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Helpers at the nest of White-banded Tanager *Neothraupis fasciata* benefit male breeders but do not increase reproductive success

Lilian Tonelli Manica · Miguel Ângelo Marini

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Abstract In cooperatively breeding birds, breeders can adjust their parental care investment without affecting nestling survival probability and save energy to invest in other activities, such as feeding, mating or territory defense. Furthermore, helpers at the nest can improve nestling nutrition and hence the reproductive performance of the breeding pair. We determined the influence of helpers on nestling feeding effort and reproductive success of breeders in the neotropical White-banded Tanager (*Neothraupis fasciata*). We monitored nests during the breeding seasons of 2006 and 2007 in central Brazil. Males showed a compensatory reduction of their food delivery rate in the presence of helpers, whereas females exhibited the same parental effort regardless of having helpers. Total food delivery rate was higher for nests with helpers, but there was no effect of helpers on reproductive performance of breeders (clutch size, hatching rate, fledgling productivity and reproductive success). Our results indicate that cooperative breeding in the White-banded Tanager appears to be important for males to reduce their parental care effort and, hence, invest in their survival or future reproductive attempts.

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L. T. Manica (✉)
Programa de Pós-graduação em Ecologia,
Instituto de Ciências Biológicas, Universidade de Brasília,
Brasília, DF 70910-900, Brazil
e-mail: lilianmanica@gmail.com

M. Â. Marini
Departamento de Zoologia, Instituto de Ciências Biológicas,
Universidade de Brasília, Brasília, DF 70910-900, Brazil

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Zusammenfassung Bei kooperativ brütenden Vögeln können Brüter ihren Brutpflegeaufwand anpassen, ohne dass dies die Überlebenswahrscheinlichkeit der Nestlinge beeinträchtigt, und Energie sparen, die dann in andere Aktivitäten, wie Nahrungsaufnahme, Paarung oder Revierverteidigung, investiert werden kann. Außerdem können Helfer am Nest die Ernährung der Nestlinge und somit die Fortpflanzungsleistung des Brutpaares verbessern. Wir haben ermittelt, wie sich Helfer auf den Nestlings-Fütterungsaufwand und den Fortpflanzungserfolg von brütenden neotropischen Flügelbindentangaren (*Neothraupis fasciata*) auswirken. Wir haben Nester während der Brutsaisons 2006 und 2007 in Zentralbrasilien überwacht. Männchen zeigten eine kompensatorische Reduktion ihrer Fütterungsrate in Anwesenheit von Helfern, während Weibchen denselben Elternaufwand zeigten, unabhängig davon, ob sie Helfer hatten oder nicht. Die Gesamtfütterungsrate war für Nester mit Helfern höher, doch Helfer hatten keinen Einfluss auf die Fortpflanzungsleistung von Brütern (Gelegegröße, Schlupfrate, Flügglingsproduktion und Fortpflanzungserfolg). Unsere Ergebnisse deuten darauf hin, dass kooperatives Brüten bei Flügelbindentangaren für Männchen wichtig zu sein scheint, um ihren Brutpflegeaufwand zu reduzieren und folglich in ihr Überleben oder weitere Fortpflanzungsversuche zu investieren.

Introduction

In cooperatively breeding birds, breeders may be assisted by helpers in caring for offspring (Brown 1987; Koenig and

Dickinson 2004) and adjust their parental care effort without affecting nestling survival probability. As a consequence, the parents may have more time and energy to invest in other activities, such as feeding, mating or territory defense. Changes in parental effort by breeders may increase their chances of survival or their reproductive attempts within the same breeding season or in future seasons (Crick 1992; Heinsohn 2004). Although cooperative breeding systems have been widely studied, a consistent direction of the effect of helpers on breeders' parental investment has yet to be found. Because of the high energy costs of parental investment, it is reasonable to expect that breeders reduce their workload with nestling care when assisted by helpers. However, studies of cooperative species have shown that, in the presence of helpers at the nest, parents can maintain the same parental effort (Emlen and Wrege 1991; Magrath and Yezerinac 1997), decrease (MacColl and Hatchwell 2003) or even increase their contribution with nestling care (Valencia et al. 2006), suggesting that factors other than parental care may affect breeders' responses.

It has been proposed that breeders' decisions about parental investment in assisted groups are affected by the costs of this activity to breeders and by the causes of nestling mortality (Hatchwell 1999). According to Hatchwell (1999), helping behavior can result in compensatory reduction of parents' efforts or additive care provided by helpers in nestling feeding. The former tends to occur when the cost of parental care is high and when nestling starvation is rare (Hatchwell 1999). In this situation, parents may reduce their workload when helped by other individuals and, therefore, gain more energy to invest in survival. Alternatively, the second situation can occur when the cost of parental care is low and nestling survival is constrained by feeding ability of adults (Hatchwell 1999; Carranza et al. 2008). In this case, breeders may not decrease their efforts when helped, but nevertheless benefit due to higher overall provisioning rates to their offspring (Emlen and Wrege 1991; Hatchwell 1999; Heinsohn 2004).

The presence of helpers can increase the chances of fledgling productivity and/or breeding success of the reproductive pair (Emlen and Wrege 1991; Cockburn 1998). Helpers can contribute with reproductive success by improving nestling nutrition or protection against predators (Cockburn 1998). Despite these predictions, the positive effect of cooperation on reproductive performance, such as fledgling productivity or reproductive success, has been refuted in some studies (Legge 2000; Eguchi et al. 2002). In these cases, the presence of helpers does not increase the overall food provisioning on nests (Legge 2000) nor the fledgling success (Legge 2000; Eguchi et al. 2002).

Helping behavior has been studied in many bird species, but most research has been focused on African, Australian or temperate region species (review in Cockburn 2006). There are few studies of cooperative breeding species in the neotropical region (Macedo 2008), and only a minor portion of these studies test hypotheses concerning breeding behavior (e.g., Rodrigues and Carrara 2004). Our purpose in this study was to determine the influence of helpers on nestling feeding effort and reproductive outcome of breeders in the neotropical White-banded Tanager (*Neothraupis fasciata*). This species is a facultative cooperative breeder (Alves 1990) in which the breeding pair may or may not be helped by other birds during chick care (Cockburn 1998). We tested whether parents would change their parental provisioning effort when aided by helpers and whether helpers′ assistance would influence brood sizes, egg hatching rates, nestling growth rates and permanence on nests, fledgling productivity, and daily nest survival.

Methods

We conducted the study in a 100-ha grid (1 × 1 km) (15°32′32″S, 47°36′49″W) covered by cerrado, a typical neotropical savanna vegetation, at Estação Ecológica de Águas Emendadas (ESECAE). This 10,500-ha reserve is located 50 km northeast of Brasília, Distrito Federal, Brazil. The climate of the region is rainy tropical with a marked seasonality: a rainy season from October to April and a dry season from May to September. Mean annual rainfall of the cerrado ranges from 1,500 to 1,750 mm, and mean temperature ranges from 20 to 26°C (Nimer 1979).

The White-banded Tanager is near-endemic to the savannas of central Brazil (Lopes 2008) and classified as near-threatened by IUCN (2004). It builds open nests usually around 1 m above the ground (Alves and Cavalcanti 1990). Clutch size ranges from one to three eggs, hatching is synchronous, incubation lasts 13 days, and nestling period is about 11.7 days (Duca and Marini 2011). This is a year-round resident species that defends 3.7 ± 0.6-ha territories on average (Duca 2007) and plays sentinel roles in mixed-species flocks (Alves 1990; Alves and Cavalcanti 1996; Ragusa-Netto 2000). This species is socially monogamous and helpers assist parents with nest or territory defense (Alves 1990) and nestling feeding (present study). Cooperative groups are composed of three to six individuals (Alves 1990; Duca 2007) and previous studies showed that some breeding units are family groups composed of the breeding pair and their progeny from the previous breeding attempt (50% of studied groups; Alves 1990; Duca 2007; Gressler and Marini, unpublished data). In our study, we did not have molecular data to determine the relatedness of all individuals in the groups. However, we knew that one non-breeder female individual (helper) in 2007 was the descendant of the breeding pair she was helping. We monitored 16 assisted (9 in 2006 and 7 in 2007) and 37 unassisted (24 in 2006 and 13 in 2007) breeding pairs in the 2 years. Group size of assisted pairs varied from three to five individuals (3.2 ± 0.5, $n = 16$). Nine individuals (helpers and breeders) were repeatedly monitored during the 2 years of the study: two breeding pairs assisted by helpers, one pair without helpers and two male helpers and one female breeder that associated with different groups in the 2 years. We monitored 71 nests (41 in 2006 and 30 in 2007), of which 23 (32.4%) belonged to breeding pairs with helpers and 48 (67.6%) to breeding pairs without helpers. Six nests in 2006 and 8 in 2007 were re-nesting attempts by the same pairs, of which 2 and 3, respectively, were assisted nests.

In the study area, birds have been captured with mist-nets since 2002. Birds were sexed and aged by plumage (following Duca 2007), and received unique combinations of three color bands, and a permanent metal band. Social groups were identified in August–September of 2006 and 2007 inside territories that were delimited in preceding years in the same area (see Duca 2007). We considered breeding males those birds that defended territories and that prevented other males within or outside the group from accessing their females, that executed sentinel behavior, that were seen singing at dawn within the group's territory or that were helping females with nest construction. We considered breeding females those that were seen incubating eggs, building nests or that were protected by males from other males. Methods to determine male and female breeding status (breeder or helper) followed Alves (1990) and Duca (2007). We also registered two copulations between the presumed breeding pair, which confirmed our pre-definition of the social role of males and females in a group. Other birds in the groups were considered helpers.

We monitored White-banded Tanagers breeding from August to December 2006 and 2007. We inspected nests every 3–4 days during the incubation period and every 2 days from near hatching to the end of nest activity. Clutch size was determined as the maximum number of eggs in two consecutive nest checks. We calculated hatching rate as the number of eggs that hatched divided by clutch size for nests that survived to hatching. We used Wilcoxon tests to test the effect of the presence of helpers on clutch size and hatching rate.

To estimate food delivery rate (FDR), we observed 29 nests for from 1–2 h (mean ± SD = 1.8 ± 0.1, $n = 53$ observations), from September to October 2006 and 2007. We observed food delivery rate in 10 nests with helpers (33 h of observation) and in 19 nests without helpers (52 h). Observations were conducted with binoculars ($n = 36$ observations) from blinds or using digital video cameras placed at least 10 m from the nest ($n = 17$ observations). We did not include data from observations in which our proximity may have disturbed normal behavior, which occurred when adults did not visit the nest to feed the nestlings but stayed nearby, repeatedly emitting short calls. We estimated total food delivery rate (FDR_T) from the total number of visits per hour of observation, and used the number of visits per hour by males, females and helpers to calculate their hourly FDR (FDR_M, FDR_F and FDR_H, respectively). We defined three nestling age categories: 0–2, 4–6 and 8–10 days old, and observed each nest at least once in each age class, unless nests failed due to predation or when we did not discover a nest until at least 2 days after hatching. We conducted observations during three time periods during the day (6:00 to 8:00, 8:00 to 10:00, 14:00 to 16:00), alternating times of nest observation each day to allow equivalent sampling for each time period in each age class. We used the mean value of all data for nests observed more than once within an age class ($n = 17$).

We used generalized linear mixed-effect models (GLMM) fitted by restricted maximum likelihood to analyze FDRs, using *lmer* function (R package *lme4*; R Development Core Team 2007) with Gaussian distribution and identity link function. We added to the models the variable "nest" and "group identity" as random effects, because there were repeated measurements of the same nest in different age classes and of the same group in different breeding attempts in the same or consecutive years. We created GLMMs to explain the variations in FDR_T, FDR_M and FDR_F relative to the presence of helpers, nestling age and year. We refrained from including time of day as a variable since sample sizes were small. Also, paired *t* tests with Bonferroni corrections and paired Wilcoxon tests showed no difference between FDRs relative to different time periods in the day ($P > 0.05$ for all comparisons). We initially related each FDR with all factors: "age" (0–2, 4–6, 8–10 days), "helper" (present/absent), "year" (2006/2007), and the interaction between "helper" and "age". We followed a stepwise procedure for model fitting, in which each variable was excluded in each step from the full model and, subsequently, pairs of models were compared through a likelihood ratio test (LRT) that is Chi-square distributed. We removed non-significant terms from final models and ran a subsequent model fitting to estimate parameters. To test if males, females and helpers differed in food provisioning, we related FDR_M, FDR_F and FDR_H estimated for assisted nests with "individual identity" (male/female/helper), "age" and the interaction between "individual identity" and "age" in a single GLMM. For this analysis, we used log(FDR+1) to correct problems with heterocedasticity and followed the same stepwise procedure for model selection as described above. We used Shapiro–Wilk tests and residual analyses (standardized residuals versus fitted values scatter plots) to evaluate normality and homogeneity of variances, respectively.

We weighed nestlings at 0–2 and 6–8 days with 10- and 50-g spring scales. For each nest, we calculated the mean nestling growth rate (r) using the formula:

$$r = (m_s - m_f)/d$$

where m_s is the nestling body mass on the second measurement, m_f is the nestling body mass on the first measurement and d is number of days between measurements. We only used data from nests with two nestlings and that did not suffer partial predation to exclude confounding variables related to clutch size and parental nestling-feeding ability. To compare the effect of helpers on nestling growth rates we used a *t* test. For this, we used data from 2006 and 2007 and assumed lack of difference between years, since there was no difference between years for nests without helpers ($t = 0.116$, $df = 4$, $P = 0.913$). It was not possible to test differences between years for nests with helpers due to low sample sizes. We also used a *t* test to compare nestling period, in days, between nests with and without helpers. We tested normality with a Shapiro–Wilk test and variances homogeneity with an *F* test.

We compared fledgling productivity (number of fledglings per nest) between pairs with and without helpers using a Wilcoxon test. We set the α level at 5% for all tests, and for all analyses we present means followed by standard deviation (SD).

We classified nest fates as: (1) successfully hatched, when incubation lasted at least 13 days, or successfully fledged, when nestlings reached at least 9 days of age (minimum age for a egg to hatch or a nestling to fledge, respectively; Duca and Marini 2011); (2) depredated, when nest contents were found damaged or disappeared before the minimum expected age of eggs/nestlings to hatch/fledge successfully; (3) abandoned, when adults were not observed attending the nest and eggs were cold; and (4) other reason, when nestlings were found dead in the nest. We used the software MARK (White and Burnham 1999; Rotella 2005; Dinsmore and Dinsmore 2007) to model daily survival rates (DSR) of nests during incubation and nestling periods, separately. We applied Akaike's Information Criterion (AIC; Burnham and Anderson 2002), adjusted for small samples (AIC_c), to make inferences about the relationship between DSR and temporal variables and the presence of helpers at the nest. We considered that only models with $\Delta AIC_c \leq 2$ had enough substantial support to explain the variation in the data (Burnham and Anderson 2002). In addition, we used Akaike weight (w_i) of each model and evidence ratio (the ratio of Akaike weights of model pairs, w_i/w_j) to make inferences about the importance of fitted models in model selection (Burnham and Anderson 2002). When w_i was less than 0.9 for the best model, we used the entire set of candidate models to calculate model-averaged parameter coefficients and unconditional standard errors for each variable of interest (Burnham and Anderson 2002). We considered that almost all premises for modeling were met (Dinsmore and Dinsmore 2007), with the exception of the premise of independence of nest fates because some nests belonged to the same breeding pair (eight nests in incubation period analysis and six nests in nestling period analysis). However, we considered this premise reasonably satisfied since these nests were found at different times and places. To standardize the number of days of incubation and nestling periods for all nests, we assumed 13 and 9 days, respectively, because these were the shorter periods recorded.

To model DSRs relative to helper presence or absence, we first included temporal variables in the models. We evaluated linear and quadratic tendencies through the season to control for possible season–day effects, such as predator number and foraging behavior or alternate prey availability (Stutchbury and Morton 2001). We also considered nest age as a predictor variable, since environmental, ecological or parental behavior changes during nest development may affect the chances of success (Skutch 1949). We included year as another effect, because previous studies showed inter-annual differences in reproductive parameters (Duca 2007). In the first stage of model selection, we ran models without predictor variables (null model) and with the following variables: (1) linear or (2) quadratic time trend through the season, (3) "nest age" at incubation or nestling period, and (4) "year" (2006/2007), using all possible combinations. In the second stage of selection, we used the best-supported models ($\Delta AIC_c \leq 2$) of the first step to include the variable "helper" (present/absent). We ran all models with predictor variables using a logit link function and models without variables with a sin-link function.

To obtain robust estimates of DSR, we used model averaging that accounts for model selection uncertainty and that is calculated based on Akaike weights (Burnham and Anderson 2002). This was done varying only the interest variable, keeping the value of the other variables constant. To calculate nest survival probability during incubation or nestling periods, we multiplied the averaged DSR mean of all models using 13 days for incubation and 9 days for nestling period.

We considered the day that we found the first active nest with an egg (incubation period) or with a nestling (nestling period) as the first day of the reproductive season for DSRs analyses. We did not include six abandoned nests in the nest survival analyses because abandonment date could not be estimated. We also excluded from analyses two depredated and two successful nests for which we were unable to determine the exact laying day of the first egg and, thus, the nest age. We lumped both categories of unsuccessful nests (predation and lost for unknown reason) because sample size for the latter category was too small to allow separate analysis (only 3 nests).

Results

Considering all 71 nests monitored, 40.8% were successful, and predation (80.9%) was the main nest failure cause, followed by abandonment (14.3%) and unknown reasons (4.8%). Eleven of the 13 nests of breeding pairs with helpers that reached the nestling stage had all helpers [one ($n = 8$) or two ($n = 3$) individuals] feeding the nestlings. Helpers were adult males ($n = 9$), subadult males ($n = 1$), juveniles ($n = 8$) and one unidentified individual. We could not determine the sex of juveniles, because immature males and females are monomorphic. All nest visits resulted in efficient food transference, that is, false-feeds did not occur.

Clutch size ranged from two ($n = 28$) to three ($n = 17$) eggs. Cooperative breeding did not affect mean clutch size, which was almost identical irrespective of helper presence (assisted: 2.33 ± 0.49 eggs, unassisted: 2.36 ± 0.49 eggs, $W = 204$, $P = 1$). For all nests that reached hatching, mean hatching rate was equivalent between nests with and without helpers (assisted: 1.0 ± 0.0 eggs hatched/clutch size; unassisted: 0.93 ± 0.15 eggs hatched/clutch size, $W = 240$, $P = 0.24$).

FDR_T increased with nestling age ($\chi^2 = 57.89$, $P < 0.01$, $n = 29$) and with the presence of helpers ($\chi^2 = 10.21$, $P = 0.02$, $n = 29$; Table 1; Fig. 1a). FDR_M increased with nestling age ($\chi^2 = 31.84$, $P < 0.01$, $n = 28$) and showed an interaction between nest age and presence of helpers ($\chi^2 = 6.36$, $P = 0.04$, $n = 28$; Table 1), being higher in the intermediate age class and decreasing in the last age class (Fig. 1b). FDR_F only increased with nestling age ($\chi^2 = 50.00$, $P < 0.01$, $n = 29$; Table 1; Fig. 1c). Helpers differed from both male and female breeders in FDR ($\chi^2 = 19.79$, $P < 0.01$, $n = 10$; Table 2) in the first age class of nestlings but fed older nestlings at similar rates to adults (Fig. 2).

The presence of helpers did not affect nestling growth rates (assisted nests = 2.5 ± 0.1 g/day, $n = 5$; unassisted nests = 2.6 ± 0.3 g/day, $n = 6$; $t = 1.18$, $df = 9$, $P = 0.87$) or nestling period (assisted nests = 10.4 ± 1.0 days, $n = 8$; unassisted nests = 10.4 ± 0.8 days, $n = 19$; $t = 0.04$, $df = 25$, $P = 0.96$). Fledgling productivity per nest was also not affected by the presence of helpers at the nest (assisted nests = 0.7 ± 1.0 nestlings/nest, $n = 23$; unassisted nests = 0.8 ± 1.1 nestlings/nest, $n = 48$; $W = 593.5$, $P = 0.59$).

Table 1 Estimated parameters for significant predictor terms of the final GLMM of food delivery rate (*FDR*) in nests of the White-banded Tanager (*Neothraupis fasciata*)

Response variable	Predictor terms	Estimate ± SE
Total FDR	Intercept	2.53 ± 0.42
	Nestling age 4–6 days[a]	2.91 ± 0.56
	Nestling age 8–10 days[a]	5.93 ± 0.65
	Helper[b]	1.27 ± 0.50
Males FDR	Intercept	1.60 ± 0.29
	Nestling age 4–6 days[a]	1.12 ± 0.43
	Nestling age 8–10 days[a]	2.74 ± 0.53
	Helper[b]	−0.41 ± 0.50
Females FDR	Intercept	1.37 ± 0.19
	Nestling age 4–6 days[a]	0.99 ± 0.25
	Nestling age 8–10 days[a]	2.46 ± 0.30

[a] Estimates relative to nestling age 0–2

[b] Estimates relative to unassisted nests

We analyzed DSR of 48 nests during the incubation and 45 during the nestling period. Thirty-three nests were sampled in both categories (incubation and nestling periods). We found three best-approximating models ($\Delta\mathrm{AIC}_\mathrm{c} \le 2$) with temporal variables in the first stage of model selection for incubation period (Table 3). In the second stage of model selection, two models with $\mathrm{AIC}_\mathrm{c} \le 2$ included helper variables combined with linear time trend, nest age and year (Table 3), indicating that the helper variable improved model fit. However, the Akaike weights of these models were low (13 and 12%) and their evidence ratios relative to the models without the helper variable ("linear + nest age" and "linear + nest age + year" models; Table 3) were also low (ER = 1.69, 2.50, respectively). Despite the fact that the relationship between presence of helpers and DSR was positive during the incubation period, the effect size was small and the 95% confidence interval (CI) overlapped with zero ($\beta_{\mathrm{helper/incubation}} = 0.18$, SE = 0.29, CI = −0.52, 0.89), suggesting that the presence of helpers may not strongly affect nest survival. Survival probability during incubation was 78.6% (CI = 50.5, 94.2) for assisted nests and 75.6% (CI = 46.1, 92.1) for unassisted nests in 2006, and was 63.0% (CI = 21.0, 87.5) for assisted nests and 59.3% (CI = 23.4, 83.0) for unassisted nests in 2007.

Temporal variables of best-approximating models for incubation period showed that DSR tended to decrease through the season ($\beta_{\mathrm{linear\ trend}} = -0.7 \times 10^{-2}$, SE = 0.01, CI = −0.18, 0.19) and with nest age ($\beta_{\mathrm{nest\ age}} = -0.14$, SE = 0.07, CI = −0.66, 0.37), and was lower in 2006 when compared with 2007 ($\beta_{2006} = -0.65$, SE = 0.39, CI = −1.73, 0.44). Daily survival rate had a low tendency to vary in a quadratic time pattern ($\beta_{\mathrm{quadratic\ trend}} = -0.65 \times 10^{-3}$, SE = 0.18×10^{-3}, CI = −0.01, 0.01). Although the best-approximating models included all these

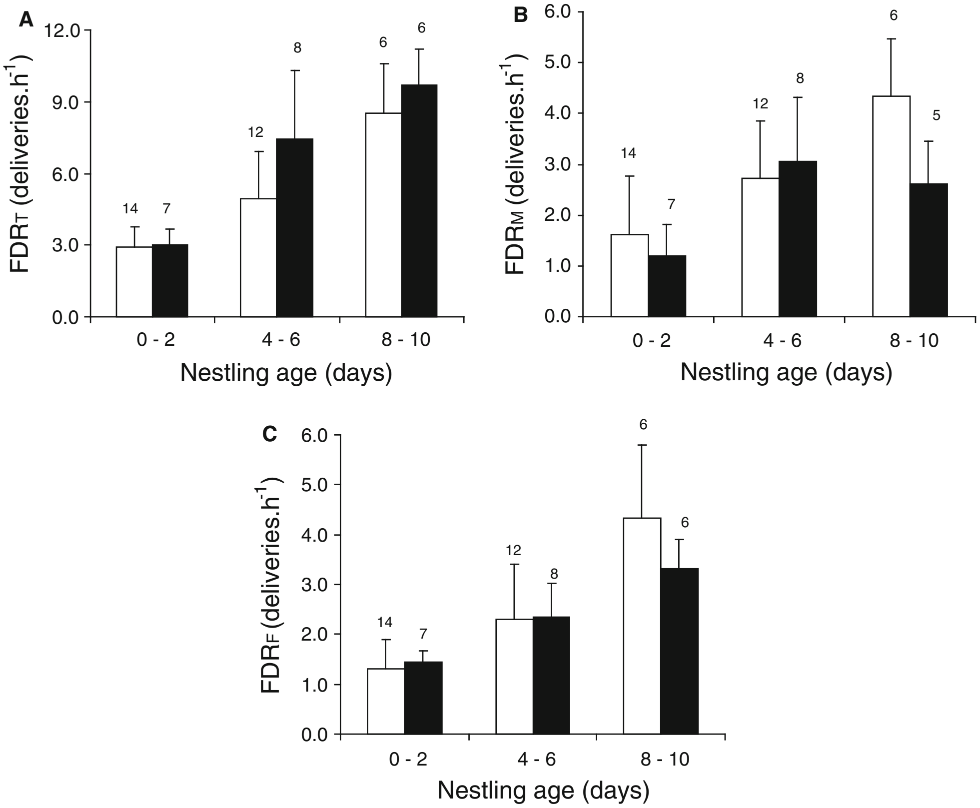

Fig. 1 Total food delivery rate (*FDR*$_T$) **a**, food delivery rate of males (*FDR*$_M$) **b** and females (*FDR*$_F$) **c** in each nestling age of non-assisted (*white bars*) and assisted (*black bars*) nests of the White-banded Tanager (*Neothraupis fasciata*). *Bars* represent mean and SD. Sample sizes indicated above the bars

Table 2 Estimated parameters on the logarithmic scale for significant predictor terms of the final GLMM of food delivery rate (*FDR*) in assisted nests of the White-banded Tanager

Response variable	Predictor terms	Estimate ± SE
FDR[a]	Intercept	0.32 ± 0.04
	Helper FDR[b]	−0.14 ± 0.04
	Males FDR[b]	−0.01 ± 0.04

[a] log (FDR + 1) transformed

[b] Estimates relative to females FDR

temporal variables, we suggest they have little influence on nest survival, given the low values of the coefficients and the large CI.

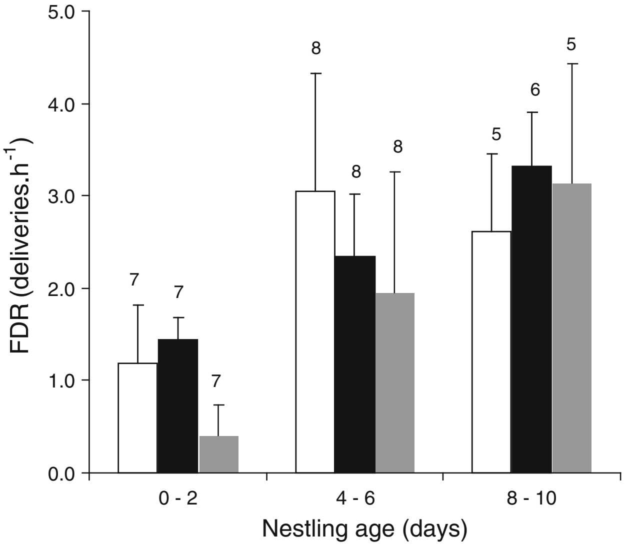

Fig. 2 Food delivery rate (*FDR*) of males (*white bars*), females (*black bars*) and helpers (*gray bars*) in assisted nests in each nestling age of the White-banded Tanager. *Bars* represent mean and SD. Sample sizes indicated above the bars

For the nestling period analysis, we found three best-approximating models ($\Delta AIC_c \leq 2$) with temporal variables in the first stage of model selection (Table 3). In the second stage of model selection, the model with the lowest AIC$_c$ for the nestling period did not include any variable (null model) and had 40% evidence of being the best model. Addition of the helper variable slightly affected model fitting ($w = 0.15$), but the evidence ratio for the model with the helper variable versus the null model (ER = 2.67) does not support superiority of the null compared with the first model. In contrast to incubation period, the presence of helpers at the nest was negatively related to DSR, but with a small effect size

Table 3 Results of the first and second stage of model selection based on Akaike's Information Criterion adjusted for small samples (AIC_c) of daily survival rates (DSR) of White-banded Tanager nests at incubation and nestling periods

Model	ΔAICc	w_i	*K*	Deviance	ER
Incubation period					
First stage					
Linear + nest age + year	0.00	0.30	4	97.47	1.00
Linear + nest age	0.95	0.19	3	100.46	1.61
Quadratic + nest age + year	1.66	0.13	5	97.08	2.30
Second stage					
Linear + nest age + year	0.00	0.30	4	101.84	1.00
Linear + nest age	0.64	0.22	3	104.19	1.38
Quadratic + nest age + year	1.27	0.16	5	106.70	1.88
Linear + nest age + helper	1.73	0.13	4	105.50	2.37
Linear + nest age + year + helper	1.77	0.12	5	101.63	2.43
Nestling period					
First stage					
Null	0.00	0.33	1	117.71	1.00
Year	1.54	0.15	2	117.22	2.20
Linear	1.99	0.12	2	117.68	2.75
Second stage					
Null	0.00	0.40	1	117.71	1.00
Year	1.54	0.19	2	117.22	2.10
Linear	1.99	0.15	2	117.68	2.67
Helper	2.00	0.15	2	117.69	2.67

ΔAICc Difference between the AICc and the minimum AICc found for the models, w_i Akaike weight of the *i* model, *K* number of parameters, *deviance* difference in the −2 log-likelihood between each model and the saturated model, *ER* evidence ratio (w_1/w_i). Models with ΔAICc > 2 are omitted

AICc of best models (ΔAICc = 0) of *incubation period*: first stage = 105.56 and second stage = 107.05; *nestling period*: first stage = 119.73 and second stage = 119.72

($\beta_{\text{helper/nestling}} = -0.02$, SE = 0.15, CI = −0.41, 0.37). The low value of regression coefficients and its 95% CI overlapping zero for the helper variable suggest that there is a very weak tendency of helpers to affect nest survival. Survival probability during the nestling period was 57.5% (CI = 26.5, 79.2) for assisted nests and 60.2% (CI = 38.4, 76.6) for unassisted nests in 2006, and was 56.9% (CI = 30.9, 76.7) for assisted nests and 55.9% (CI = 32.7, 74.3) for unassisted nests in 2007. Temporal variables included in best models showed a slight tendency for DSR to decrease through the season ($\beta_{\text{linear trend}} = -0.2 \times 10^{-2}$, SE = 0.02×10^{-2}, CI = −0.04, 0.05) and that DSR was lower in 2006 than 2007 ($\beta_{2006} = -0.08$, SE = 0.12, CI = −0.45, 0.28).

Discussion

Our study suggests that the effect of helpers in White-banded Tanagers is limited to a reduction in parental effort by breeding males and an increase in total food delivery rate at the nest. Although helpers contributed to nestling nutrition, nestling growth rate did not increase nor did nestlings leave the nest earlier when compared with those from unassisted nests. In addition, the presence of helpers did not affect daily nest survival probability during incubation nor during the nestling period. Additionally, helpers had no effect on clutch sizes, egg hatching rates or fledgling productivity.

We found that breeding males and females showed different responses in nestling care in the presence of helpers. The effect of helpers was compensatory for males, because they reduced their number of food deliveries, whereas females maintained the same delivery rate. This sex-related difference can be associated with the cost–benefit for each sex for parental investment (Hatchwell 1999; Heinsohn 2004). Males' reproductive success is generally constrained by access to females, and consequently males can benefit from saving energy for future investment in breeding attempts (Cockburn 1998). In addition, males can take advantage of their load-lightening response by increasing their chances of survival. In fact, studies have been shown that in cooperative breeding species breeders may have increased survival in assisted groups (e.g., Woolfenden and Fitzpatrick 1984; Curry 1988; Russell et al. 2007; Kingma et al. 2010), and that low male survival rates is probably related to their compensatory response (Hatchwell 1999). However, we could not access males' survival rates in the White-banded Tanager due to the short-term period of our study and the difficulty in distinguishing between mortality and dispersal of an individual that was not recaptured in successive years.

Another possibility is that paternity uncertainty could explain the compensatory reduction of breeding males, since their breeding partner may copulate with extra-pair males (Cockburn 1998; Griffith et al. 2002). However, plenty of evidence shows that most social groups of White-banded Tanager are probably familiar, in which helpers are the progeny of the breeders from a previous reproductive attempt (Alves 1990; Duca 2007; Gressler and Marini, unpublished data; present study). Therefore, incest avoidance mechanisms may be frequent in our study population, as in other cooperative breeders (Koenig and Haydock 2004). Indeed, in the White-banded Tanager, dispersal is female-biased (Duca 2007) which could reduce the chances of incest.

Total food delivery rates increased with helpers' assistance, corroborating an additive effect of cooperative behavior on parental care combined with the compensatory reduction by males. The additive response in assisted nests indicates that the contribution of helpers may benefit the development of nestlings. Following Hatchwell's (1999) predictions, it was expected that the additive response should be associated with high levels of starvation among nestlings. However, most nestling deaths were caused by predation and we found evidence of nestling starvation or malnutrition in only 4.8% of the nests, in which nestlings were found dead on the last monitoring day or had a slower growth rate. Similar results have been found for other species (Carranza et al. 2008). For example, in the Azure-winged Magpie (*Cyanopica cyanus*), breeders increased their feeding effort when aided by helpers, even though starvation risk was a minor cause of nest failure (Valencia et al. 2006). Also, in the Laughing Kookaburra (*Dacelo novaeguineae*), although brood reduction was the main cause for nest failure, additional helpers did not increase food delivery rates (Legge 2000). Therefore, parental investment by breeders may be driven by factors other than nestling mortality risk, such as nest defense (Valencia et al. 2006) or nestling body condition (review in Carranza et al. 2008). Considering the high rates of nest predation in the White-banded Tanager (Alves and Cavalcanti 1990; Duca 2007), we predicted that protection against predators may be the most important role of helpers. However, we found no support for this prediction.

Nestling age was also an important variable that explained the variation of provisioning rates in nests. Total food delivery rate and adult delivery rate increased with nestling age. This result was expected, because nestlings increase their energetic demand during development. In altricial bird species, nestling growth rate can be fitted in a logistic curve, in which rapid growth occurs until the last few days before fledging (Ricklefs 1984). Adults may guarantee appropriate nestling nutrition by increasing the number of visits and choosing suitable food item size or quality.

The presence of helpers did not affect nestling growth rate and the number of days they stayed in the nest, although total food delivery rate increased. Provisioning made by helpers could have compensated for short or low-quality food availability in breeders′ territories, such that larger number of food deliveries at assisted nests would result in similar growth rates of nestlings than that of unassisted nests. Considering that harsh environmental conditions favor cooperation in reproduction among individuals (Rubenstein and Lovette 2007), breeders of the White-banded Tanager might have accepted helpers in such severe situation to improve nestling nutrition, even if subjected to potential costs (e.g., competition for food). In our study area, a large variation of food biomass (arthropods and fruits) exists across territories, as estimated in 2009–2010 (Pereira 2011); therefore, if nestling feeding help outweighs low food availability, we expect that assisted pairs will occur preferentially in low-quality territories. This hypothesis remains untested and we suggest that it should be considered in further studies with this species.

An alternative explanation for inconsistency between increased food provisioning at the nest and no effect on nestling development is that each adult reduced the amount of food delivered in each nest visit, resulting in similar nestling growth rates in assisted and unassisted nests. This reduction in food amount may be compensatory and benefit breeders, because they can reduce the effort in seeking food for nestlings and save energy for other activities. We did not test this prediction because we could not assess food item size provided by each adult, given the high degree of nest concealment. We also have to consider that our sample sizes and statistical power for nestling growth rate and period analyses were too small to make definitive conclusions.

Contrary to our expectations, nests with helpers did not have higher daily survival rates during incubation or nestling periods. We anticipated an enhancement in the survival of nests with helpers, since, in addition to helping with chick feeding, helpers behave as sentinels together with male breeders while females are incubating (Alves 1990). Furthermore, even though predation is the main cause of nest failure, helpers cannot increase predator detection during incubation (Skutch 1949) because they do not incubate the eggs and do not feed females during incubation (Alves 1990; Duca 2007). Other studies have also found no effect of helpers on the probability of nest survival (Magrath and Yezerinac 1997; Legge 2000; Hatchwell et al. 2004; Blackmore and Heinsohn 2007, 2008), even when controlling for individual or territory effects (Eguchi et al. 2002). Such findings suggest that cooperative breeding does not necessarily increase the reproductive success of breeders and, alternatively, other benefits may explain the occurrence of this behavior.

We suggest that, if helpers contribute to offspring survival, it may be through other mechanisms, such as improving post-fledgling survival (Hatchwell et al. 2004). Nestlings of the White-banded Tanager, compared with other altricial neotropical species, have relatively short developmental periods at the nest and fast growth rates (Alves and Cavalcanti 1990). Thus, after leaving the nest, fledglings are totally dependent on parental care, a period that may be critical for their survival and that can be prolonged and/or maintained by helpers (e.g., Ridley and Raihani 2007). In addition, helpers′ auxiliary work during post-fledgling stage may directly benefit breeders by reducing their current parental investment and by increasing new chances of breeding attempts (Langen 2000). Helpers may also increase the ability to defend larger or higher quality territories, which may be especially important to post-fledging survival, as well as increasing clutch size, hatching rate or nest productivity (Emlen and Wrege 1991; Komdeur 1994; Eguchi et al. 2002; Russell et al. 2007). Although territory size is known to be related to the number of individuals in the groups of White-banded Tanagers (Duca 2007) and probably to food availability, we did not find significant effects on number of eggs laid or hatched and number of nestlings fledged in assisted nests.

Habitat saturation and life-history characteristics of White-banded Tanagers are together a plausible explanation for the occurrence of cooperative breeding in this species. Cooperatively breeding birds are most common in unpredictable environments, such as savanna-like habitats in tropical and subtropical areas (Russell 1989; Rubenstein and Lovette 2007). In these habitats, precipitation is highly seasonal and food availability can be limited in harsh periods. Constrained habitats may restrict appropriate breeding conditions to few individuals and reduce survival of non-residents, favoring delayed dispersal and cooperative breeding (Kokko and Lundberg 2001). Recent estimates of population size at the study site in ESECAE indicate that the White-banded Tanager population is near carrying capacity, with few vacant territories (Duca 2007). Since it is a resident territorial species with high adult survival rates (77%, Duca 2007), high density population and habitat saturation possibly occur in our study population. Other potential benefits of helpers accrue from the fact that in the White-banded Tanager all birds from a group defend territories against co-specifics and that territory size increases with group size (Duca 2007). Thus, helpers may have direct benefits increasing their own survival and territory acquisition by inheritance or by the vacancy of neighboring territories. Detailed data of territory turnover, habitat quality variation and survivor difference of residents and non-residents are required to clearly explain how cooperation evolved in the White-banded Tanager.

On the other hand, indirect benefits to helpers also appear to be important in our study species. Social groups in the White-banded Tanager are commonly composed by close-related individuals, with the progeny from the previous breeding season acting as helpers at nests of their parents (Alves 1990; Duca 2007; Gressler and Marini, unpublished data; present study). Helpers can increase their inclusive fitness component by increasing their relatives' survival or reproductive success (kin selection theory; Hamilton 1964). Even if reproductively constrained by environmental or social conditions, helpers may recognize related individuals and improve their nutrition during the nestling phase. Kin selection has been largely studied in birds and is one of the most accepted explanations for delaying dispersal and reproduction of some individuals in cooperative breeding species (West et al. 2007).

In conclusion, this is the first study in a neotropical savanna showing that helpers at the nest contribute with nestling feeding and with a reduction in parental effort of breeding males. Helping behavior, however, was not shown to favor several other characteristics related to the reproductive outcome of the breeding pair. Considering that parental care investment can constrain breeders' survival and future reproductive attempts (Heinsohn 2004), cooperative breeding in the White-banded Tanager may be an advantage for breeding males. Furthermore, in the studied population, habitat limitation due to saturation and positive effects on inclusive fitness may favor individuals that remain as helpers as a way to increase their own survival and/or reproduction (Kokko and Lundberg 2001) or their relatives' future reproductive outcome (Hamilton 1964). Therefore, we suggest that future studies with the White-banded Tanager take into account benefits to helpers from cooperative breeding behavior.

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