

Parental and alloparental investment in campo flickers (*Colaptes campestris campestris*): when relatedness comes first

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Abstract

In cooperative species, parental investment may be shared with auxiliaries. Kin selection and other types of benefits have been proposed to explain the evolution of helping behavior. Auxiliaries are expected to be more helpful when closely related to the breeders. In this context, breeders may adjust parental investment in at least three ways: (a) reducing their effort and being compensated by the auxiliaries' investment (compensatory effect); (b) maintaining their effort, with an increase in total investment (additive effect); or (c) partial compensation, i.e., a decrease in care by the parents but not by as much as the increase in care from the auxiliaries. We studied the cooperative species *Colaptes campestris campestris* and tested the following hypotheses: (1) partial compensation effect occurs, (2) parents modulate their investment relative to the auxiliaries' investment, (3) auxiliaries adjust their investment according to their relationship to the offspring, and (4) groups whose members are in better physical

condition fledge more young or these are in better condition. We determined relatedness within groups and monitored parental and alloparental behavior during breeding. Breeders in cooperative groups presented the same investment as unattended breeders. Restricting the analysis to cooperative groups revealed that the investment made by auxiliaries reflected their relatedness to the young and positively affected the investment by breeders. Results suggest that a partial compensation occurs in the species, with breeders reducing their effort despite the small increase in overall nest investment. Results highlight the importance of kin selection in the evolution of cooperative breeding in campo flickers.

Significance statement

Cooperatively breeding birds may have auxiliaries that help rear their brood. The evolution of helping behavior may derive from kin selection, where auxiliaries could gain a genetic benefit by helping to rear kin, which occurs when groups are composed of closely related individuals. However, it is often the case that some offspring may not be closely related to the auxiliaries due to the species' mating system. We used the cooperatively breeding campo flickers to investigate whether and how the presence of auxiliaries might affect parental care patterns and nest productivity. We found that breeders did not reduce their investment in the presence of auxiliaries and that cooperative groups present the same overall investment when compared with unassisted pairs, indicating that the investment made by auxiliaries was not large enough to affect the total investment nor the breeders' investment. Our results also show that auxiliaries increased their investment when they were more closely related to the brood.

Keywords Additive effect · Compensatory effect · Cooperative breeding · Kin selection · Parental care · Relatedness · Sociality

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Introduction

Parental care is time demanding, energetically expensive, and involves a trade-off between increasing the survival of the current offspring relative to future breeding opportunities, which may decline due to losses in fecundity and mating opportunities (Trivers 1972; Clutton-Brock 1991). Countless factors influence parental investment, ranging from partner quality (Burley 1988; de Lope and Møller 1993; DeMory et al. 2010) to resource availability (Whittingham and Robertson 1994; Eikenaar et al. 2003). Among cooperative breeders (i.e., social systems where more than a pair help rear young during a nesting attempt, Brown 1987), parental investment can be shared with other individuals, which are known as auxiliaries or helpers.

The investment made by auxiliaries can influence, among other factors, the provisioning effort of the group breeders (Heinsohn 2004; Johnstone 2011). Parents can react to the presence of auxiliaries, adjusting their parental investment in at least two ways. They may reduce their parental effort, which is compensated by the investment of auxiliaries, thus maintaining the same overall provisioning rate—“compensatory effect” (Hatchwell and Russell 1996; Khan and Walters 2002; Russell et al. 2008; but see Koenig and Walters (2012)). Conversely, parents may not change their original effort, accumulating a higher overall investment when accounting for the auxiliaries’ effort—“additive effect” (Emlen and Wrege 1991; Magrath and Yezerinac 1997; Cockburn 1998); but in this case, they obtain an increment in investment without increasing the costs associated with parental care. This latter pattern is expected in species with high chances of nest failure due to starvation where parents would rarely be able to breed successfully without help (Hatchwell 1999; Liebl et al. 2016; but see Legge (2000b)). Another possibility is the occurrence of partial compensation (Russell et al. 2008; Kingma et al. 2010; Meade et al. 2010; Brouwer et al. 2014). In this case, although the parents may reduce their effort somewhat, they can still gain a higher overall investment in the offspring due to an increase in auxiliary effort. This is the only scenario where all group members would benefit from the presence of auxiliaries. Feeders may reduce their individual effort and offspring still benefit from a higher investment.

Different strategies evidently may generate different outcomes. For species in which a compensatory effect occurs, a reduction in parental workload is expected (load lightening), which may result in an increase in breeder survival (Russell and Rowley 1988; Khan and Walters 2002; Kingma et al. 2010), earlier initiation of nesting (Koenig and Stacey 1990), and reduced intervals between breeding attempts (Woxvold and Magrath 2005; Canestrari et al. 2008). On the other hand, additive care should improve the current breeding attempt, increasing productivity and nestling survival rates (Hatchwell 1999; Kingma et al. 2010; but see Legge (2000a)).

Kin selection is one of the most accepted explanations for the investment of auxiliaries in helping to rear non-descendent young (Hamilton 1964). This phenomenon is widespread in cooperative breeders, because auxiliaries acquire indirect fitness benefits helping kin, since most groups are formed by closely related individuals (Brown 1987; Emlen 1997; Dickinson and Hatchwell 2004). However, it is often the case that some of the offspring may not be closely related to the auxiliaries due to the mating system, occurrence of extra-pair fertilizations, or joint nesting. Different studies have shown that auxiliaries may be more prone to help relatives or help them at higher rates as compared to help provided to unrelated individuals. This pattern has been observed when considering specific kinship classes (siblings, half-sibs, unrelated) as well as in cases of linear variation in relatedness (Komdeur 1994; Dickinson et al. 1996; Russell and Hatchwell 2001; Richardson et al. 2003). In other cases, however, auxiliaries may provide care regardless of the degree of relatedness they have to the offspring they are provisioning (Dunn et al. 1995). As a way to maximize the benefits obtained by helping, auxiliaries are expected to adjust their investment according to their relatedness to the offspring whenever possible (Savage et al. 2013). Kin discrimination has been shown to occur consistently in several species and may be favored in species presenting a variable level of relatedness within the group (Griffin and West 2003; Cornwallis et al. 2009). Interestingly, even the mechanisms leading to kin discrimination have been revealed for some species, such as the long-tailed tit (*Aegithalos caudatus*), where young exposed to calls made by the provisioning adults learn kin recognition cues through association (Sharp et al. 2005).

We studied the tropical campo flicker (*Colaptes campestris campestris*), a facultative cooperative breeder with a complex social and mating system. Cooperative groups are usually composed of individuals that are related in varying degrees. Auxiliary females, for instance, may be completely unrelated to all members of the group. Breeding pairs without the assistance of auxiliaries also occur in the population (Dias et al. 2013a). Nest losses in the studied population occur due to predation (60% of all nest failures) and to starvation of nestlings, although the latter only happens to breeding pairs without auxiliaries. Here, we focused on parental care patterns and productivity as reflected by breeding parameters such as the presence or absence of auxiliaries, parental and group physical condition, nest success, number of nestlings produced, and the sex of the nest auxiliaries. Specifically, we hypothesized that (1) partial compensation occurs in cooperative groups. Considering that cooperative breeding is facultative in campo flickers and that starvation only happened in nests of unassisted pairs, we expected to observe a reduction of the breeders’ investment associated with an overall increase in nest investment by auxiliaries; (2) parents modulate their investment in relation to the investment of auxiliaries; (3) auxiliaries adjust their investment relative to their degree of relatedness to the

offspring; and (4) higher overall investment in the nest occurs in groups whose members generally present a better physical condition, leading to more successful nesting attempts and a higher production of young.

Methods

Study species

Campo flickers (*Colaptes campestris campestris*) are medium-sized woodpeckers widely distributed across South America (Short 1972). The subspecies is a facultative cooperative breeder and presents mixed mating strategies that include joint nesting, intra-specific brood parasitism, and a variable mating system. Cooperative breeding was observed in 42% of the groups and assisted groups had one to three auxiliaries. Clutch size was statistically smaller for pairs (4.10 ± 0.11 eggs; mean \pm SE) than for cooperative groups (6.00 ± 0.64 eggs; mean \pm SE) as was nesting success (59 vs 72%), respectively (Dias et al. 2013b). Relatedness within groups was high, with a mean of 0.34 ± 0.13 (mean \pm SE) for male dyads and 0.37 ± 0.09 for female dyads (Dias et al. 2013a). Monogamy prevails for unassisted pairs, and both monogamy and polygyny are common in cooperative groups (Dias et al. 2013a). In groups with parents and auxiliaries, all individuals contribute to the success of the breeding event by participating in incubation and feeding of nestlings (Dias et al. 2013b).

Study site and general procedures

We conducted our study at Fazenda Água Limpa (FAL; 15° 56' S, 47° 55' W), a 4500-ha property of the University of Brasilia. The area is located in central Brazil, within the savanna biome (Cerrado). The climate of the region is highly seasonal, with two distinct periods, dry and wet. Field data were collected across 4 years (2006–2009) that encompassed three breeding seasons. It was not possible to record data blind, because our study involved focal animals in the field.

During the study, we used playbacks and mist nets to attract and capture the woodpeckers. Captured individuals were individually color banded, measured to the nearest 0.02 mm (tarsus, wing, beak, and tail length), and weighted to the nearest gram. We used the scaled mass index (Peig and Green 2009) as an index of condition for group members (more details as follows). The condition was usually measured before and sometimes during the breeding attempt. Additionally, we took blood samples (100 μ l) from captured individuals, which were stored at room temperature in a lysis buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 2% SDS). Individuals were sexed based on the malar stripe coloration, which is red in males and black in females.

We monitored the groups throughout the year and identified potential nesting cavities within the study area, recording their location with a GPS. We checked cavity contents using a flashlight and a mirror attached to a pole. Active nests ($N = 57$) were monitored every 2–3 days. Near fledging (25th day after hatching), we measured, banded and took blood samples from nestlings, similarly to adults. Groups were monitored until chicks fledged. We considered a nest to be successful when at least one nestling fledged the nest within 5 days of the expected fledging date (around the 29th day after hatching). The number of young leaving the nest within this period was used as an index of productivity. A previous study documented an average nesting success of 65.5% (Dias et al. 2013b).

During the 4 years, we monitored a total of 11 groups and 15 pairs to determine group composition and general behavioral and mating patterns. We only classified as a new cooperative group one case where a drastic change in composition occurred, with dispersal of some previous members and immigration of new ones. Alterations in socially monogamous pairs occurred more frequently ($N = 4$), so that whenever one of the pair members changed, we classified it as a new pair. On the other hand, we did not consider as new those groups that changed from cooperative groups to socially monogamous pairs if the same breeders persisted (see “Statistical analysis” section). We classified the auxiliaries as two types: 1—primary auxiliaries, for males or females that were usually offspring from the previous breeding season and that did not breed; and 2—secondary auxiliaries, for subordinate females that mated with the dominant male and contributed with some eggs to the nest.

Parental and alloparental behavior

In 2008 and 2009, we performed nest focal observations from a blind (approximately 20–30 m from nests) with binoculars or a spotting scope. We also used video cameras (Sony DCR-HC52) to conduct some of the observations. During incubation, on both the fifth and tenth days after clutch completion, we recorded nest activity for each nest during 1 h. Incubation bouts last an average of 15.2 ± 14.5 min (mean \pm SE), and during 1 h of observation, it is possible to observe from one to eight incubation bouts. During the nestling period, we recorded nest activity (from 1 h 40 min to 2 h) during five different days for each nest (days 4, 10, 16, 22, and 28 after hatching). For all observations, we identified the visiting adult and recorded the number of visits performed (i.e., when the individual entered the nest) and the time spent inside the cavity. Because observation within the nest cavity was impossible, we assumed that every time an adult entered the cavity during the egg phase, it was for provisioning care in the form of incubation. Conversely, if the same behavior occurred during the nestling period, we assumed that it was for provisioning food. Consequently, we defined provisioning rate as the

number of times a specific adult went inside the nest per hour, either to incubate eggs or to feed nestlings. In the case of food provisioning rate, this was defined as the number of visits per nestling per hour.

Molecular analysis

We conducted a genetic analysis as detailed by Dias et al. (2013a). Concisely, we stored blood samples in a lysis buffer and extracted DNA using Qiagen DNeasy Blood and Tissue Kit®. We used 10 polymorphic microsatellite markers, originally isolated from the northern flicker (*Colaptes auratus*, Kuhn et al. 2009), in a multiplex polymerase chain reaction (PCR) and visualized the amplification products on the Applied Biosystems (ABI) 3100 automated capillary sequencer. We used GeneMapper® (version 4.1; Applied Biosystems) to evaluate the electropherograms. For the parentage analysis, we used the program CERVUS version 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007) and for the pairwise relatedness (r) estimation, we used the software SPAGeDi (Hardy and Vekemans 2002), based on Queller and Goodnight's (1989) formula. The average relatedness was 0.5067 between putative fathers and offspring and 0.5713 for putative mothers and offspring.

Statistical analysis

All analyses were conducted in the free software R 3.3.1 (R Core Team 2016). We performed generalized linear models (GLM) for binomial and count response variables fitted considering a Binomial and Poisson distribution, respectively. Linear mixed models for continuous response variables with Gaussian distribution were also used. Mixed models were implemented using the “lmer” function in the “lme4” package (Bates et al. 2015). We evaluated the effect of parental condition (see as follows), sex of the provisioning adult, and the presence of auxiliaries on the number of visits to the nest and on the time spent inside the cavity for all group members. We fitted random factors in the model to correct for hierarchical repeated sampling. We incorporated the random terms “Group ID,” “Individual ID,” and “Days after hatching” to all models that involved investment during the nestling period. For the models concerning investment during incubation, we only incorporated the random terms Group ID and Individual ID because we averaged the results of the two focal observations (i.e., conducted on the fifth and tenth days of incubation). When we evaluated the effect of provisioning on breeding parameters (i.e., nest success and number of nestlings fledged), we only incorporated the random terms Group ID and Days after hatching because we considered the whole group investment in these analyses. For the analysis concerning the nestling period, we used brood size as a factor to control for possible differences in investment. To obtain the

scaled mass index (see Peig and Green (2009)), we used the slope of a standardized major axis (SMA) regression on ln-transformed data using the “sma” function from the “smatr” package. We considered the averaged condition index of all group members as the group average condition. Q-Q plots of residuals were examined to confirm normality of error terms. The models were progressively simplified by removing variables starting with higher-level interactions. We used likelihood ratio tests (LRTs) using the change in deviance as a chi-squared approximation. The model simplification was retained if the simpler model did not differ in terms of fit. Results are shown as mean \pm 1SE.

Results

Factors affecting parental investment patterns

During the incubation period, and considering both assisted and unassisted breeders, we found that the parental condition ($\chi^2_1 = 0.34$; $P = 0.556$), the presence of auxiliaries ($\chi^2_1 = 2.75$; $P = 0.09$), or the interaction between the presence of auxiliaries and parental sex ($\chi^2_1 = 1.74$; $P = 0.185$) were not associated with the time spent at the nest. However, we did find a significant effect of sex ($\chi^2_1 = 8.23$; $P = 0.004$, Fig. 1), with mothers spending more time than fathers inside the nest during incubation (Table 1).

During the nestling period, we also observed that parental condition did not affect parental provisioning rate ($\chi^2_1 = 0.19$; $P = 0.658$). Somewhat surprisingly, we found a negative

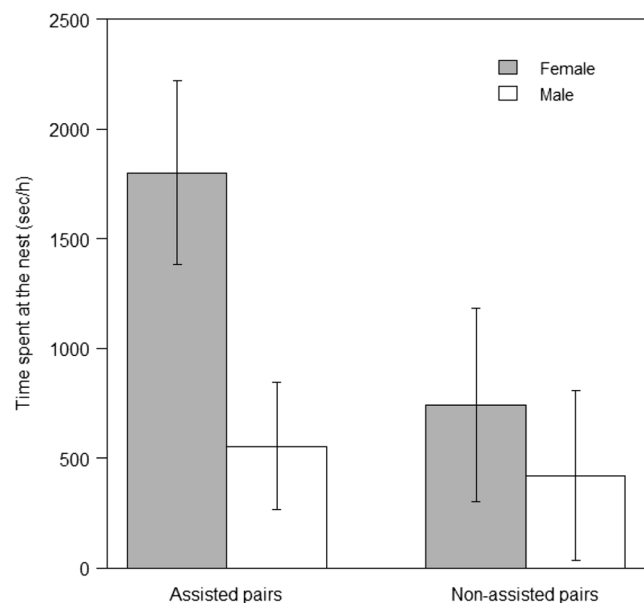


Fig. 1 Average time spent at the nest during incubation of campo flickers (*Colaptes campestris campestris*) for assisted (12) and non-assisted (26) parents in relation to sex in central Brazil. Bars represent 95% confidence intervals of the mean

Table 1 Results from the LMMs testing the effects of the parents' condition, the sex, and the presence of auxiliaries on the number of parental visits and time spent at the nest of campo flickers (*Colaptes campestris campestris*) during incubation and nestling periods

Variable	Estimate ± SE	χ^2	P
Time spent at the nest—incubation			
The parents' condition	7.17 ± 13.59	0.34	0.556
Sex (male)	−997.25 ± 311.00	8.23	0.004
Presence of auxiliaries (no)	596.96 ± 360.66	2.75	0.097
Presence of auxiliaries × sex	−895.04 ± 714.40	1.74	0.185
Number of visits—nestling period			
The parents' condition	−0.00 ± 0.00	0.19	0.658
Sex (male)	0.03 ± 0.07	0.21	0.647
Presence of auxiliaries (no)	0.10 ± 0.10	1.11	0.291
Presence of auxiliaries × sex	−0.00 ± 0.17	0.00	0.939
Number of nestlings	−0.06 ± 0.03	6.30	0.012

relationship between the provisioning rate and the number of surviving nestlings ($\chi^2_1 = 6.30$; $P = 0.012$, Fig. 2). However, there were no effects of parental sex ($\chi^2_1 = 0.21$; $P = 0.647$), presence of auxiliaries ($\chi^2_1 = 1.11$; $P = 0.291$, Fig. 3), or their interaction ($\chi^2_1 = 0.00$; $P = 0.939$) on parental provisioning rate (Table 1). Despite this lack of significant effect, non-assisted pairs made 35% more visits to the nest than assisted pairs.

Do parents modulate their investment in relation to the investment of auxiliaries?

When we restricted our analysis to cooperative groups, we found that the number of visits per hour made by parents during the nestling period was positively correlated with the

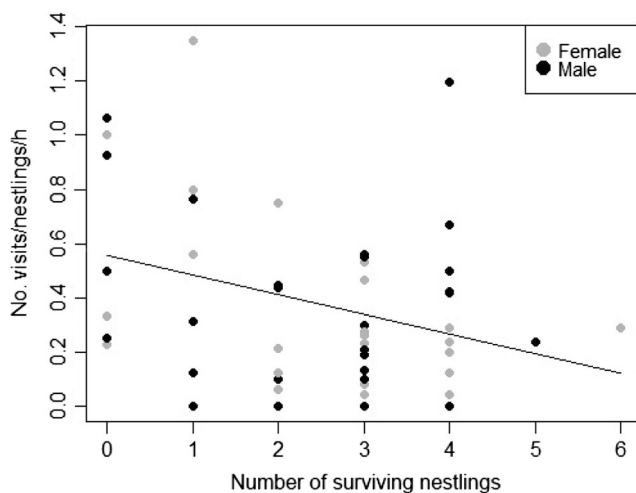


Fig. 2 Effect of the number of nestlings on the number of visits per nestling per hour by parents of campo flickers (*Colaptes campestris campestris*) during the nestling period in central Brazil

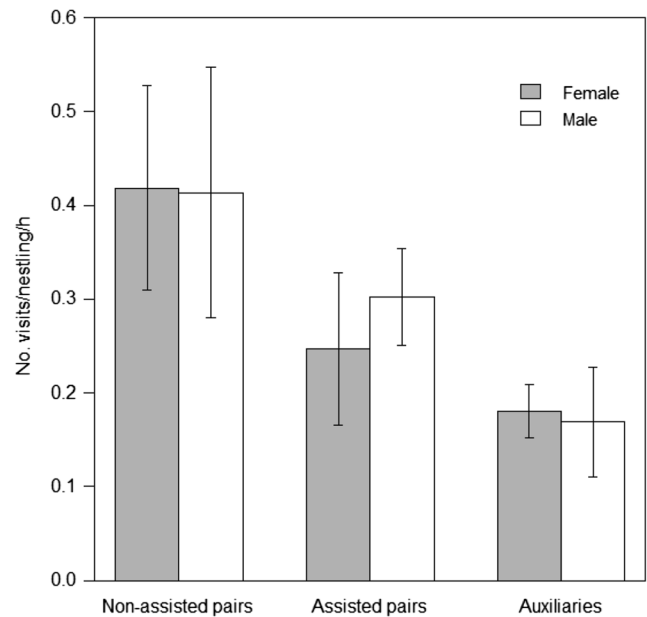


Fig. 3 Average number of visits per nestling per hour by parents and auxiliaries of campo flickers (*Colaptes campestris campestris*) in relation to sex and occurrence of helping behavior during the nestling period in central Brazil. Bars represent 95% confidence intervals of the mean

number of visits made by auxiliaries ($\chi^2_1 = 14.59$; $P < 0.001$; Fig. 4), but was not associated with the number of nestlings ($\chi^2_1 = 2.76$; $P = 0.096$). Conversely, the time spent at the nest by parents during the nestling period was not affected by the time spent at the nest by auxiliaries ($\chi^2_1 = 0.62$; $P = 0.429$) nor by the number of nestlings ($\chi^2_1 = 0.64$; $P = 0.422$).

Do auxiliaries adjust their investment relative to their degree of relatedness to the offspring?

We found that auxiliaries visited nests more frequently when they were more closely related to the offspring in the nest

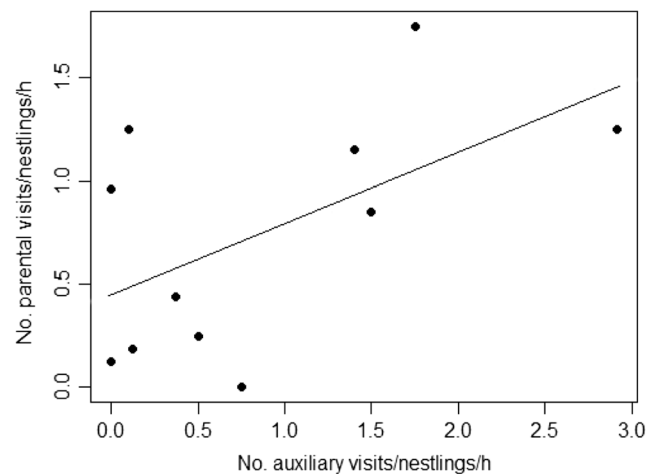


Fig. 4 Effect of the number of visits per nestling per hour made by auxiliaries on the number of visits per nestling per hour made by campo flicker parents (*Colaptes campestris campestris*) in central Brazil

($\chi^2_1 = 4.78$; $P = 0.028$; Fig. 5) and when there were more nestlings in the brood ($\chi^2_1 = 5.81$; $P = 0.016$; Fig. 5). However, the type of auxiliary (i.e., primary or secondary; $\chi^2_1 = 0.02$; $P = 0.864$), their condition ($\chi^2_1 = 0.12$; $P = 0.682$), or sex ($\chi^2_1 = 0.00$; $P = 0.93$) did not seem to be important in determining nest visitation rates. None of the evaluated predictor variables (level of relatedness to the offspring, number of nestlings, type of auxiliary, condition, and sex) influenced the time that the auxiliaries spent in the nest (all $\chi^2_1 < 1.29$; all $P > 0.255$).

Does overall group condition affect nest productivity?

Our data show that neither the social group's average condition (GLM; $Z = -0.32$; $P = 0.742$), nor the total number of visits to the nest by all group members ($Z = 1.03$; $P = 0.299$), or even the total time they spent at the nest ($Z = -0.67$; $P = 0.499$) affected the number of fledglings. Similarly, nest success was also unaffected by the predictor variables: average group condition ($Z = 0.02$; $P = 0.879$), total number of visits to the nest ($Z = 0.10$; $P = 0.681$), and total time spent at the nest ($Z = 0.18$; $P = 0.482$). Interestingly, we observed that fledgling weight was affected by the average condition of group members ($Z = 287.66$; $P = 0.04$; Fig. 6), but not by the total number of visits to the nest ($Z = 89.99$; $P = 0.289$) or the total time spent at the nest ($Z = 1.42$; $P = 0.897$).

Finally, we observed that the overall number of visits by group members to the nest was not significantly affected by the presence of auxiliaries ($Z = -0.80$; $P = 0.432$), or by the number of nestlings ($Z = 2.39$; $P = 0.262$). When considering the total time spent at the nest, we observed that assisted groups did not spend more time as a whole at the nest than unassisted groups ($Z = -1.01$; $P = 0.323$). However, we did

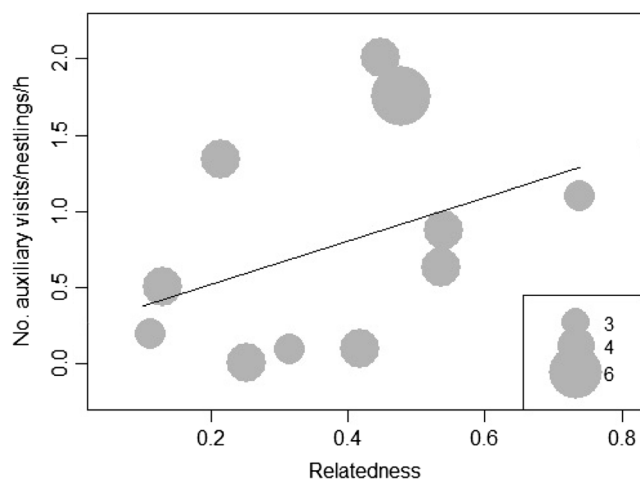


Fig. 5 Effect of the level of relatedness on the number of visits by auxiliaries of campo flickers (*Colaptes campestris campestris*) during the nestling period in central Brazil. The number of nestlings is represented by circle size

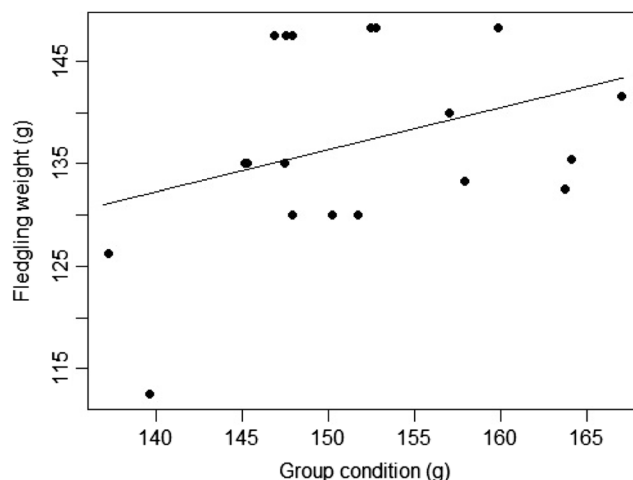


Fig. 6 Effect of the overall group condition (residuals of the regression between body mass and tarsus length) on the weight of fledglings of campo flickers (*Colaptes campestris campestris*) in central Brazil

observe a negative effect by tendency of the number of hatchlings upon the total time spent at the nest ($Z = 1.79$; $P = 0.087$).

Discussion

Our results suggest that campo flickers may exhibit provisioning patterns that reflect a partial compensation effect, characterized by a decrease in the care provided by the parents but not by as much as the increase in investment made by the auxiliaries. In this case, the contribution of auxiliaries may not directly affect the effort of breeders, but may instead provide an additive effect in the overall provisioning of nestlings (Emlen and Wrege 1991; Magrath and Yezerinac 1997). Alternatively, assisted breeders may reduce their own provisioning effort, but this would not change the overall provisioning rate, because the investment made by the auxiliaries may compensate the reduction in the care provided by the parents (Brown et al. 1978; Legge 2000b; Khan and Walters 2002). Studies have shown that the occurrence of an increase in the productivity is possible even with the reduction of parental workload (Kingma et al. 2010; Meade et al. 2010). In red-winged fairy wrens (*Malurus elegans*), the social environment affects the probability of load lightening. Group members reduced their effort in the presence of male but not female auxiliaries (Brouwer et al. 2014). We speculated that this might be the case for campo flickers due to the facultative nature of cooperation in our study population, and because only breeding pairs without help lose broods to starvation (Dias et al. 2013a). Our data show that the mere presence of auxiliaries does not seem to directly affect parental investment. And although we did not observe a statistical effect of the presence of auxiliaries on parental provisioning levels, non-assisted pairs seem to invest proportionally more than assisted pairs during

the nestling period. Similarly to the cooperatively breeding purple-crowned fairy wren (*Malurus coronatus*, Kingma et al. 2010), we found that assisted breeders reduced their effort by an average 25–35% in comparison to non-assisted breeders. Additionally, the investment made by the auxiliaries was high and comparable to that of breeders.

All these adjustments in the overall provisioning rate are known to directly affect several aspects of breeder life history, such as increasing the number of breeding attempts per season (Russell and Rowley 1988) and survival until the next breeding season (Koenig and Mumme 1987), among other possible effects. For example, in the purple-crowned fairy wren, auxiliaries contributed to the reduction of the breeders' workload favoring higher breeder survival (Kingma et al. 2010). Because campo flickers have very long life spans, it was impossible to estimate breeder survival across the period of the present study.

We predicted that parents would modulate their investment relative to the investment made by auxiliaries, since several studies have established that the presence of auxiliaries can affect the investment level of the breeders (Hatchwell 1999). However, only a few studies have addressed the direct effects of auxiliary investment upon breeder investment (for birds: Wright and Dingemanse 1999; McDonald et al. 2009; for fish: Zöttl et al. 2013). Our assessment of how parents within cooperative groups modulate their investment in face of the investment made by auxiliaries revealed that the number of visits made by parents during the nestling period was positively affected by the number of visits made by auxiliaries. This result reinforces the idea that parents may attempt to increase overall investment and maybe productivity in favorable situations, when the investment of the auxiliaries is higher. It is important to highlight the fact that campo flickers lose a substantial number of nestlings due to starvation (Dias et al. 2013b), a context that may be mitigated in the presence of additive care (Hatchwell 1999).

One focus of the present study was to assess whether auxiliaries adjust their investment relative to their degree of relatedness to the offspring. We found that the investment provided by auxiliaries (i.e., visitation rate) was directly affected by the level of relatedness of the auxiliary to the offspring, as well as by the number of nestlings. However, the type of auxiliary (primary or secondary) and its condition were not important in predicting investment level. This may be due to the fact that secondary auxiliaries were sometimes sisters and thus highly related to the dominant females (Dias et al. 2013a). Cooperative breeders generally occur within a kin-based framework, because auxiliaries are usually offspring from previous years (Brown 1987). This situation seems to favor kin-selected benefits. However, in some specific cases, the strength of kin selection may be even stronger, as auxiliaries preferentially assist close kin or assist them at a higher rate (Mumme 1992; Komdeur 1994; Dickinson et al. 1996;

Russell and Hatchwell 2001; Richardson et al. 2003; but see Legge 2000b; Canestrari et al. 2005). Recent studies with the long-tailed tit (*Aegithalos caudatus*) and the bell miner (*Manorina melanophrys*) show that the investment made by auxiliaries was affected by fine-scale differences in relatedness and occurred at higher levels in broods to which they were related (Nam et al. 2010; Wright et al. 2010). Auxiliaries are known to be able to discriminate in favor of kin (Griffin and West 2003), and kin discrimination is likely to occur in species that exhibit a variable relatedness component within groups (Cornwallis et al. 2009), which seem to be the case for the campo flicker (Dias et al. 2013a). It is thus not surprising that we found kin discrimination in this species, although the mechanism supporting this capability remains to be studied.

We failed to find evidence that a higher overall investment or the condition of the entire group influences the number of nestlings produced or nesting success, as has been found in a few other studies (Doerr and Doerr 2007; Kingma et al. 2010). Despite this, previous analyses for the campo flicker, controlling for individual and territory quality, have shown that the presence of auxiliaries itself enhances fledgling production (Dias et al. 2015), suggesting that there may be benefits associated with the presence of auxiliaries other than provisioning rate. One possibility to explain the lack of an overall investment enhancement in cooperative groups may be that auxiliaries are bringing more food in their crops, without necessarily increasing the rates of provisioning. This may be the reason for the unexpected finding that fledgling weight was affected by the average condition of group members, but was not affected by overall nest contribution, as observed in other studies (Hatchwell et al. 2004; Lloyd et al. 2009). This result suggests that the condition of the produced fledglings was directly related to the quality of the group that reared the fledglings. A study of the congener northern flicker (*Colaptes auratus*) revealed that larger broods induced an increase in the foraging time of the feeders, but did not influence their visitation rate to the nest (Wiebe and Elchuk 2003).

In conclusion, we have found that the condition of group members may be even more important than the presence of auxiliaries in determining the provisioning rates of the breeders and condition of the produced fledglings. Moreover, results suggest that similarly to other species, campo flickers may present some characteristics compatible with partial compensatory effects during the nesting effort, with breeders reducing their investment but the group presenting a higher overall investment per nest in cooperative groups. Additionally, this study demonstrated that auxiliaries adjusted their provisioning based on their levels of relatedness to the offspring. Auxiliaries increased investment when they were more closely related to the brood, suggesting that kin selection in the campo flicker may be a strong component that favored the evolution of cooperative breeding.

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Compliance with ethical standards All applicable international, national, and institutional guidelines for the use and capture of animals were followed. The study complied with the current laws of Brazil under permits 14368 and 2056 from Instituto Brasileiro de Recursos Renováveis.

Conflict of interest The authors declare that they have no conflicts of interest.

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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