

# Helping enhances productivity in campo flicker (*Colaptes campestris*) cooperative groups

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**Abstract** Reproductive adults in many bird species are assisted by non-breeding auxiliary helpers at the nest, yet the impact of auxiliaries on reproduction is variable and not always obvious. In this study, we tested Hamilton's rule and evaluated the effect of auxiliaries on productivity in the facultative cooperative breeder campo flicker (*Colaptes campestris campestris*). Campo flickers have a variable mating system, with some groups having auxiliaries and others lacking them (i.e., unassisted pairs). Most auxiliaries are closely related to the breeding pair (primary auxiliaries), but some auxiliaries (secondary auxiliaries) are unrelated females that joined established groups. We found no effect of breeder quality (body condition) or territory quality (food availability) on group productivity, but the presence of auxiliaries increased the number of fledglings produced relative to unassisted pairs. Nonetheless, the indirect benefit of helping was small and did not outweigh the costs of delayed breeding and so seemed insufficient to explain the evolution of cooperative breeding in campo flickers. We concluded that some ecological constraints must limit dispersal or independent breeding, making

staying in the group a “best-of-a-bad-job” situation for auxiliaries.

**Keywords** Altruism · Assistantship · Group size effect · Helper · Reproductive success · Sociality

## Introduction

The presence and behavior of non-breeding auxiliaries in cooperative breeding systems have been prevailing topics in behavioral studies for decades. Among cooperatively breeding insects, fish, birds and mammals, auxiliaries are typically young from previous years that delay dispersal and remain at the natal site to help rear their siblings (Ekman et al. 2004). How these auxiliaries affect group reproduction and why they help are key questions that still stimulate extensive debate (Emlen 1991; Dickinson and Hatchwell 2004; Brouwer et al. 2012; Manica and Marini 2012). The presence of auxiliaries is generally thought to have a positive effect on breeder fitness, such as enhanced group productivity (Emlen and Wrege 1991; Conner et al. 2004; Brand and Chapuisat 2014), increased quality of young produced (Hatchwell 1999; Brouwer et al. 2012), or increased breeder survival (Reyer 1984; Russell et al. 2007; Cockburn et al. 2008). There are even unusual cases of species that are unable to breed without assistance, such as the white-winged chough (*Corcorax melanorhamphos*, Heinsohn 1992) and the apostlebird (*Struthidea cinerea*, Woxvold and Magrath 2005). However, some studies have found no effect—or even a negative effect—of the presence of auxiliaries on breeder productivity (Caffrey 2000; Eguchi et al. 2002; Cockburn et al. 2008).

These contrasting results relative to the effect of auxiliaries on breeder success (productivity) may be due to the difficulty of teasing apart this variable from other masking or

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confounding factors, such as territorial or individual quality (Brown 1987; Emlen 1991; Cockburn 1998; Legge 2000; Dickinson and Hatchwell 2004). Different approaches have been used to evaluate the effect of auxiliaries (Dickinson and Hatchwell 2004), and they can be separated into at least three different categories: (1) experimental studies with the removal of auxiliaries (Brown et al. 1978; Mumme 1992; Hatchwell and Russell 1996, but see Brintjes et al. 2013), (2) observational studies that compared the reproductive output of the same breeders in years with and without assistance (Caffrey 2000; Legge 2000; Eguchi et al. 2002), and (3) studies that used statistical methods to control the effects of auxiliaries, separating their influence on group breeding parameters from other unimportant traits (Hatchwell et al. 2004).

Several studies have also attempted to elucidate the possible benefits to auxiliaries (Dickinson and Hatchwell 2004). Both direct and indirect benefits have been proposed as explanations for the investment made by auxiliaries, although the relative roles of such benefits in the evolution and maintenance of helping behavior remain unclear (Cockburn 1998; Clutton-Brock 2002; Dickinson and Hatchwell 2004). Some studies have shown that possible direct benefits to auxiliaries include enhanced survival (Gaston 1978; Brown 1987), increased chances of future breeding (Ligon and Ligon 1978; Carlisle and Zahavi 1986; Heinsohn et al. 1988), and acquisition of skills needed for independent breeding (Komdeur 1996, but see Khan and Walters 1997). Other studies, however, have not found any direct benefits of helping (e.g., Dickinson et al. 1996), and it is possible that helping behavior may generate no immediate gain for auxiliaries, but by providing help, they are allowed to stay on the natal territory in a “pay to stay” situation (Mulder and Langmore 1993; Kokko et al. 2002).

One of the main explanations for the evolution of cooperation requires that auxiliaries be related to the individuals that they are helping, so they can reap the inclusive fitness benefits associated with producing relatives (Hamilton 1964). Within this context, the assumptions are that the auxiliaries and the assisted individual must be genetically related and that there should be a measurable benefit to the assisted individual due to the behavior of the auxiliary (Hamilton 1964; Lucas et al. 1996). In some social and ecological contexts, helping behavior may be maladaptive to auxiliaries or may be only slightly helpful to breeders (Emlen 1982). However, it is generally established that auxiliaries accumulate lower fitness by helping than they would by breeding independently (Stacey and Koenig 1990; Dickinson and Hatchwell 2004), though, in some cases, it appears that kin-selected benefits may be enough to favor natal philopatry and helping behavior (McGowan et al. 2003; Hatchwell 2009). Thus, the comparison of systems and species of cooperative breeders exposed to different selective pressures may provide particularly relevant data to answer questions about the evolution of helping behavior.

In this study, we calculate Hamilton’s rule and test two hypotheses based on the facultative cooperative breeding system of the campo flicker (*Colaptes campestris campestris*), a woodpecker endemic to savannas of South America. First, we test whether helping behavior by auxiliaries enhances the productivity of breeders. Second, we examine the direct and indirect fitness costs of helping to auxiliaries to test the hypothesis that helping behavior is favored by kin selection in this system. To test these hypotheses, we compare the productivity (number of fledglings produced) of groups that contained more than two adults (cooperative breeding) with groups composed of only two adults (i.e., the breeding pair). Due to the short period of the study, it was not possible to evaluate auxiliaries’ effects on breeders’ survival or even their acquisition of skills for future breeding. In campo flicker groups that breed cooperatively, auxiliaries occasionally breed within the group (Dias et al. 2013b). The fitness of male and female auxiliaries may differ because secondary males usually do not breed, while it is common to find multiple breeding females in groups (Dias et al. 2013b). Auxiliaries may be classified as follows: (a) offspring of both sexes from the previous breeding season; (b) siblings (male or female) of one of the breeders; or (c) non-kin, typically females that joined the group (Dias et al. 2013a, b). We refer to auxiliaries closely related to the breeding pair as “primary auxiliaries” and non-related female auxiliaries as “secondary auxiliaries.” To test whether breeder productivity is enhanced by the presence of auxiliaries, we use behavioral, ecological, and demographic data collected over a period of 4 years. Using these results, combined with estimates of genetic relatedness, we examine the direct and indirect fitness costs of helping to auxiliaries. The campo flicker is a particularly interesting species to study in this regard, because some female auxiliaries are close relatives of the breeding pair whereas others are not, raising the possibility that different individuals reap varying fitness benefits through helping (see Reyer 1984).

## Methods

### Study species

Campo flickers are terrestrial, medium-sized woodpeckers with a subtle sexual dichromatism based on plumage ornaments (Short 1972). The species is widely distributed across South America and comprises two subspecies: *C. campestris campestris* and *Colaptes campestris campestroides* (Short 1972). The subspecies under study, *C. campestris campestris*, has a complex social and mating system with facultative cooperative breeding associated with monogamy or simultaneous polygyny (Dias et al. 2013a, b). We studied 27 groups across 4 years (Oct. 2006–Dec. 2009), encompassing three breeding seasons, which coincided with the rainy months

(detailed in Dias et al. 2013a). We monitored 17 of these groups in only 1 year, six in 2 years, and four in 3 years of study. Group size ranges from two to five individuals ( $2.61 \pm 0.94$ ; mean  $\pm$  SD) during breeding and affects levels of provisioning to nestlings. Auxiliaries are of both sexes, most of which are offspring of one or both of the primary breeders; however, some auxiliaries are siblings of the breeders or even unrelated to them (Dias et al. 2013b). Year-round, groups occupy territories ranging in size from approximately 20 to 80 ha, and during the breeding season, nest in cavities excavated in termite mounds and occasionally in trees (Dias et al. 2013a). Thus, termite mounds are the main substrate used for nesting (Dias et al. 2013a) and termites are the most frequent item of the campo flicker diet (Dias et al. unpublished data).

### Study area and general procedures

The study was conducted at Fazenda Água Limpa (FAL;  $15^{\circ} 56' S$ ,  $47^{\circ} 55' W$ ), an area of 4500 ha in central Brazil within the Cerrado biome (tropical savanna). The region is characterized by a strong seasonality, with a rainy season from October to March and vegetational landscapes that range from open grasslands to gallery forests.

We used playbacks and mist nets to capture individuals that were then banded with a unique combination of three plastic color bands and a numbered metal band from the Brazilian environmental regulatory agency (IBAMA). We measured (nearest 0.02 mm: tarsus, wing, beak, and tail lengths) and weighed (nearest gram) each captured bird and collected a blood sample ( $\sim 100 \mu\text{l}$ ) from the brachial vein for genetic analyses. Blood samples were initially stored in lysis buffer and DNA extracted using Qiagen DNeasy Blood and Tissue Kit<sup>®</sup>.

During the study, we searched for nests in new cavities in both termite mounds and trees, checked the contents of preexisting cavities, and also used behavioral cues from adults to identify potential nests. After finding an active nest or one under construction, we monitored it systematically every 2–3 days using a flashlight and mirror attached to a pole to check cavity contents. We recorded all cavity locations with a GPS. We identified brooders and provisioners that visited each active nest to help us interpret results. Parental and alloparental activities were recorded for approximately 2 h per day at each nest for 5 days during the nestling period (days 4, 10, 16, 22, and 28 after hatching). When nestlings approached fledging (25th day after hatching), we manually removed them from the nest, measured, banded, and took blood samples similarly to the protocol for adults. We defined laying date as the day when the first egg was laid in each nest, relative to a continuous succession of days, starting on June 1, which is prior to the occurrence of the first breeding activities (e.g., copulations, cavity excavation). We defined productivity as the

number of fledglings produced by a social pair or a cooperative group in a given breeding attempt.

We used the residuals of the regression of body mass on tarsus length as an index of body condition for the genetic parents. We used the number of termite mounds as an indication of territory quality, estimated as the total number of mounds within a 200-m radius around the nest. During the breeding season, campo flickers are often found foraging within this area. In all but one case, there was only a single male breeder in each of the groups, but several groups contained multiple breeding females (see Dias et al. 2013b). We defined primary breeders as those individuals that produced a higher proportion of nestlings per breeding attempt, as determined by genetic analyses (below). For the objectives of this study, we considered two possibilities for the auxiliaries: (a) those that did not breed within the group and (b) those that did breed within the group. In the comparative analyses of group productivity with and without assistance, we considered that groups with multiple breeding females were assisted, since in these cases, both primary and secondary females acted simultaneously as breeders and auxiliaries. Both female types invested heavily in brooding eggs and feeding nestlings (Dias et al. unpublished data). In addition, secondary females were, in some cases, identified as a full sibling of the primary female, allowing a gain in indirect benefits. We classified as a new group a single observed case of an existing group that suffered a drastic change in composition due to both dispersal of previous group members and immigration of new ones. We also considered as new groups those socially monogamous pairs in which one of the pair members was replaced. Groups that we sampled repeatedly over the years were considered non-independent samples. Nests that were depredated early in development (e.g., few days after laying) did not enter the analyses, because in preliminary exploration of the data, we found no effect of auxiliary presence on occurrence of predation.

### Calculations of Hamilton's rule

We used molecular analysis to determine parentage of nestlings and the degree of relatedness among group members, as detailed elsewhere (Dias et al. 2013b). In brief, we used ten polymorphic microsatellite markers and generated electropherograms that were examined using GeneMapper<sup>®</sup> (version 4.1; Applied Biosystems). For the parentage analysis, we used the program CERVUS version 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007). Pairwise relatedness ( $r$ ) was estimated with the software SPAGeDi (Hardy and Vekemans 2002), based on Queller and Goodnight's (1989) formula.

We calculated Hamilton's rule for both primary and secondary auxiliaries. We defined primary auxiliaries as being either male or female offspring from previous years, and secondary auxiliaries were defined as females that joined the

group and that had a low level of relatedness ( $r < 0.15$ ) to the breeders (Dias et al. 2013a). Hamilton's rule defines the likely spread of altruism (helping behavior) via kin selection only if  $rB - C > 0$ , that is, when the indirect fitness gained through the helping behavior is greater than the loss of direct fitness. The indirect fitness gained by the auxiliary can be estimated by multiplying the average coefficient of relatedness between auxiliaries and breeders ( $r$ ) by the average number of extra fledglings produced due to that help ( $B$ ). The cost of the helping behavior ( $C$ ) can be calculated by estimating the number of offspring that the auxiliary would produce if it had bred independently. Floating could be considered an alternative strategy for breeding independently, in which case, the indirect fitness benefits of helping probably would outweigh the costs if the fitness of floating individuals is zero. However, we did not consider floating as an alternative strategy when estimating the cost because we have never observed any floaters in the study area. For these estimates, we pooled together all groups with auxiliaries regardless of number of auxiliaries, because calculating the estimates separately by group size would result in parameters based on small sample sizes. As most groups had only a single auxiliary, we understand that this is a valuable simplification of a more complex scenario that can shed some light on the benefits of helping. For this calculation, we separately estimated the variables for male and female auxiliaries and also for primary and secondary auxiliaries. We only used groups with complete data sets that included blood samples (for molecular analysis) for all group members. Five groups had at least one auxiliary male, and seven groups had at least one auxiliary female. The level of relatedness ( $r$ ) was calculated between the auxiliaries and the primary breeders of both sexes. The benefit of helping (i.e., number of extra fledglings generated by auxiliaries) ( $B$ ) was calculated as the difference between the mean fitness of assisted breeders and the mean fitness of unassisted breeders (calculated for male and female auxiliaries separately). The cost of helping ( $C$ ) for auxiliaries was calculated as the difference between the mean productivity of unassisted individuals and the direct fitness of the auxiliaries (i.e., number of own offspring produced by an auxiliary).

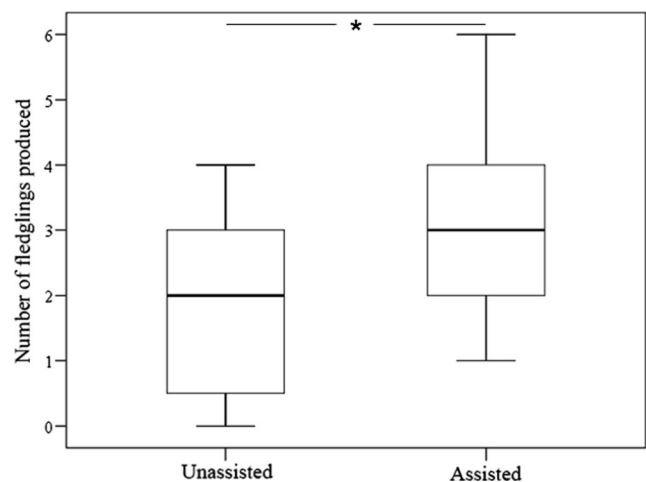
### Statistical analysis

We used generalized linear mixed models (GLMM) for binomial and count response variables considering a Binomial and Poisson error distribution, respectively. Linear mixed models for continuous response variables with Gaussian error distribution were also used. Models were implemented using the "glmer" function in the "lme4" package (version 1.1-7 R Development Core Team 2014). We incorporated the random term "Group ID" to all models to avoid pseudo-replication because of the repeated sampling of some of the groups over the years of study. We evaluated the effects of the explanatory

variables, which included presence of auxiliaries (presence/absence), group size, breeders' condition, territory quality and year on the number of fledglings produced, nest success (determined as the fledging of at least one chick), nestling body weight (mean body weight for the brood), and laying date. Preliminary exploratory data analysis revealed that there were no associations between the explanatory variables. The models were progressively simplified by removing variables starting with higher-level interactions. We used likelihood ratio tests (LRT) using the change in deviance as a chi-square approximation. The model simplification was retained if the simpler model did not differ in terms of fit. The Tukey post hoc test ("glht" in the R package "multcomp") was used to evaluate differences between levels of dummy variables. We visually inspected the presence of outliers in the variables by plotting the values by the Group ID. We examined residuals of the models to check for the assumption of normality. All analyses were conducted in the free software R 3.1.2. (R Development Core Team 2014). Results are shown as mean  $\pm$  1 standard error.

### Results

Group size averaged  $2.46 \pm 0.16$  (range 2–5), and successful groups produced only a single brood per year. Clutch size was, on average,  $4.61 \pm 0.03$  (range 3–9), and the number of fledged nestlings was, on average,  $2.41 \pm 0.03$  (range 0–6). Approximately 83 % of the nests were successful, with predation occurring in almost 10 % of the nests and the remaining 7 % failing due to nestling starvation. Around 30 % of the groups contained at least one auxiliary, but over the study period, two groups changed status from assisted to unassisted and two other groups changed in the opposite direction.



**Fig. 1** Comparison of the number of fledglings produced by assisted and unassisted pairs of campo flickers (*Colaptes campestris*) in the central savanna region of Brazil. Asterisk represents statistical significance at  $P = 0.01$  level

The number of fledglings produced per group (productivity) was positively associated with the presence of auxiliaries (Fig. 1) but was not associated with other measured parameters, which included group size, breeders' condition, territory quality, or year (Table 1). Groups with auxiliaries fledged more nestlings (3.14±0.35) than unaided pairs (2.03±0.27). However, nest success (at least one chick surviving) was not affected by the presence of auxiliaries, group size, breeders' condition, territory quality, or year (Table 1). We found that nestling body mass (near fledging at 25 days) was strongly affected by year (Fig. 2), by the presence of auxiliaries, and by group size, but not by breeders' condition or territory quality (Table 1). More specifically, the main difference in nestling body mass occurred between 2007 and 2008:

nestlings were much heavier in 2007 (143.33±2.92 g) than in 2008 (132.08±4.78 g; Tukey post hoc test;  $Z=-3.53$ ;  $P<0.01$ ). No other difference was observed among years (all  $Z<2.04$ ;  $P>0.10$ ). Additionally, body mass was slightly higher for nestlings produced by groups (133.68±13.22 g) in comparison to that of nestlings produced by pairs (132.43±10.64 g).

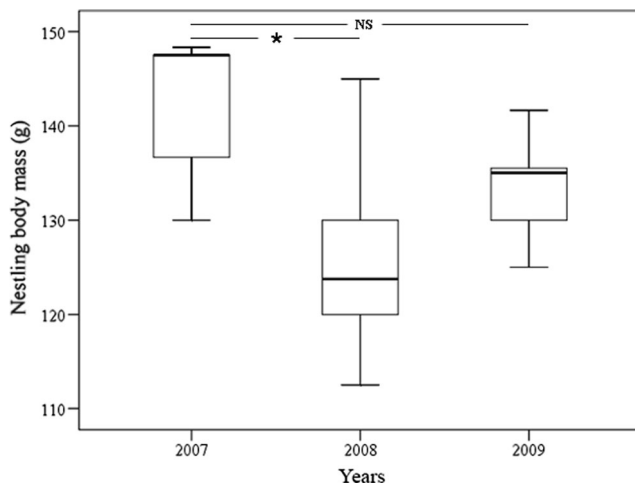
Groups with auxiliaries began breeding earlier than groups without auxiliaries (Fig. 3), particularly so for the larger groups. Breeding date was also affected by year: in 2007, laying date occurred 22.23±6.86 days later when compared to 2008 (Tukey post hoc test;  $Z=-2.62$ ;  $P=0.02$ ) and 2009 ( $Z=-4.15$ ;  $P<0.01$ ). There was no significant difference between 2008 and 2009 ( $Z=-1.36$ ;  $P=0.36$ ). On the other hand,

**Table 1** GLMM results from the effects of the presence of auxiliaries, group size, breeders' condition, territory quality, and year on the number of fledglings produced, nest success, nestling body weight, and laying date

Predictor	Standardized coefficient (SE)	$\chi^2$	df	P value
<b>Number of fledglings produced</b>				
Presence of auxiliaries <sup>a</sup>	1.26 (0.76)	5.90	1	0.01
Group size	-0.32 (0.40)	1.15	1	0.28
Breeder's condition	0.00 (0.03)	0.05	1	0.82
Territory quality	-0.00 (0.00)	0.11	1	0.73
Year <sup>b</sup>		0.27	2	0.87
2008	-0.07 (0.35)			
2009	0.07 (0.39)			
<b>Nest success</b>				
Presence of auxiliaries <sup>a</sup>	-0.13 (0.10)	0.50	1	0.48
Group size	0.13 (0.12)	0.50	1	0.48
Breeder's condition	-0.02 (0.02)	0.05	1	0.82
Territory quality	0.05 (0.08)	0.03	1	0.85
Year <sup>b</sup>		1.56	2	0.45
2008	-0.01 (0.02)			
2009	0.02 (0.01)			
<b>Nestling body weight</b>				
Presence of auxiliaries <sup>a</sup>	-18.63 (9.42)	4.00	1	0.04
Group size	10.02 (4.30)	4.26	1	0.03
Breeder's condition	0.52 (0.45)	2.66	1	0.10
Territory quality	-0.00 (0.01)	0.10	1	0.75
Year <sup>b</sup>		11.23	2	<0.01
2008	-13.52 (4.38)			
2009	-7.38 (4.66)			
<b>Laying date</b>				
Presence of auxiliaries <sup>a</sup>	-1.03 (0.19)	32.29	1	<0.01
Group size	0.39 (0.09)	17.00	1	<0.01
Breeder's condition	-0.00 (0.00)	1.34	1	0.24
Territory quality	0.00 (0.00)	3.14	1	0.07
Year <sup>b</sup>		7.50	2	0.02
2008	-0.07 (0.07)			
2009	-0.22 (0.08)			

<sup>a</sup> Estimate is relative to the presence of auxiliaries

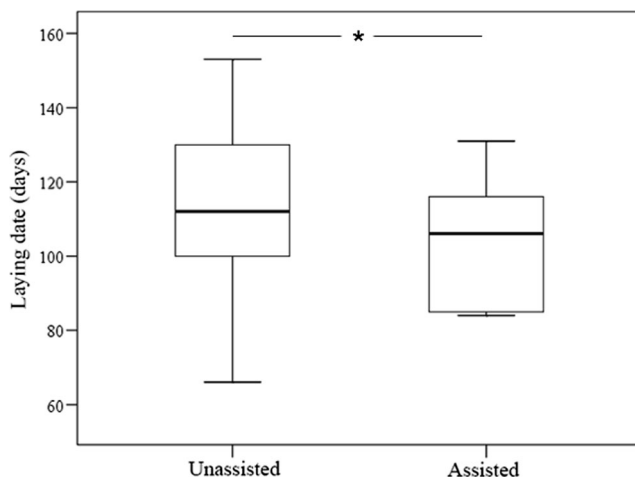
<sup>b</sup> The years are 2007, 2008, or 2009. Estimates are relative to 2007



**Fig. 2** Comparison of nestling body mass of campo flickers (*Colaptes campestris*) among the study years in the central savanna region of Brazil. Asterisk represents statistical significance at  $P < 0.01$  level

breeding date was not influenced by breeders' condition or territory quality. Despite the effects of year on some breeding parameters, the number of auxiliaries in groups did not change among years (chi-square test:  $\chi^2_1 = 0.98$ ;  $P = 0.61$ ).

The calculation of Hamilton's rule revealed that the benefits of helping do not outweigh the costs to auxiliaries (Table 2). For male auxiliaries, the benefit ( $B$ ) generated was estimated as 1.51 offspring per male and the cost ( $C$ ) was equal to 2.29 offspring. Thus, helping appears to be a costly behavior, leading to an overall net cost (rather than benefit) of helping estimated as  $-1.69$  offspring per male auxiliary (from Hamilton's rule). This scenario was slightly more complicated for females, in part because there are some joint nesting groups ( $N = 4$ ) where female auxiliaries sometimes produce young in the nest (Table 2). Nonetheless, for primary female auxiliaries, the cost ( $C$ ) was 0.79



**Fig. 3** Comparison of the laying date for assisted and unassisted groups of campo flickers (*Colaptes campestris*) in the central savanna region of Brazil. Asterisk represents statistical significance at  $P < 0.01$  level

offspring and the benefit ( $B$ ) was estimated as 0.51 offspring, leading to a final weighted net cost of  $-0.62$  offspring per female (Table 2). The outcome was similar for secondary female auxiliaries, but with an even greater net cost due to the low levels of relatedness between secondary females and the breeders (Table 2). Thus, the extra production of nestlings by breeders would have to be more than fourfold higher, on average, for the inclusive fitness of auxiliaries to outweigh the cost in lost production of offspring via independent breeding.

## Discussion

Our results revealed that the presence of auxiliaries increased the number of fledglings produced by breeders, compared with unassisted pairs. Other factors, such as territory or breeder quality, did not seem to have much impact on group productivity, though our sample sizes were limited. Similar results pointing toward a positive effect of auxiliaries on breeder productivity have been found in other studies encompassing mammals, fish, and insects (e.g., Powell and Fried 1992; Brouwer et al. 2005; Doerr and Doerr 2007; Canestrari et al. 2008; Brand and Chapuisat 2014, but see Dunn et al. 1995). However, in our study, having more than one auxiliary did not seem to influence the number of surviving offspring. Among other things, this means that, similar to most cooperative breeders (reviewed in Pruett-Jones 2004), unassisted pairs of campo flickers are able to produce nestlings successfully, although at a lower rate when compared with assisted pairs.

The positive effect of auxiliaries on the number of fledglings extended to improved nestling condition at fledging. Nestlings produced by groups were heavier at fledging, a factor that was also positively related to group size. Auxiliaries in other species have been found to have both a positive effect on fledgling condition (e.g., white-fronted bee eaters *Merops bullockoides*: Emlen and Wrege 1991) as well as no effect (e.g., American crow *Corvus brachyrhynchos*: Caffrey 2000). Our data for the campo flicker suggest that the additional offspring produced by assisted pairs may in fact be of superior quality relative to the fewer offspring produced by unassisted pairs, which could be interpreted as a positive effect overall. However, we need to acknowledge the limitations of the observational approach used here. Future experimental studies may be needed to demonstrate possible cause and effect relationships between evaluated variables.

In addition to the effect of the presence of helpers on nestling condition, we found that the variable *year* also had a strong effect on nestling body mass. Interestingly, 2007 was a harsh year, with a very long dry season (Dias et al. 2013a),

**Table 2** Calculation of Hamilton's rule,  $rB-C > 0$ , for campo flickers in central Brazil

Variable	Description	Auxiliary type			
		No aux	Male aux	Primary female aux	Secondary female aux
$r$	Coefficient of relatedness between helper and primary breeder		0.40	0.33	0.13
	Fledglings produced by breeding pair	2.29	3.80	2.80	3.00
	Fledglings produced by auxiliary		0.00	1.50	0.50
$B$	Benefit to primary breeder		1.51	0.51	0.71
$C$	Cost to helper		2.29	0.79	1.79
Net	$rB-C$		-1.69	-0.62	-1.70

but nonetheless, nestlings produced in 2007 were, on average, 11 g heavier than those of 2008, thus apparently in better condition. Moreover, when evaluating laying patterns, we observed that the presence and number of auxiliaries and the year affected the date that females started laying eggs. Assisted groups started laying earlier than unassisted groups, and laying started later in 2007 when compared to other years. Laying date in campo flickers is influenced by rainfall (Dias et al. 2013a), a link that has been also established for other birds dependent upon invertebrate prey in regions of strong seasonality in rainfall. A study in the Brazilian savanna revealed that termite abundance usually peaks in the first half of the wet season (Pinheiro et al. 2002), a pattern that could have been disrupted by the long dry season in 2007, resulting in a later laying date and, possibly, lower food availability for the offspring. Despite considering 2007 a poor year due to the extended dry period (Dias et al. 2013a), the delay in the rains may have postponed the beginning of laying so that offspring production coincided with a higher abundance of insects later in the season, positively affecting nestling body condition. Regardless of that year's effect, we did not observe differences in the number of assisted groups between years, differently from the study of azure-winged magpies, which had more assisted nests in the poorer years (Canário et al. 2004).

Despite the fact that auxiliaries increased productivity in campo flickers, the calculation of Hamilton's rule revealed that the net cost of helping was still very high for auxiliaries of both sexes and types (primary and secondary), compared to the indirect fitness benefit of helping, despite the fact that female auxiliaries sometimes contributed young directly to the brood (Table 2). This indicates that kin selection alone is not sufficient to account for helping behavior in this species and suggests that cooperative breeding must occur in campo flickers in cases when independent breeding is not possible (see Emlen 1982, 1991; Du-Plessis et al. 1995). Due to ecological constraints, such as lack of territories or breeding positions, some campo flicker fledglings may be forced to stay in their natal territory and act as auxiliaries, thus being trapped in a "best-of-a-bad-job" situation (Dickinson et al.

1996). Indeed, some female auxiliaries (i.e., secondary auxiliaries) are completely unrelated to the breeding pair (Dias et al. 2013b) and thus cannot be reaping any kin selected benefits at all. It is possible that there are direct benefits of being an auxiliary that we did not measure in this study, such as increased survival while waiting in the natal site (Kokko et al. 2001), higher chances of dispersal (Clutton-Brock 2002), acquisition of other skills necessary for independent survival or breeding (Komdeur 1996), or signaling suitability as future breeders (Carlisle and Zahavi 1986). Indeed, auxiliaries may be helping breeders as a form of "payment of rent" so that they are allowed to remain (Gaston 1978). Since auxiliaries are often young from previous years, one possibility is that auxiliary males may be constrained from breeding independently due to female mating preferences for more experienced males. Additionally, other variables associated to successful production of offspring were not evaluated in this study and we may have underestimated the benefits of indirect fitness. For instance, it was found that when the number of auxiliaries increased in the long-tailed tit (*Aegithalos caudatus*), there was an elevated recruitment of offspring as breeders (Hatchwell et al. 2004). A further consideration is the potential bias that could be introduced if there is an effect of age or breeding experience on the probability of a breeder receiving help. A first-time breeder may have low fitness compared with more experienced birds and, additionally, is likely to have no assistance, thereby inflating the apparent cost of helping. Thus, future comparisons of fitness of helped and non-helped birds in cooperative species could be improved if analyses control for the effects of breeding experience, something we could not do in our study of this long-lived bird.

In conclusion, we have shown that the presence of auxiliaries increased breeding productivity in campo flickers, resulting in indirect fitness benefits for auxiliaries genetically related to the breeding pair. However, this indirect fitness gain did not compensate the direct fitness costs of not breeding. Consequently, we suggest that helping behavior in campo flickers must result from ecological constraints that restrict independent breeding.

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## References

- Brand N, Chapuisat M (2014) Impact of helpers on colony productivity in a primitively eusocial bee. *Behav Ecol Sociobiol* 68:291–298
- Brouwer L, Heg D, Taborsky M (2005) Experimental evidence for helper effects in a cooperatively breeding cichlid. *Behav Ecol* 16:667–673
- Brouwer L, Richardson DS, Komdeur J (2012) Helpers at the nest improve late-life offspring performance: evidence from a long-term study and a cross-foster experiment. *PLoS One* 7, e33167
- Brown JL, Dow DD, Brown ER, Brown SD (1978) Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behav Ecol Sociobiol* 13:115–124
- Brown JL (1987) *Helping and communal breeding in birds*. Princeton University Press, Princeton
- Bruinijes R, Heg-Bachar Z, Heg D (2013) Subordinate removal affects parental investment, but not offspring survival in a cooperative cichlid. *Funct Ecol* 27:730–738
- Caffrey C (2000) Correlates of reproductive success in cooperatively breeding western American crows: if helpers help, it's not by much. *Condor* 102:333–341
- Canário F, Matos S, Soler M (2004) Environmental constraints and cooperative breeding in the azure-winged magpie. *Condor* 106:608–617
- Canestrari D, Marcos JM, Baglione V (2008) Reproductive success increases with group size in cooperative carrion crows, *Corvus corone corone*. *Anim Behav* 75:403–416
- Carlisle TR, Zahavi A (1986) Helping at the nest, allofeeding and social status in immature Arabian babblers. *Behav Ecol Sociobiol* 18:339–351
- Clutton-Brock TH (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72
- Cockburn A (1998) Evolution of helping behaviour in cooperatively breeding birds. *Annu Rev Ecol Syst* 29:141–177
- Cockburn A, Sims RA, Osmond HJ, Green DJ, Double MC, Mulder RA (2008) Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? *J Anim Ecol* 77:430–438
- Conner RN, Saenz D, Schaefer RR, McCormick JR, Rudolph DC, Burt DB (2004) Group size and nest success in red-cockaded woodpeckers in west gulf coastal plain: helpers make a difference. *J Field Ornithol* 75:74–78
- Dias RI, Webster MS, Goedert D, Macedo RH (2013a) Cooperative breeding in the campo flicker I: breeding ecology and social behavior. *Condor* 115:847–854
- Dias RI, Macedo RH, Goedert D, Webster MS (2013b) Cooperative breeding in the campo flicker II: patterns of reproduction and kinship. *Condor* 115:855–862
- Dickinson JL, Koenig WD, Pitelka FA (1996) Fitness consequences of helping behavior in the western bluebird. *Behav Ecol* 7:168–177
- Dickinson J, Hatchwell BJ (2004) Fitness consequences of helping. In: Koenig WD, Dickinson JL (eds) *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge, pp 48–66
- Doerr ED, Doerr VA (2007) Positive effects of helpers on reproductive success in the brown treecreeper and the general importance of future benefits. *J Anim Ecol* 76:966–976
- Dunn PO, Cockburn A, Mulder RA (1995) Fairy-wren helpers often care for young to which they are unrelated. *Proc R Soc Lond B Bio* 259:339–343
- Du-Plessis MA, Siegfried WR, Armstrong AJ (1995) Ecological and life-history correlates of co-operative breeding in South African birds. *Oecologia* 102:180–188
- Eguchi K, Yamagishi S, Asai S, Nagata H, Hinos T (2002) Helping does not enhance reproductive success of cooperatively breeding *Rufous vanga* in Madagascar. *J Anim Ecol* 71:123–130
- Ekman J, Dickinson L, Hatchwell J, Griesser M (2004) Delayed dispersal. In: Koenig WD, Dickinson JL (eds) *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge, pp 35–47
- Emlen ST (1982) The evolution of helping I. An ecological constraints model. *Am Nat* 119:29–39
- Emlen ST (1991) The evolution of cooperative breeding in birds and mammals. In: Krebs J, Davies N (eds) *Behavioural ecology*, 3rd edn. Blackwell Scientific Publications, Oxford
- Emlen ST, Wrege PH (1991) Breeding biology of white-fronted bee-eaters at Nakuru—the influence of helpers on breeder fitness. *J Anim Ecol* 60:309–326
- Gaston AJ (1978) The evolution of group territorial behavior and cooperative breeding. *Am Nat* 112:1091–1100
- Hamilton WD (1964) The genetical theory of social behavior. I and II. *J Theor Biol* 7:1–52
- Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol Ecol Notes* 2:618–620
- Hatchwell BJ (1999) Investment strategies of breeders in avian cooperative breeding systems. *Am Nat* 154:205–219
- Hatchwell BJ, Russell AF (1996) Provisioning rules in cooperatively breeding long-tailed tits. *Proc Royal Soc B* 263:83–88
- Hatchwell BJ, Russell AF, MacColl ADC, Ross DJ, Fowlie MK, McGowan A (2004) Helpers increase long-term but not short-term productivity in cooperative breeding long-tailed tits. *Behav Ecol* 15:1–10
- Hatchwell BJ (2009) The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philos T R Soc B* 364:3217–3227
- Heinsohn RG, Cockburn A, Cunningham RB (1988) Foraging, delayed maturity and cooperative breeding in white-winged choughs (*Corcorax melanorhamphos*). *Ethology* 77:177–186
- Heinsohn RG (1992) Cooperative enhancement of reproductive success in white-winged choughs. *Evol Ecol* 6:97–114
- Khan MZ, Walters JR (1997) Is helping a beneficial learning experience for red-cockaded woodpecker (*Picoides borealis*) helpers? *Behav Ecol Sociobiol* 41:69–73
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106
- Kokko H, Johnstone RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. *Proc R Soc Lond B Bio* 268:187–196
- Kokko H, Johnstone RA, Wright J (2002) The evolution of parental and alloparental care in cooperatively breeding groups: when should helpers pay to stay? *Behav Ecol* 13:291–300



- Komdeur J (1996) Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav Ecol* 7:326–333
- Legge S (2000) The effect of helpers on reproductive success in laughing kookaburra. *J Anim Ecol* 69:714–724
- Ligon JD, Ligon SH (1978) Communal breeding in green woodhoopoes as a case for reciprocity. *Nature* 276:496–498
- Lucas JR, Creel SR, Waser PM (1996) How to measure inclusive fitness, revisited. *Anim Behav* 51:225–228
- Manica LT, Marini MA (2012) Helpers at the nest of white-banded tanager *Neothraupis fasciata* benefit male breeders but do not increase reproductive success. *J Ornithol* 153:149–159
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7:639–655
- McGowan A, Hatchwell BJ, Woodburn RJW (2003) The effect of helping behaviour on the survival of juvenile and adult long-tailed tits *Aegithalos caudatus*. *J Anim Ecol* 72:491–499
- Mulder RA, Langmore NE (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim Behav* 45:830–833
- Mumme RL (1992) Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behav Ecol Sociobiol* 31: 319–328
- Pinheiro F, Diniz IR, Coelho D, Bandeira MPS (2002) Seasonal pattern of insect abundance in the Brazilian Cerrado. *Austral Ecol* 27:132–136
- Powell RA, Fried JJ (1992) Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. *Behav Ecol* 3:325–333
- Pruett-Jones S (2004) Summary. In: Koenig WD, Dickinson JL (eds) *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge, pp 228–238
- Queller DC, Goodnight K (1989) Estimating relatedness using genetic markers. *Evolution* 43:258–275
- R Development Core Team (2014): R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL (<http://www.R-project.org>)
- Reyer HU (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim Behav* 32:1163–1178
- Russell AF, Langmore NE, Cockburn A, Astheimer LB, Kilner RM (2007) Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* 317:941–944
- Short LL (1972) Systematics and behavior of South American flickers (Aves: Colaptes). *B Am Mus Nat Hist* 149:1–110
- Stacey PB, Koenig WD (1990) *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, Cambridge
- Woxvold IA, Magrath MJL (2005) Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *J Anim Ecol* 74:1039–1050