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How do helpers help? Helper contributions throughout the nesting cycle in the cooperatively breeding brown-headed nuthatch

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Abstract
Breeder investment in offspring reflects a trade-off between the benefits realized from current reproductive efforts and the benefits expected from future reproductive opportunities. When assisted by nonbreeding helpers that provide care for offspring, breeders may modify reproductive investments to minimize the costs of producing offspring, or in ways that maximize productivity and offspring survival. How helpers assist breeders can vary with different stages of reproduction, and how breeders alter investment in response to helpers may change depending on the stage of reproduction. We assessed how helpers contribute to reproduction and how breeders alter their investment in response to helper contributions in the cooperatively breeding brown-headed nuthatch (*Sitta pusilla*). We assessed helper contributions across three stages of reproduction: (1) nest excavation, (2) maternal egg production, and (3) nestling care and development at days 8–12 post-hatching, a period of rapid nestling growth. We also investigated how breeders responded to helper contributions and the relationship of helper behavior with breeders' reproductive success. Helpers contributed to offspring care but not nest excavation. Breeders assisted by helpers did not alter investments in nest excavation, offspring production, or offspring care. As a result, offspring raised by cooperative groups received more food and weighed more. Nests with helpers were more likely to fledge at least one offspring, even when considering variation in territory characteristics and breeder experience. Results indicate breeders likely benefit from the favorable breeding conditions helpers provided for current breeding efforts, which influenced the quality of offspring produced and their likelihood of fledging in this study.

Significance statement
Helpers may contribute to breeders' reproductive effort during many stages of reproduction. The presence of nonbreeding helpers should therefore influence the investments made by breeders during different stages of breeding. Investment decisions in one stage should furthermore influence later investment decisions. We demonstrated that helpers assisted breeders primarily during the offspring rearing stage in brown-headed nuthatches (*Sitta pusilla*), a facultative cooperative breeder. Breeders with helpers maintained their level of investments in offspring similar to the investments documented for breeders without helpers. As a result, chicks in nests with helpers received more food and were heavier, and adults with helpers were more likely to fledge at least one young. Our results suggest that the combined effects of parental and helper investment provided benefits for current broods with potentially important survival consequences for offspring.

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The care a parent invests in offspring frequently reflects a trade-off between the benefits gained from the current reproductive effort and the costs incurred in terms of survival and future reproduction (Williams 1966). Trade-offs in individual reproductive decisions are complicated in cooperatively breeding species where nonbreeding caregivers contribute to reproductive efforts. When nonbreeding helpers are present, both parents and helpers are expected to adjust their investment based on the contributions provided by others. The

predictability of investment by additional caregivers (Russell et al. 2007) and the type of investment they provide should influence the individual investment decisions of group participants.

Breeders should adjust their investments when assisted by helpers, but the specific adjustments made likely depend on how helpers assist across the breeding season. For example, Hatchwell (1999) predicted that sources of chick mortality among birds should influence how breeders respond to additional caregivers. When offspring perish due to predation more frequently than starvation, breeders with helpers should reduce their provisioning investment to avoid attracting predators to nests. In contrast, if food limitation is a major source of offspring mortality, breeders should maintain high levels of provisioning in the presence of helpers. These predictions have not been consistently observed. In some species where chicks experience high predation rates and helpers are present, parents maintain consistent effort (e.g., Mumme et al. 1990) or even increase their investments in offspring (Valencia et al. 2006), suggesting that investment in reproduction depends on factors other than chick mortality risk.

Departures from Hatchwell's (1999) predictions could be explained if helpers contribute by means other than provisioning and influence how breeders invest in reproduction during stages other than offspring care (Carranza et al. 2008). For example, increasing evidence suggests females may adjust their investment in offspring even before young hatch (e.g., Fox et al. 1997; Cunningham and Russell 2000; Russell et al. 2007; Canestrari et al. 2011). In addition to providing care to chicks or influencing how females invest in egg production, helpers can also contribute to reproduction through defense of territory and/or resources, guarding nests against predation (Cockburn 1998; Carranza et al. 2008), or assisting with nest construction and maintenance (e.g., Balshine-Earn et al. 1998). These contributions and their effects on investments have not been considered extensively in empirical work or theoretical models (except see Carranza et al. 2008). It is important to consider how the presence of helpers might affect investment decisions across all stages of reproduction, even before young are fed. Helper contributions made at the beginning of reproduction (i.e., nest construction) could affect later breeders' investment decisions because investments in one phase of reproduction likely affect later investment decisions for all participants (Carranza et al. 2008; Savage et al. 2012, 2015).

The brown-headed nuthatch (Sitta pusilla) is an excellent species in which to test hypotheses about helper contributions and parental investments in the presence of helpers across different stages of the breeding process. The brown-headed nuthatch is a facultative cooperative breeder, which allows cooperative and noncooperative groups to be compared directly in a single population. In our study population, only 20–30% of the breeding pairs are assisted by one or more

auxiliary helpers, which are typically young males. Cooperative breeding groups form months before reproduction begins (Cox and Slater 2007) and therefore provide reliable information on whether or not a pair will be assisted by helpers. This predictability could lead to changes in the investments breeders make to early stages of reproduction, like nest construction. Brown-headed nuthatches typically excavate a new nesting cavity each year (Cox and Slater 2007). Excavations can take weeks to complete and potentially have direct reproductive consequences because earlier nests are more successful (Lloyd and Slater 2007). If helpers expedite cavity excavation, the process could be a form of assistance affecting later investment decisions made by breeders (e.g., Carranza et al. 2008). Helper predictability could also influence the investments females make in egg production, which could in turn affect investments in offspring care and chick fledging success (Russell et al. 2007; Canestrari et al. 2011). Finally, nuthatches face a high risk of predation during nesting (ca. 60% of nests fail as a result of predation in this population, unpublished data), especially later in the nesting cycle when snakes in the genus Elaphe use adult provisioning activity as a cue to find nests (Mullin and Cooper 1998). These characteristics provide clear predictions based on the theory developed and enable us to assess how helper contributions might influence breeder investments across several different stages of reproduction.

We investigated how helpers contribute and how breeders altered their breeding investments in response to helper contributions across three stages of reproduction: (1) nest excavation, (2) maternal egg production (e.g., clutch size and egg volume), and (3) offspring provisioning and nest sanitation. We also investigated the relationship between helper contributions and breeder investment on fledging success. Based on the breeding biology of the brown-headed nuthatch, we expect helpers to assist in nest excavation because nest initiation dates affect nesting success. We also expect breeders to reduce their investment in offspring provisioning when assisted by helpers because predation risks are higher than starvation risks. Finally, if additional caregivers simply lighten the provisioning load borne by breeding adults, we expect to see comparable offspring survival and fledging success among breeders with and without helpers.

Methods

Study area

The study was conducted from 2013 to 2017 on Tall Timbers Research Station (TTRS; 30° 39′ 23″ N, 84° 12′ 32″ W) in north Florida where a color-marked brown-headed nuthatch population has been monitored since 2010. TTRS contains 854 ha of mature upland pine forests (Crawford and

Brueckheimer 2012) that are dominated by shortleaf (*Pinus echinata*) and loblolly (*Pinus taeda*) pines with dominant trees > 80 years old. Approximately 60% of the pine-forest area was burned annually to maintain the open habitat structure preferred by nuthatches and other species associated with the pinelands of the region (Engstrom 1992).

General field methods—nest monitoring and nuthatch marking

Annual nest searching began mid-February. Brown-headed nuthatches typically excavate nest cavities in dead boles (referred to as "snags") < 3 m from the ground. Less frequently, cavities are excavated in taller snags and the dead limbs of living trees 5–10 m high (Cox and Slater 2007; Lloyd et al. 2009). Potential nest sites were located by searching for excavations underway and adults carrying food or nest-lining material. Once confirmed by the presence of eggs or young, nest locations were entered into a geographic information system. The average distance separating nests monitored in this study was 201 m. To assess the importance of pine habitat, we calculated the area of upland pine habitat within 100 m of each nest (hereafter "pine cover"). The density of large pines (> 25 cm diameter) is associated with high-quality nuthatch territories (Slater 1997) and has been shown to improve nestling productivity (Lloyd and Slater 2007). Large pines also produce proportionally more seeds than younger pines; pine seeds are an important winter staple that may have carryover effects during the breeding seasons (Cox and Slater 2007).

Nests were visited every 3–4 days to determine status and record the individuals associated with the nesting attempt. Flashlights and dental mirrors were used to check nest contents. Most nests were discovered during nest construction, but when nests were discovered later in the nest cycle, date of nest initiation was estimated using the age and number of young present, an incubation length of 14 days, and an egg-laying rate of one egg per day (Norris 1958). Nests were tracked until they either fledged chicks or failed. To prevent losses due to fire, nests were protected by clearing the ground-level fuels within 2 m before prescribed burns were conducted.

Nestlings were extracted from cavities 8 to 12 days post-hatching by removing the face of the cavity (Ibarzabal and Tremblay 2006). Young were banded and placed back in the cavity after it was repaired using duct tape and wood putty. At the time of banding and 4 days after banding, we measured chicks' weight (g), tarsus length (mm), and wing chord (mm). Adults were captured using mist nets placed near nests or by luring individuals into nets using conspecific vocalizations broadcast through an MP3 player. Adults and nestlings were both marked with unique band combinations consisting of two plastic color bands on one leg and a single anodized federal band on the other. Sex for marked adults and nestlings was determined using DNA samples collected from feathers or blood at time of marking (Fridolfsson and Ellegren 1999; Haas et al. 2010; Han et al. 2015). Sex-specific vocalizations and behaviors (e.g., only females incubate) were used to assign sex to unmarked adults (Norris 1958; Han et al. 2015). Age categories (and acronyms) used to describe marked individuals were as follows: (1) hatch year (banded nestling), second year (SY; individual resighted in first year post-hatching), after second year (ASY; individual resighted ≥ 2 years post-hatching), and after-hatch year (AHY; adults marked at an unknown age).

The social status of adults (breeder vs. helper) was assigned using behavioral observations. Breeders were defined as individuals observed copulating, mate guarding, and incubating eggs. The age and previous breeding status of marked individuals were also used to classify breeders and helpers (Cox and Slater 2007). These field procedures have been corroborated using paternity assessments (Han et al. 2015). In contrast to breeding pairs, which consisted of the breeding male and breeding female, cooperative breeding groups assessed here contained at least one nonbreeding male helper.

Behavioral observations, maternal investment, and nesting success

Data on breeder and helper contributions and resulting reproductive success were gathered using observations of adult activities at 79 nests in 2013 and 2014. Behavioral monitoring of adult activities began during nest excavation and continued until the nest either failed or fledged. Observations made every 2–3 days quantified individual contributions to cavity excavation and offspring care. Observation times ranged from 0730 to 1430; the daily sequence in which territories were visited was determined using a random number generator (Microsoft Excel 2008).

Daily excavation dynamics were monitored at 12 snags that eventually became active nests (i.e., where at least one egg was laid). Hour-long observations were made from a distance of 15–20 m using a 20–60x spotting scope. Activities recorded included individuals tapping at snag surfaces and entering a cavity and removing wood. We recorded (1) the identity of marked individuals and activities they performed, (2) the frequency and duration of each activity, and (3) the other marked individuals present (either on the snag or in nearby trees). Each nest was observed (mean ± SE, hereafter) 3.2 ± 0.7 times during excavation.

Adult activities during offspring care were recorded at 24 nests for 2 h using high-definition video cameras (Canon VIXIA HFM500 or HF20) mounted 8 m from cavities on metal garden stakes. Videos were also used to identify the marked individuals tending nests. Provisioning events were scored when (1) an adult entered the nesting cavity with food and left the cavity without food or (2) an adult was observed feeding a nestling. Nest sanitation events were scored when an

adult left the cavity with a fecal sac. For nests where eggs and young were produced, each nest was monitored using a combination of direct observation and video recordings 4.1 ± 0.5 times during incubation and 4.9 ± 0.3 times when nestlings present. To assess the influence that human observers may have had, we used separate video and human observations to monitor excavation and offspring care at a subset of nests ($N = 8$). Rates of excavation and offspring care did not differ for these two types of observations ($\chi^2 = 0.002$, $df = 1$, $p = 0.9$).

We quantified maternal egg investment as (1) clutch size and (2) egg volume at 34 nests from 2013. To ensure the relationship we detected was robust, we augmented this sample size with an additional 64 nests from the years 2015 to 2016 and found the same results as in the single-year analyses. We therefore report the analyses of the expanded dataset here ($n = 98$ nests). Eggs were accessed and removed as described for the young (Ibarzabal and Tremblay 2006) after the clutch was completed. Length and width were measured to the nearest 0.1 mm, and egg volume was calculated using the standard equation for the volume of an ellipsoid (Hoyt 1979).

We quantified reproductive success for active nests ($n = 79$ nests from 2013 to 2014) using three metrics: (1) a binary measure of whether any nestlings survived 12 days post-hatching ("12-day survival" hereafter), (2) a binary measure of whether ≥ 1 chick fledged, and (3) the total fledglings produced. We did not assess an effect of helpers on renesting as failed breeders rarely attempt to renest. Fledging was confirmed using direct observation of chicks leaving the nest, video recordings of chicks fledging, fecal sacs observed on the face of the cavity, and observations of banded nestlings in trees.

Video recordings of offspring care were scored using SONY Movie Study V.11 (Sony Creative Software, Inc.). Marked individuals could be identified in 99.7% of the 897 behavioral events recorded. We excluded nests with more than one unbanded bird from the analyses or nests with redirected helpers (individuals from failed nests that assisted neighboring nests). We monitored offspring care throughout the nesting cycle but limited our analyses of offspring provisioning to a period when chicks were 8–12 days post-hatching. This period of nestling development features rapid growth and high rates of offspring provisioning (unpublished data). Variation in adult provisioning behavior should be most evident during this period of nestling development and provide a biologically relevant time frame for assessing helper contributions to offspring care. Finally, blind data could not be recorded because our study involved field observations of focal animals.

Statistical analyses

All statistical analyses were conducted in R v3.2.1 (R Core Team 2014). A nonparametric Kruskal-Wallis test was used to assess differences in excavation behavior because the measurements were not normally distributed (Shapiro-Wilk, $W = 0.82$, $p < 0.0001$). Other assessments of investment were conducted by fitting GLMMs using the glmmADMB (Fournier et al. 2012; Skaug et al. 2015) and lme4 packages (Bates et al. 2014; R Core Team 2014). We included all the biologically relevant factors expected to influence our response variables in a global model (Table 1 global models, Table 2 definition of fixed effects). Pair ID and nest ID were included as random effects when our data included information on multiple individuals at each nest over multiple years.

We generated a set of models with all combinations of the terms found in each global model using the *dredge* function in the R package *MuMIn* (Burnham and Anderson 2002). Top models were compared and selected using AIC$_c$ values with a $\Delta AIC_c > 2$ as the threshold for a substantial reduction in fit relative to our top models (Burnham et al. 2010; Grueber et al. 2011). When support for multiple models existed (i.e., $\Delta AIC_c < 2$), we used the natural average method to generate robust parameter estimates (Arnold 2010; Grueber et al. 2011; Symonds and Moussalli 2011) because the effects of specific parameters were of interest (Nakagawa and Freckleton 2010). We report final predictor variables after model averaging, and we used two criteria to evaluate the importance of each predictor: (1) relative importance value of each predictor calculated by summing the Akaike weights for each model in which the term appears (Arnold 2010; Symonds and Moussalli 2011) and (2) whether the 95% and 85% confidence intervals (CI) for each predictor included zero (Arnold 2010). Use of the 85% CI has been recommended (Arnold 2010), but we found no differences when both were compared and report only the 95% CI. The relative importance value of each term was calculated after model averaging by summing the Akaike weight of all models where $\Delta AIC_c < 2$.

We assessed variation in chick mass using GLMMs (Gaussian distribution, identity link function) in 21 nests sampled in 2017. We included the presence of helpers, brood size, date of first chick, cavity type, and chick age (defined in Table 2) as fixed effects. Nest ID and chick ID were included as random effects in the models, and the same model selection processes were used.

We assessed the effect of previous breeding experience on nesting success, using a subset of nests where the breeding experience of adults was known ($N = 74$ nests). We assessed variation in likelihood of fledging at least one offspring using a GLMM (a binomial distribution with logit link function) and the same fixed and random effects as described previously (Tables 1 and 2). We also included the fixed effect "previous breeder experience" as a binomial term. The same model selection processes were used.

We tested the effect of helper age on helper provisioning and sanitation efforts using a GLMM (Poisson distribution), with number of provisioning events by helpers as the response

Table 1 Global models assessing the effect of helpers on breeder investment in egg volume and clutch size, offspring care, and reproductive success

Question	Response variable	Distribution	Fixed effects in the global model	Random effects
(1) Do females alter egg investment when assisted by helpers?	Egg volume	Gaussian Identity link function	Presence of helpers, pine cover, laying date, clutch size	Pair ID
	Clutch size	Poisson Log link function	Year, laying date, pine cover, presence of helpers	Pair ID
(2) Do breeders alter offspring care when assisted by helpers?	Number of visits with food (per individual)	Poisson Log link function	Year, social status, number of helpers, pine cover, minutes observed, brood size, start time, social status * number of helpers	Nest ID
	Number of nest sanitation events (per individual)	Poisson Log link function	Year, social status, number of helpers, pine cover, minutes observed, brood size, start time, social status * number of helpers	Nest ID
	Number of visits with food (male helpers only)	Poisson Log link function	Year, number of helpers, pine cover, minutes observed, brood size, start time, age	Nest ID
	Total provisioning per nest	Poisson Log link function	Provisioning effort (breeding female), provisioning effort (breeding male), brood size, minutes observed, start time, number of helpers, pine cover, helper presence (YN), year	Pair ID
	Total nest sanitation effort per nest	Poisson Log link function	Nest sanitation effort (breeding female), nest sanitation effort (breeding male), brood size, minutes observed, start time, number of helpers, pine cover, helper presence (YN), year	Pair ID
(3) Does nesting success differ when helpers are present?	Survival to day 12 (YN)	Binomial Logit link function	Year, laying date, pine cover, presence of helpers	Pair ID
	Fledging success (YN)	Binomial Logit link function	Year, laying date, pine cover, presence of helpers	Pair ID
	Number of fledglings (for successful nests only)	Poisson Log link function	Year, laying date, pine cover, presence of helpers	Pair ID

Fixed effects are defined in Table 2

variable. We used only data on helper age because most breeders under assessment were ASY ($N = 25$ compared to SY breeders $N = 1$), precluding analysis of age effects on provisioning behavior. In addition to including age as a fixed effect, we used the same fixed and random effects as in the offspring care analysis (Table 1), with the exception of social status because only helpers were analyzed. We used the same model selection methods described previously.

Data availability Data are available from the corresponding author on reasonable request.

Results

Excavation

Helpers were not observed excavating cavities though they were frequently observed nearby when breeding males and females were excavating. Breeding females and breeding males excavated 47 ± 7.30 and $53 \pm 7.01\%$ of the total excavation time, respectively, and did not differ significantly in the average time spent excavating (Kruskal-Wallis, $\chi^2 = 0.12$, $df = 1$, $p = 0.73$, $N = 12$ nests). Excavation times for breeders in cooperative groups (15.8 ± 8.5 min h^{-1}) did not differ significantly from excavation times for pairs (19.9 ± 5.7 min h^{-1}; $\chi^2 = 0.28$, $df = 1$, $p = 0.60$, $N = 12$).

Female investment in egg production—clutch size and egg volume

Helpers did not influence female investment in egg production. Clutch size and the volume of eggs (Fig. 1) laid by females assisted by helpers were similar to the values observed for unassisted females. Helper presence was retained in only one of the top models assessing clutch size (Table 3a) and egg volume (Table 3b), but helper presence had the lowest relative importance in both cases and the 95% CI overlapped zero (Table 3). Laying date and pine cover also did not affect clutch size (Table 3a), but laying date was strongly related to egg volume such that eggs laid earlier had greater volume

Table 2 Definition of parameters included in models analyzing helper effects on reproduction across different stages of nesting

Fixed effect	Definition	Notes
Breeding female effort	Number of provisioning or nest sanitation events by the breeding female at the nest	Included to test if one sex contributed more to the overall provisioning or nest sanitation effort
Breeding male effort	Number of provisioning or nest sanitation events by the breeding male at the nest	Included to test if one sex contributed more to the overall provisioning or nest sanitation effort
Brood size	Number of chicks in brood	
Chick age	Age of chick at time of measurement	Only used for assessing chick mass
Clutch size	Number of eggs in the nest	
Date of first chick	Date the first chick of the clutch hatched	Recorded as days since January 1st; only used for chick weight analyses
Laying date	Date of first egg	Recorded as days since January 1st
Minutes observed	Total number of minutes observation occurred	Predicted to have no effect because there was little variation in recording duration (120–130 min of recording time per nest)
Number of helpers	Number of helpers associated with the nest	Analyzed as a continuous variable
Pine cover	Proportion of upland pine foraging habitat available within 3.14 ha of a nest	Range 0.05–1.00; mean = 0.80
Presence of helpers	Whether the nest was attended by any helpers	Analyzed as a binomial variable
Social status	Breeder or helper	
Start time	Time of day video recording began	
Year	Year data was collected	Year was included as a fixed effect because only 3 years of data were assessed (Zuur 2009).

All continuous predictor variables were standardized using the scale function in base R (sqrt(sum(x^2)/($n-1$))) (Becker et al. 1988). Standardizing the input variables in the global model is important for interpreting parameter estimates after model averaging (Grueber et al. 2011). See Table 1 for which parameters were included in each model. All terms were assessed for violations of collinearity, but no violations were detected. Correlations of fixed effects for terms used were $r < 0.3$

(Table 3b). Egg volume was also strongly influenced by clutch size (Table 3b), indicating that females with larger clutches laid smaller eggs. Collectively, our data show strong support
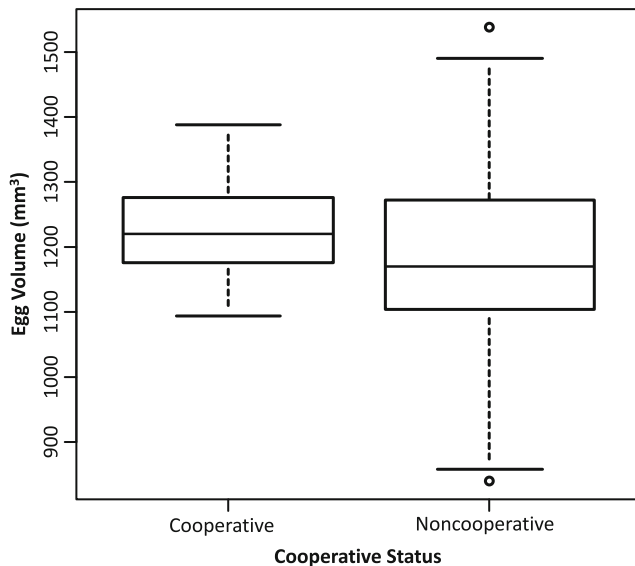

Fig. 1 Box and whisker plots (median, 1st/3rd quartiles, 1.5× IQR, and outliers) show egg volume was unrelated to whether females were assisted by helpers. The volume of eggs laid by breeding females assisted by helpers (mean ± SE = 1225.4 ± 10.7 mm^3, N = 42 eggs) did not differ significantly from the volume of eggs laid by females without helpers (mean ± SE = 1188.3 ± 10.9 mm^3, Table 3b)

for an effect of clutch size and laying date on egg volume, but no effect of helper presence on egg volume or clutch size.

To assess whether females assisted by helpers laid eggs earlier compared to unassisted females, we tested for an effect of helper presence on laying date but found no support (helper presence 0.077 ± 0.052, Z = 1.45; 95% CI −0.066, 0.14; relative importance = 1). The null model was retained as one of the top six models ($\Delta AIC_c < 2$) of this analysis suggesting that the presence of helpers and other factors were not strong predictors of laying date.

Offspring care—patterns of provisioning and nest sanitation behavior

Helpers did contribute to offspring care by provisioning offspring and removing fecal sacs (i.e., nest sanitation). The investment provided by breeders assisted by helpers was similar to the investment provided by unassisted breeders (Fig. 2). Collectively, breeders provisioned at a higher rate than helpers (breeders = 6.08 ± 0.82 visits h^{-1} vs. helpers = 4.55 ± 0.79 visits h^{-1}). We found strong support for the interaction between social status and the number of helpers on provisioning behavior. The interaction ranked high in importance and the 95% CI did not overlap zero (Table 4a). Mean provisioning rate per helper decreased when more helpers were present

Table 3 Presence of helpers was not strongly associated with female investment in egg production

Response variable	Coefficient	Estimate	Std. error	Z value	95% CI	Relative importance	No. of top models containing variable	No. of top models used for model averaging
(a) Clutch size	Laying date	−0.048	0.058	0.83	−0.16, 0.066	0.58	3	5
	Year	0.061	0.100	0.61	−0.14, 0.26	0.42	2	
	Presence of helpers	−0.0068	0.041	0.16	−0.089, 0.075	0.10	1	
(b) Egg volume	**Clutch size**	**−28.49**	**8.45**	**3.36**	**−45.10, −11.89**	**1.00**	**4**	**4**
	Laying date	**−14.86**	**11.08**	**1.34**	**36.60, 6.88**	**0.83**	**3**	
	Pine cover	11.11	10.54	1.05	−9.57, 31.80	0.73	3	
	Presence of helpers	1.60	8.96	0.86	−19.19, 15.98	0.16	1	

Data presented were the results after model averaging. A GLMM with a Poisson distribution was used to assess (a) clutch size and three models were found to have comparable support ($\Delta AIC_c < 2$). A GLMM with a Gaussian distribution was used to assess (b) egg volume ($N = 514$ eggs from 98 nests) and five models were found to have comparable support ($\Delta AIC_c < 2$). Terms in bold indicate important and informative parameters because 95% confidence intervals (reported here) and 85% confidence intervals did not overlap zero, and these terms had a high relative importance rank

(Fig. 3). This relationship was robust even when a rare three-helper nest was removed from the assessment because it might have undue influence in the model. The presence of helpers was unrelated to the provisioning behavior of breeding males and females (Table 4a, Fig. 2a). Brood size and year had little influence on provisioning behavior (Table 4a). For helpers, age was not strongly related to provisioning behavior (age 0.38 ± 0.40, $Z = 0.93$; 95% CI −0.42, 1.18; relative

Fig. 2 Breeding females and breeding males in cooperative groups did not differ significantly in either their provisioning rate (**a**) or nest sanitation rate (**b**) when compared to breeders unassisted by helpers. Breeding males did provision significantly more often than breeding females and helpers, regardless of whether the group was assisted by helpers. Bars indicate mean provisioning rate ± SE. Twenty-four nests attended by 69 individuals were used in these analyses, and sample size of individuals of each status type is shown in each bar

importance = 0.53, $N = 19$ helpers at 11 nests). We found no strong trends explaining variation in nest sanitation effort (Table 4b). Ten models, including the null model, had comparable support ($\Delta AIC_c < 2$). The 95% CIs for these uninformative predictors also all overlapped zero (Table 4b).

The total number of provisioning events was higher at nests with helpers compared to nests without helpers (Fig. 4). Helper presence had a strong influence on total provisioning effort (Table 5a). The provisioning behaviors of the breeding male and breeding female were also strongly related to the total provisioning effort at the nest (Table 5a). In contrast to provisioning results, nests attended by helpers did not differ in the total number of nest sanitation events compared to nests without helpers (Fig. 4, Table 5b). We found strong support for a positive effect of female nest sanitation behavior on total nest sanitation effort (Table 5b).

The mass of chicks raised by cooperative groups at days 9–10 post-hatching (9.6 ± 0.11 g) was greater than the mass of chicks raised by breeding pairs (8.9 ± 0.12 g). Two models assessing chick mass had comparable support ($\Delta AIC_c < 2$). Variation in chick mass was strongly positively associated with helper presence (pair only compared to cooperative −1.24 ± 0.30, $Z = 4.13$; 95% CI −1.83, −0.65; relative importance = 1.00, $N = 95$ chicks from 21 nests). Variation in chick mass was also strongly associated with brood size (brood size −0.86 ± 0.27, $Z = 3.14$; 95% CI −1.40, −0.32; relative importance = 1.00, $N = 95$ chicks from 21 nests) and chick age (chick age 1.18 ± 0.13, $Z = 9.08$; 95% CI 0.93, 1.44; relative importance = 1.00, $N = 95$ chicks from 21 nests). These latter results suggest that, as expected, chicks in larger broods weighed less and chicks weighed more as they aged. We detected no interaction between the presence of helpers and chick age (presence of helpers * age 0.30 ± 0.26, $Z = 1.46$; 95% CI −0.30, 0.47; relative importance = 0.29, $N = 95$ chicks from 21 nests) suggesting that the effect of helpers does not differ at different chick ages.
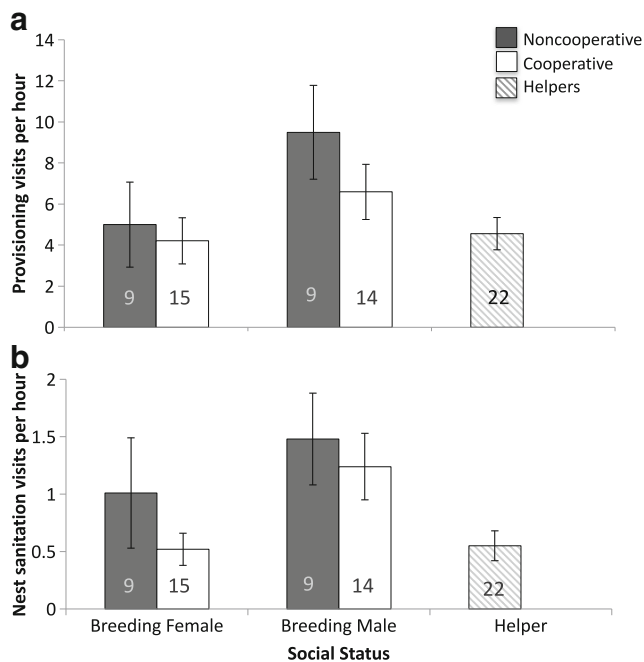
Table 4   Breeders and helpers' provisioning rate was affected differently when helpers were present, but nest sanitation effort was unaffected

Response variable	Model terms	Estimate	Std. error	Z value	95% CI	Relative importance	No. of top models containing variable	No. of top models used for model averaging
(a) Provisioning per individual	**Social status**	**1.01**	**0.26**	**3.86**	**0.50, 1.52**	**1.00**	**3**	**3**
	Number of helpers	0.11	0.20	0.52	− 0.29, 0.50	1.00	3	
	Social status * number of helpers	**− 0.69**	**0.15**	**4.53**	**− 1.0, − 0.39**	**1.00**	**3**	
	Brood size	− 0.074	0.15	0.48	− 0.37, 0.22	0.32	1	
	Year	0.07	0.31	0.31	− 0.38, 0.53	0.21	1	
(b) Nest sanitation per individual	Start time	− 0.29	1.15	1.86	− 0.60, 0.015	0.93	9	10
	Social status	−0.23	0.45	0.52	− 1.12, 0.65	0.82	8	
	Number of helpers	−0.13	0.16	0.81	− 0.46, 0.19	0.59	6	
	Pine cover	−0.10	0.14	0.73	− 0.38, 0.17	0.47	4	
	Social status * number of helpers	−0.079	0.23	0.35	− 0.53, 0.37	0.17	2	
	Brood size	−0.0072	0.046	0.16	− 0.10, 0.084	0.07	1	

Data presented were the results after model averaging. A GLMM with a Poisson distribution was used to assess the number of provisioning and nest sanitation events per individual ($N = 69$ individuals at 24 nests recorded for 2901 h). Three top models with comparable support ($\Delta AIC_c < 2$) were found for provisioning behavior. Ten top models, including the null model, had comparable support ($\Delta AIC_c < 2$) nest sanitation behavior. Terms in bold indicate important and informative parameters because 95% confidence intervals (reported here) and 85% confidence intervals did not overlap zero, and these terms had a high relative importance rank

Consequences of helpers for reproductive success

Breeders at 79 monitored territories (33% attended by cooperative groups and 67% attended by only a breeding pair) produced at least one egg and were considered in the following analyses of reproductive success. Earlier laying date, but not the presence of helpers, was strongly associated with chick survival to day 12 (Table 6a). All other retained parameters were not strongly associated with early chick survival

(Table 6a). We found that 33 nests successfully fledged at least one offspring (42%), while 46 nests (58%) failed.

The presence of helpers was strongly associated with increased likelihood of at least one offspring fledging (Table 6b). Sixty-two percent of the 26 nests attended by cooperative groups fledged at least one offspring, whereas only 32% of the 53 pair-only nests fledged at least one offspring. Nests that were initiated earlier in the breeding season were also more likely to be successful compared to nests initiated

Fig. 3 Individual helpers provisioned at a lower rate when more helpers were present (see Table 4). In contrast, helper number was unrelated to breeder provisioning behavior. This interaction remained significant even when the single nest with three helpers was removed from analyses. Squares denote breeder provisioning rate and diamonds denote helper provisioning rate, with error bars denoting SE. Sample sizes in parentheses indicate number of nests filmed for provisioning analyses for each group size ($N = 24$ nests)
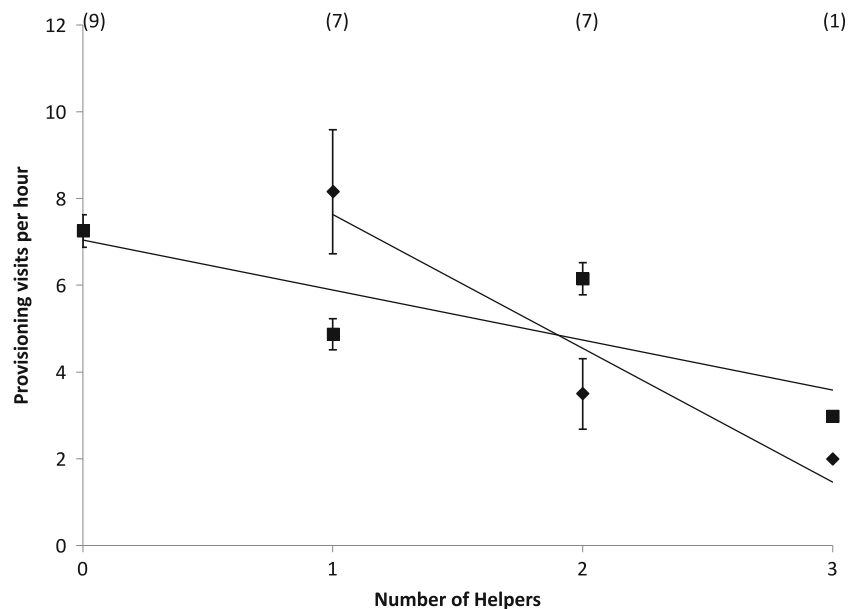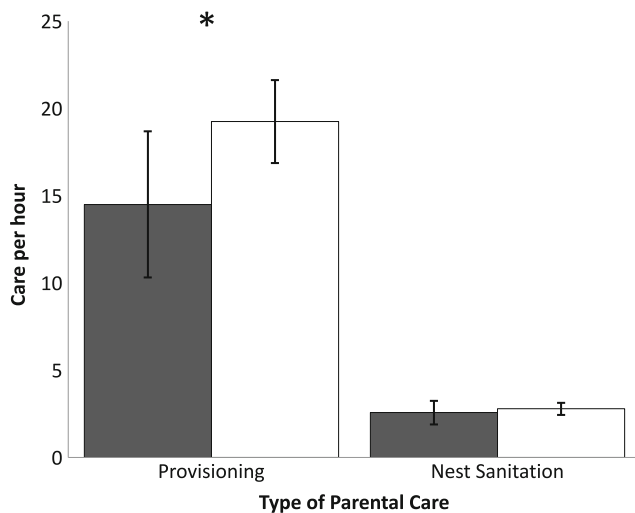
Fig. 4 Nests attended by helpers (white bars, $N = 15$) had a significantly higher total provisioning rate (mean visits per hour $\pm$ SE) compared to nests attended only by the breeding pair (black bars, $N = 9$) ($N = 24$ nests, Table 5a). There was no significant difference in the total nest sanitation rate at nests attended by helpers and nests only attended by the breeding pair ($N = 24$ nests, Table 5b). Significant differences are indicated by an asterisk

helper presence on the likelihood of fledging at least one chick. Of the 66 nests attended by at least one experienced breeder, 45% fledged at least one offspring. Meanwhile, of the eight nests attended by two novice breeders, 75% fledged at least one offspring. Previous breeder experience was not strongly associated with fledging success (previous experience -0.20 ± 0.59, $Z = 0.33$; 95% CI -1.38, 0.98; relative importance $= 0.25$, $N = 74$ nests). We also compared nests where both breeders had previous experience ($N = 28$ nests) to those where both breeders were novices and again found no support for an effect of breeder experience on likelihood of fledging offspring (previous experience -0.32 ± 0.73, $Z = 0.42$; 95% CI -1.77, 1.14; relative importance $= 0.32$, $N = 36$ total nests). Laying date remained strongly associated with likelihood of fledging as this term was retained in all three top models and had a relative importance of 1.00 (laying date -1.07 ± 0.40, $Z = 2.66$; 95% CI -1.86, -0.28; $N = 74$ nests).

Discussion

Helpers are hypothesized to provide significant benefits for breeders during reproduction. However, few studies identify the range of potential helper contributions and their impact on breeder investment. We assessed how helpers contribute across three major stages of reproduction, how breeders respond to these contributions, and the effect of these investment decisions on nesting success. We found that helpers in the brown-headed nuthatch had a positive effect primarily via their contribution during offspring rearing in the years of our study. Contrary to our predictions, helpers did not participate in excavation and breeders in cooperative groups did not differ in their excavation behavior. Breeders assisted by helpers also

later in the season (Table 6b). Though year was retained in one of the top models, it had no substantive relationship with likelihood of fledging (Table 6b). Some breeders were assisted by more than one helper, but we found that group size was not strongly related to fledging success (helper number 2.19 ± 1.85, $Z = 1.12$; 95% CI -2.31, 3.92; $N = 26$ nests). When we investigated the number of fledged chicks, rather than the likelihood that any chick in the nest fledged, we found no effect of the presence of helpers.

We found no substantial support for effects of breeder experience or an interaction between breeder experience and

Table 5 Nests attended by helpers received more food deliveries but did not differ in total nest sanitation compared to nests not attended by helpers

Response variable	Coefficient	Estimate	Std. error	Z value	95% CI	Relative importance	No. of top models containing variable	No. of top models used for model averaging
(a) Provisioning per nest	**Presence of helpers**	**0.56**	**0.086**	**5.86**	**0.37, 0.74**	**1.00**	**2**	2
	Breeding female provisioning effort	**0.18**	**0.045**	**3.57**	**0.080, 0.28**	**1.00**	**2**	
	Breeding male provisioning effort	**0.38**	**0.045**	**7.59**	**0.28, 0.48**	**1.00**	**2**	
	Start time	-0.033	0.044	0.72	$-0.12, 0.057$	0.45	1	
(b) Nest sanitation per nest	**Breeding female nest sanitation effort**	**0.28**	**0.094**	**2.72**	**0.077, 0.48**	**1.00**	**2**	2
	Start time	-0.21	0.19	1.11	$-0.58, 0.16$	0.63	1	
	Breeding male nest sanitation effort	0.093	0.13	0.68	$-0.17, 0.36$	0.37	1	

Data presented were the results after model averaging. Analyses consisted of total counts of provisioning and nest sanitation visits per nest performed by all attending adults (i.e., helpers and breeders). A GLMM with a Poisson distribution was used to assess the factors influencing the number of provisioning and nest sanitation events per nest ($N = 24$ nests). Two top models with comparable support ($\Delta AIC_c < 2$) were found for provisioning and for nest sanitation behavior, respectively. Terms in bold indicate important and informative parameters because 95% confidence intervals (reported here) and 85% confidence intervals did not overlap zero, and these terms had a high relative importance rank

Table 6 Nests attended by helpers were more likely to fledge, but cooperative status was unrelated to differences in chick survival to day 12

Response variable	Coefficient	Estimate	Std. error	Z value	95% CI	Relative importance	No. of top models containing variable	No. of top models used for model averaging
(a) Survival to day 12	**Laying date**	**− 0.84**	**0.28**	**2.99**	**− 1.39, − 0.83**	**1.00**	**4**	4
	Pine cover	0.051	0.15	0.33	− 0.27, 0.74	0.21	1	
	Presence of helpers	0.10	0.31	0.32	− 0.59, 1.56	0.21	1	
	Year	0.054	0.24	0.23	− 0.67, 1.31	0.17	1	
(b) Fledging success	**Presence of helpers**	**1.14**	**0.54**	**2.06**	**0.055, 2.22**	**1**	**2**	2
	Laying date	**− 0.71**	**0.28**	**2.46**	**− 1.27, − 0.14**	**1**	**2**	
	Year	0.64	0.64	0.99	− 0.62, 1.90	0.65	1	

A GLMM with a binomial distribution was used for the following global models: (a) survival to day 12 (binary assessment of whether nestlings hatched and survived to day 12) and (b) fledging success (a binary assessment of whether a nest fledged any offspring). Results presented are the outcome of model averaging top retained models ($\Delta AIC_c < 2$). Terms in bold indicate important and informative parameters because 95% confidence intervals (reported here) and 85% confidence intervals did not overlap zero, and these terms had a high relative importance rank

did not differ in timing of reproduction and did not reduce their investment in offspring production or care. As a result of the differential care provided to nestlings, offspring raised by cooperative groups were provisioned more frequently and had higher mass. The consequences of these helper contributions were that nests tended by cooperative groups were more likely to have at least one chick fledge compared to nests tended by breeding pairs.

Female breeders assisted by helpers did not differ in their pre-hatching investment (egg volume and clutch size) compared to unassisted females. A reduction in clutch size is predicted for cooperatively breeding species when offspring production costs are higher than rearing costs (Savage et al. 2012) or when reduced pre-hatching investment can be compensated for with increased post-hatching investment (Russell et al. 2007; Savage et al. 2015). Breeding females can also increase their investment when assisted by helpers, a pattern found in some other cooperative breeding species (i.e., Valencia et al. 2017). Brown-headed nuthatches produce a small number of offspring (average 4–5 eggs; range 3–7 eggs), similar to other primary cavity nesters (Martin 1993). Females may be more limited in their ability to produce additional offspring because of energetic costs (Savage et al. 2012). When brood size is limited, females are predicted to modify their investment in the quality of each offspring (Savage et al. 2012, 2015), as has been reported in many cooperatively breeding species (e.g., birds: Canestrari et al. 2011; Santos and Macedo 2011; Paquet et al. 2013; fish: Taborsky et al. 2007). Although we cannot rule out the possibility that eggs varied in characteristics such as steroid hormones (Paquet et al. 2013) or nutritional content (Russell et al. 2007) when helpers were present, we did not observe a difference in egg volume, an indicator of pre-hatching investment (Russell et al. 2007; Valencia et al. 2017).

Though helpers contributed to offspring care, breeders did not reduce their provisioning effort when assisted by helpers. Chicks raised in cooperative groups received more food and were heavier (~ 7%) compared to chicks raised by a breeding pair. The proportional gain in weight that we observed was comparable or even larger than that reported in other species where chicks raised by helpers were heavier (Marvelde et al. 2009; Dias et al. 2015; Mumme et al. 2015). When future breeding conditions are unpredictable, breeders are expected to maintain (Savage et al. 2015) or even increase their investments when helpers are present (Valencia et al. 2006; Carranza et al. 2008; Russell and Lummaa 2009; Savage et al. 2015). In our study population, breeding conditions can be unpredictable, and in some years, adults do not attempt to breed (Slater 1997). The unpredictable conditions lead to variation in nesting success across years (20–60% nest success annually, unpublished data). Heavier offspring are arguably of better quality as greater chick mass has been associated with greater fledging success (Magrath 1991; Hatchwell et al. 2004) and higher post-fledging survival (e.g., Mumme et al. 2015) in other passerine birds. We observed that chicks raised in cooperative groups were heavier and more likely to fledge.

Though we expected breeders to reduce their provisioning effort when assisted by helpers, our data failed to support this hypothesis. The brown-headed nuthatch thereby joins many species that deviate from the patterns predicted by Hatchwell (1999) (e.g., Innes and Johnston 1996; Langen and Vehrencamp 1999; Legge 2000; Hatchwell et al. 2004; Valencia et al. 2006, 2017). Consistent breeder effort regardless of presence of helpers may be because the additional care provided by helpers results in heavier, more robust offspring that are more likely to fledge. Alternatively, maintenance of breeder investment is predicted if helper investment increases the likelihood of reproductive success beyond that which parents could achieve alone (Carranza et al. 2008). This could occur, for example, if helpers participate in nest defense. Indeed, helpers in our study population have been recorded defending nests against nest predators and against heterospecific nest competitors (e.g., eastern bluebirds, *Sialis*

sialis) (JAC et al., unpublished data). In other brown-headed nuthatch populations, cooperative groups have been documented defending their nests against heterospecific competition (E. Niemasik, pers. comm.) and Thompson (2000) found that nest guarding occurred more frequently at nests with helpers than nests with pairs. Though they did not participate in excavation itself, helpers could be serving as sentinels or defending against conspecifics during early stages of the nesting cycle (e.g., reviewed in Bednekoff 1997; Yasukawa and Cockburn 2009). Additional work should consider the benefits of larger groups on the ability to defend against nest and territory threats.

Although we did not observe a reduction in breeder investment in larger groups, we did observe a decrease in helper investment when more helpers were present. It is not uncommon to observe individuals of different social status alter their investment when additional caregivers are present (Cockburn 1998) and helper load-lightening is likely to occur when costs of providing care for helpers are greater than costs endured by breeders (Savage et al. 2012). Additionally, helpers in the study population often become breeders (Cox and Slater 2007), suggesting that changing investment strategies when additional helpers are present might reduce current costs and have implications for future breeding efforts (Clutton-Brock et al. 2006).

Our finding that breeders assisted by helpers were more likely to fledge at least one offspring was not confounded by territory quality, similar to findings in other cooperatively breeding species (Dias et al. 2015), though others have reported such effects (Saino et al. 2012; Germain and Arcese 2014). More specifically, our findings are in line with other assessments in brown-headed nuthatches where measures of territory quality (e.g., height of nest tree, midstory density) were not related to likelihood of fledging (Dornak et al. 2004; Lloyd et al. 2009). Our study area likely contained high (or at least consistent) habitat quality, as it supported 10–12 red-cockaded woodpecker (*Picoides borealis*) territories during this study (Cox and McCormic 2016). This endangered species serves as an indicator of high-quality habitat for the brown-headed nuthatch (Hannah et al. 2017). We tested one plausible measure of territory quality (Slater 1997; Lloyd and Slater 2007), and future work might consider alternative measures, such as the height of available snags or overall snag densities within a territory (Thompson 2000), or measures of predation risks (Martin et al. 2000) and interspecific competition (Jones et al. 2014).

Several lines of evidence further suggest that the presence of helpers, and not differences in breeder quality, improved fledging success in the brown-headed nuthatch in the years assessed. Similar to findings in other cooperatively breeding species (e.g., Dias et al. 2015), we found neither previous breeding experience nor the interaction of breeding experience

and helper presence to be strongly associated with likelihood to fledge offspring. We also did not find a strong relationship between helper age and helper provisioning behavior, although our ability to detect a relationship may have been limited by the small sample size. We also did not detect a relationship between breeder experience and the presence of helpers, and many failed breeders nevertheless had SY helpers (JAC et al., unpublished data). The relationship between breeder experience, age, and reproductive success can be complicated (Nol and James 1987; Schiegg et al. 2002). In some species, breeder experience is unrelated to the number of hatched or fledged offspring (Baran and Adkins-Regan 2014), while in others, inexperienced breeders benefit more from helpers (Magrath 2001; Paquet et al. 2015; Valencia et al. 2017). We find that in the brown-headed nuthatch, the presence of helpers, rather than indirect effects of breeder experience or quality, is most clearly related to nesting success.

We observed that, regardless of cooperative status, breeders initiating reproduction earlier were more successful, both in whether chicks survived to day 12 and the likelihood of fledging any offspring. Higher reproductive success for early breeders has been observed in many species (e.g., Herenyi et al. 2014) for reasons that include higher predation risk associated with later breeding (Gotmark 2002). In our study population, later lay date was associated with increases in predator activity (e.g., snakes and ants), but the prescribed burns applied at TTRS from March to April may reduce habitat cover available for these predators and reduce predation risk for some later breeders. Food resources may also change across the breeding season (e.g., Perrins 1970; Siikamäki 1998), and chicks that hatch later may be fed different or lower quality food and therefore be less likely to fledge. The relationship between lay date and likelihood of fledging was robust across many different analyses and supports previous work on this species (Cox and Slater 2007). How predation risk and resources change over the course of the breeding season should be explored in greater detail.

This study investigated how helpers contribute across multiple stages of reproduction and the consequences of this help for fledging success. Helpers did not contribute to nest excavation, and breeders did not alter investment in excavation, egg production, or offspring care. As a result, chicks raised by groups with helpers received more food and weighed more than chicks raised by the breeding pair. Chicks raised in cooperative groups were more likely to fledge in the years of our study, demonstrating a reproductive benefit to having helpers. We considered possible confounding effects of breeder experience and of territory quality as estimated by pine cover and found that only helper presence was related to nest success. Future work should continue to consider additional ways that helpers assist in reproduction, specifically offspring and nest defense.

Compliance with ethical standards

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

Ethical statement All applicable national and institutional guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards approved by the Florida State University Animal Care and Use Committee (protocol 1505) and by the Tall Timbers Institutional Animal Care and Use Committee (protocol 1042). There has been no evidence of any effects of marking, handling, nest monitoring, or methodology on the behavior and survival of individuals in the study population.

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