5	4.8	5.1	4.8 (2.5)
Chicks missing[b] per nest	2.4	2.4	1.6	2.2 (2.4)
Fledged per nest	2.1	2.5	3.6	2.6 (2.0)
Overall percent of eggs apparently tossed[a]	25.8	15.4	27.7	23.0
Overall percent of disappeared eggs	9.2	13.7	9.6	10.8
Overall percent of incubated eggs that hatched	74.4	63.9	71.9	69.8
Overall percent of eggs that fledged	22.5	23.1	34.0	26.0
Overall percent of chicks that disappeared	53.5	49.1	30.4	45.2

[a] Eggs found on ground.
[b] Includes chicks that died as result of starvation, predation, infanticide, or other cause.

young that fledged ($r = -0.67$, $P < 0.05$; Fig. 5).

DISCUSSION

In communally breeding birds, group membership yields few, if any, per capita reproductive benefits (Vehrencamp 1977, 1978, Koenig 1981b, Emlen and Vehrencamp 1983). Koenig (1981b) found that in Acorn Woodpeckers (*Melanerpes formicivorus*), per capita reproductive success declines with increasing group size. An-

other example is the Groove-billed Ani, where per capita reproductive success roughly decreases across different group sizes (Vehrencamp 1977, 1978).

In cooperative species, however, where only one pair reproduces, helpers may enhance the breeders' reproductive success, although the per capita reproductive benefits do not increase with group size (Fry 1972, Emlen 1981, Woolfenden 1981, Woolfenden and Fitzpatrick 1984, Rabenold 1985).

TABLE 6. Reproductive output (averages, with ranges in parentheses) according to group size (small, 2 to 5 birds; medium, 6 to 8; and large, 9 to 13). Includes only nests where at least one young fledged, and for which group size known.

	Group size (n)		
	Small (6)	Medium (14)	Large (7)
Eggs laid	8.0 (5–13)	9.6 (4–13)	13.4 (8–20)
Eggs apparently tossed[a]	1.5 (0–5)	2.0 (0–5)	3.4 (0–12)
Eggs disappeared	0.3 (0–1)	0.8 (0–3)	1.9 (0–5)
LT/L[b]	0.23	0.30	0.40
Chicks disappeared	1.0 (0–3)	1.4 (0–5)	2.3 (0–7)
C/L[c]	0.13	0.15	0.17
Chicks fledged	3.0 (1–6)	3.1 (2–5)	3.6 (2–6)
F/L[d]	0.38	0.32	0.27

[a] Eggs found on ground.
[b] Lost/laid = overall proportion of eggs lost (includes eggs apparently tossed and those that disappeared).
[c] Chicks disappeared/laid = overall proportion of chicks that disappeared.
[d] Chicks fledged/laid = overall proportion of chicks that fledged.

TABLE 7.   Correlation coefficients (Pearson's r) among reproductive and group parameters for Guira Cuckoos in central Brazil (1987, 1988 and 1990).[a]

Variable	Variable							
	CS	%CL	%EL	HAT	CHL	CHF	GS	EGGSL
Clutch size (CS)	—	0.12	0.24	0.48**	0.31	0.25	0.66**	0.72**
Percent chicks lost (%CL)		—	0.17	0.15	0.72**	−0.69**	0.11	0.09
Percent eggs lost (%EL)			—	−0.21	−0.10	−0.16	0.28	0.80**
Chicks hatched (HAT)				—	0.69**	0.46**	0.33	0.08
Chicks lost (CHL)					—	−0.33	0.18	0.03
Chicks fledged (CHF)						—	0.20	0.07
Group size (GS)							—	0.56**
Eggs lost (EGGSL)								—

*, $P < 0.05$; **, $P < 0.01$.

[a] All sample sizes 33 except for group size, where $n = 32$. Analyses involve only incubated clutches.

Because data on cooperative and communal breeders point to an overall reproductive disadvantage for group members, Koenig and Pitelka (1981) proposed that resource localization (e.g. limited number of breeding sites, sexual partners, etc.) may play the primary role in selecting for cooperative/communal breeding. Habitat saturation (i.e. lack of suitable unused breeding habitat) has been the most popular hypothesis for explaining the occurrence of cooperative and communal breeding (Selander 1964, Stacey 1979, Brown 1987). For two species, the Acorn Woodpecker and Florida Scrub Jay, multigenerational data are consistent with this hypothesis. Helpers only remain in their natal territories until a territorial vacancy occurs, at

which time they disperse (Koenig 1981a, Woolfenden and Fitzpatrick 1984, Hannon et al. 1985).

However, group membership may also confer individual advantages (e.g. increased foraging efficiency and protection from predators) that outweigh the loss in breeding success. Within this context, Stacey and Ligon (1987) proposed an alternative model for the evolution of cooperative breeding, based on the lifetime rewards associated with philopatry rather than on ecological constraints.

One purpose of my study was to evaluate possible explanations for social behavior in Guira Cuckoos. Habitat saturation is said to occur when territories "suitable for breeding" are scarce (Brown 1987). Distinguishing suitable
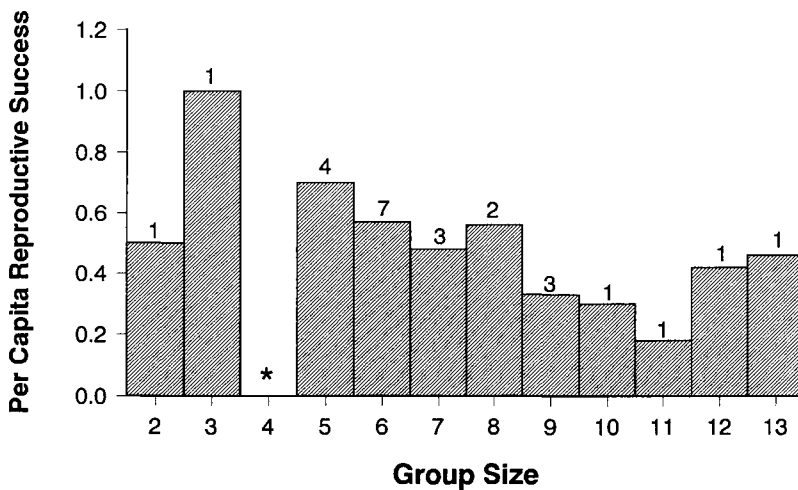

Fig. 5.   Per capita reproductive success (number of chicks fledged divided by total number of adults for each group category) according to group size for Guira Cuckoo nests in central Brazil. Sample sizes shown above bars; asterisk for group size 4 indicates that no nests were evaluated. Includes only nests where at least one young fledged and group size was known.

from unsuitable habitat, as viewed by the animals themselves, turns out to be a tricky problem. The habitat occupied by guiras in the study site is relatively homogeneous, composed mostly of well-tended lawns and introduced ornamental trees. To the degree that my criteria for identifying potential nesting sites are valid, an average of about 65% of such sites were occupied in a given year (71% in 1987; 58% in 1988; and 65% in 1990). There were cases of nest sites left vacant one year and used another year (64.5% of 31 breeding sites). On other occasions, a group nested adjacent to what appeared to be a suitable unoccupied breeding site, such that group members presumably could have left the group to breed as pairs (25.8% of 31 breeding sites). When the estimated occupied area of active groups was increased (e.g. radius of 600 m), the number of empty nest sites available for breeding (i.e. not included within an active group's area) drops considerably. Nonetheless, even with this more conservative measure, empty nest sites were still available each year (the percent available ranged from 10 to 26%). The experimental introduction of lure birds around empty but presumably suitable adjacent sites attracted guiras from neighboring breeding groups in only one case, when the testing distance was less than 300 m.

These preliminary tests and the distribution patterns observed in guira groups suggest that some habitat may have been unoccupied every year. However, to evaluate objectively the habitat-saturation model, a thorough analysis of habitat quality (including some precise evaluation of the nesting tree) and true territory size (through estimates of foraging area) is needed. In Guira Cuckoos, within-group relatedness of some adults (Quinn et al. in press) could play a role in group cohesiveness.

In some cooperative and communal breeders, studies have shown that, despite the availability of nearby suitable breeding space, nonbreeding group members frequently do not disperse (e.g. Splendid Wrens, *Malurus splendens*, Rowley et al. 1986; Acorn Woodpeckers, Stacey and Ligon 1987; Harris' Hawks, *Parabuteo unicinctus*, Bednarz and Ligon 1988; Red-cockaded Woodpeckers, *Picoides borealis*, Walters et al. 1988). Available suitable habitat in itself sometimes is not sufficient to ensure successful breeding. For Stripe-backed Wrens (*Campylorhynchus nuchalis*) in Venezuela, for instance, the limiting resource for dispersing young is a set of helpers,

not empty habitat (Rabenold 1990, Wiley and Rabenold 1984). In another study of this same species, DNA fingerprinting revealed that male auxiliaries sometimes shared paternity with the dominant male. This reproductive benefit may help explain the delayed dispersal of auxiliary males in this population (Rabenold et al. 1990).

Most Guira Cuckoo groups moved to a different tree within their territories when attempting to breed a second time in the same season. It may be advantageous for a group to have territories that allow nesting in different trees. By moving to a different site a group may decrease the effects of nest infestation by parasitic mallophaga (Abrahamovich and Cicchino 1985). A second advantage may be related to nest detection by potential predators.

The guira association with the Araucaria *per se* may be a behavioral novelty, dating from the planting of these trees throughout the savanna region of central Brazil. At present, it is unknown whether similar preference for Araucaria is displayed by other guira populations in other parts of the range. Comparative studies could determine whether there is an increased susceptibility to nest predation in those populations in regions devoid of Araucaria (or other thorny trees in general).

The most common Guira Cuckoo egg-loss pattern, where early eggs are laid and subsequently tossed, is similar to that of the anis. For Guira Cuckoos, however, egg losses frequently occurred throughout incubation. Sometimes almost all eggs (Tables 3 and 4) were lost (i.e. found on the ground) simultaneously. Occasionally, eggs were lost after incubation started, or only part of a clutch was lost. A few times one or two eggs were lost as the time of hatching approached.

To the extent that lost eggs are evicted by group members (i.e. tossing), the pattern found in Guira Cuckoos suggests two alternative systems—subtle recognition or "sabotage." If individual females are capable of recognizing their own eggs within a mixed clutch, they presumably can toss out only those belonging to other females. As nest space and food are limited, a breeding individual, thus, could increase the proportion of her offspring in the nest by selectively tossing other females' eggs. Whether such an egg-recognition mechanism is in operation in this species is uncertain. In other species there apparently are more reliable cues characterizing eggs from different females.

Vehrencamp (1976) indicated that Groove-billed Ani eggs belonging to individual female clutches can be distinguished based on size, shape, and color differences. Egg-recognition capability has been documented for Ostriches (*Struthio camelus*; Bertram 1979), where the dominant female effectively increases her own fitness by rolling other females' eggs away from the communal nest.

Despite the use of several egg variables, I was unable to assign Guira Cuckoo eggs objectively to different females based on egg characteristics. I discovered no reliable physical differences between eggs from different females. If the birds are unable to distinguish between clutches in the nest, it is unlikely that they would toss eggs indiscriminately and risk losing some of their own investment.

One alternative sabotage explanation for the protracted tossing occurring during incubation is that the nonbreeding birds (Quinn et al. in press) in the group are attempting to undermine the group's breeding effort altogether. If an individual is prevented from breeding (e.g. due to lack of mate, social subordination, etc.), it may be advantageous to sabotage that particular nesting attempt so that a new nest may be initiated at a shorter time interval. A group member that does not contribute to the clutch during the first breeding effort could be more successful in subsequent nesting attempts. During my research, 10 nests (11.6% of 86 breeding attempts) never went past the egg-laying stage, since eggs were lost continuously. Such groups eventually abandoned the nest after as many as 15 eggs had been tossed. On three occasions, activity by the same group resumed within five to eight weeks. To test this sabotage hypothesis, one would predict that egg destruction be primarily done by nonbreeding group members, and that such individuals enjoyed higher reproductive success as a result.

As with many other communal/cooperative breeders, there appears to be little short-term breeding advantage gained from group membership. The positive correlation between clutch and group sizes suggests the communal nature of reproduction; many of the members are not just "helpers" but potential parents. However, per capita reproductive success (no. fledglings/no. group members) declines with increasing group size (Fig. 5), and the probability of nesting successfully is not known to be affected by group size. Of course, status inequalities among group members could make group breeding advantageous for some birds and disadvantageous for others, even over a short time span.

In the population of Groove-billed Anis studied by Vehrencamp (1976), 49% of the groups had only one female contributing to the clutch. In my study area, only 5.8% ($n = 86$) of the groups possibly had only one female in the nest. Single-female clutches were suspected when all three of the following criteria were applicable: (1) fewer than seven eggs were laid (an estimated maximum clutch size for Guira Cuckoos, taking into consideration Davis' [1942] and Vehrencamp's [1976] assessments for other crotophagines); (2) no eggs were found on the ground; and (3) only one egg was found in the nest each 24-h period. Apparently, in the study area, very few individuals engaged in noncommunal breeding.

Correlations between group size and clutch size, number of eggs hatching, and eggs lost are to be expected in a communal species. Communal clutch size increases with group size, but the number of young that fledge does not follow the same pattern. Although egg loss contributes to a decrease in clutch size, there is no significant correlation between clutch size and percent of eggs lost. Thus, between incubation and fledging, some additional factor(s) limit the number of young that survive. Possibilities include predation, starvation, fatal nest falls, and infanticide (Macedo 1991).

The foraging habits of the Guira Cuckoos are similar to those of the Groove-billed and Smooth-billed anis (Vehrencamp 1976, Loflin 1983). More specifically, the "sentinel" behavior described by Loflin (1983) for Smooth-billed Anis is similar to the nest attendance behavior seen in the Guira Cuckoo and may have comparable functional value. He pointed out that having sentinels may be one of the primary advantages for group living in that species.

Nest-attendance behavior seen in Guira Cuckoos also occurred during the nesting period, especially after the nestlings hatched. Most of the time, one guira perched near the nesting tree and remained alert while the remaining group members foraged out of sight of the nest. The approach of a human, for example, elicited loud staccato calls from these birds, resulting in the immediate convergence of group members on the nest. Nest attendance may provide a major benefit of sociality for crotophagines in general.

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