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GROUP COMPOSITION, MATING SYSTEM, AND RELATEDNESS IN THE COMMUNALLY BREEDING GUIRA CUCKOO (*GUIRA GUIRA*) IN CENTRAL BRAZIL

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Abstract.—Guira Cuckoos (*Guira guira*) are cooperative breeders with joint nests, where several breeding and nonbreeding males and females remain in a cohesive unit through repeated breeding attempts within a single territory. We used nine microsatellite markers to analyze parentage and relatedness in a population of Guira Cuckoos in central Brazil, comprising 225 progeny from 51 breeding attempts. The Guira Cuckoos presented a variety of mating patterns, polygynandry and monogamy being the most common. We found low levels of extragroup fertilization, and cobreeding males and females within groups shared reproduction to some extent. Relatedness among group members varied. In some groups, adult males were more related to each other than expected by chance and, overall, males within groups were genetically more similar than background genetic relatedness. In addition, for some of the groups, males were more genetically similar than expected by chance in different years, which indicates some degree of male philopatry or possible joint dispersal by male kin. Male Guira Cuckoos were more likely to breed closer to their natal territories than females, a pattern of dispersal commonly found in birds. We also found that nonbreeding adult males had a higher number of nondescendent kin (chicks and embryos) in the nest than expected from background genetic relatedness, which implies that possible indirect reproductive benefits may have been a significant factor in the evolution of this breeding system. *Received 10 October 2010, accepted 7 May 2011.*

Key words: cooperative breeding, genetic parentage, *Guira guira*, joint-nesting, microsatellite, relatedness

Composición de Grupos, Sistema de Apareamiento y Parentesco en la Especie con Cría Comunal *Guira guira* en el Centro de Brasil

Resumen.—La especie *Guira guira* presenta cría cooperativa con nidos comunales, donde varios machos y hembras reproductores y no reproductores se mantienen en una unidad cohesiva a través de varios intentos de cría dentro de un mismo territorio. Empleamos nueve marcadores microsatélites para analizar la paternidad y el parentesco en una población de *G. guira* del centro de Brasil, teniendo en cuenta 225 crías producto de 51 intentos reproductivos. Las aves presentaron una variedad de patrones de apareamiento, entre los que la poliginandría y la monogamia fueron los más comunes. Encontramos niveles bajos de fertilización extragrupo, y los machos y hembras que se reprodujeron juntos en los grupos compartieron la reproducción en algún grado. El grado de parentesco entre miembros de los grupos fue variable. En algunos grupos, los machos adultos eran más relacionados entre sí que lo esperado por azar y, en general, los machos de los grupos eran más similares entre sí en relación con el grado de relación genética general de la población. Además, en algunos de los grupos, los machos eran genéticamente más similares que lo esperado por azar en diferentes años, lo que indica algún grado de filopatría en los machos o que machos emparentados se dispersan juntos. Los machos fueron más propensos a reproducirse cerca de sus territorios natales que las hembras, un patrón de dispersión observado comúnmente en las aves. También encontramos que los machos adultos no reproductores tenían un número mayor de parientes no descendientes (pichones y embriones) en los nidos que lo que se esperaría con base en el grado general de parentesco de la población, lo que implica que los beneficios reproductivos indirectos podrían haber sido un factor significativo en la evolución de este sistema reproductivo.

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Communal breeding is a rare form of cooperative breeding in which more than one group member of the same sex breeds synchronously using the same nest (Brown 1987, Vehrencamp and Quinn 2004). The evolution of cooperative breeding may have been favored by gains through indirect inclusive fitness (Brown 1987). Indeed, in some cooperative species helpers can be genetically related to breeding adults (Cockburn 1998), and relatedness among cobreeding adults has also been detected in some communal breeders (Jamieson 1997, Haydock et al. 2001). However, indirect fitness benefits are not a requirement for cooperative breeding to occur, because direct benefits to group members can be sufficient for the maintenance of cooperative breeding (Clutton-Brock 2002).

The Crotophaginae consist of a monophyletic group of four species of Neotropical cuckoos that are all communal breeders (Davis 1942, Hughes 2003). The two genera in the subfamily, *Crotophaga* and *Guira*, are quite different in their social and breeding behavior. The three *Crotophaga* species occur in groups of varying sizes but generally breed as monogamous pairs. The Greater Ani (*C. major*), for instance, breeds in groups that typically contain two or three socially monogamous pairs (Riehl and Jara 2009). Groove-billed Ani (*C. sulcirostris*) groups usually contain two monogamous breeding pairs, but single pairs without helpers are also common (Vehrencamp et al. 1986, Koford et al. 1990), whereas Smooth-billed Anis (*C. ani*) form larger groups that frequently contain nonbreeders (Vehrencamp and Quinn 2004). By contrast, Guira Cuckoos (*G. guira*) can have up to seven females laying in joint nests (Cariello et al. 2002), and a previous preliminary study, based on a small number of nests, suggests that these birds have a polygynandrous mating system with nonmonogamous mating relationships among adult group members (Quinn et al. 1994).

Female joint nesting in crotophagines comes at a cost because competitive reproductive behaviors are frequently exhibited by group members in the form of egg destruction (Vehrencamp and Quinn 2004) and infanticide (Macedo and Melo 1999, Quinn et al. 2010). In Groove-billed and Greater Anis, females rarely begin laying synchronously, and early-laid eggs are at a higher risk of ejection, and this typically ends only when all females enter the laying sequence (Vehrencamp et al. 1986, Riehl and Jara 2009). Because females apparently cannot recognize their own eggs, they eject any eggs they find in the nest prior to the beginning of their own laying (Vehrencamp 1977, Riehl 2010a). As a result, early-laying females have more eggs ejected than late-laying females, whereas the last female to enter the laying sequence rarely loses eggs (Vehrencamp 1977, Riehl and Jara 2009).

Egg ejection in Guira Cuckoos and Smooth-billed Anis (also egg burial in the latter) continues throughout the laying period and affects all females independently of their position in the laying sequence (Macedo et al. 2004a, b; Schmaltz et al. 2008). Brood reduction also occurs in Guira Cuckoos, in which ~50% of chicks are eliminated through infanticide (Macedo and Melo 1999). There is circumstantial evidence that infanticide also occurs in Smooth-billed and Greater anis (Riehl and Jara 2009, Quinn et al. 2010).

The costs associated with communal breeding in the crotophagines are probably compensated by the direct benefits that group members may experience because of social living. For instance, nest predation in the Greater Ani is lower for groups that consist of three pairs than for groups of two pairs (Riehl 2010b), whereas adult Groove-billed Anis that nest in groups have a lower predation risk than solitary nesters (Vehrencamp 1978). Also, cooperation occurs during nest building, territory defense, incubation, parental care, and sentinel behavior during foraging, although relative effort varies among individuals (Macedo 1992, Vehrencamp and Quinn 2004, Rielh and Jara 2009). In addition, group members that help to rear nondescendent kin may also gain some indirect fitness benefits (Brown 1987).

Apart from the Greater Ani, in which it has been shown that groups are composed of unrelated, socially monogamous pairs (Riehl 2010b), very little is known about the genetic breeding system of crotophagines; to date, only one group of Smooth-billed Ani (Quinn et al. 2010) and four groups of Guira Cuckoo (Quinn et al. 1994) have been genetically assessed. Thus, there is no clear understanding about the general patterns of kinship within and among groups. Without information concerning the potential indirect fitness benefits of communal breeding, we remain largely ignorant about the evolutionary pathways that may lead to this rare social breeding system.

We investigated the genetic basis of communal breeding for Guira Cuckoos in central Brazil to describe their mating system, dispersal patterns, and group composition. The complexity of the social and mating system expressed in various degrees in the other crotophagines, as well as the preliminary study of genetic relations in Guira Cuckoos, led us to test the following hypotheses: (1) cobreeders within groups have low levels of kinship, (2) polygynandry is the most common mating pattern, (3) females disperse greater distances from their breeding territories than males, and (4) breeding philopatry is exhibited by both sexes.

Methods

Study site and group monitoring.—The study took place in a 3,000-ha suburban area of central Brazil, close to Brasília (15°47'S, 47°56'W; altitude 1,158 m) in four breeding seasons (1997, 1998, 2000, and 2001). The area contains fragments of savanna, housing developments, cultivated fields, and residential gardens. The preferred nesting sites for Guira Cuckoos were introduced Paraná Pine trees (*Araucaria angustifolia*), with breeding activity concentrated in the rainy season (August–March).

Before the breeding season, we searched for nests in previously used sites because groups typically reuse old nests. These were visited every other day to check for breeding activity and then daily when nesting started in order to monitor egg laying and ejection. We collected ejected eggs during 2000 and 2001 by placing camouflaged nylon fishing nets (mesh = 15 mm) beneath all active or inactive nests. We are certain that almost all ejected eggs were collected by using these nets because practically all egg ejections we ever observed consisted of individuals dropping the eggs directly over the nest's rim. We also counted the number of adults around the nest during successive visits to estimate group size from repeated maximum counts.

Embryo and chick sampling.—During the 1997 and 1998 breeding seasons, we banded chicks and took 0.1-mL blood samples by venipuncture on the first day after hatching. Chicks were banded using a combination of different-colored plastic straws cut and fitted to their tarsi. Blood samples were stored at –20°C in lysis buffer (0.1 M Tris HCl, 4 M urea, 0.2 M NaCl, 0.01 M EDTA and 0.5% n-lauroylsarcosine). Ejected eggs from these two breeding

TABLE 1. Polymorphic microsatellite loci used in genotyping the Guira Cuckoo of central Brazil. For each locus, we list number of alleles (k), primer annealing temperature (T_a) in Celsius (°C), $MgCl_2$ concentration, observed heterozygosity (H_o), expected heterozygosity (H_e), probability of Hardy-Weinberg equilibrium (P), and exclusion probabilities for one parent (Excl 1) and the second parent when the first parent is known (Excl 2). Data refer to 284 individuals.

Locus	k	T_a	$MgCl_2$ mM	H_o	H_e	P	Excl 1	Excl 2	Source
G398	17	60	1.5	0.848	0.892	0.09	0.360	0.219	Muniz et al. 2003
G1	14	60	1.0	0.821	0.869	0.38	0.416	0.261	Muniz et al. 2003
G963	8	58	1.0	0.774	0.857	0.42	0.454	0.290	Muniz et al. 2003
G30	13	60	0.5	0.865	0.862	0.91	0.440	0.280	Muniz et al. 2003
Ani450B2	20	57	0.5	0.879	0.885	0.10	0.379	0.234	Blanchard and Quinn 2001
G5	16	58	1.0	0.871	0.847	0.43	0.472	0.306	Muniz 2002
G17	13	58	0.5	0.824	0.871	0.33	0.417	0.262	Muniz 2002; Robyn Strange
CL9	32	59	1.5	0.927	0.933	0.05	0.240	0.137	Robyn Strange
G463[a]	12	57	0.5	0.422	0.828	0.01	0.512	0.340	Muniz et al. 2003
Total							>0.999	>0.999	
Total excluding G463							>0.999	>0.999	

[a]Significantly different from Hardy-Weinberg equilibrium due to a frequency of 32% null alleles. Not used in CERVUS analysis.

seasons were not incubated in the laboratory and were therefore not genotyped.

Under natural circumstances, when infanticide occurs it takes place soon after hatching (Macedo and Melo 1999). To avoid the loss of data, eggs in the 2000 and 2001 seasons were substituted with dummy plaster eggs on the 10th day of incubation (mean incubation period = 12 days). Plaster eggs were hand painted and had the average weight of a Guira Cuckoo egg, and in almost every case the birds incubated the clutch of dummy eggs (Macedo et al. 2004b). The removed eggs were incubated in a commercial incubator IP.70 (Ecológica Ltda) at 38°C with humidity at 50%. After hatching (0–6 h) we took 0.1-mL blood samples from the chicks as described above, and within 12 h we returned the chicks to their nests in the order that they hatched in the laboratory. To ensure that the adult birds would brood and feed chicks after they were returned to the nest, we always left one randomly chosen real egg in the nest to provide the stimuli of chick vocalizations within the egg and during hatching. The chicks that hatched from the single egg remaining in the nest were processed in the same way as the ones incubated in the laboratory. Ejected eggs collected from nets below the nests were incubated for 5 days, after which we opened the eggs and collected tissue samples, which were stored in lysis buffer at –20°C.

In the four breeding seasons, we sampled 148 chicks (40 in 1997; 10 in 1998; 40 in 2000; 58 in 2001) and 77 embryos (64 in 2000; 13 in 2001) produced by 26 breeding groups. We collected genetic data for 51 clutches, of which 34 hatched successfully, whereas 17 were abandoned. This high pattern of nest desertion is typical for the species and usually occurs after numerous eggs have been laid and consistently ejected from the nest (Macedo 1992).

Adult banding.—During the 2000 and 2001 breeding seasons, we captured adults using a funnel trap surrounded by mist nets (mesh = 61 mm). The trap was a wire-mesh-covered aluminum cube (1.2 m on each side) with funneled openings on all four sides in addition to a slit in the cage ceiling, which allowed birds to enter but not leave. We used a hand-reared Guira Cuckoo together with playbacks of calls to lure the birds into the trap. The lure bird was enclosed in an individual cage within the trap, which allowed visual but not physical contact between it and other birds inside the trap. In 1997 and 1998, birds were captured in the same way, but we also used entangling monofilament "noose mats" surrounding the cage of the lure bird (Macedo 1992). We collected 0.5-mL blood samples from the jugular vein of captured birds and stored them in lysis buffer at –20°C. Birds were banded with a numbered metal ring from Brazil's bird-banding agency (CEMAVE) and three other plastic colored rings for individual identification. Because we were only successful in capturing adults by simulating territorial intrusions, we had a strong male bias in our captures: 48 males (4 in 1997; 2 in 1998; 26 in 2000; and 16 in 2001) and 11 females (2 in 1997; 1 in 1998; 6 in 2000; and 2 in 2001), for a total of 59 adults.

Laboratory procedures and population genetic diversity analysis.—Genomic DNA was extracted from blood and embryo samples using a standard protocol with overnight digestion with proteinase K and subsequent phenol–chloroform extraction and alcohol precipitation (Sambrook and Russell 2001). All adults, chicks, and embryos were molecularly sexed using specific markers P2 and P8 for the ZW chromosomes (Griffiths et al. 1998), and we used nine microsatellites for DNA genotyping analysis (Table 1). Two of these were developed for Smooth-billed Anis (ANI450B2 and CL9) and the others for Guira Cuckoos (Muniz 2002). Polymerase chain reaction (PCR) was performed in 20-μL reactions that contained ~20 ng of template DNA, 1× Promega buffer, 0.5–1.5 mM of $MgCl_2$, 2 pmol of each primer, 0.05 mM each of dNTP, and 0.5 units of Taq polymerase (Bioline) made up to 20 μL with sterile H_2O. The reactions were denatured at 94°C for 4 min followed by 31 cycles of 94°C for 15 s, primer-specific annealing temperature for 40 s, 72°C for 40 s and a final elongation step at 72°C for 5 min (Table 1). The PCR products were run on a Beckman Coulter CEQ 8000XL system using the Fragment 3 program following the manufacturer's protocol.

We used GENEPOP, version 3.4, to analyze deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium for all nine loci with 10,000 iterations (Raymond and Rousset 1995). We used MICRO-CHECKER (Van Oosterhout et al. 2006)

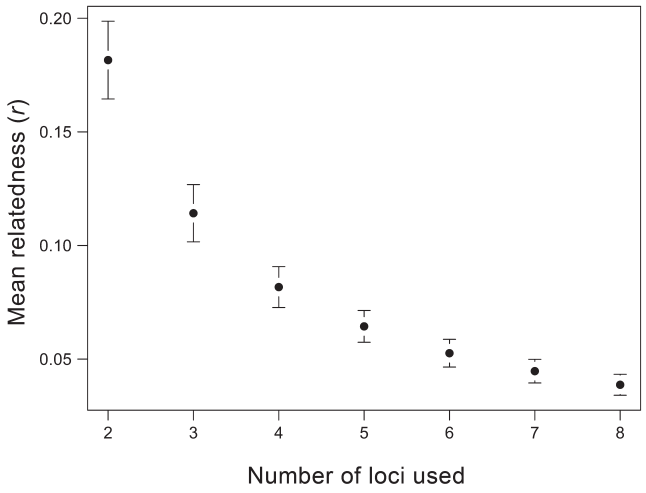

FIG. 1. Rarefaction analysis of Guira Cuckoos from central Brazil showing the relationship between the number of loci used and the mean difference between consecutive relatedness (*r*) estimates and standard deviation for 1,000 simulations.

to check for null alleles, large allele dropout, and stuttering. G463 presented high levels of null alleles and was dropped from analyses in CERVUS (Table 1).

Relatedness estimation.—We used SPAGEDI, version 1.2 (Hardy and Vekemans 2002), to estimate genetic relatedness (1) among all captured adults; (2) among all sampled chicks, including ejected eggs; and (3) among adults and chicks, including ejected eggs. We calculated estimates of pairwise relatedness (*r*) using Queller and Goodnight (1989), Li et al. (1993), Lynch and Ritland (1999), and Wang (2002). We tested which of the four estimates performed best on a data set consisting of parent–offspring (PO) pairs assigned by CERVUS using all captured males as potential fathers, by testing their deviation from the expected value of 0.5 using two-tailed *t*-tests.

We performed a rarefaction analysis to determine the change in relatedness estimates with additional loci. For this we used the loci in HWE, Queller and Goodnight's *r*, and the web-based software RE-RAT (Schwacke et al. 2005). Loci were added without replacement one-by-one until all eight loci were selected at the same time (Girman et al. 1997). This was repeated 1,000 times, and changes in relatedness estimates were determined by calculating the mean relatedness difference as loci were added. There was little change to the Queller and Goodnight relatedness *r* estimator after seven to eight loci were sampled (Fig. 1), which suggests that the use of more than seven loci would have little effect on our estimates of relatedness.

Parentage analysis.—We used CERVUS, version 3.0, to assign parentage with a default typing error rate of 1% (Kalinowski et al. 2007), and 97.3% of loci were typed. G463 was excluded because of high levels of null alleles. We had a strong male bias in captured birds, so we ran different simulations for the different estimates of the numbers of unsampled candidate parents. Assuming an equal sex ratio and using maximum counts of adults, we estimated that an average of 47% of males and 13% of females were genotyped in each nest.

As recommended by Marshall et al. (1998), we first ran analyses with females, the sex with fewer samples. We used all 11 females as potential mothers and allowed up to one mismatch between mother–offspring (MO) pairs. We could not establish every nestling with its mother because many females were not sampled, and both MO pairs and offspring without maternity assignments were used in the paternity analysis. We proceeded with two analyses for the fathers, using different numbers of potential fathers. In the first analysis, we used the number of males captured at the nest as the number of potential fathers ($\bar{x}$ = 5.3 ± 1.9 SD). In the second simulation, we used as candidate fathers all adult males in the study area (n = 48). We accepted as PO pairs those that were significantly assigned by CERVUS with up to one mismatch, provided that they had pairwise *r* values ≥0.34, the minimum value found for PO pairs with zero mismatches (see below); this was also the lowest value found for PO pairs in nests where we sampled all chicks and where monogamy was the established mating pattern. When more than one male was assigned as parent as a result of the different simulations, we considered the male that was an active group member (i.e., participated in nest defense and parental behavior) the parent.

We also used the list function in ML-RELATE (Kalinowski et al. 2006) to infer parentage, allowing locus G463 to be included in the analyses (Table 1). This analysis accommodates null alleles, calculates the log-likelihood of four relationships (unrelated [U]; half sib [HS]; full sib [FS]; and PO), and lists the highest-likelihood relationship. If PO was the most likely relationship and presented up to one mismatch, we accepted the pair as PO.

Pedigree analysis.—Pedigrees for each nest were drawn by looking first at PO assignments and then at offspring relatedness, and the latter was evaluated with ML-RELATE using the list function. We checked the results with Queller and Goodnight's (1989) *r* value and tested for possible deviations from the expected (0.5 for FS and 0.25 for HS) using two-tailed *t*-tests. This indicated the number of adults breeding in a nest. For example, two chicks can be assigned by ML-RELATE as FS without the adult birds having been sampled (Fig. 2). Therefore, most of our mating-system analyses were based on chick and embryo relatedness within nests, because we successfully sampled chicks from eggs that were not ejected as well as ejected eggs that were caught by nets (i.e., 63% of all eggs laid; $\bar{x}$ = 0.67 ± 25 SD; Appendix).

Relatedness among adults.—We used GROUPRELATE (Valsecchi et al. 2002) to estimate the relationship among adults. The program calculates Queller and Goodnight's (1989) *r* for all pairwise relations, partitions the results by sex within groups, and tests whether the mean *r* is above chance level.

We classified as breeders those adults assigned to offspring by either CERVUS or ML-RELATE. We classified as nonbreeders any adults that were not assigned as breeders but that were captured in the group and participated in nest vigilance, incubation of eggs, and feeding of nestlings. We also calculated average relatedness for dyads of males in five categories: adult males captured at the same nest (all males pooled together within the group, irrespective of their breeding condition); breeding males that belonged to the same nest; breeding and nonbreeding males that belonged to the same nest (dyads in this analysis necessarily had a different reproductive condition; thus, only breeding males with nonbreeding males); nonbreeding males and progeny (chicks and embryos) from the same nest; and nonbreeding

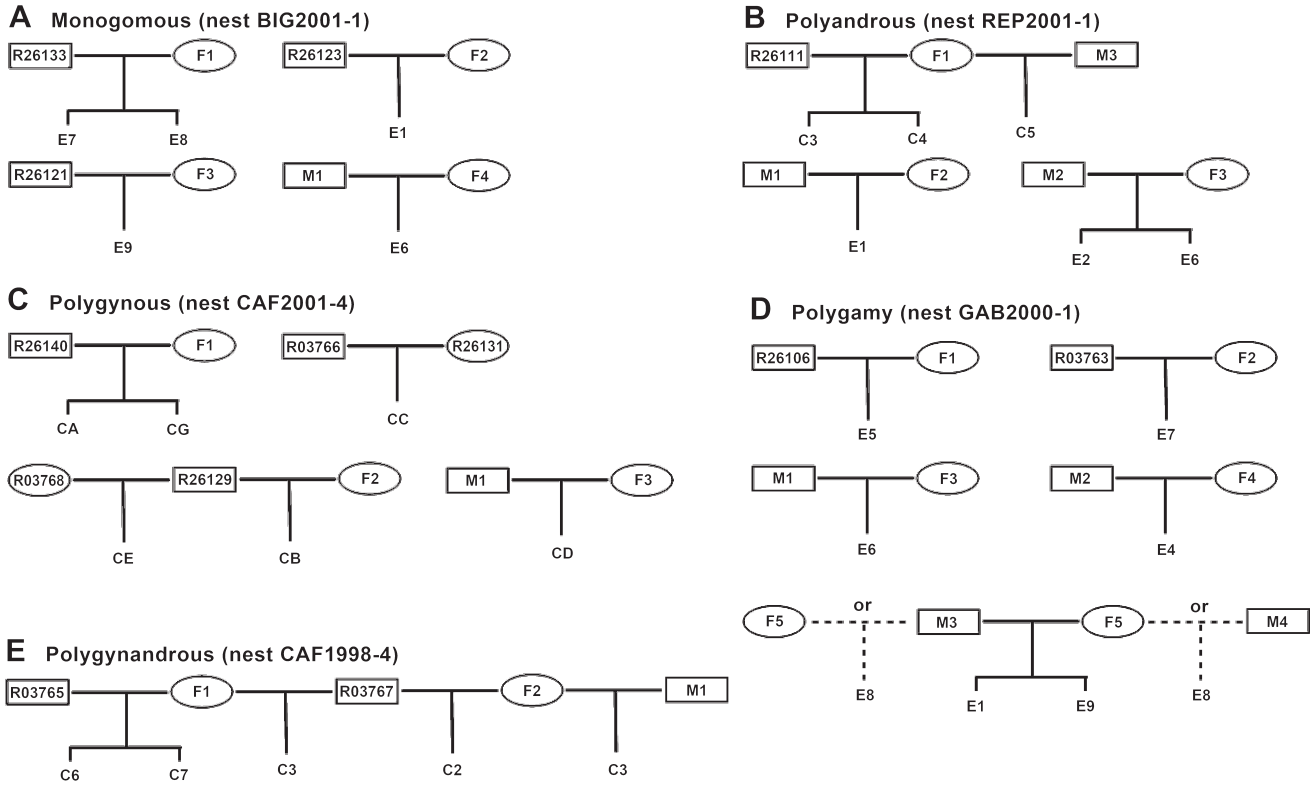

FIG. 2. Genetic mating patterns of five Guira Cuckoo groups from central Brazil using parentage assignments of CERVUS and offspring relatedness based on ML-RELATE's most likely relationship estimate (using list function). Monogamous mating was considered when we found no extrapair copulations (A); polyandrous when at least one of the breeding females bred with more than one male (B); polygynous when at least one of the breeding males bred with more than one female (C); polygamy when we were unable to determine the sex of the extra-pair adult (D); and polygynandrous when a male and female bred with more than one mate (E). M = male; F = female; C = chick; and E = embryo. Squares represent males and circles females, and a code (one letter followed by five numbers) indicates identity of the captured adult.

males and progeny from different nests. For all dyads, we compared only individuals known to be alive during the same period. We then compared the average relatedness values of the different dyads with a random distribution of average relatedness values for all adult males, when dyads consisted of only adult males, and the whole population, when dyads consisted of adult males and progeny. The random distribution was obtained by permutation of genotypes (1,000 times) using IDENTIX, version 1.1, which uses a Monte Carlo resampling procedure that generates a null distribution of genotypes based on population-wide allele frequencies (Belkhir et al. 2002). We considered the average relatedness of our categories to be significantly greater than the average relatedness of our null distribution if it occurred in the 5% tail of the highest average relatedness values of the random distribution. We looked at the relationship of nonbreeding adults with chicks and embryos from the nest because we were unable to sample all the adults. We assumed that if some sampled adults were related to the chicks, but not assigned as parents by CERVUS, then they must be related to unsampled adults as well. We tested the above predictions using adult males, but not females because of their small sample size.

We used partial Mantel tests (Manly 1997) to examine whether there was an association of pairwise genetic *r* values (Queller and Goodnight 1989) with nest distance, using a distance of zero for adults that belonged to the same group, while controlling for the effect of an interaction matrix. The interaction matrix consisted of individuals sampled in the same year, thus guaranteeing that *r* values were from individuals known to be alive at the same time. We also tested for any association between dyads of all adults: male–male, male–female, and female–female dyads. Partial Mantel tests were conducted using the software ZT with 10,000 permutations. *P* values represent the proportion of times that the correlation coefficient was equal to or greater than the observed Mantel correlation (Bonnet and Van de Peer 2002). All other statistical tests were conducted in R (R Development Core Team 2008), and normality of data, when needed, was checked with Q-Q plots. Data are presented as means ± SD.

RESULTS

All loci were in HWE after correction for multiple testing, except G463, which was significantly out of HWE with an estimated 32% null alleles (Table 1). There was no significant linkage disequilibrium among the nine loci.

Likelihood-based parentage assignment and different relatedness estimators.—When PO pairs assigned by CERVUS were

TABLE 2. Different relatedness (*r*) estimators of parent–offspring pairs (PO) for Guira Cuckoos from central Brazil assigned by CERVUS, allowing up to two ($n = 122$), one ($n = 87$), and zero ($n = 41$) mismatching loci. Values in bold are significantly different from the expected *r* value (0.5) of PO pairs ($P \leq 0.02$).

	Queller and Goodnight 1989		Lynch and Ritland 1999		Wang 2002		Li et al. 1993	
CERVUS	(*r* ± SD)	(*t*)	(*r* ± SD)	(*t*)	(*r* ± SD)	(*t*)	(*r* ± SD)	(*t*)
2 mismatches	**0.40 ± 0.13**	8.99	**0.34 ± 0.17**	10.51	**0.38 ± 0.14**	9.61	**0.38 ± 0.13**	9.97
1 mismatch	**0.45 ± 0.09**	5.36	**0.40 ± 0.15**	6.60	**0.44 ± 0.09**	6.07	**0.44 ± 0.09**	6.62
0 mismatches	0.49 ± 0.08	0.86	**0.44 ± 0.16**	2.43	0.48 ± 0.07	1.30	0.48 ± 0.08	1.44

allowed to have up to one or two mismatching loci, all mean measures of PO pairs were significantly lower than the expected 0.5 (Table 2). When we identified as PO pairs only those with no mismatches, we found that only Lynch and Ritland's (1999) relatedness method deviated significantly from the expected 0.5 (Table 2). Because the three methods had similar results and variances (Queller and Goodnight: $s^2 = 0.91$; Wang: $s^2 = 0.86$; Li et al.: $s^2 = 0.87$), we used Queller and Goodnight's (1989) *r* estimator, the most commonly used method.

Maternity assignments were made for 39 (17%) of 225 progeny (i.e., 28 chicks and 11 embryos). CERVUS assigned 15 maternities at 95% and an additional 12 at 80% confidence level. The remaining 12 assignments were made using ML-RELATE. Paternity assignments were made for 99 progeny (44%). CERVUS assigned 57 paternities at the 95% and 30 at 80% confidence level, whereas the other 12 paternities were assigned by ML-RELATE. Exclusion probabilities per locus ranged from 0.240 for locus CL9 to 0.512 for locus G463. If one parent was assigned, it ranged from 0.137 to 0.340 (Table 1). Total combined exclusion was higher than 0.99 for one parent and for both when the first parent was known. The log-likelihood ratios (LOD scores) for mothers and fathers assigned by CERVUS and ML-RELATE that matched at seven or eight loci were all positive, with no overlap for females and little overlap for males (Fig. 3).

Mating patterns.—We eliminated 12 nesting attempts from analyses in which we sampled only one of the chicks or embryos. Of the remaining 39 nesting attempts (mean proportion of progeny sampled per nest = 0.67 ± 0.25), mating patterns were as follows: 28.2% polygynandrous, 28.2% monogamous, 15.4% polygynous, 10.3% polyandrous, with the remaining 17.9% presenting some form of polygamy (either polyandry or polygyny) (Appendix; see Fig. 2 for description of mating patterns). In 21 of the nesting attempts in which some form of polygamy occurred, there were also monogamous pairs in addition to the polygamous birds (Appendix). However, because we did not sample all the nestlings, it is possible that some of the monogamous nests were in fact polygamous, except for nests BCE2001-2 and EST2001-2, in which all chicks were genotyped.

Breeding patterns of females.—Of the 11 females genotyped, 8 laid eggs (73%), and by looking at the genetic relationship

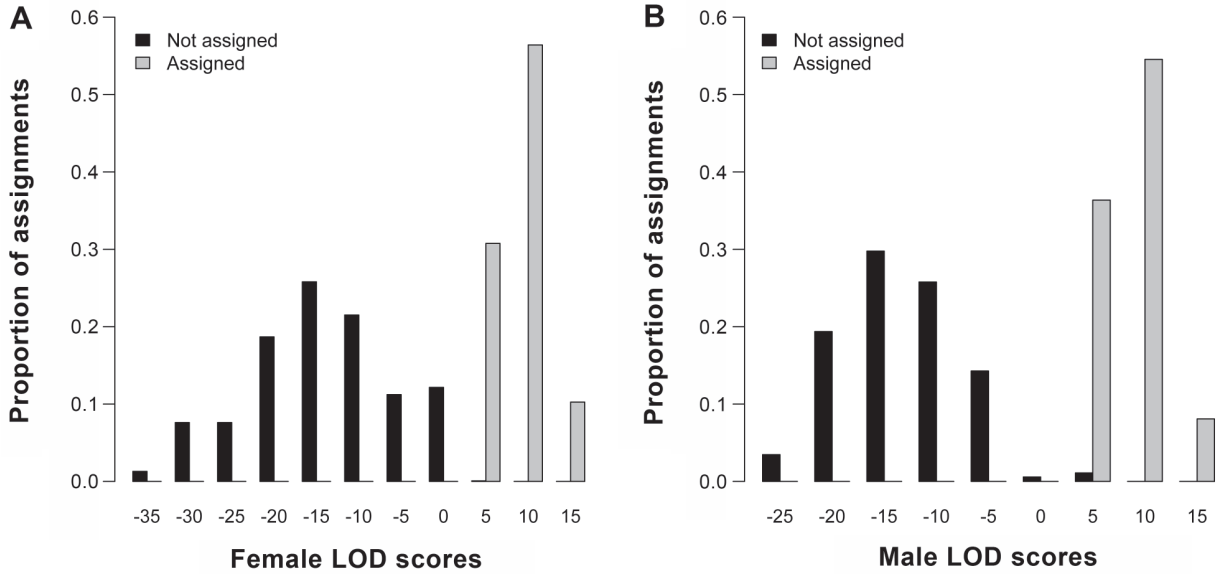

FIG. 3. Distribution of LOD scores of Guira Cuckoos from central Brazil for (A) females and (B) males. Represented in each graph is the proportion of LOD scores for both categories, when parentage was not assigned and when parentage was assigned by CERVUS and ML-RELATE.

Table 3. Sampled adult Guira Cuckoos from central Brazil that bred in nests other than the ones where they were captured. "Group" refers to where adults were caught and "Reproduced" to where they were known to breed. Males in bold were captured in more than one group in the same breeding season.

Adult	Sex	Group (year)	Reproduced (year)	Distance (m)
R26136	Female	DAN(2001)	EST(1998)/VAL(1997)	3,071/5,573
R26118	Female	WAR(2000)	COU(1997)/IRE(2000)	4,959/6,540
R26131	Female	CAF(2001)	COI(2000)	1,655
R03768	Female	EST(1998)	CAF(2000,2001)/IRE(2001)	1,260/1,789
R26121	Male	BIG(2000)	BCE(2000,2001)	367
R26123	Male	BCE(2000)	BIG(2001)	367
R26133	Male	BCE(2001)	BIG(2001)	367
R26140	Male	CAF(2001)	EST(2000)	1,260
R26129	Male	CAF(2001)	VIL(2000)	3,596
R26132	Male	CAF(2001)	PAS(2000)	1,699
R26191	Male	COI(2000)	TCH(2000)/VAL(1997)	2,140/1,699
R03763	Male	EST(1997)	GAB(2000)	3,407
R26127	Male	EST(2000)	CAF(2000)/PIT(2000,2001)	1,260/113
R26111	Male	EVA(2000)	AGU(2000)/REP(2001)	200/1,862
R26104	Male	IRE(2000)	PIR(2000)	309
R26196	Male	PIR(2001)	IRE(2000)	309
R26126	Male	PIT(2001)	EST(2000,2001)	113
R26197	Male	VAR(2001)	WAR(2000)	285
R26134	Male	VAR(2001)	WAR(2000)	285

among chicks of the same nesting attempt (ML-RELATE's list function), we were able to identify at least 108 females that were not captured (Appendix). Thus, we estimate that there were ~116 breeding females in the population (8 sampled females assigned parentage plus 108 unsampled females). During nest visits, we found 212 adults by maximum counts; assuming a 1:1 sex ratio, we would expect 106 females, a number very close to the estimate derived from the parentage assignments and genetic relationships among chicks within clutches. Three females bred in more than one nesting bout of the same group, two of which also bred in the same group in different breeding years. Therefore, at least some female cobreeder associations were maintained in repeated nesting attempts.

All nests had more than a single breeding female except for nests BEL2001-1 and EST1997-2, in which there was only one breeding female, although both of these nests had group sizes larger than two (Appendix). Four females were found breeding in a different group than the one in which they were captured, and in one case this happened in the same breeding season (Table 3). In the other three cases this change in sites occurred from one to three seasons later. The mean distance between sites was 3,263 ± 2,130 m.

Breeding patterns of males.—By looking at the relatedness of chicks in each nest, we estimated indirectly that a minimum of 80 breeding males were not captured (Appendix). Therefore, we estimate that ~114 breeding males were present during the study period (34 sampled males assigned by CERVUS and ML-RELATE plus 80 unsampled males). Male cobreeders were retained in repeated breeding attempts: 11 males bred in more than one breeding event of the same group in the same season 21 times. Nineteen males also bred in the same group in different breeding years, whereas six males that bred (i.e., fathers to either chicks or embryos) in one event did not do so in subsequent nesting events despite retaining group membership.

Reproduction in the Guira Cuckoo was shared among male group members; in other words, all nests had more than one breeding male except for one nest (EST1997-2). Fifteen males (31.2%) were identified as breeding at more than one nest, seven of which bred in two nests during the same breeding season, and four of them were also captured in both groups (Table 3). For the other males, breeding events in different nests were separated by at least 2 months. The mean distance between such nests was 1,053 ± 1,091 m, significantly less than the mean for females ($\bar{x}$ = 3,263 ± 2,130 m; W = 26, df = 19 and 8, $P \leq 0.01$). Eight of the males that bred in more than one nest used sites very close together (<380 m), whereas seven males did so at nests >1,200 m away from where they were caught, two of which were in the same season (Table 3). Thus, our data point to the existence of extragroup paternity (11.1% of all progeny). However, there is a possibility that simultaneous breeding at two nests occurred in two instances (EVA2000 and AGU2000; EST2000 and PIT2000), because the same individuals were responsible for most of the progeny and nests were very close together. When we excluded these events from the analyses, extragroup paternity dropped to 5.8%.

Within-group patterns of relatedness.—We assessed the accuracy of our pedigree methodology by comparing Queller and Goodnight's (1989) pairwise r values for progeny with the highest likelihood relationship encountered by ML-RELATE. We found no significant deviation for half sibs from the predicted relatedness of 0.25 ($\bar{x}$ = 0.27 ± 0.09, t =1.77, P = 0.08, n = 75), but we found a significant deviation for full sibs ($\bar{x}$ = 0.54 ± 0.14, t = 2.03, P = 0.05, n = 52). Because the mean r value for full sibs was 0.54, our methodology for full sibs was probably more conservative than for half sibs.

The relatedness among adults within groups varied from low (mean r = −0.215) to high (mean r = 0.508) in different nesting events (Appendix). Relatedness among adult group members

TABLE 4. Average dyadic relatedness among and between adult males and adult females for 20 groups of breeding Guira Cuckoos from central Brazil and the number of comparisons. We pooled all nesting events over the four breeding seasons (1997, 1998, 2000, and 2001), and only adults captured at the nesting site were considered. In bold are *r* values significantly higher than expected by chance ($P \leq 0.05$), calculated using GROUPRELATE.

Group	M:M	F:F	M:F	All
AGU	–0.005 (6)	—	—	–0.005 (6)
BCE	–0.045 (3)	—	—	0.045 (3)
BEL	**0.411 (1)**	—	—	**0.411 (1)**
BIG	**0.214 (3)**	—	—	**0.214 (3)**
CAF	**0.145 (21)**	—	**0.130 (7)**	**0.141 (28)**
COI	**0.186 (21)**	—	0.073 (7)	**0.157 (28)**
CON	0.197 (1)	—	–0.039 (2)	0.039 (3)
DAN	–0.215 (1)	—	–0.098 (2)	–0.137 (3)
EST	–0.100 (3)	0.194 (1)	–0.031 (6)	–0.029 (10)
EVA	–0.157 (3)	—	—	–0.157 (3)
GAB	—	—	–0.004 (1)	–0.004 (1)
IRE	–0.049 (1)	—	0.137 (1)	0.044 (2)
ITA	—	—	—	—
PAS	**0.304 (3)**	—	—	**0.304 (3)**
PIR	–0.210 (1)	—	—	–0.210 (1)
PIT	–0.100 (3)	—	–0.031 (6)	–0.024 (9)
TCH	–0.098 (1)	—	0.191 (2)	0.094 (3)
VAR	0.049 (10)	—	—	0.049 (10)
VIL	**0.508 (1)**	—	0.052 (2)	0.135 (3)
WAR	—	—	**0.441 (1)**	**0.441 (1)**

changed little when we pooled all nesting events over the 4 years (Table 4). Mean relatedness values for all males within groups were significantly higher than expected by chance for 6 of 20 groups (30%). Among females, we were able to analyze relatedness for only one group (EST), in which females were not more related to each other than expected by chance. In 11 groups, we inferred relatedness between males and females; in only two groups (CAF and WAR) were male–female dyads more related to each other than expected by chance. For WAR (one pairwise comparison), the highest-likelihood relationship found by ML-RELATE was PO. Furthermore, we found a very low rate (0.99%) of close inbreeding (2 of 225 progeny, 2 nests). Thus, in Guira Cuckoos, inbreeding between close relatives may occur only rarely.

Adult males that belonged to the same group were more genetically related than randomly selected adult males from the studied population (Table 5). However, when we partitioned relatedness within groups between breeding and nonbreeding adult males, we found that average relatedness dropped, but it was still significantly higher than among randomly selected males from the study population. Thus, it seems that breeding adults are genetically related and that nonbreeding adults are also related to breeding adults. In support of this latter point, nonbreeding adults presented significantly higher relatedness to progeny (chicks and embryos) that they helped to rear (i.e., belonged to the same group) than randomly assigned individuals from the whole population, which implies that nonbreeding adults were probably related to unsampled breeding adults. Additionally, the same did not happen when average relatedness was calculated between nonbreeding adults and progeny from other nests (Table 5). However, *r* values had very large ranges and standard deviations were also high (Table 5), which indicates that not all dyads are related and that there is a high degree of asymmetry in the extent of relatedness among group members.

Partial Mantel tests showed that there was a significant decrease in male relatedness with geographic distance (Mantel $r_{AB.C} = -0.10$, $P = 0.001$; Fig. 4A). The same was found for male–female dyads (Mantel $r_{AB.C} = -0.09$, $P = 0.002$; Fig. 4B). However, female dyads presented the opposite pattern: females that were farther away were more related than females close by (Mantel $r_{AB.C} = -0.10$, $P = 0.003$; Fig. 4C). With partial Mantel tests, the direction of the relationship cannot be inferred from the Mantel *r* statistic because the distance (or matrix similarity) matrices are used for the statistical test. Negative signs indicate that large differences in one variable are associated with small differences in the second variable (Reynolds and Houle 2003).

DISCUSSION

Interpretation of our results was complicated because we were unable to capture all adult group members and had low sample sizes, especially for females. Despite these logistical problems, we were able to sample 63% of the eggs and chicks for the 39 Guira Cuckoo nests studied, which yielded considerable information. These data show that Guira Cuckoos have a remarkably variable mating system and a great deal of plasticity in their social behavior. We found that Guira Cuckoos mated polygamously in 72% of nests, of which polygynandrous matings were the most common variant. Monogamous breeding was found at a maximum of 28% of the nesting attempts (because not all eggs were sampled) and a minimum of 5% (two groups had all their eggs sampled), and, in general, groups consisted of more than one breeding pair (one exception: EST1997-2, with only one breeding pair). These mating patterns contrast quite sharply with those inferred from behavioral observations of two other crotophagine species. Groove-billed Ani groups appear to be composed mainly of two breeding monogamous pairs, with the occasional occurrence of helpers (Vehrencamp et al. 1986, Koford et al. 1990), and Smooth-billed Ani groups seem to be composed of several cooperating monogamous pairs that frequently have helpers (Vehrencamp and Quinn 2004). However, the incidence of nonmonogamous matings may be higher for the latter species (Vehrencamp and Quinn 2004). Whether or not monogamous breeding is the only mating strategy within groups in these species needs to be confirmed by genetic analyses. Recent genetic analyses of the Greater Ani show that the mating system is overall socially monogamous (Riehl 2010b), but extrapair copulations were widespread, with at least one extrapair chick in every nest examined (C. Riehl pers. comm.). Thus, it seems that *Crotophaga* species are socially monogamous, whereas Guira Cuckoos have a more diverse array of mating patterns. However, these results need to be interpreted cautiously, because our sampling was limited to 47% of adult males and 13% of adult females in the population.

Our population size estimate was based on field counts that yielded minimum group sizes. If we applied a 1:1 sex ratio, we would expect to have 106 females and males, very close to the minimum number of breeding females and males identified genetically in the present study (114 and 116, respectively). We identified four females breeding in different groups in different years,

TABLE 5. Average pairwise genetic relatedness between adult male Guira Cuckoos from central Brazil and between adult males and progeny (chicks and embryos) in relation to their breeding condition and group membership. Dyads were considered only if both individuals were known to be alive in the same year. Relatedness values are presented as $r \pm$ SD, sample size (n) refers to number of sampled dyads, range refers to the range of r values, and background average relatedness refers to mean relatedness values for randomly assigned dyads in the population with 1,000 permutations (with 95% confidence intervals in parentheses). Values in bold are significantly different from randomly selected dyads in the population.

Dyads being compared	n	$r \pm$ SD	Range	Background average relatedness
Adult males within groups	51	**0.132 ± 0.229**	–0.219 to 0.642	–0.021 (–0.02118 to –0.02113)
Breeding adult males from the same group	40	**0.061 ± 0.181**	–0.243 to 0.593	–0.021 (–0.02118 to –0.02113)
Breeding and nonbreeding adult males from the same group	29	**0.076 ± 0.174**	–0.201 to 0.461	–0.021 (–0.02118 to –0.02113)
Nonbreeding adult males and progeny from the same group	126	**0.079 ± 0.172**	–0.286 to 0.578	–0.003 (–0.00342 to –0.00339)
Nonbreeding adult males and progeny from other groups	1,243	0.003 ± 0.130	–0.312 to 0.435	–0.003 (–0.00342 to –0.00339)

and also one case in which one female had chicks in two different nests within the same season. Except for this one case, the periods did not overlap and we do not believe that these are cases of brood parasitism. Instead, we suggest that females may have changed groups (i.e., dispersed). In the case in which breeding occurred in two nests within the same season, nests were >6 km apart, which suggests that brood parasitism is unlikely.

Alternatively, CERVUS may have assigned a closely related female other than the true parent as a likely mother to the offspring (Marshall et al. 1998); if so, these four events would be linked to female dispersal. We also found low levels of extragroup paternity (13 progeny; 5.8%). If we also accept the dispersal explanation above for these parentage assignments, then females disperse significantly greater distances from their breeding (and possibly natal) territories than do males, as in many avian species (Greenwood 1980). In support of this view, relatedness among adult males dropped significantly with distance, whereas adult females showed the opposite pattern. Although the apparent level of extragroup paternity was low and we do not suspect the occurrence of brood parasitism, we cannot rule out these possibilities, given that we could not genetically sample all adults in the nests studied. In the Greater Anis, for instance, brood parasitism is quite common (Riehl 2010a). However, Guira Cuckoos are highly territorial and have considerable home ranges ($\bar{x}$ = 57.0 ± 10.8 ha; M. R. Lima and R. H. Macedo unpubl. data), and nests were very far apart ($\bar{x}$ = 4,370 ± 1,791 m), which could lead to low levels of both extragroup parentage and brood parasitism.

Relatedness among adult group members varied considerably across breeding groups. Across all 4 years, males were more related to each other than expected by chance in 6 of 20 groups. Adult male relatedness within groups was also significantly greater than background genetic relatedness, which indicates that male philopatry, joint dispersal by male kin, or both are responsible for male group composition in Guira Cuckoos. In support of this view, nonbreeding adults were more related to progeny produced at their nests than background genetic relatedness, whereas this was not true when relatedness was calculated with progeny from other nests. This indicates that nonbreeding males were related to unsampled breeders in the nesting attempt. Thus, in some groups adult males may be highly related and the occurrence of male helpers may be favored through indirect fitness benefits. The lack of indirect fitness benefits for females that share the nest seems plausible given the female dispersal patterns established in our study, but we cannot determine this as a fact because of the low sample sizes of captured females.

Evolution of cooperative breeding, according to kin selection theory, could be favored if group members are related (Brown 1987). However, Guira Cuckoos show strong reproductive conflict

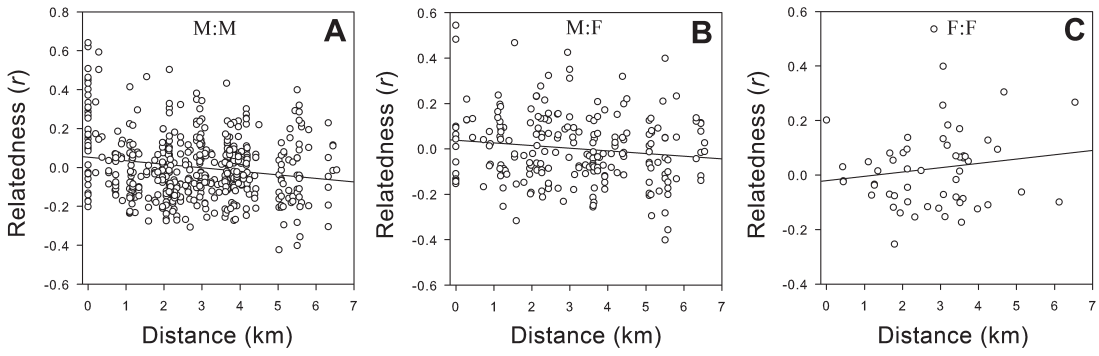

FIG. 4. Distance (km) between Guira Cuckoo nests from central Brazil and pairwise genetic relatedness (r) of adults (Queller and Goodnight 1989) for (A) male–male dyads for all years, (B) male–female dyads for all years, and (C) female–female dyads for all years. Dyads were considered only if adults were known to be alive in the same year. Fitted least-squares regression lines are included within each plot for illustrative purposes only.

in the form of both egg ejection and infanticide (Macedo et al. 2004a, b). This probably happens because groups consist of adults with mixed relatedness. For instance, it seems that females are less likely to gain indirect inclusive fitness benefits, and not all males receive indirect inclusive fitness benefits, because relatedness is highly asymmetric, at least among male group members. Therefore, cooperation and conflict will inevitably coexist and may vary according to the type of social and genetic environment within a group, which includes levels of kinship and male:female ratio of breeders and nonbreeders. It has been shown that egg survival increases with the proportion of group females that participate in egg laying in this species (Macedo et al. 2004a). Thus, we can hypothesize that infanticide is negatively associated with the proportion of males and females that breed, or possibly with levels of kinship, so that nests with related males and females may exhibit lower levels of infanticide.

Genetic data on group composition for the other crotophagines are available only for Greater Anis and one breeding group of Smooth-billed Anis. In the Greater Anis, adult group members are unrelated and young rarely remain in their natal groups in the following year (Riehl 2010b). In the one breeding group of Smooth-billed Anis studied, adults at the nest were not related (Quinn et al. 2010). Behavioral observations in the Groove-billed Ani show that a small fraction (12%) of male young that survive to adulthood are recruited into their natal territories. Most males disperse to sites close to their natal territories, whereas females disperse longer distances (Bowen et al. 1989). Thus, for *Crotophaga* species, the direct fitness benefits linked with sociality, such as reduction of nest predation and acquisition of breeding sites with lower predation pressures (Riehl 2010b), may compensate for any negative effects associated with reproductive competition. For these species, direct fitness benefits may be sufficient for the maintenance of communal breeding, or, at least, indirect fitness benefits may not be a prerequisite for group formation, a common element of other cooperative-breeding vertebrates (Clutton-Brock 2002). For Guira Cuckoos, however, we suggest that indirect fitness benefits may play an important role in the formation of groups, given that the patterns of relatedness within groups are much more variable than those in the *Crotophaga* species.

Despite the logistic difficulties that the Guira Cuckoo system presents in terms of field data collection, we believe that underlying genetic relations within and among groups in this species may contribute greatly to the understanding of the evolution of cooperative societies. This is because this species presents high levels of asymmetry in relatedness within groups across the population, which could lead to variability in how individuals resolve reproductive conflicts. The intense reproductive competition in Guira Cuckoos provides an ideal opportunity to investigate how cooperative and competitive behaviors may vary with kinship.

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APPENDIX. Characteristics of breeding groups of Guira Cuckoos from central Brazil. Nest ID has group code followed by year and breeding bout within the reproductive season. Values in parentheses for males and females indicate the number of genotyped individuals breeding in the nest; for clutch size the values in parentheses indicate the number of genotyped chicks and embryos; and for adult relatedness the values in parentheses indicate the number of comparisons. Figures in bold indicate $P \leq 0.05$.

Nest ID	Mating pattern[c]	Monogamous pairs	Group size	Breeding adults[a]			Clutch size	Adult relatedness[b]			
				Males	Females	Unknown		M:M	F:F	M:F	All
AGU2000-1	Polygamy	1	6	3 (1)	3 (0)	2	8 (6)	0.005 (6)	—	—	0.005 (6)
BCE2000-1	Polygynandry	0	4	3 (1)	2 (0)		11 (4)	**0.214** (3)	—	—	**0.214** (3)
BCE2001-2	Monogamy	3	4	3 (2)	3 (0)		5 (5)	−0.040 (3)	—	—	−0.040 (3)
BEL2000-1	Polyandry	1	6	3 (2)	2 (0)		5 (5)	**0.411** (1)	—	—	**0.411** (1)
BEL2001-1	Polygyny	0	6	2 (1)	1 (0)		3 (3)	**0.411** (1)	—	—	**0.411** (1)
BIG2000-1	Monogamy	2	5	2 (1)	2 (0)		7 (2)	—	—	—	—
BIG2001-1	Monogamy	4	4	4 (3)	4 (0)		10 (5)	0.049 (3)	—	—	0.049 (3)
CAF1998-4	Polygynandry	0	7	3 (2)	2 (0)		9 (5)	0.055 (1)	—	—	0.055 (1)
CAF2000-1	Polygyny	1	3	3 (2)	4 (1)		12 (5)	0.050 (3)	—	0.001 (3)	0.025 (6)
CAF2001-1	Polygamy	3	7	4 (3)	4 (1)	1	8 (7)	**0.186** (10)	—	0.099 (5)	**0.157** (15)
CAF2001-2	Monogamy	3	6	3 (2)	3 (1)		13 (4)	0.073 (1)	—	0.039 (2)	0.051 (3)
CAF2001-4	Polygyny	2	7	4 (3)	5 (2)		7 (6)	**0.183** (6)	−0.052 (1)	−0.033 (8)	0.052 (15)
COI2000-2	Polygyny	1	7	2 (1)	3 (0)		12 (4)	**0.170** (3)	—	—	**0.170** (3)
COM1997-1	Monogamy	2	5	2 (0)	2 (0)		3 (2)	—	—	—	—
CON1997-1	Monogamy	5	8	5 (1)	5 (0)		11 (9)	0.197 (1)	—	−0.039 (2)	0.039 (3)
CON2001-1	Polygamy	0	6	3 (0)	3 (0)	1	6 (5)	—	—	—	—
CON2001-3	Polygamy	0	1	3 (1)	2 (0)	1	10 (6)	—	—	—	—
COU1997-1	Polygynandry	4	7	6 (1)	5 (0)		13 (9)	—	—	—	—
DAN1997-2	Polygyny	2	8	3 (2)	4 (1)		10 (5)	−0.215 (1)	—	−0.024 (2)	−0.088 (3)
EST1997-2	Monogamy	1	5	1 (0)	1 (1)		6 (3)	−0.188 (1)	—	0.075 (2)	−0.012 (3)
EST1998-3	Polygynandry	0	5	3 (0)	3 (3)		5 (5)	—	**0.201** (3)	—	**0.201** (3)
EST2000-1	Polygynandry	1	4	4 (2)	3 (1)		8 (7)	0.029 (3)	—	−0.080 (3)	−0.025 (6)
EST2001-2	Monogamy	4	5	4 (2)	4 (0)		4 (4)	−0.108 (1)	—	−0.074 (2)	−0.085 (3)
EVA2000-1	Polygynandry	4	8	5 (1)	5 (0)	1	14 (6)	0.005 (6)	—	—	0.005 (6)
GAB2000-1	Polygamy	4	3	5 (2)	5 (0)	1	9 (7)	0.109 (3)	—	0.071 (3)	0.009 (6)
IRE2000-1	Monogamy	5	8	5 (3)	5 (1)		8 (7)	−0.049 (3)	—	0.137 (3)	0.044 (6)
IRE2000-2	Polygamy	2	6	3 (1)	3 (2)	1	8 (6)	—	−0.004 (1)	0.107 (2)	0.070 (3)
IRE2001-1	Monogamy	3	6	3 (0)	3 (1)		7 (3)	—	—	—	—
ITA1997-1	Monogamy	4	4	4 (0)	4 (1)		8 (6)	—	—	—	—
PIR2000-1	Polyandry	2	6	7 (2)	4 (1)		14 (9)	−0.021 (1)	—	−0.033 (2)	−0.029 (3)
PIR2001-1	Polygyny	1	7	2 (2)	2 (1)		6 (4)	−0.049 (3)	—	0.137 (3)	0.044 (6)
PIT2000-1	Polygynandry	2	3	4 (2)	4 (0)		9 (7)	−0.108 (1)	—	−0.074 (2)	−0.085 (3)
PIT2001-1	Polygynandry	2	7	4 (2)	4 (1)		9 (7)	−0.108 (1)	—	−0.074 (2)	−0.085 (3)
REP2001-1	Polyandry	2	4	4 (1)	3 (0)		6 (6)	—	—	—	—
TCH2000-2	Polyandry	3	4	5 (3)	4 (0)		13 (6)	0.128 (3)	—	0.232 (3)	0.180 (6)
VAL1997-1	Polygynandry	1	6	3 (1)	4 (1)	3	21 (8)	—	—	—	—
VAR2000-2	Polygynandry	0	6	2 (1)	2 (0)		06 (3)	—	—	—	—
VIL2000-3	Polygamy	1	4	2 (0)	2 (0)	1	03 (3)	**0.508** (1)	—	0.052 (2)	0.135 (3)
WAR2000-2	Polygynandry	3	10	8 (5)	6 (2)		18 (13)	0.052 (10)	0.029 (1)	0.062 (10)	0.055 (21)

[a]Minimum number of adults breeding in the nest, calculated using PO assignments (CERVUS) and offspring relatedness (Queller and Goodnight 1989) relatedness *r* estimator and ML-Relate's most likely relationship estimate (using "list function"). Adding up the minimum number of males and females breeding at a nest differs from results in the main text because some of the sampled adults bred in the same group in different years as well as in different groups.

[b]Relatedness *r* estimator calculated using GroupRelate. In some groups some captured adults were not assigned as parents (CERVUS) and relatedness was calculated using the captured adults in that nesting event and the assigned parents.

[c]We considered as a monogamous mating pattern cases where none of the adults were polygamous, therefore monogamous pairs that used the same nest also resulted in the nest being classified as a monogamous mating pattern.