

## COOPERATIVE BREEDING IN THE CAMPO FLICKER I: BREEDING ECOLOGY AND SOCIAL BEHAVIOR

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**Abstract.** Cooperative breeding and complex social systems are known in woodpeckers, but most available information concerns species of the North Temperate Zone. The social behavior and breeding ecology of tropical woodpeckers are poorly documented. Here we present data on the breeding behavior and ecology of a tropical woodpecker, the Campo Flicker (*Colaptes campestris campestris*). We confirm for the first time, through behavioral observations, facultative cooperative breeding in this species. Both males and females were observed visiting the nest during the incubation and nestling period. In cooperative groups some helpers were identified as young from the previous year, but others seem to be unrelated individuals that joined the groups. In addition, our behavioral observations strongly suggest both polygyny (a male breeding with more than one female simultaneously) and joint nesting (multiple females contributing eggs to a single nest) in some but not all cooperative groups. These observations reveal a complex social system in this tropical species, with high potential for reproductive conflicts both within and among groups, due to the presence of new potential breeders or through advantages emerging from the effects of group size.

**Key words:** *Colaptes campestris*, communal breeding, cooperative breeding, joint nesting, mating system, tropics.

### Cría Cooperativa en *Colaptes campestris campestris* I: Ecología Reproductiva y Comportamiento Social

**Resumen.** La cría cooperativa y los sistemas sociales complejos son conocidos en los carpinteros, pero la mayoría de la información disponible se refiere a especies de la zona templada norte. El comportamiento social y la ecología reproductiva de los carpinteros tropicales han sido pobremente documentadas. Aquí presentamos datos sobre el comportamiento reproductivo y la ecología de un carpintero tropical, *Colaptes campestris campestris*. Confirmamos por primera vez, a través de observaciones de comportamiento, cría cooperativa facultativa en esta especie. Los machos y las hembras fueron observados visitando el nido durante el período de incubación y pichón. En los grupos cooperativos se identificaron algunos ayudantes como jóvenes del año anterior, pero otros parecen ser individuos no relacionados que se unieron a los grupos. Además, nuestras observaciones de comportamiento sugieren con firmeza tanto poliginia (un macho criando con más de una hembra simultáneamente) como anidación conjunta (varias hembras que contribuyen huevos a un único nido) en algunos pero no todos los grupos cooperativos. Estas observaciones revelan un sistema social complejo en esta especie tropical, con un alto potencial para conflictos reproductivos tanto dentro como entre grupos, debido a la presencia de nuevos reproductores potenciales o a través de ventajas emergentes del efecto del tamaño de grupo.

## INTRODUCTION

Cooperative breeding has been recorded in about 9% of bird species (Cockburn 2006), and in many cases helpers are non-breeding young that remain at the natal site and help to care for their own siblings (Skutch 1961). In other cases, helpers are unrelated individuals that may produce offspring within the group, either by copulating with the group's breeding female, in the case of helper males, or by contributing eggs to the nest ("joint nesting"), in the case of helper females (Brown 1987). Despite much effort toward understanding

the evolution of cooperative breeding, the main factors responsible for the evolution and maintenance of this behavior in most species remain unclear. Ecological, demographic, and life-history factors have been proposed to explain variation in patterns of sociality among different species (Ligon and Burt 2004). The most common explanations are the "habitat-saturation hypothesis," which proposes that sexually mature individuals will remain in the natal territory when all suitable breeding habitats are occupied (Koenig and Pitelka 1981), and the "benefits-of-philopatry hypothesis," which proposes

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that individuals may enhance their fitness by remaining on high-quality territories instead of dispersing to low-quality territories (Stacey and Ligon 1991). These and other hypotheses have been evaluated in several taxonomically diverse cooperatively breeding species, leading to significant conceptual and empirical progress in the last few decades (Koenig and Dickinson 2004, Hatchwell 2009).

The family Picidae includes approximately 216 species distributed worldwide, found on all continents except Australia and Antarctica (Winkler et al. 1995). Most species of woodpeckers that have been studied are socially monogamous, each breeding pair caring unaided for its own young (Winkler and Christie 2002). Several species of woodpecker, however, breed cooperatively. One such well-studied example is the Acorn Woodpecker (*Melanerpes formicivorus*), in which groups of up to 15 individuals defend territories year-round and store acorns, which are an important source of nutrients for the group, especially during the winter. The mating system of the Acorn Woodpecker ranges from monogamy to polygyny, and all group members usually care for the offspring (Koenig and Pitelka 1979, Koenig 1981, Haydock and Koenig 2003, Koenig et al. 2009). In another cooperative species that has been well investigated, the Red-cockaded Woodpecker (*Picoides borealis*), a similar form of social organization has evolved, but in this case groups consist of a pair of breeders aided by helpers that are usually male offspring from the previous year (Ligon 1970, Walters et al. 1988, Khan and Walters 1997, Malueg et al. 2009).

Studies of North American and European woodpeckers (e.g., Pechacek et al. 2005, Rudolph et al. 2007, Drever et al. 2008, Wiebe and Kempnaers 2009), which represent 7% of the species of Picidae, account for approximately 70% of the publications on breeding ecology of woodpeckers published between 1985 and 2004 (Mikusiński 2006). Only 3% of these studies were conducted in Latin America, where more than half of the world's woodpeckers occur (Mikusiński 2006). Moreover, cooperative breeding has been well studied in only a few temperate-zone woodpeckers. Thus it remains unclear whether cooperative breeding is common or rare in tropical woodpeckers, or whether insights from studies of temperate-zone woodpeckers can be generalized to tropical species. Anecdotal observations suggest that two tropical woodpeckers (the Yellow-fronted, *Melanerpes flavifrons*, and White-fronted, *M. cactorum*) are cooperative breeders (Yamashita and Lo 1995, Oniki and Willis 1998). Additionally, cooperative breeding in a previously described non-cooperative tropical woodpecker was reported recently (Great Slaty Woodpecker, *Mulleripicus pulverulentus*; Lammertink 2004).

The genus *Colaptes* is widely distributed in the New World and includes species with well-developed social behavior. *Colaptes* differs from most other woodpeckers by its terrestrial foraging habits (Short 1972). The Campo Flicker (*C. campestris*) is a conspicuous medium-sized woodpecker

with a wide distribution in South America. It consists of two subspecies: *C. c. campestris*, distributed from northeastern Brazil to central Paraguay, as well as in isolated patches of Amazonian upland savanna (Silva et al. 1997), and *C. c. campestroides*, found from southern Paraguay and Brazil to northeastern Argentina (Short 1972). The subspecies differ mainly in throat coloration, black on *campestris* and white on *campestroides* (Short 1972). In spite of the species' abundance, most aspects of the natural history of the Campo Flicker are poorly known. The breeding biology and social system of subspecies *campestroides* have been described only briefly. In Argentina, this subspecies has been observed either in pairs or in groups of up to five individuals (Di Giacomo 2005). Short (1972) suggested that it may live in small social groups and proposed that some individuals could be from the previous year's brood, but emphasized that studies were needed to establish this speculation.

Given prior observations of sociality in this species, our primary goal in this study was to describe the breeding biology of the Campo Flicker (subspecies *campestris*), including its social system, mating behavior, and timing of breeding relative to seasonality. We also interpret our results in the context of hypotheses that have been applied to cooperative breeding in other woodpeckers, such as the explanation of limiting resources, granaries in the case of the Acorn Woodpecker (Gutiérrez and Koenig 1978, Koenig and Benedict 2002) and cavities in pine trees in the case of the Red-cockaded Woodpecker (Walters et al. 1992).

## METHODS

### STUDY AREA AND GENERAL PROCEDURES

We conducted field work at Fazenda Água Limpa (15° 56' S, 47° 55' W), an area of 4500 ha in Brasília, central Brazil, from October 2006 to December 2009. The area is within the cerrado (tropical savanna) biome and comprises several natural vegetation types, including open grassland (*campo limpo*), grassland dotted with shrubs (*campo sujo*), scrub forest (*cerrado sensu stricto*), gallery forests, and some grazed areas as well. We obtained weather data from a meteorological station within the study area. The climate is strongly seasonal with a marked rainy season from October through March.

We searched for Campo Flickers by surveying the study site at least four times each week, broadcasting recorded vocalizations. Whenever we discovered a social group, we used recorded vocalizations to capture the birds in mist nets. We banded all captured individuals with a unique combination of three color bands and a numbered metal band from the Brazilian regulatory agency, the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). We weighed the birds (to nearest gram), measured their tarsus, wing, beak, and tail lengths with calipers (to nearest 0.02 mm), and collected approximately 100 µL of blood from the brachial vein of adults for genetic analyses of parentage and kinship (see Dias et al. 2013).

We defined a social group as any aggregation of two or more individuals that remained together within a specific area (usually being found in the same place) of the study site over at least 6 months. We categorized each social group as either a socially monogamous pair (two adults of the opposite sex) or a cooperative group (more than two adults).

During the breeding season (July–November) we used a mirror attached to a pole and flashlight to check the contents of potential nesting cavities within the study area, independently of having detected a group nearby, and recorded the location (GPS coordinates) of all active nests found, which we subsequently monitored every 2 or 3 days. We defined hatching success (per nest) as the percentage of eggs of the total clutch that hatched. Unhatched eggs that disappeared within 5 days after hatching of the remaining eggs in the clutch we considered to be unhatched, rather than depredated, because adults sometimes removed unhatched eggs from the nest. We considered predation to have been the cause of nest failure when eggs or nestlings disappeared and the nest entrance was abruptly enlarged and/or there were blood and feathers in the vicinity of the nest. We present the number of eggs depredated as a mean for all nests of the social unit (pairs or groups). We attributed nest failure to starvation when we found nestlings dead within the nest cavity over successive days. We defined nesting success as the percentage of nests that fledged at least one young, and we considered a brood to have fledged successfully whenever a nestling disappeared from the nest within 5 days of the expected date of fledging (expectations based on prior field observations of the Campo Flicker) with no sign of predation (as described above).

#### PARENTAL ACTIVITY

We recorded the adults' parental activity during 1 hr of observation at each nest twice during the incubation period (years two and three of the study), on the fifth and tenth days after the last egg of the clutch was laid. After hatching, we recorded parental activity at each nest on five days during the nestling period (days 4, 10, 16, 22, and 28 after hatching). These data were obtained either through 2-hr focal observations (for most nests) from a blind approximately 20–30 m from the nest cavity (to avoid disturbing the birds) or by video cameras (Sony DCR-HC52) whose tapes lasted 1 hr, 40 min. During all observation periods we recorded the identity of the individuals visiting the nest. Near the end of the nestling period (day 25 after hatching), we measured and banded nestlings and took blood samples for genetic analyses, as for adults (see Dias et al. 2013).

#### HOME RANGE AND TERRITORY

At least three times per week during the study period we located all focal groups and used GPS to map the locations of individuals, noting all aggressive interactions with neighbors and occurrence of territorial displays. Usually we recorded no more than three points with the GPS per day for any social

group: the points were taken whenever the group was found or when territorial displays or aggressive interactions were observed. In 2008, to facilitate the location of a subset of groups and more easily define their territories, we fitted one individual from each of 12 social groups with a backpack transmitter that weighed 4.0–5.0 g, approximately 2–3% of an adult's weight (Sopb-2190 HWSC; Wildlife Materials, Inc.). We did not observe adverse effects of the transmitters on the birds, and all radio-tagged individuals survived to the next year (see also Vukovich and Kilgo 2009). We calculated the size of a home range as the 95% fixed-kernel contour (Seaman and Powell 1996) with the software Home Ranger 1.5 (Hovey 1999). Because kernel estimates of home ranges are influenced by sample size (Seaman et al. 1999), for these analyses we only included social groups with more than 40 sampled points. The points resulted from approximately 15 to 40 days of sampling for each group.

#### STATISTICAL ANALYSES

We compared the clutch sizes and hatching success of pairs with those of cooperative groups with Mann–Whitney *U*-tests, nesting success with a chi-squared test. To avoid pseudoreplication, we used mean values for individuals that bred in more than one year. Values are presented as mean  $\pm$  standard error. For all analyses we used R 2.7.2 (R Development Core Team 2009). Statistical tests were two-tailed, and we rejected the null hypothesis at  $P < 0.05$ .

## RESULTS

#### GROUP SIZE AND COMPOSITION

We captured and banded 160 individuals (71 adults and 89 nestlings), monitored 26 social groups, and found 57 nests during the three-year study period. Each social group could be classified unambiguously as either a socially monogamous pair (58%;  $n = 15$ ) or a cooperative group (42%;  $n = 11$ ). Membership of individuals in a group was generally very stable, and despite some changes in composition (e.g., through dispersal of former helpers out of, or addition of new individuals into, a group), the same groups were found at the same sites through two ( $n = 4$ ), three ( $n = 6$ ), or four ( $n = 2$ ) years of the study. However, some groups were found before others, so the persistence of groups in territories is likely underestimated. Outside the breeding season, the size of a social unit ranged from 2 to 7 individuals, but a few weeks before the observation of the first reproductive behaviors (e.g., cavity excavation and copulations) some individuals of larger groups disappeared from the area and may have dispersed to unidentified areas. During the breeding season the size of a social unit varied from 2 to 5 individuals (mean =  $2.67 \pm 0.14$ ). Most cooperative groups (7 of 11, or 64%) had more females than males, and group composition varied from one male and three females to two males and three females (see Dias et al. 2013 for further details). Of the

remaining four groups, two (18%) had multiple (two or three) males with a single female, and the other two groups (18%) contained two males and two females. Socially monogamous pairs ( $n = 15$ ) were very stable, most persisting through at least one year and three (20%) maintaining the bond for the entire duration of the study.

#### HOME RANGE AND TERRITORIALITY

Campo Flickers are year-round residents and defend their territory intensively throughout the year, displaying 1–12 times per hour. Territories were found in various habitats such as grasslands with scattered shrubs and trees (*campo sujo*), rocky grasslands, floodplain grasslands with mounds of earth, *cerrado sensu stricto* (dominated by trees and shrubs often 3 to 8 m tall), gallery forest borders, and grazed pastures. Territory owners (pairs or whole groups) approached intruders and attempted to repel them with a conspicuous wing flicking display and vocalizations ( $n = 39$  observations). In cases where the intruder persisted, territory owners sometimes attacked and poked the intruder with their bill ( $n = 7$ ). We observed physical combat, at territory borders, on only three occasions. Intruders were never observed wandering within other groups' territories, since group members appeared to detect them at territory borders. It appears that Campo Flicker territories coincide with their home ranges, since individuals defended all areas where they were ever observed. For all social units, territory borders made contact with at least one neighboring territory, territories appearing to saturate the available suitable habitat. In the three cases where one of the breeding adults in a group died (found dead), it was replaced in 5–12 days by an individual of the same sex, either an unbanded individual or a banded one from a nearby territory. In all the cases of the breeding adult dying, the social group was composed of a pair without helpers. Mean territory size was  $48.50 \pm 3.93$  ha, ranging from 20.84 to 81.21 ha.

#### BREEDING PERIOD AND NEST SITES

Observations of copulation were rare and occurred in late July and August ( $n = 6$ ), during the period when most nest excavation took place. We observed nesting behavior from July through November; egg laying peaked in September, when 45% of the nests received their first eggs (Fig. 1). The beginning of the breeding season seemed to be strongly associated with precipitation, since the date of laying varied from year to year and coincided with the first rains in the region (Fig. 1). The dry season of 2007 was exceptionally long, with no significant rain during September (0.5 mm), when the first nests were initiated (Fig. 1). In contrast, in 2009 the dry season was very short, restricted to the month of July, and egg laying started in early August (Fig. 1). Nevertheless, the duration of the breeding season seemed to be constrained, since all five nests starting late in the season (October and November) failed, and since these failures did not have the

typical indicators associated with predation, we attributed them to undefined effects of seasonality that may have led to the nestlings' starvation.

Of the 57 nests found, 84% were excavated in termite mounds, the remaining 16% in tree cavities. The latter nests occurred in areas of the study site that lacked large termitaria, suggesting that tree cavities were less preferred as nest sites. Only nests in tree cavities were reused in successive years (44% of all tree cavity nests). Even when a tree cavity was reused, adults always excavated to deepen the cavity prior to egg laying. Re-use of the same termitarium mound was always associated with the excavation of a new cavity, since the termites often closed nest cavities after the young fledged ( $n = 6$ ). Nest excavation

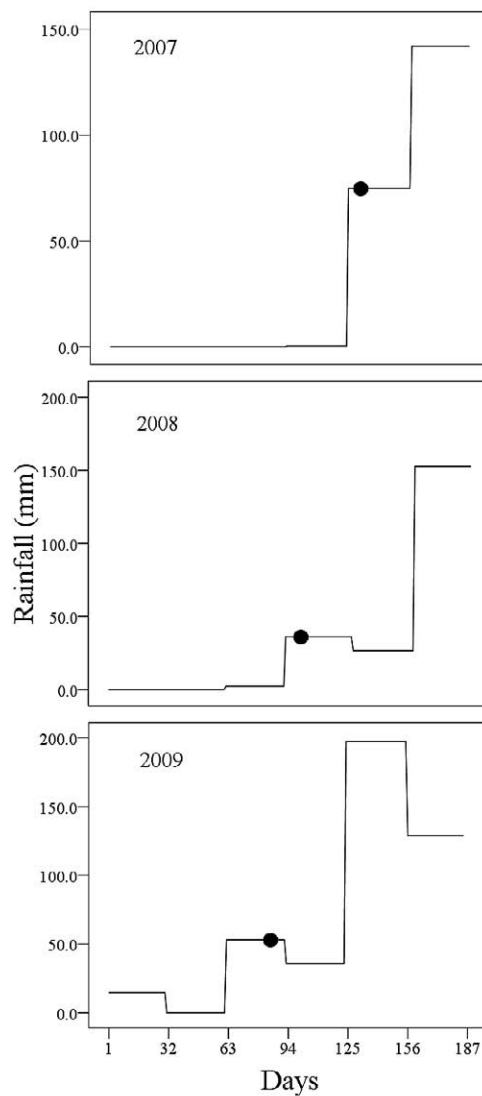


FIGURE 1. Mean date of laying of the Campo Flicker in central Brazil over three breeding seasons. Lines show monthly rainfall (mm) each year. The “days” axis starts on 1 June (day 0) and ends on 30 November (day 183). The mean date of laying each year is marked with a symbol on the line for that year.

lasted for up to four weeks but sometimes occurred swiftly in one week (mean =  $21.66 \pm 3.71$  days;  $n = 9$ ). Males and females both excavated nests, and all members of cooperative groups were observed to help with cavity excavation and vigilance.

#### EGGS AND NESTING BEHAVIOR

Eggs were plain white and elliptical in shape with a mean length of  $30.41 \pm 0.25$  mm and width of  $21.51 \pm 0.15$  mm. Clutch size ranged from 3 to 9 eggs, and the mean clutch size for pairs ( $4.10 \pm 0.11$  eggs, range 3–5,  $n = 15$ ) was significantly smaller than that for cooperative groups ( $6.00 \pm 0.64$  eggs, range 4–9,  $n = 11$ ; Mann–Whitney  $U$ -test,  $U = 78.00$ ;  $P = 0.01$ ; Table 1). Typically, one egg was laid each day until the clutch was completed, but there were three cases of a two-day interval between laying of successive eggs.

The Campo Flicker appears to be single-brooded, as we never observed a group fledge more than one brood per season, although we did observe up to three nesting attempts within a breeding season after the previous nest failed. Hatching success averaged 76% and tended to be higher for pairs (85%,  $n = 15$ ) than for cooperative groups (67%,  $n = 11$ ; Table 1), although this difference was not quite statistically significant (Mann–Whitney  $U$ -test,  $U = 74.50$ ;  $P = 0.06$ ). The incubation and nestling periods lasted  $15.67 \pm 0.33$  days ( $n = 15$ ) and  $29.11 \pm 0.35$  days ( $n = 18$ ), respectively. Nesting success averaged 65.5% but was seemingly higher for cooperative groups (72%) than for pairs (59%; Table 1), although again this difference was not statistically significant ( $\chi^2_1 = 0.91$ ,  $P > 0.10$ ). Nests lost to predation accounted for 60% of the failures; only pairs experienced losses apparently caused by starvation or parasitism, and these represented 40% of all nest losses pooled (and 50% of pairs' total losses). Partial losses were observed in 18% of pairs' nests and 6% of cooperative groups' nests. Interestingly, in some nests of cooperative groups ( $n = 6$ ), but none of pairs, we observed cases of all eggs in the clutch vanishing without any sign of predation,

followed by renesting in the same nest cavity. Renesting in the same cavity never occurred when the eggs disappeared because of predation ( $n = 8$ ).

#### PARENTAL AND ALLOPARENTAL CARE

More than two individuals were involved in the incubation of eggs and feeding of young in all cooperative groups ( $n = 11$ ), and both males and females were observed visiting the nest during the incubation and nestling periods. For three groups for which we have longer banding records, we were able to determine that helpers assisting at nests were male ( $n = 2$  groups) or female ( $n = 1$  group) nestlings from previous years. In all cases where an adult helper joined a group and was known not to be an offspring from a previous season ( $n = 3$  groups), the helper was a female. In two of these three cases we observed the breeding group's female aggressively interacting with the immigrant female, seemingly attempting to drive the potential helper female away.

#### DISCUSSION

Our 3-year study establishes that the Campo Flicker is a facultative cooperative breeder, as nearly half of all breeding units had adult helpers in addition to the breeding pair. Cooperative groups had three to five individuals helping to rear the offspring. In some cooperative breeders, helpers are nonbreeding young that remain at the natal site and help to care for their own siblings (Skutch 1961). In other cases, helpers are unrelated individuals that may produce offspring within the group, either by copulating with the group's breeding female if they are males or contributing eggs to the nest ("joint nesting") if they are females (Brown 1987). In our study of the Campo Flicker we found that helpers were of two types: either male or female offspring of the breeding pair from the previous breeding season ("primary helpers") or adult females that joined the group ("secondary helpers"). In the latter case the females had immigrated from outside the study site and were of unknown origin, but they were likely unrelated to the breeding pair (see Dias et al. 2013).

Year-round territoriality and adults' high rate of survival in the Campo Flicker may lead to habitat saturation, which may be an important factor favoring philopatry and low territory turnover (see Baglione et al. 2005). This idea is supported by our observations of the rapid replacement that followed the death of some paired individuals, suggesting that the population contains adults waiting for an opportunity to breed. Thus primary helpers are probably constrained in terms of opportunities to disperse, such that the best option in most cases may be to remain on the natal territory. This agrees with predictions of the habitat-saturation hypothesis, although our study design does not allow us to conclude that it is the main factor maintaining cooperative breeding. It is also likely that, as for other cooperative breeders, there are several

TABLE 1. Measures of the breeding of the Campo Flicker in central Brazil. We defined pairs as social units composed of two adults of opposite sex and groups as social units containing more than two adults.

|                                       | Mean $\pm$ SE (range) |                       |
|---------------------------------------|-----------------------|-----------------------|
|                                       | Pairs ( $n = 15$ )    | Groups ( $n = 11$ )   |
| Eggs laid                             | $4.10 \pm 0.11$ (3–5) | $6.00 \pm 0.64$ (4–9) |
| Eggs hatched                          | $3.63 \pm 0.20$ (3–5) | $3.90 \pm 0.45$ (3–7) |
| Eggs depredated                       | $0.69 \pm 0.26$ (2–4) | $0.36 \pm 0.36$ (4–4) |
| Chicks depredated                     | $0.28 \pm 0.19$ (3–4) | $0.60 \pm 0.41$ (4–5) |
| Chicks died (starved/<br>parasitized) | $0.88 \pm 0.30$ (1–4) | $0.20 \pm 0.14$ (1–2) |
| Chicks fledged                        | $1.58 \pm 0.29$ (0–4) | $2.45 \pm 0.59$ (0–6) |

potential benefits for primary helpers that favor delaying dispersal, including possible inheritance of the natal territory or abutting areas (Stacey and Ligon 1991), as well as possible indirect fitness benefits (Hamilton 1964a,b).

In contrast, secondary helpers were not previous young constrained from natal dispersal but may have been dispersing females attempting to find a mate or resources (e.g., food, nesting sites, territory). These females may join existing groups when they could benefit in some way, for example, by directly contributing eggs to the nest and/or by establishing a pair bond with a male for future breeding (see Reyer 1980). The evolutionary origins of helping by primary and secondary helpers may not necessarily be different, but these helpers' behavior can also be viewed as two different strategies that emerge under the constraints of habitat saturation. Atypically large clutches of social groups with multiple females and our genetic analyses (see Dias et al. 2013) support this hypothesis and suggest that the Campo Flicker belongs to a small group of species that are joint-nesting cooperative breeders, i.e., multiple females laying eggs in the same nest. This is a relatively rare breeding system that has been documented for only about 14 species (Vehrencamp and Quinn 2004), including only one woodpecker, the Acorn Woodpecker (Mumme et al. 1988). Interestingly, during our study, eggs vanished from the nest without any sign of predation only from nests of cooperative groups, and when this happened the group re-nested in the same nest cavity within a few days. In contrast, in cases of nest predation, the group did not re-nest in the same cavity. This suggests that females may be destroying each others' eggs, as has been documented in other joint-nesting species such as the Acorn Woodpecker (Mumme et al. 1983), three species of anis (Vehrencamp 1977, Loflin 1983, Riehl and Jara 2009), and the Guira Cuckoo (*Guira guira*; Macedo 1992). In addition, we observed aggressive behaviors among a group's females during nesting. In one case, the dominant female displaced a subordinate female every time the latter approached the nest (R. I. Dias, pers. obs.).

Our results also suggest that groups of Campo Flickers with secondary helpers may bear a cost. Hatching success tended to be lower for joint-nesting cooperative groups than for monogamous pairs, suggesting a possible limitation of cavity size for the effective incubation of large clutches (but see Wiebe and Swift 2001). An alternative possibility is that unhatched eggs were not fertilized. On the other hand, the absence of total losses of broods to starvation and the reduction of partial losses for cooperative groups suggest that helpers, whether primary or secondary, have an important role in determining nest fate. Studies of several species, including woodpeckers, have demonstrated that the presence of helpers has a positive effect on the number of young that fledge per nest (Conner et al. 2004).

The mating system of most woodpeckers is social monogamy, though there are some cases of polyandry (Williamson et al. 1991, Winkler et al. 1995, Kotaka 1998, Pechacek

et al. 2005). A congener, the Northern Flicker (*Colaptes auratus*), is essentially genetically monogamous but may use some alternative reproductive tactics, such as polyandry and brood parasitism (Wiebe and Kempenaers 2009). It is usually assumed that in woodpeckers biparental care is essential to rearing a brood (Winkler et al. 1995, Wiktander et al. 2000), and in this study we observed that incubation and feeding were shared by males and females of both social pairs and cooperative groups. Our field data and genetic analyses (see Dias et al. 2013) indicate that the Campo Flicker's variable mating system ranges from social monogamy to simultaneous polygyny and some cases of joint nesting. Polygyny is considered to be rare among woodpeckers (but see Wiktander et al. 2000).

Campo Flicker groups maintained a stable social organization and defended territories year round, in some cases for several years. Suitable habitats in our study area seem to be saturated, with territories abutting each other, and territory sizes are comparable to those observed in other woodpecker species (Winkler and Christie 2002). The Campo Flickers we studied nested primarily in termite mounds and used tree cavities only when there were few or no termitaria available. Thus termitaria may be a limiting and valuable resource, which could contribute to the value of the natal territory and thus limit juveniles' options for dispersal. This pattern differs from that observed for subspecies *campestroides*, which prefers tree cavities in Argentina, for example (Short 1972; Di Giacomo, pers. comm.), and for which cooperative breeding is not reported (but see Di Giacomo 2005). Possibly, there are tradeoffs between using termitaria near the ground (e.g., greater vulnerability to predators) and nesting in trees. Group size and composition may determine whether a group nests in a tree or a termitarium, and these alternative options may influence reproductive success; a study of such possibilities is needed.

Campo Flickers began breeding at the end of the dry season and nestlings usually fledged at the beginning of the wet season, suggesting that rainfall is intrinsically linked to reproduction in this species. Other studies have demonstrated an effect of rainfall and other weather conditions on the timing of tropical birds' breeding in seasonal climates (Hau 2001, Monadjem and Bamford 2009). Among woodpeckers, such an association has been found in the Middle Spotted Woodpecker (*Dendrocopos medius*) and the Northern Flicker, both of which initiate certain aspects of breeding earlier in warmer springs (Pasinelli 2001, Wiebe and Gerstmar 2010). In the case of the Campo Flicker, greater availability of termites and ants during the rainy season may be the ultimate cause of breeding at the end of the dry season. The breeding ecology of the Campo Flicker is similar to that of most members of the family Picidae (del Hoyo et al. 2002), but detailed comparisons with other congeners is difficult due to a lack of information (but see Wiebe 2001, Wiebe and Swift 2001).

The data we present here for the Campo Flicker illustrate a complex breeding system that includes variability in both mating and social relationships, revealing the potential for conflict as well as cooperation in this species. The integration of these life-history data with the genetic analyses of group composition and maternity/paternity (see Dias et al. 2013) will contribute toward a more sophisticated interpretation of the evolution of cooperation in tropical woodpeckers and other birds.

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## LITERATURE CITED

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