

COOPERATIVE BREEDING IN THE CAMPO FLICKER II: PATTERNS OF REPRODUCTION AND KINSHIP

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Abstract. Understanding the evolution of cooperative breeding systems remains a central issue in evolutionary biology. In this context, molecular tools have contributed greatly toward understanding kinship patterns within groups and resolving long-standing issues regarding mating systems and parentage. We used such molecular tools to examine patterns of kinship in the Campo Flicker (*Colaptes campestris campestris*), a facultative cooperative breeder, to answer questions concerning its mating system and patterns of reproductive skew. Genetic analysis revealed that the species is predominantly monogamous in both cooperative groups and socially monogamous pairs, but in several cooperative groups auxiliary females contributed eggs to the nest. In contrast, within groups direct reproduction by auxiliary males was rare. We observed no cases of extra-group paternity but detected cases of quasi-parasitism in socially monogamous pairs. Levels of relatedness within groups were high; auxiliaries of both sexes were often offspring or siblings of the primary breeding pair but were sometimes unrelated to the breeding pair. The structural genetic complexity of groups and high intragroup relatedness generate a social system in which cooperation among group members coexists with competition for opportunities to breed.

Key words: *Cooperative breeding, joint nesting, mating system, molecular analysis, relatedness, relationship, tropics.*

Cría Cooperativa en *Colaptes campestris campestris* II: Patrones de Reproducción y Parentesco

Resumen. Entender la evolución de los sistemas de cría cooperativa aún representa un tema central de la biología evolutiva. En este contexto, las herramientas moleculares han contribuido enormemente para entender los patrones de parentesco dentro de los grupos y a resolver temas de larga data sobre los sistemas de apareamiento y parentesco. Empleamos estas herramientas moleculares para examinar los patrones de parentesco en *Colaptes campestris campestris*, un ave con un sistema de cría cooperativo facultativo, para responder preguntas concernientes a su sistema de apareamiento y a los patrones de sesgo reproductivo. Los análisis genéticos revelaron que la especie es predominantemente monógama tanto en grupos cooperativos como en parejas socialmente monógamas, pero en varios grupos cooperativos las hembras auxiliares contribuyeron con huevos al nido. En contraste, dentro de los grupos la reproducción directa por parte de machos auxiliares fue rara. No observamos casos de paternidad extra grupo pero detectamos casos de cuasi parasitismo en parejas socialmente monógamas. Los niveles de relacionamiento adentro de los grupos fueron altos; los auxiliares de ambos sexos fueron usualmente crías o hermanos de la pareja reproductiva original pero a veces no estuvieron relacionados a la pareja reproductiva. La complejidad genética estructural de los grupos y el alto relacionamiento adentro del grupo generan un sistema social en el cual la cooperación entre los miembros del grupo coexiste con la competencia por las oportunidades reproductivas.

INTRODUCTION

Cooperative breeding, known in both vertebrates and invertebrates, is a social system in which more than two individuals help care for offspring (Brown 1987). In most of these systems, cooperative breeding is facultative, with some but not all breeding adults receiving help during breeding from other individuals, called “auxiliaries” or “helpers.” Thus cooperative breeding represents a rather rare but widespread form of reproductive altruism, and considerable research has

focused on understanding the evolution and maintenance of such systems. The advent of molecular genetic markers has opened new doors for examining the fitness costs and benefits involved, and in turn these methods have revealed considerable hidden complexity (Koenig and Dickinson 2004).

In general, a better understanding of cooperative breeding requires that two issues be addressed. First, identification of auxiliaries and their relationship to the individuals being aided is crucial to understand the effects of helping on both direct and indirect fitness. In most species of birds

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that breed cooperatively, auxiliaries usually are young male offspring from previous breeding seasons that delay dispersal and remain in the natal territory and thus may reap indirect fitness benefits by helping to rear younger siblings (Koenig and Dickinson 2004). But exceptions to this general pattern are numerous, including auxiliaries that are female rather than male (Berg et al. 2009, Eikenaar et al. 2010) and auxiliaries that are unrelated to the breeding pair (Dunn et al. 1995, Magrath and Whittingham 1997, Legge and Cockburn 2000). Thus there may be considerable diversity across cooperative species in the expression of helping behavior and in its relative costs and benefits. Data from more species are necessary to further our understanding of the ultimate mechanisms favoring helping behavior within cooperative groups.

A second issue necessary for furthering our understanding of cooperative systems concerns the patterns of mating and reproduction within cooperative groups, as this also has important consequences for individuals' fitness. Mating patterns of cooperatively breeding birds range from strict monogamy, which is common, to rarer and more complex patterns such as polygynandry (Cockburn 2004). Joint nesting (i.e., more than one female contributing eggs to a single nest; Brown 1987) occurs in some cooperative species, either because multiple monogamous pairs use the same nest or because several females attempt to contribute eggs to the nest in polygynandrous groups (Vehrencamp and Quinn 2004). Moreover, in some cases, auxiliaries may be able to breed directly: auxiliary males may sire young by copulating with females within or outside of the social group (extra-group paternity), and auxiliary females may lay fertile eggs in the nests of other females without providing maternal care (intraspecific brood parasitism; Davies 2000). Indeed, although extra-group paternity is generally infrequent among cooperative species (Cornwallis et al. 2010), it may be common in some populations (Mulder et al. 1994, Webster et al. 2004, Berg 2005, Eimes et al. 2005), possibly as a strategy to avoid the costs of close inbreeding (Brooker et al. 1990, Blomqvist et al. 2002, Tarvin et al. 2005, Varian-Ramos and Webster 2012). Cases of intraspecific brood parasitism or even quasi-parasitism, in which an extra-group female lays parasitic eggs in the nest, fertilized by the group's breeding male, have also been observed in cooperative breeders, albeit rarely (Emlen and Wrege 1986, Li et al. 2009, Du and Lu 2010). Overall, these patterns of reproduction may determine whether auxiliaries have the opportunity to reproduce directly and also affect the relative magnitude of indirect fitness benefits, since they will affect the degree of relatedness between auxiliaries and the young being reared (Webster et al. 2004).

Our goal here was to apply molecular genetic analyses to provide insights into the breeding system of the Campo Flicker (*Colaptes campestris campestris*), a cooperatively breeding woodpecker endemic to South American savannas. Observations of this species' natural history suggest a high

degree of social complexity in addition to a low rate of territory turnover and, apparently, low levels of dispersal (Dias et al. 2013). We investigated genetic relatedness within and between groups to elucidate patterns of reproduction and kinship. Specifically, we addressed the following questions: (1) What are the patterns of relatedness among adults within groups? (2) Who produces young within cooperative groups?

METHODS

STUDY SPECIES

The Campo Flicker is a conspicuous, sexually dimorphic, medium-sized woodpecker that is poorly known, despite its wide distribution across the savannas of South America (Short 1972). In central Brazil, site of our study, groups defend large territories year round, usually start breeding in the middle of the dry season in August, and males invest heavily in parental care (Dias et al., unpubl. data). Two subspecies are recognized: *C. c. campestris*, distributed from northeastern Brazil to central Paraguay, and *C. c. campestroides*, found from southern Paraguay and Brazil to northeastern Argentina (Short 1972). Field observations indicate that this species often breeds cooperatively and suggest that breeding relationships vary considerably; not only are there auxiliaries, females may nest jointly as well (Dias et al. 2013).

STUDY AREA AND GENERAL PROCEDURES

We searched for and captured virtually all Campo Flickers within the study area (see Dias et al. 2013 for details). We categorized social groups as either socially monogamous pairs (only two adults) or cooperative groups (more than two adults), within which we could generally identify the primary pair (potential breeders in the group) by their behavioral dominance and greater investment in caring for nestlings (Dias et al. 2013). For each individual captured we measured body mass (to nearest gram) and length of the tarsus, wing, beak, and tail (to nearest 0.02 mm), collected approximately 100 μ L of blood from the brachial vein for genetic analyses, and applied an individually unique combination of colored leg bands (see Dias et al. 2013).

At each nest, near the end of the nestling period (25th day after hatching), we measured and banded nestlings, as for adults. We observed the behavior of identified group members (banded individuals), monitoring their interactions with other identified adults and their activity at nests when brooding and provisioning young. We considered adults to belong to the same social group if they maintained a long-term social affiliation and occupied the same territory (more details in Dias et al. 2013). We used data from both the breeding and nonbreeding seasons to evaluate the structure of social groups. We also include data from some social groups for which we had blood samples but little information on behavior or breeding because they could still contribute to the understanding of

group structure. We defined the primary pair by behavioral data (interactions with other group members, high investment in the nestlings, and frequent territorial vocalizations) rather than by offspring production.

When group composition changed drastically, for example, with substitution of breeding individuals, we classified the newly formed group as new ($n = 5$). In one case a new group resulted from both dispersal of some original group members and immigration of new individuals. Similarly, when there was a substitution of one member of a socially monogamous pair we also classified it as a new pair ($n = 4$). Groups that changed from cooperative to a socially monogamous pair through the loss of all auxiliaries, but without the replacement of either of the pair, were treated as non-independent samples of the same group ($n = 3$). We took behavioral information and group composition into consideration during paternity analyses. Social pairings between individuals that had a coefficient of relatedness (r) between 0.0625 and 0.5 we considered as inbred matings (Koenig and Haydock 2004). We could determine the sex of the few unbanded birds ($n = 8$) by the species' slight sexual plumage dichromatism. Adults' survival rate was high in our study population, and group composition was fairly stable.

DNA EXTRACTION AND ANALYSIS

We stored blood samples in a lysis buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 2% SDS) at room temperature and extracted the DNA with a DNeasy blood and tissue kit (Qiagen). We initially screened 12 loci, all originally isolated from the Northern Flicker (*Colaptes auratus*; Kuhn et al. 2009), for amplification and polymorphism, and in the end we used the 10 polymorphic microsatellite markers that we could amplify (Table 1). We applied a multiplex polymerase chain reaction (PCR) in 10- μ L reactions with 1 μ L of template DNA, 0.1 μ L of JumpStart *Taq* DNA polymerase (Sigma-Aldrich), 1 μ L of 10 \times PCR buffer, 3.25 mM of MgCl₂, 0.2 mM of dNTP and 0.10–0.45 μ M of each primer. The PCR profile was as follows: initial incubation at 94 °C for 1 min; 30 cycles of amplification at 94 °C for 1 min, 52–57 °C (depending on locus) for 1 min, and 72 °C for 1 min; and a final extension step at 72 °C for 5 min. One primer within each pair was labeled at the 5' end with a fluorescent dye (VIC, NED, 6-FAM or PET). After PCR we diluted the amplification products to optimize the product signal and visualized it on an ABI 3100 automated capillary sequencer, using the GS500 LIZ size standard (Applied Biosystems). We analyzed electropherograms with GeneMapper (version 4.1; Applied Biosystems). For each locus in these analyses, we used Genepop 4.0 (Raymond and Rousset 1995) to determine observed and expected heterozygosities, probabilities of parental exclusion, and frequency of null alleles (Table 1).

PARENTAGE AND KINSHIP ANALYSES

We analyzed the parentage of offspring with Cervus (version 3.0.3), which uses a likelihood approach to assign parentage

TABLE 1. Summary statistics from loci used for analysis of paternity and relatedness of Campo Flickers. The data include number of alleles (k), range of allele size in base pairs (bp), observed (H_O) and expected (H_E) heterozygosity, non-exclusion probability assuming no parents known (NEP_{1p}) and one parent known (NEP_{2p}), and estimated frequency of null alleles (F_{Null}).

Locus	k	Size (bp)	H_O	H_E	NEP _{1p}	NEP _{2p}	F_{Null}
Cau1	10	199–233	0.686	0.765	0.626	0.448	0.0535
Cau2	7	148–163	0.757	0.779	0.618	0.441	0.0128
Cau3	6	177–222	0.700	0.728	0.687	0.513	0.0161
Cau5	7	145–170	0.886	0.775	0.619	0.439	–0.0761
Cau8	16	235–274	0.914	0.868	0.436	0.277	–0.0321
Cau9	18	225–264	0.800	0.914	0.313	0.185	0.0644
Cau10	9	108–140	0.643	0.629	0.758	0.570	–0.0014
Cau11	11	241–290	0.786	0.695	0.705	0.524	–0.0746
Cau12	8	170–191	0.743	0.630	0.772	0.596	–0.0957
Cau13	3	212–215	0.314	0.345	0.941	0.848	0.0385

(Marshall et al. 1998, Kalinowski et al. 2007), and entered genotype data from chicks and adults, along with population allelic frequencies from all adults genotyped. The sampling of parents in the study area was thorough, and we estimate that approximately 90% of the adults were sampled. As a result of the high polymorphism and low frequency of null alleles, the exclusionary power of the combined loci was 0.9913 if neither parent was known and 0.9996 if one parent was known (Table 1). The overall test demonstrated that the allelic frequencies were in Hardy–Weinberg equilibrium (chi-squared test: $\chi^2 = 5.39$; $P = 0.145$). Assignments were carried out at a strict level of 95%. We ran the parentage analyses with all known adults as potential parents and allowed Cervus to assign the pair with the highest likelihood of being the true parents, accepting assignment if the trio “female/chick/candidate male” had zero or one mismatch.

We used genetic data to estimate relatedness (r), defined as the proportion of alleles individuals share through descent from a common ancestor (Wright 1922). We used SPAGeDi (Hardy and Vekemans 2002) to estimate r for all possible combinations of pairs of individuals within and among groups, on the basis of Queller and Goodnight's (1989) formula. Subsequently, to avoid pseudoreplication, we randomly selected one individual of each sex from all groups and compared its average relatedness within its group and in relation to the members of other groups for all dyad combinations: female–female, male–male, and male–female. We used paired t -tests to evaluate differences within and among groups.

On the basis of both behavioral observations and genetic analysis, we also estimated the relationship between pairs of individuals by category of genealogical relationship, such as parent–offspring or full sibs (Blouin 2003). For each pair of individuals, we used ML-RELATE (Kalinowski et al. 2006) to estimate the likelihood of four common relationships: unrelated, half sibs, full sibs, and parent–offspring. This program

accommodates null alleles by using a maximum-likelihood estimate of the frequency of null alleles in all calculations. Subsequently, we used the program's function "confidence sets," and whenever more than one relationship was consistent with the genotypes of the individuals, we used the a priori suspected relationship based on behavioral data in a likelihood-ratio test, rejecting the alternative hypothesis when the P -value of the test was below 0.05. In some cases we also used field observations to determine or confirm relationship category (e.g., when young from the previous year remained in the natal group or joined a new group).

STATISTICAL ANALYSES

We used two-way repeated-measures ANOVA to evaluate differences in the level of relatedness among individuals with respect to dyad type (combination of sexes) and group (within and among groups). For these analyses we used the software R (2.11.1; R Development Core Team 2010). All tests were two-tailed, and we present results as means \pm SE.

RESULTS

RELATEDNESS AMONG INDIVIDUALS

Mean relatedness among adults within cooperative groups was high for both male dyads (0.34 ± 0.13) and female dyads (0.37 ± 0.09 ; Fig 1). Between individuals of the same sex, relatedness within a group was significantly higher than between groups ($F_{1,10} = 22.39$; $P < 0.001$; Fig. 1), and the sexes did not differ in this pattern ($F_{1,10} = 0.00$; $P = 0.96$). Neither was the interaction of group type and sex significant ($F_{1,10} = 0.21$; $P = 0.65$). We found that individuals of opposite sexes were more related within their groups (0.16 ± 0.06) than when compared to opposite-sex individuals of other groups, whether male (0.03 ± 0.01 ; paired t -test: $t_6 = 3.07$; $P = 0.022$) or female (0.02 ± 0.01 ; paired t -test: $t_6 = 3.210$; $P = 0.018$; Fig. 1). These results remained significant after the Bonferroni correction was applied. Breeders within cooperative groups did not differ in degree of relatedness (r) to each other (0.16 ± 0.10) from socially monogamous pairs (0.07 ± 0.04 ; $t_{17} = 0.913$; $P = 0.374$). We compared the relatedness between primary female breeders and auxiliary females who produced offspring (0.26 ± 0.15) with that between primary breeders and auxiliary females who did not produce offspring (0.44 ± 0.09) and found no difference between them (t -test: $t_4 = -1.013$; $P = 0.368$).

The analysis of relationships within seven cooperative groups revealed that in three cases the dominant pair was unrelated to each other. In two additional cases it specified that the breeders were unrelated to each other but could not statistically exclude the possibility that they were related at the level of half-siblings. In one of the two remaining cases the dominant pair was related to each other at the level of full or half siblings; in the other the dominant pair appeared to be related as parent and offspring.

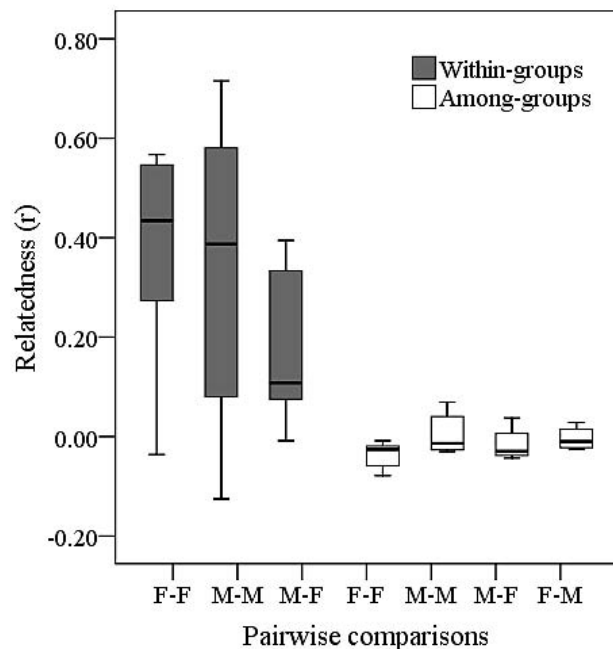


FIGURE 1. Level of relatedness (r) between dyads of individuals of both sexes within and among groups of the Campo Flicker in central Brazil. Sample sizes: female (F)–female, 6; male (M)–male, 6; M–F, 7.

Relationships of auxiliaries to the breeders were complex and variable. Of six male auxiliaries (from five groups), three (50%) were classified as offspring of one or both of the dominant breeders, one (17%) was a full sibling of the dominant male, and two (33%) were unrelated to the dominant pair. Of 13 female auxiliaries from nine groups, six (46%) were classified as offspring of one or both of the dominant breeders, three (23%) were full siblings of the dominant female, and four (31%) were apparently unrelated to either of the dominant breeders. Thus auxiliaries of both sexes were sometimes offspring, siblings of the dominant breeder of the same sex, or unrelated individuals who joined the group.

SOCIAL ORGANIZATION, PARENTAGE, AND MATING SYSTEM

We collected data from 36 social groups that ranged from two to seven individuals (see Dias et al. 2103). Of these, 21 were socially monogamous pairs and 15 were cooperative groups. We located 57 nests within the study site, and from 32 of these we obtained samples from adults and/or nestlings for genetic analyses. In 78% of these groups we were able to capture all group members; in the remaining groups we sampled all nestlings and most adults but missed one or two of the adults. In total, we genotyped 162 individuals, 72 of which were adults (36 males, 36 females) and 90 were nestlings (45 males, 44 females). The sex ratio of adults did not differ from the expected ratio of 1:1 ($\chi^2_1 = 0.01$; $P = 0.91$).

Twenty sampled nests were from socially monogamous pairs without helpers, and genetic analyses revealed that 45 (90%) of 51 offspring from these nests matched the social parents. The only exceptions were nestlings in two nests that were apparently the result of intraspecific brood parasitism, representing 6% of all 32 broods sampled and 5.5% of all nestlings. In both of these nests all young genetically matched the social father (i.e., for each offspring, at least one allele at each locus matched the social father) but not the social mother, indicating quasi-parasitism. In both nests the parasitic nestlings were full siblings ($r = 0.46 \pm 0.07$), indicating that they were produced by a single female parasite that mated with the social father and was responsible for the entire brood. Yet in our behavioral observations of these pairs' nest attendance (~10 hr per nest) and activities before and after the breeding season (~13 hr per pair), we recorded only the social female with the male or visiting the nest to incubate and feed nestlings. At one nest, we identified the genetic mother of the nestlings as a female from an adjacent territory. At the other, we could not identify the genetic mother, so she was likely an unsampled female.

Over the three years of our study, 10 cooperative groups raised young in 13 nests (Table 2), and in eight of these all young were produced by the primary pair and not by auxiliaries (i.e., strict monogamy, though from two of these nests we sampled only a single nestling). At the other five nests the pattern was more complex. Four groups showed simultaneous polygyny, with a single breeding male siring the young of multiple joint-nesting females. There was no difference in the sex ratio of cooperative groups with polygynous males (0.64 ± 0.14 males/females) in comparison to groups with a monogamous pair (0.70 ± 0.14 males/females; Student's t -test: $t_7 = 0.332$; $P = 0.75$). All cooperative groups had multiple females, so our results suggest that polygyny is common in cooperative

groups, occurring in four of nine such groups from which we analyzed more than a single chick.

In contrast to frequent breeding by auxiliary females, of those cooperative groups with multiple males and more than a single nestling analyzed ($n = 6$), in only one case (17%) did more than a single male sire offspring: in group F (2008) the breeding male sired offspring with both of the group's females and his son also sired an offspring with one of the females. As with socially monogamous pairs, there were no cases of offspring sired by males from other groups.

DISCUSSION

While Campo Flickers often breed as simple pairs without helpers, approximately half of the breeding units that we monitored were cooperative groups consisting of multiple adults. These cooperative groups consisted of a primary pair with one or more auxiliaries of either sex. Auxiliaries of both sexes were usually related to at least one member of the primary pair and often appeared to be offspring from the previous year and/or siblings of one of the primary breeders. In some cases, however, the auxiliaries were unrelated to the primary breeding pair.

These results provide insight into the evolution of sociality in the Campo Flicker, in particular by showing that auxiliaries can arise via multiple routes. First, our data show that many auxiliaries are offspring of the primary pair that delay dispersal from the natal group. This is a typical "helper at the nest" social system seen in many other cooperatively breeding birds (Brown 1987), including other species of woodpecker such as the Red-cockaded (*Picoides borealis*; Haig et al. 1994) and Three-toed (*P. tridactylus*; Li et al. 2009). In many cooperative birds it is the males that remain in their natal group as helpers at the nest, but our results indicate that both sexes may do so in the Campo Flicker. Second, many other auxiliaries were siblings (or half-sibs), rather than the offspring, of the primary breeder of the same sex. This suggests that individuals of the same sex may sometimes disperse together to create a new group or join an existing group, as has been described in the Acorn Woodpecker (*Melanerpes formicivorus*; Koenig and Stacey 1990) and other cooperative birds (e.g., Heinsohn et al. 2000). This pattern could also occur if a solitary individual joins a group that already contains relatives.

An additional scenario for the patterns of relatedness among group members containing dyads of sibs and half sibs could arise with the death of a male breeder that was assisted by more than one of his own sons. In such cases the older auxiliary could inherit the breeding position and the remaining auxiliary could become a sibling helper (Koenig et al. 1998, but see Komdeur and Edelaar 2001). However, this scenario should be rare because of the high possibility of incestuous mating with the dominant female breeder (the mother). Finally, in some groups, auxiliaries appeared to be unrelated to other group members, suggesting that individual males or

TABLE 2. Number of males and females in each social group and number of young fledged per female. Each row represents a nest of a social group in a given year.

Group	Year	Males	Females	No. of fledglings produced by each female of a group		
				Female 1	Female 2	Female 3
F	2007	2	3	3	0	0
G	2008	2	3	1	0	0
R	2009	2	3	2	0	0
D	2007	2	3	1	1	0
D	2008	1	3	2	1	0
B	2007	2	2	4	0	—
E	2007	2	2	3	1	—
F	2008	2	2	2	2	—
K	2008	2	2	4	0	—
AG	2008	2	2	1	0	—
F	2009	1	2	4	2	—
AA	2008	1	2	3	0	—
AB	2009	1	2	3	0	—

females may sometimes join unrelated groups and/or form coalitions with unrelated birds. In these cases the auxiliaries may be potential breeders waiting for an opportunity to breed (Cockburn 2004).

These results also reveal the potential for both cooperation and conflict within Campo Flicker groups. In many species it appears that the main benefit to breeders of group formation is increased productivity (e.g., Emlen and Wrege 1991, Conner et al. 2004) and/or survival (e.g., Russell et al. 2007), and this may be the case for the Campo Flicker as well (Dias et al., unpubl. data). However, the benefits for auxiliaries are less clear and may vary by type of auxiliary. Indirect kin-selected benefits (Hamilton 1964, Brown 1987) are possible in many groups, at least for auxiliaries that are closely related to the breeding pair. Finally, it is clear that in the Campo Flicker auxiliaries are sometimes able to reproduce directly within their group—auxiliary males may sire young with the breeding female and auxiliary females may contribute eggs to a joint nest. Accordingly, conflicts may arise between breeders and auxiliaries of the same sex, especially in those cases where the breeders and auxiliaries are unrelated (Emlen 1995, Webster et al. 2004).

Our data show that, despite the significant social and reproductive complexity observed in many groups, monogamy is the Campo Flicker's primary mating system, whether birds are organized socially as cooperative groups or as isolated pairs. However, in some groups we observed joint nesting, with multiple females laying eggs in the same nest. Although cooperative breeding has been described for a few woodpecker species, joint nesting by females has been described only for the Acorn Woodpecker (Vehrencamp and Quinn 2004). We found no difference in the relatedness of the dominant female breeder with female auxiliaries producing young and with those that did not. However, our sample size was small, and there was a non-significant trend for auxiliary females that produced young to be less closely related to the primary female than were female auxiliaries that did not produce young, as would be expected from reproductive skew theory (Emlen 1995, Magrath et al. 2004). In this respect the Campo Flicker differs from the Acorn Woodpecker, as in the latter species joint-nesting females are almost always close relatives (Koenig and Haydock 2004).

In contrast, male auxiliaries appear to sire young within the group only rarely. In the single case we observed, a subordinate son of the dominant male produced a nestling with one of the two females of the group (his aunt), while his father copulated with both of the group's females, producing three nestlings. Accordingly, in most groups with multiple breeding females, all young produced were sired by the dominant breeding male. Such simultaneous polygyny is rare in woodpeckers (Wiklander et al. 2000), most of which appear to be genetically monogamous (Winkler et al. 1995), possibly because of their dependence upon biparental care

for successful reproduction (Winkler and Christie 2002). We also observed no cases of extra-pair paternity or extra-group paternity, and this agrees with the general pattern of little to no extra-pair paternity in nonpasserines (Griffith et al. 2002; but see Huyvaert et al. 2000 and Mee et al. 2004), including woodpeckers (but see Pechacek et al. 2005). Thus male auxiliaries appear to have few opportunities for direct reproduction. Instead, their benefits may be indirect through kin selection and/or delayed (as they wait to inherit a breeding position).

Although we found no cases of extra-group paternity, we did find, albeit at a low level, intraspecific brood parasitism of the nests of monogamous pairs, which has been detected in other woodpeckers also (Wiklander et al. 2000, Bower and Ingold 2004, Pechacek et al. 2005, Li et al. 2009). In our study, these cases of intraspecific brood parasitism were in fact examples of quasi-parasitism, as the social male at each parasitized nest sired the parasitic nestlings. In both cases we are confident that the parasitic female was not a member of the social group, and indeed in one case the female was from a neighboring social group. Quasi-parasitism of this sort is rare in birds and poorly understood (Lyon and Eadie 2008). Both the absence of extra-pair paternity and the low level of intraspecific brood parasitism may reflect the high level of paternal investment in the Campo Flicker (Dias et al. 2013, unpubl. data) and in woodpeckers in general. For woodpeckers, nesting entails a demanding process of nest excavation, long bouts of incubating and brooding, and frequent feeding of nestlings (Winkler and Christie 2002).

Our results reveal a complex social system in the Campo Flicker, ranging from monogamous pairs to cooperative groups, and with the latter including an array of reproductive patterns and diverse kinship relationships among group members. Thus the costs and benefits associated with the evolution of sociality in the Campo Flicker vary by group and by individual within a group. For auxiliaries, group membership may provide the indirect benefits of kin selection, an opportunity for direct reproduction (for females), and the opportunity to fill a future vacancy of a primary breeder. For primary breeders, the presence of auxiliaries likely provides benefits via assistance with parental duties in some cases (Dias et al. 2013), but in many groups auxiliaries (particularly females) also may be reproductive competitors. Studies of species like the Campo Flicker, with complex and variable social systems, are important for understanding the dynamic interplay of reproductive cooperation and competition in highly social organisms.

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