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Research Paper

Evidence of a load-lightening helper effect in Florida Scrub-Jays: implications for translocation

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ABSTRACT. The Florida Scrub-Jay (*Aphelocoma coerulescens*) is an imperiled cooperatively breeding species endemic to Florida scrub habitats. Translocation of non-reproductive helpers has been proposed as a conservation tool to increase population size and connectivity. However, the potential consequences of helper removal on the source population remain unclear because the benefits provided by helpers are complex and not consistently observed. We used nest monitoring and nest camera data to examine the effects of helpers on provisioning rates, nestling mass, nest survival, and productivity for 111 family groups at Ocala National Forest, which supports the largest remaining population of Florida Scrub-Jays. In groups with helpers, male breeders and helpers provisioned nestlings at higher rates than did female breeders. In contrast, provisioning rate of female breeders was reduced by half in groups with helpers compared to groups without helpers, revealing a load-lightening helper effect in this population. The compensatory benefit of helpers on maternal provisioning rates in this study may have easily been overlooked without the use of nest cameras. Helpers provisioned less and nestling mass was lower in 2019 than 2018. Helpers did not influence nestling mass, nest survival, or nest productivity, suggesting that the effect of helpers on these metrics is either minimal or masked by other environmental factors. Future study is needed to understand how indirect helper benefits may affect female breeder survival and future productivity. In the meantime, the load-lightening effect of helpers on maternal provisioning and its potential effect on the donor population should be acknowledged when evaluating the net benefits of future translocation projects proposing the removal of helpers.

Indications d’un effet des auxiliaires dans l’allègement de la charge chez le Geai à gorge blanche: répercussions pour le déplacement d’auxiliaires

RÉSUMÉ. Le Geai à gorge blanche (*Aphelocoma coerulescens*), espèce en péril qui niche en coopération, est endémique aux milieux broussailleux de Floride. Le déplacement d’auxiliaires non-nicheurs a été proposé comme outil de conservation destiné à augmenter la taille et la connectivité des populations. Cependant, les conséquences potentielles du retrait d’auxiliaires sur la population d’origine ne sont pas claires, car les avantages fournis par les auxiliaires sont complexes et ne sont pas observés de manière régulière. Nous avons utilisé des données de suivi des nids et de caméras aux nids pour examiner les effets des auxiliaires sur le taux de ravitaillement, le poids des oisillons, la survie au nid et la productivité de 111 groupes familiaux dans la forêt nationale d’Ocala, qui abrite la plus grande population restante du Geai à gorge blanche. Dans les groupes comportant des auxiliaires, les mâles nicheurs et les auxiliaires ont approvisionné les oisillons à des taux plus élevés que celui des femelles nicheuses. En revanche, le taux de ravitaillement des femelles nicheuses était réduit de moitié dans les groupes avec auxiliaires par rapport aux groupes sans auxiliaires, révélant un effet d’allègement de la charge par les auxiliaires dans cette population. Dans la présente étude, l’avantage compensatoire des auxiliaires sur le taux d’approvisionnement maternel aurait pu être facilement ignoré sans l’utilisation de caméras aux nids. Les auxiliaires ont fourni moins de nourriture et le poids des oisillons était plus faible en 2019 par rapport en 2018. Les auxiliaires n’ont pas eu d’effet sur le poids des oisillons, la survie au nid ou la productivité des nids, ce qui indique que l’effet des auxiliaires sur ces paramètres est soit minime, soit masqué par d’autres facteurs environnementaux. D’autres études devront être entreprises pour nous permettre de comprendre comment les bénéfices indirects des auxiliaires peuvent toucher la survie des femelles nicheuses et leur future productivité. Entre-temps, l’effet d’allègement de la charge par les auxiliaires sur le ravitaillement maternel et son effet potentiel sur la population donneuse doivent être pris en compte au moment de l’évaluation des bénéfices nets des futurs projets de déplacement proposant le retrait d’auxiliaires.

Key Words: *cooperative breeding; helper effects; load-lightening; nest cameras; nestling mass; provisioning rates; translocation*

INTRODUCTION

Cooperative breeding is a social system where group members assist the breeding pair in the rearing of young (Stacy and Koenig 1990). Assisting individuals may be nonbreeding “helpers” (related or unrelated) or co-breeders. In birds, helping typically involves provisioning food to young, but in some species may also include territorial defense, vigilance against predators, nest building, and incubation (Stacy and Koenig 1990). In response to provisioning by helpers, breeders can maintain or reduce their level of investment. Maintaining their provisioning rate increases the total provisioning rate, resulting in an additive benefit of helping and potentially increased nestling mass and survival (Mumme 1992, Russell et al. 2007, Koenig et al. 2019). Alternatively, provisioning helpers may present a compensatory benefit to breeders, whereby they decrease their individual level of investment (i.e., “load-lightening” sensu Brown 1978),

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resulting in little or no increase in total provisioning rate. Load-lightening allows breeders to decrease investment in the current brood in favor of their future survival and reproduction (Hatchwell 1999, Cockburn et al. 2008, Russell et al. 2008). Understanding all the ways helpers may benefit a breeding pair can be difficult, and in many cases, helper benefits may be concealed or difficult to isolate because of confounding factors such as territory quality and breeder experience (Mumme 1992, Mumme et al. 2015, Downing et al. 2020), stage in the nesting cycle (Rensel et al. 2010), or annual and spatial variability in ecological conditions (Jetz and Rubenstein 2011, Koenig et al. 2011).

The Florida Scrub-Jay (*Aphelocoma coerulescens*) is a cooperatively breeding species endemic to Florida scrub, an early successional shrubland plant community in peninsular Florida (Myers 1990, Florida Natural Areas Inventory 2010), historically maintained by periodic fire (FWC 2019) and more recently by fire and mechanical disturbance (Menges and Gordon 2010, Weekley et al. 2013). Suitable habitat is often saturated by breeding pairs, limiting the availability of new territories for nonbreeding individuals. Monogamous breeding pairs maintain year-round territories and breeding vacancies typically become available only after the death of a breeder. Our understanding of the role of helpers in this species comes primarily from a single, well-studied population on the Lake Wales Ridge in southern Florida. At this site, the most common source of helpers are first-year offspring that have delayed dispersal; ca. two-thirds of helpers assist at the nests of their full parents, and 90% assist at least one parent, leading to high mean levels of relatedness between helpers and the young they tend (Woolfenden and Fitzpatrick 1984). Florida Scrub-Jay helpers may assist groups by reducing predation through sentinel duty, territorial defense, and by provisioning nestlings and dependent fledglings, which in turn increases reproductive success for the breeding pair (Woolfenden 1975, Mumme 1992, Mumme et al. 2015, Fitzpatrick and Bowman 2016, Breininger et al. 2023). Nest construction, egg-laying, and incubation are performed exclusively by the breeding female (Woolfenden and Fitzpatrick 1984, 1996), and breeders usually prevent helpers from tending nestlings until nestlings are about one week old (Rensel et al. 2010). However, less is known about the role of helpers at other sites where habitat structure and composition differ considerably from the Lake Wales Ridge. The number of helpers per family group varies by site. Most pairs are assisted in the breeding season by at least one helper in southern Florida (annual mean = 0.6–1.5 helpers per pair; Woolfenden and Fitzpatrick 1984) and the Atlantic coast populations (annual mean = 0.4–1.6 helpers per pair; Breininger et al. 2022), but fewer pairs have helpers in north-central Florida (e.g., annual mean = 0.3–0.7 helpers per pair in Ocala National Forest; Cox 1984, Miller et al. 2023).

The Florida Scrub-Jay was placed on the Endangered Species List as Threatened in 1987 (USFWS 1987). Habitat loss, habitat fragmentation, and management challenges associated with early successional habitat have resulted in widespread population declines (U.S. Fish and Wildlife Service [USFWS] 2007, 2019). The Florida Scrub-Jay Recovery Plan (USFWS 2019) has proposed conservation translocation (i.e., human-assisted movement of wild animals from one location to another location; IUCN/SSC 2013; hereafter "translocation") as a strategy to maintain landscape connectivity among the most viable populations, to assist those populations in growing and recolonizing suitable habitat, and to preserve genetic diversity. Cooperative breeding can add another level of complexity when considering translocation as a conservation tool. Translocation of other cooperatively breeding birds has involved breeders or entire family groups (Clarke et al. 2002, Bennett et al. 2013) or only nonbreeding helpers (Carrie et al. 1999), with mixed results. A previous study about Florida Scrub-Jay translocation recommended that older nonbreeding helpers may be the best candidates, given their persistence rates at recipient sites and the minimal impact their removal had on reproduction (fledged young) and breeder survival (3 months after helper removal) at the donor site (Mumme and Below 1999). However, removal of helpers may have different effects on different populations, especially if helper benefits are masked by study design, environmental variability, or other confounding issues (Downing et al. 2020).

Here, we assessed the role of helpers in the Florida Scrub-Jay population in Ocala National Forest (hereafter Ocala NF) in north Florida. We used a two-year nest monitoring dataset to explore the effect of helpers on nestling provisioning rates, nestling mass, nest survival, and nest productivity to better understand the potential consequences of removing helpers from this population for translocation. During 2018-2019, Florida Fish and Wildlife Conservation Commission (FWC) staff removed 22 helpers from 10 family groups as part of a pilot translocation research project (K. Miller, unpublished data), which provided three treatments for our study: helpers, no helpers, or helpers experimentally removed. However, the sample size of groups with helpers removed was small, and these groups were often pooled with groups containing no helpers in our analyses. We addressed the following five questions related to the benefits of helpers at Ocala NF: 1) do nestling provisioning rates differ among female breeders, male breeders, and helpers? 2) does the presence of helpers in a family group result in an additive or compensatory benefit on provisioning rates? 3) is nestling mass higher in family groups with helpers? 4) do family groups with helpers have higher daily nest survival rates? 5) do family groups with helpers produce more fledglings?

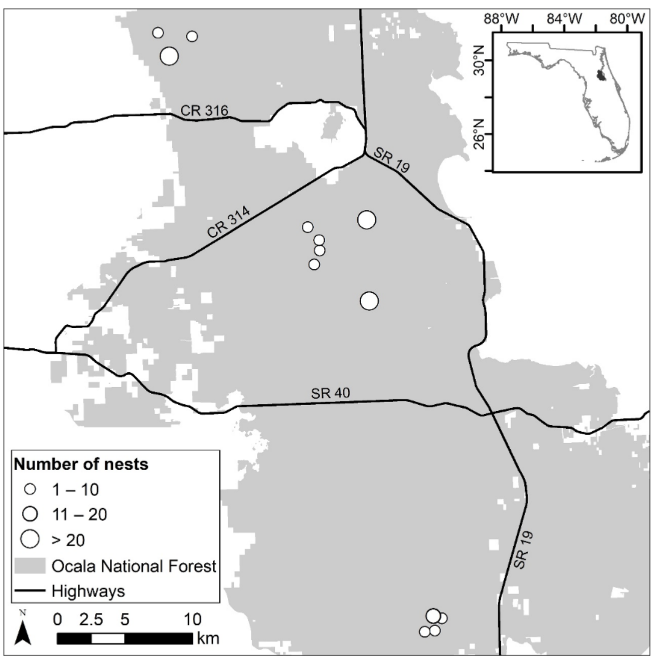
METHODS

Study area

Ocala NF in north-central Florida supports the largest remaining Florida Scrub-Jay population (≥1900 family groups; Miller et al. 2023). Ocala NF encompasses approximately 225,000 acres (91,000 ha) of scrub and sand pine (*Pinus clausa*) plant communities, which are managed for multiple objectives including commercial forest products, wildlife habitat, and recreation. The Ocala NF landscape is unique in that most habitat suitable for Florida Scrub-Jays occurs in hundreds of small (mostly <100 ha) clearcut stands of regenerating scrub embedded within an extensive matrix of young seral stands of sand pine forest. Scrub in Ocala NF is characterized by three species of oaks: myrtle (*Quercus myrtifolia*), Chapman's (*Q. chapmanii*), and sand live (*Q. geminata*) oak (Myers 1990). All types of Florida scrub are pyrogenic plant communities historically maintained in an early successional state by infrequent but high-intensity wildfires. Without disturbance, most scrub at Ocala NF eventually becomes sand pine forest, which has been managed for commercial harvesting since the 1940s (Hinchee and Garcia 2017). Ocala NF is bordered on the west by the Ocklawaha River and on the east by the St. Johns River and is characterized by nutrient-poor sandy soils (Astatula-Paola association) on gently rolling dune-like ridges formed during the Pleistocene (Myers 1990).

We studied Florida Scrub-Jays in regenerating clearcut stands located within focal areas established in 2011 for long-term monitoring (Miller and Shea 2021) and in more recently established Scrub-Jay Management Areas (Hinchee and Garcia 2017). At these sites, a subset of Florida Scrub-Jay adults and nestlings was color-banded annually to improve the accuracy of territory mapping and population monitoring and to assist in ongoing demographic study (Miller et al. 2015). From this pool of stands, we selected those with suitable habitat (Miller and Shea 2021) in 2018 for monitoring (Fig. 1). We monitored Florida Scrub-Jay family groups in stands ranging in age from 3 to 13 yr post-disturbance (mean = 7.8 yr) and ranging in size from 14.3 to 97.1 ha (mean = 35.2 ha).

Fig. 1. Florida Scrub-Jay (*Aphelocoma coerulescens*) study stands at Ocala National Forest, Florida, with the number of nests monitored in each stand, 2018–2019.



Nest monitoring and nestling mass

We located and monitored Florida Scrub-Jay nests during March–June in 2018 ($n = 69$) and 2019 ($n = 64$). Within focal areas described previously, we attempted to locate nests for all family groups that were encountered within our study stands (Fig. 1). Most adults had been banded with unique combinations of color bands and sexed by genetic analysis in conjunction with ongoing population studies (Miller et al. 2021, Miller and Shea 2021, Miller et al. 2023). For each nest, we recorded the color band combinations of the breeding adults and helpers (when present). Helpers were confirmed as family group members through repeated visits during the nesting season. We marked nests with flagging tape at least 5 m away and collected spatial coordinates for each nest using a handheld GPS unit. We found most nests during the building stage when adults were often seen carrying sticks and palmetto (*Sabal etonia*) fibers to the nest site. We used mirrors to examine nest contents every 3–5 days to identify laying, hatching, and fledging dates, and record clutch size, number of nestlings, and number of fledglings. For nests discovered in the incubation stage, we conducted more frequent monitoring until hatch day to allow for more accurate assignment of nestling age. For nests that were found during the nestling phase, we were able to estimate hatch date by backdating from the age of the nestlings using Woolfenden (1978) and a photographic guide to aging nestlings that we developed.

Florida Scrub-Jays typically lay one egg per day in the morning and begin incubation on the day that the last egg is laid: incubation time averages 18 d, with hatch day counting as day 0 (Woolfenden 1978, Woolfenden and Fitzpatrick 1984). We visited nests at midday, kept our visits brief, and varied our approach and departure paths to reduce disturbance and minimize predation (Martin and Guepel 1993). Mean age of fledging for the southern Florida population is 17 d (12–21 d; Woolfenden 1978); in our study area, we could not confirm exact fledging date for all nests, but we frequently found nests fledging at ≤16 d. We, therefore, considered nests surviving to 16 d without evidence of predation disturbance as successful in analyses. In our study area, Florida Scrub-Jays were observed renesting multiple times, but there was no evidence of double brooding.

We measured nestling mass when the oldest nestling in the brood was age day 11 (when flight feathers begin to break from their sheaths; Woolfenden 1978). On banding day, we transferred all nestlings to a clean paper bag and transported them ca. 10 m away from the nest. We weighed each nestling with a digital scale (precision 0.01 g). After weighing, we banded nestlings >35 g with one U.S. Geological Survey (USGS) aluminum band and a unique combination of three plastic color bands. Nestlings 30–35 g were banded with a USGS band only, and nestlings <30 g received no bands. Nestlings were returned to the nest and nests were monitored from a distance to verify the return of at least one adult.

Nest cameras

To quantify nestling provisioning rates of tending Florida Scrub-Jay adults, we installed nest cameras at a subset of accessible nests (<4 m height above ground) from family groups containing 0–2 helpers ($n = 33$ nests from 33 family groups; Appendix 1). We installed cameras (GoPro Hero 3+ Silver Edition, GoPro Inc., San Mateo, California) at nests when the oldest nestling was 8–10 d old (one camera session per nest). We fitted cameras with extended batteries (Wasabi Power Extended Batteries, Wasabi Power, Pomona, California) and altered camera settings (720 p video resolution, 60 fps, medium field of view, and 1280 x 720 p screen resolution) to allow for up to eight hours of HD video recording (in 20 min clips). Cameras were installed no later than 1.5 hr after sunrise (the period corresponding to greatest feeding activity; Stallcup and Woolfenden 1978). We attached cameras to a nearby branch with green zip ties at least 0.3 m from the nest cup and added camouflage duct tape to the camera housing to conceal it. After camera installation, we monitored nests from a distance (5-10 m) to confirm an adult's return. Cameras were to be removed if adults failed to return within 30 min, but this never occurred. We left cameras in place for 4–6 hr and removed them during midday.

Provisioning analysis

We used VSDC Free Video Editor software (https://www.videosoftdev.com/, Multilab LLC) to splice together the 20 min video clips for each nest, truncating the first 15 min and the last 5 min to eliminate bias associated with disturbance during camera installation and removal. We obtained a total of 147.6 hr of camera footage (mean = 4.5 hr/nest; after truncation). Videos were reviewed in real time using VLC Media Player (VideoLAN, Paris, France) by a single observer. We recorded each visit to the nest by an adult Florida Scrub-Jay as either a feeding visit (approaching the edge of the nest or landing on the nest carrying a food item) or a non-feeding visit (sitting in the nest shrub without coming to the nest). For each visiting bird, we recorded the band ID, group status (breeder vs. helper), sex (when banded), arrival time, departure time, total time at nest, and feeding behavior (feeding vs. non-feeding visit). Color-banded birds were previously sexed by genetic analysis and were usually of known age. For unbanded jays, we determined sex and breeding status through vocalizations (i.e., the female-specific rattle call) and behavioral characteristics (e.g., only females incubate eggs; breeders exhibit dominance behaviors over nonbreeders; Woolfenden and Fitzpatrick 1977, 1996). The relatedness of helpers to the breeders and nestlings was unknown for many of the groups in our study when either a breeder or helper was unbanded. We assigned feeding visits to the adult that brought the food to the nest, regardless of which individual ultimately passed the food to the nestling. For example, a breeding male bringing food to the nest was assigned as the feeding individual even if he gave the food to the female who then fed the nestlings.

For all analyses, we defined the provisioning rate for each tending adult as the mean number of feeding visits to the nest per hour of video recording (feeds/hr). Only one family group had a second helper, and it was never observed feeding nestlings. We used data from the first helper and ignored the presence of the second helper rather than calculating the mean provisioning rate across two helpers. For 10 nests, the sex of the breeding adults could not be assigned because both breeders were unbanded. For one additional nest with a helper, the breeders and helper were all unbanded and only total provisioning rate was available.

We ran a single linear mixed model to examine the fixed effect of individual status (female breeder, male breeder, or helper [sexes pooled]) on provisioning rate in groups with helpers. We included a random effect (nest ID) to control for lack of independence of provisioning behavior within each family group. Model analysis was performed using the lme4 package (Bates et al. 2015) in R (version 4.0.3; R Core Team 2020). We considered there to be a significant difference in provisioning rate when the 95% confidence interval for the mean slope coefficient (β) of the pairwise comparison did not include zero.

To examine the role of helpers on provisioning rates, we used a series of linear models to examine the effects of year (2018, 2019), ordinal date of camera recording (20 Apr–16 Jun), nestling age (8–10 d), brood size (1–4), and the presence/absence of helpers on three different response variables describing provisioning rates of female breeders, male breeders, and all adults in the group (breeders and helpers pooled). To examine the effect of helpers, we compared two alternative covariates: a 3-level covariate (helpers, no helpers, and helpers experimentally removed) and a 2-level covariate (helpers and no helpers [including groups with helpers experimentally removed]). We did not include 2-level and 3-level helper covariates in the same model and instead used model selection methods to determine the helper-level covariate describing the most variability in provisioning rates. We also ran a linear model examining the same effects (except the presence of helpers) on a fourth response variable representing the provisioning rate of helpers (sexes pooled) on the subset of family groups with helpers. Prior to analysis, we looked for collinearity among the covariates of year, ordinal date, nestling age, brood size, and helpers by estimating generalized variance inflation factors ($GVIF^{1/2df}$; car package in R; Fox and Weisberg 2019). All $GVIF^{1/2df}$ were <3 indicating negligible collinearity (except for the alternate covariates for helper presence); therefore, all covariates were retained when constructing models (Fox and Weisberg 2019).

For each response variable, we used a three-step sequence when evaluating covariates (Step 1: year and ordinal date, Step 2: nestling age and brood size and, Step 3: helper effects). Models were established in this order to control for sources of variation on nestling provisioning rates, thus maximizing power to detect effects for each subset of variables while reducing the number of total models in the candidate set. We assessed relative model support by using the Akaike Information Criterion (AIC) corrected for small sample size (AIC_c; Burnham and Anderson 2002). We disregarded models that were apparently competitive (i.e., $\Delta AIC_c < 2$) with the top model if they differed from the top model by 1 parameter and the 95% confidence interval (CI) for the slope coefficient of that parameter overlapped zero (Arnold 2010). In all steps, a single model with the lowest AIC_c value was used as the base model for the next step and all covariates were subject to exclusion. We confirmed model fit by assessing residual plots.

For the first step, we created a set of five models using all possible additive combinations of the effects of year (linear), ordinal date (linear), and quadratic ordinal date (second-order orthogonal polynomial). We also included a null model containing no effects. For the second step, we created eight additional models containing all possible additive interactions of nestling age (linear), quadratic nestling age (second-order orthogonal polynomial), brood size (linear), and quadratic brood size (second-order orthogonal polynomial). For the helper provisioning rate response variable, models containing polynomial covariates for ordinal date, nestling age, and brood size failed to converge, so only models with linear effects were included in the model selection process for the first and second steps. For the third step, we created six additional models representing helper presence (2-level and 3-level), multiplicative interactions between the two helper covariates and year, and multiplicative interactions between the two helper covariates and brood size. Interactions were only included in the model set if the year or brood size covariates were retained in steps one and two for a specific response variable.

Nestling mass analysis

We measured mass on day 11 from 61 Florida Scrub-Jay nestlings from 23 broods in 2018, and 43 nestlings from 17 broods in 2019 (Appendix 1). Only one nest from each family group was included in a given year. Our dataset included two territories that had nests in both 2018 and 2019; the breeders were unbanded, so we were unable to determine whether they were the same individuals in consecutive years. All other territories were represented only once.

We ran a series of linear mixed models to examine the fixed effects of year (2018, 2019), ordinal date of banding (23 Apr to 19 Jun), brood size (1–4), and the presence/absence of helpers (sexes pooled) on day 11 nestling mass. To examine the effect of helpers, we compared two alternative covariates: a 3-level covariate (helpers, no helpers, and helpers experimentally removed) and a 2-level covariate (helpers and no helpers [including groups where helpers were experimentally removed]). For all models, we added a random effect term (nest ID) to account for the non-independence of nestlings within a brood. Models were created and compared using the lme4 package (Bates et al. 2015). Collinearity among covariates was negligible ($GVIF^{1/2df}$ for covariates were <3, except for the alternate covariates for helper presence).

We used a three-step model selection sequence when examining nestling mass to maximize power for detecting important predictors for each variable subset (Step 1: year and ordinal date, Step 2: brood size and, Step 3: helper effects). We assessed relative model support using AIC_c, following the same procedures as the provisioning rate analysis, excluding of the nestling age covariate because all nestlings were the same age. Model fit was assessed and determined as acceptable using residual analyses in the DHARMa package (Hartig and Hartig 2017). Prediction plots include the predicted marginal means and 95% confidence intervals conditioned on the fixed effects.

Nest survival analysis

Of the 133 Florida Scrub-Jay nests discovered, four had an unknown fate because of infrequent monitoring late in the breeding season. We used Shaffer's (2004) logistic exposure method to estimate daily nest survival probability for all Florida Scrub-Jay nests in our sample that survived to the incubation stage (*n* = 131 nests [Appendix 1]; 2604 exposure days, 728 nest-check intervals; 79 failed, 49 successful, 3 unknown fate). We compared logistic exposure models using the generalized linear model function GLM assuming a binomial response distribution with a modified power-logistic link function, where *e* is the number of exposure days (Bolker 2014).

We first examined random effects to check for potential non-independence of observations within sampling units: stand ID and territory ID. Likelihood ratio tests indicated limited support ($P > 0.05$) for the random effect terms when compared to the reduced model, which set the random effect variance to zero, so we pooled nest data from all stands and territories and treated each nest check as independent.

We considered the following covariates for each exposure period: year (2018, 2019), ordinal date of the nest visit (25 Mar to 18 Jul), nest stage (incubation or brooding), and the presence/absence of helpers (sexes pooled) on daily nest survival. For the nest stage covariate, we aged most nests directly because they were discovered in the building (*n* = 40), laying (*n* = 15), or nestling stages (*n* = 15), or they were found in the incubation stage but survived long enough to be observed with nestlings (*n* = 38). The remaining 23 nests (18%) were discovered in the incubation stage but failed prior to being observed with nestlings, so we estimated the nest stage at failure based on the midpoint of possible failure dates. To examine the effect of helpers, we compared two alternative covariates: a 2-level covariate (helpers and no helpers, including groups where helpers were experimentally removed) and a 3-level covariate (helpers, no helpers, and helpers experimentally removed). Collinearity among covariates was negligible ($GVIF^{1/2df}$ for covariates were <3, except for the alternate covariates for helper presence).

We used a similar three-step model selection sequence as used previously, when evaluating effects on daily nest survival. For the first step, we created a set of models using all possible additive combinations of the effects of year, linear ordinal date, and quadratic ordinal date (second-order orthogonal polynomial). We also included a null model containing no effects. For the second step, we created one additional model containing the effect of nest stage (incubation, brooding). For the third step, we created six additional models representing helper presence (2-level or 3-level), the multiplicative interactions between the two helper covariates and year, and the multiplicative interactions between the two helper covariates and nest stage (based on the observation that helpers do not assist with incubation [Woolfenden and Fitzpatrick 1984] and, therefore, the effect of helpers on nest survival may be greater during the brooding period). We assessed relative model support using AIC_c, following the same procedures as the provisioning rate and nestling mass analyses. We calculated the modeled probability of nest survival over a typical nest cycle by exponentiating the daily point estimate by 35 days (assumes an 18-day incubation period and a 17-day nestling period; Woolfenden 1978) and calculated 95% confidence intervals based on the standard error estimated using the delta method (deltavar function of the emdbook package; Bolker 2020).

Productivity

We estimated productivity on 128 nests with known fate (Appendix 1). The number of fledglings was assigned to each successful nest based on the number of nestlings observed on the nest check prior to fledging. We examined the effects of year (2018, 2019), ordinal date of nest initiation (4 Mar to 20 Jun), and the presence/absence of helpers on the number of fledglings per nest (using a series of negative binomial models) and the number of fledglings per successful nest (using a series of zero-truncated Poisson models). We created and compared negative binomial models using the MASS package in R (Venables and Ripley 2002) and zero-truncated Poisson models using the glmmTMB package in R (Brooks et al. 2017). To examine the effect of helpers, we compared two alternative covariates: a 3-level covariate (helpers, no helpers, and helpers experimentally removed) and a 2-level covariate (helpers and no helpers, including groups where helpers were experimentally removed). Collinearity among covariates was negligible ($GVIF^{1/2df}$ for covariates were <3, except for the alternate covariates for helper presence).

We used a two-step model selection sequence when examining productivity to maximize power for detecting important predictors for each variable subset (Step 1: year and ordinal date, Step 2: helper effects). We assessed relative model support using AIC_c, following the same procedures as the provisioning rate analysis, with the exclusion of the nestling age, and brood size covariates because those covariates do not apply to this analysis.

RESULTS

We monitored the territories of 56 Florida Scrub-Jay family groups in 2018 and 55 family groups in 2019 and discovered a total of 133 nests (Appendix 1–2, Fig. 1). Mean group size was 2.43 adults, and 32 of 110 (29%) helpers were color banded (years pooled). In both years, most banded helpers were male (2018: 64%; 2019: 78%) and second-year helpers were the most common age-class (2018: 50%; 2019: 94%; Appendix 2).

Provisioning

Years pooled, we observed a total of 1,110 feeding visits during 147.6 hr of camera footage (mean = 4.5 hr/nest; Methods). For family groups without helpers, male breeders provisioned at higher rates on average than females (Appendix 3). For family groups with helpers, male breeders provisioned at higher rates than female breeders ($\beta = 2.311$, 95% CI: 0.902–3.721; Fig. 2). Helpers also provisioned at higher rates than female breeders ($\beta = 1.869$, 95% CI: 0.520–3.230), but there was no difference in provisioning rates between male breeders and helpers ($\beta = 0.442$, 95% CI: -0.919–1.791; Fig. 2). The among-nest (nest ID) standard deviation of the intercept was 0.827. Helpers exhibited more individual variation in provisioning rate than breeders, ranging from 0–7 feeds/hr (Appendix 3).

The presence of helpers did not increase the total provisioning rate of the brood, instead, total provisioning rate was positively correlated with nestling age and brood size (model 10; Tables 1 and 2, Fig. 3). The provisioning rate of female breeders was also positively correlated with nestling age and brood size, however, female breeders fed nestlings at lower rates in groups with helpers than in groups without helpers (2-level helper effect; model 14, Tables 1 and 2, Fig. 4a). Female breeders in groups without helpers provisioned their nestlings twice as frequently as female breeders from groups with helpers (3.36 vs. 1.64 feeds/hr; model-predicted values for nests with the median nestling age [9] and median brood size [3]). A model containing the 3-level helper covariate was competitive (model 16, Table 1), but the only supported pairwise difference in female breeder provisioning rate was between groups with helpers and groups without helpers (Table 2); female breeders from groups where helpers were removed had intermediate provisioning rates (Fig. 4b). The presence of helpers did not alter the provisioning rate of male breeders, instead, male breeder provisioning rate was positively correlated with linear ordinal date (model 2, Tables 1 and 2). The provisioning rate of helpers varied only by year and was higher in 2018 than 2019 (model 1, Tables 1 and 2, Fig. 5).

Fig. 2. Predicted mean nestling provisioning rates (with 95% confidence intervals) of Florida Scrub-Jay (*Aphelocoma coerulescens*) female breeders, male breeders, and helpers in family groups containing at least one helper from the Ocala National Forest population, Florida, USA (2018–2019). Means are predicted from a linear mixed model containing the random effect of nest ID and the fixed effect of status and 95% confidence intervals are estimated based on the variance of the fixed effects only. Letter notations represent groups that are statistically different (the 95% confidence intervals surrounding the slope coefficient for a given comparison pair did not contain zero).

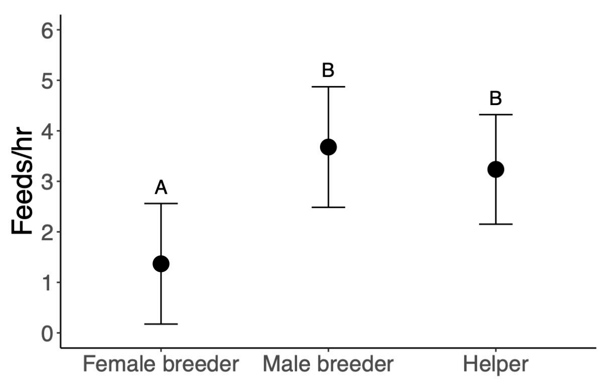


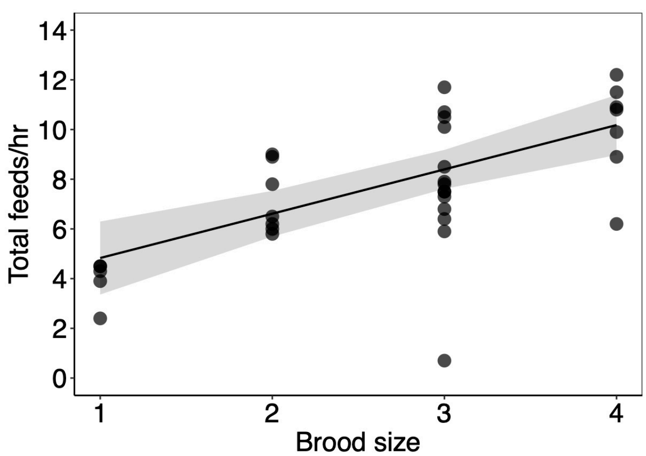
Table 1. Step 3 model selection tables for linear models of Florida Scrub-Jay (*Aphelocoma coerulescens*) provisioning rates (feeds/hr) from Ocala National Forest, Florida, USA (2018–2019). Provisioning rates were estimated as four different response variables (total [all tending adults pooled], female breeders, male breeders, and helpers). Models are listed by number (No.) and ranked according to their difference in Akaike information criterion score (corrected for small sample size; ΔAIC_c) compared to the model with the lowest AICc in each set. Other columns include the number of model parameters (K), the model likelihood (-2Log(L)), and the Akaike weight (wi). Steps 1 and 2 evaluated support for the effect of year (Year), ordinal date (Ord), nestling age (Age), and brood size (Size). Step 3 evaluated support for the effect of helpers as either a 2-level covariate (Helper2L; helpers, no helpers) or a 3-level covariate (Helper3L; helpers, no helpers, removed). The asterisk (*) indicates a multiplicative interaction between covariates.

Response	No.	Steps 1 & 2	Step 3	K	-2Log (*L*)	AIC_c	ΔAIC_c	w_i
Total	10	Age + Size		4	-68.05	145.50	0.00	0.70
	14	Age + Size +	Helper2L	5	-68.02	148.30	2.73	0.18
	15	Age + Size +	Size*Helper2L	6	-67.29	149.80	4.28	0.08
	16	Age + Size +	Helper3L	6	-68.01	151.20	5.72	0.04
	17	Age + Size +	Size*Helper3L	8	-67.09	156.20	10.65	0.00
Female breeder	14	Age + Size +	Helper2L	5	-29.79	73.10	0.00	0.59
	16	Age + Size +	Helper3L	6	-28.55	74.30	1.25	0.31
	15	Age + Size +	Size*Helper2L	6	-29.78	76.80	3.71	0.09
	17	Age + Size +	Size*Helper3L	8	-27.78	81.80	8.75	0.01
	10	Age + Size		4	-37.09	84.40	11.29	0.00
Male breeder	2	Ord		3	-39.18	85.60	0.00	0.76
	14	Ord +	Helper2L	4	-39.03	88.30	2.65	0.20
	16	Ord +	Helper3L	5	-39.01	91.60	5.93	0.04
Helper	1	Year		3	-18.30	46.00	0.00	0.77
	8	Year + Size		4	-17.29	49.20	3.23	0.15
	6	Year + Age		4	-18.13	50.90	4.91	0.07
	10	Year + Age + Size		5	-16.95	55.90	9.87	0.01

Table 2. Mean coefficient estimates with lower (LCL) and upper (UCL) 95% confidence limits for top ranking linear models (No.) of Florida Scrub-Jay (*Aphelocoma coerulescens*) provisioning rates (feeds/hr) from Ocala National Forest, Florida, USA (2018–2019). Provisioning rates were estimated as four different response variables (total [all tending adults pooled], female breeders, male breeders, and helpers).

Response	No.	Covariate	Estimate	LCL	UCL
Total	10	Intercept	-6.696	-15.127	1.735
	10	Nestling age	1.083	0.135	2.030
	10	Brood size	1.783	1.050	2.517
Female breeders	14	Intercept	-10.272	-15.689	-4.854
	14	Nestling age	1.031	0.452	1.610
	14	Brood size	0.876	0.414	1.337
	14	Helper2L (no helpers)	1.724	0.845	2.603
Male breeders	2	Intercept	-4.172	-11.034	2.690
	2	Ordinal date	0.063	0.010	0.115
Helpers	1	Intercept	4.967	3.123	6.810
	1	Year (2019)	-2.379	-4.541	-0.217

Fig. 3. Predicted mean total provisioning rate (feeds/hr; all tending adults pooled) increases with brood size for Florida Scrub-Jays (*Aphelocoma coerulescens*) from Ocala National Forest, Florida, USA. Raw data for total feeds/hr (black dots) and 95% confidence limits for model predicted values (shaded region) are shown. Nestling age is fixed at the median value (9 days old) for predicted values.



Nestling mass

The top model for nestling mass (model 1) included the random effect of nest ID and the fixed effect of year (Table 3), where day 11 nestlings were 4.3 g heavier on average in 2018 (47.2 g) than 2019 (42.9 g; β = -4.34, 95% CI: -7.55–1.12; Fig. 5). The among-nest (NestID) standard deviation of the intercept for nestling mass was 3.99. The model containing the 3-level helper effect was competitive (Table 3), but the 95% CI for all pairwise beta estimates contained zero, indicating that the effect of helpers on nestling mass was not supported.

Fig. 4. Mean provisioning rates and 95% confidence intervals for female breeder Florida Scrub-Jays (*Aphelocoma coerulescens*) in Ocala National Forest, Florida, USA (2018–2019). Predicted means are shown from the best model (A: 2-level helper effect: groups where helpers were experimentally removed pooled with groups containing no helpers) and second-best model (B: 3-level helper effect). Both models also contain effects of brood size and nestling age fixed at their median values (3 nestlings and 9 days old, respectively). Letter notations represent groups that are statistically different (the 95% confidence intervals surrounding the slope coefficient for a given comparison pair did not contain zero).

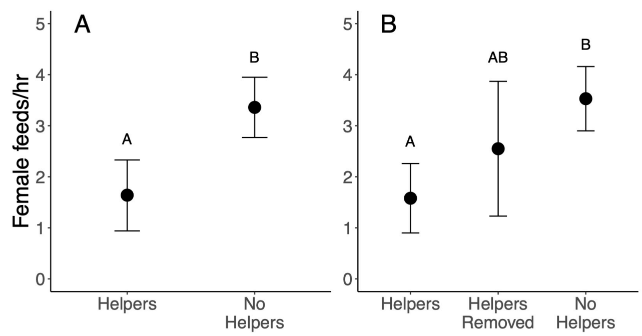


Table 3. Step 3 model selection table for mixed linear models of Florida Scrub-Jay (*Aphelocoma coerulescens*) nestling mass (g) on day 11 from Ocala National Forest, Florida, USA (2018–2019). Models are listed by number (No.) and ranked according to their difference in Akaike information criterion score (corrected for small sample size; ΔAIC_c) compared to the model with the lowest AIC_c in each set. Other columns include the number of model parameters (K), the model likelihood (-2Log (L)), and the Akaike weight (wi). All models contain the random effect of nest ID. Steps 1 and 2 evaluated support for the fixed effects of year, ordinal date, and brood size. Step 3 evaluated support for the fixed effect of helpers (2-level [Helper2L] and 3-level [Helper3L]). The asterisk (*) indicates a multiplicative interaction between covariates.

No.	Steps 1 & 2	Step 3	K	`-2Log(L)	AIC_c	ΔAIC_c	w_i
1	Year		4	-326.60	661.60	0.00	0.52
9	Year +	Helper3L	6	-325.29	663.40	1.85	0.21
8	Year +	Helper2L	5	-326.49	663.60	2.00	0.19
10	Year +	Year*Helper2L	6	-326.45	665.80	4.16	0.07
11	Year +	Year*Helper3L	8	-325.12	667.80	6.16	0.02

Nest survival

Of the 129 nests with known fate, 47 fledged at least one young (36.4% apparent survival). The top model for daily nest survival (model 2) was supported over a null model (ΔAIC_c = 8.1) and contained the effect of linear ordinal date (Table 4). Daily nest survival declined linearly with season (β = -0.02, 95% CI: -0.02 – -0.01), from 0.985 (95% CI: 0.974–0.991) at the start of the season (25 May) to 0.915 (95% CI: 0.850–0.954) by the end of the season

Fig. 5. Annual variation in mean provisioning rate (feeds/hr) by Florida Scrub-Jay (*Aphelocoma coerulescens*) helpers (open diamonds) and mean nestling mass (g; black circles) in Ocala National Forest, Florida, USA (2018–2019). Mean helper provisioning rate was predicted from the top-ranking linear model containing the effect of year. Mean nestling mass was predicted from the top ranking linear mixed model containing the random effect of nest ID and the fixed effect of year (95% confidence intervals are shown and estimated based on the variance of fixed effects only).

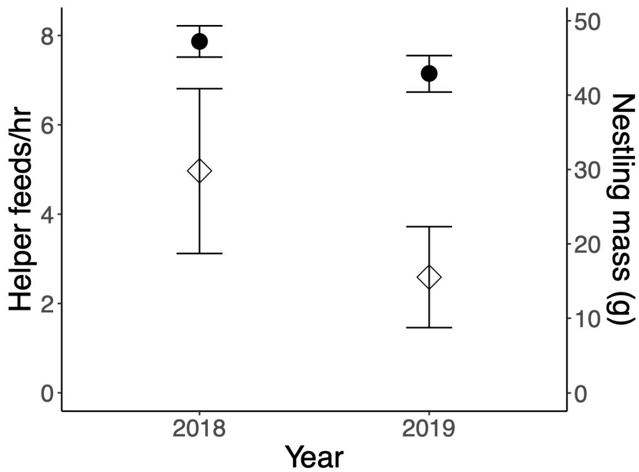


Table 4. Step 3 model selection tables for logistic exposure models of Florida Scrub-Jay (*Aphelocoma coerulescens*) daily nest survival from Ocala National Forest, Florida, USA (2018–2019). Models are listed by number (No.) and ranked according to their difference in Akaike information criterion score (corrected for small sample size; ΔAIC_c) compared to the model with the lowest AIC_c in each set. Other columns include the number of model parameters (K), the model likelihood (-2Log(L)), and the Akaike weight (wi). Steps 1 and 2 evaluated support for the effect of year (Year), ordinal date (Ord), and nest stage (Stage). Step 3 evaluated support for the effects of helpers as either a 2-level covariate (Helper2L; helpers, no helpers) or a 3-level covariate (Helper3L; helpers, no helpers, removed).

No.	Steps 1 & 2	Step 3	K	`-2Log(L)	AIC_c	ΔAIC_c	w_i
2	Ord		2	-242.43	488.9	0.00	0.45
7	Ord	Helper2L	3	-241.61	489.3	0.37	0.37
8	Ord	Helper3L	4	-241.31	490.7	1.80	0.18

(18 Jul). Daily nest survival at the median ordinal date (4 May) was 0.972 (95% CI: 0.964–0.978). The daily nest survival rate exponentiated across a 35-d nest cycle (on the median ordinal date: 4 May) resulted in a cumulative nest survival probability of 37.1% (95% CI: 27.9–46.3%). None of the helper effects was included in the top model, and while the second-best model (model 7) containing the 2-level helper effect appeared competitive based on model weight (36.8%; Table 4), the 95% CI surrounding the beta estimate for that term contained zero (helper2L [no helper] β = -0.31, 95% CI: -0.80–0.16), indicating low support for a helper effect.

Productivity

The number of fledglings per nest declined slightly with ordinal date of nest initiation (Table 5; Ordinal date β = -0.02, 95% CI: -0.04 – -0.01). The mean number of fledglings per nest was 1.18 ± 1.48 SD for family groups with helpers and 0.79 ± 1.31 SD for family groups without helpers, but none of the helper effects was included in the top model. Although the second-best model (model 4) containing the 2-level helper effect appeared competitive based on model weight (32%, Table 5), the 95% CI surrounding the beta estimate for that term contained zero (helper2L [no helper] β= -0.37, 95% CI: -1.0–0.25), indicating low support for a helper effect. Among successful nests, mean number of fledglings was 2.79 ± 0.79 SD for family groups with helpers and 2.36 ± 1.19 SD for family groups without helpers. The number of fledglings per successful nest did not vary with year, ordinal date of nest initiation, or the presence of helpers (the top model was the null model [model 0]; β = 0.82 95% CI: 1.03–0.82; Table 5).

Table 5. Step 2 model selection table for negative binomial and zero-truncated Poisson models of Florida Scrub-Jay (*Aphelocoma coerulescens*) fledglings per nest and fledglings per successful nests (respectively), from Ocala National Forest, Florida, USA (2018–2019). Models are listed by number (No.) and ranked according to their difference in Akaike information criterion score (corrected for small sample size; ΔAIC_c) compared to the model with the lowest AIC_c in each set. Other columns include the number of model parameters (K), the model likelihood (-2Log (L)), and the Akaike weight (wi). Step 1 evaluated support for the effects of year and ordinal date. Step 2 evaluated support for the effect of helpers (2-level [Helper2L] and 3-level [Helper3L]).

Response	No.	Step 1	Step 2	K	`-2Log(L)	AIC_c	ΔAIC_c	w_i
Fledglings	1	Ord		3	-163.00	332.2	0.00	0.47
per nest	4	Ord	Helper2L	4	-162.32	333.0	0.76	0.32
	5	Ord	Helper3L	5	-161.68	333.9	1.66	0.21
Fledglings	0	(.)	(.)	1	-70.99	144.1	0.00	0.43
per successful	4	(.)	Helper3L	3	-69.08	144.7	0.65	0.31
nest	5	(.)	Helper2L	2	-70.43	145.1	1.07	0.25

DISCUSSION

We discovered a compensatory (load-lightening) effect of helping on maternal provisioning rates in Florida Scrub-Jays at Ocala NF. Female breeders reduced their level of nestling care when helpers were present, and because helpers fully compensated for this reduction, total provisioning rate, nestling mass, nest survival rate, and productivity did not differ between groups with and without helpers. Load-lightening effects are one of the most commonly reported benefits of helping in cooperatively breeding birds (review in Hatchwell 1999) but could have been easily overlooked in this system without provisioning data from camera recordings or behavioral observations.

Despite being frequently reported in other cooperatively breeding species, load-lightening effects have not been consistently recognized as a helper benefit for Florida Scrub-Jays. Previous studies on the Lake Wales Ridge in southern Florida did not find evidence for load-lightening. Mumme (1992) instead discovered an additive increase in total feeding rate and increased nestling mass for groups with helpers compared to groups where all helpers had been experimentally removed. McGowan and Woolfenden (1990) also observed an additive effect of helpers that extended into the fledgling stage; male and female breeders did not decrease their feeding rates when helpers were present. Another study found that female breeders had much lower food contribution rates (sum of food bolus size scores divided by hours of observation) than male breeders and most helpers (Stallcup and Woolfenden 1978); however, their study did not consider groups without helpers, so it is unknown if the low food contribution by female breeders was a compensatory reaction to helper presence.

Small family group size may partially explain why we did not observe an additive effect of helpers in our study in north-central Florida (mean group size = 2.43 adults; this study) in contrast to long-term studies in southern Florida (mean group size = 2.65-3.52 adults; Woolfenden and Fitzpatrick 1984). A longitudinal study on the Lake Wales Ridge population in southern Florida revealed a positive effect of Florida Scrub-Jay group size on nestling mass and post-fledging survival to day 30, but nestling mass was only higher in groups with two or more helpers (Mumme et al. 2015: Figure 2c). Similarly, in cooperatively breeding Long-Tailed Tits (*Aegithalos caudatus*), breeders reduced their provisioning rate when one helper was present, but no additional adjustments were made when two or more helpers were present; therefore, the level of care was fully compensatory for 1-helper groups but additive for 2-helper groups (Hatchwell and Russell 1996).

The difference in maternal response to helper provisioning between our study and previous studies from southern Florida also may be driven by site differences in the probability of nestling starvation or the relative costs of care (Hatchwell 1999, Russell et al. 2008, Johnstone 2011). Breeders in cooperatively breeding species are predicted to compensate care when nestling starvation rates for that species are low and use additive care when the risk of nestling starvation is high (Hatchwell 1999). If food resources are more available at Ocala NF than on the Lake Wales Ridge, this may explain why we observed a compensatory response to helper provisioning at Ocala NF. Nestling starvation is considered rare for Florida Scrub-Jays on the Lake Wales Ridge (<10% of nestling deaths; Woolfenden 1978, McGowan 1987, Mumme 1992), but there is a positive relationship between nestling mass and fledgling survivorship (McGowan 1987, Fitzpatrick et al. 1988, Mumme et al. 2015), in part because small, poorly fed nestlings and fledglings may attract more predators because they beg more frequently (Mumme 1992, Grubb et al. 1998).

Our results also indicate considerable annual variation in breeding conditions. Helper provisioning rates and nestling mass were both higher in 2018 than in 2019 (Fig. 5) and it is possible that the helpers chose to reduce their level of care in a year when resources were lower. For cooperatively breeding Acorn Woodpeckers (*Melanerpes formicivorus*), the benefits associated with having a helper were significant only in "good years" (high acorn crop years) contrary to previous analysis and theory; in poor years, there was little or no effect of helpers on productivity and survival metrics (Koenig et al. 2011). Helper provisioning rate was positively associated with food supplementation in other cooperatively breeding bird species (e.g., Eden 1987, Boland et al. 1997). In addition, food supplementation positively influences Florida Scrub-Jay nestling survival (Reynolds et al. 2003) and annual fecundity (Breininger et al. 2023). Continued research on this topic with larger sample sizes (i.e., more years), including assessment of food availability and the size and quality of prey deliveries, might reveal more complex interactions between annual variation in breeding conditions and adult provisioning rates.

Implications for translocation

It is challenging to fully understand the benefits that helpers provide to breeders because helper effects vary among or within sites because of spatial and temporal differences in food availability, habitat quality, and other environmental factors (Breininger et al. 2023). Some helper effects, such as load-lightening, are subtle and could be easily overlooked without the collection of detailed behavioral data. Therefore, it is difficult to predict the full consequence of removing helpers for translocation. Our results tentatively suggest that removing Florida Scrub-Jay helpers from Ocala NF may not result in a reduction of total provisioning rates, nestling mass, nest survival, or productivity (Franzreb 2007) in a given year. This conclusion is congruent with Mumme and Below's (1999) conclusion that the removal of helpers for translocation may not cause short-term detriment to the donor population.

However, we caution that site-specific differences in resource availability should be considered prior to making translocation decisions. Our findings suggest that it may be more strategic to remove helpers from sites with higher primary productivity, especially if the compensatory response by female breeders to helper provisioning observed at Ocala NF is an indication of reduced risk of nestling starvation. Removing helpers from sites with an additive effect of helper provisioning and a higher risk of nestling starvation may have greater consequence to nestling mass and fledging success. The number of helpers in the donor family may also be relevant when making collection decisions. Conclusions from studies where one helper was removed from groups with multiple helpers (Mumme and Below 1999), may differ substantially from our study where the removal of helpers resulted in experimental groups with no remaining helpers. The age and sex of the helpers targeted for removal and translocation may also be relevant; Stallcup and Woolfenden (1978) showed that older male helpers contribute more food units to nestlings than first-year male helpers, and females and, therefore, the removal of younger male helpers or female helpers may have less impact on the donor family.

Finally, removing helpers also may have long-term consequences on the donor population that have yet to be studied. In the Lake Wales Ridge population, helpers increased fledgling survival (McGowan 1987), but this potential helper benefit has not been studied at Ocala NF. The load-lightening benefit provided by Florida Scrub-Jay helpers to female breeders is also important to consider when planning translocation projects. A reduction in maternal care in response to helper provisioning is predicted to decrease female breeder reproductive costs and thereby result in higher survival and future reproduction of that female (Hatchwell 1999). Adult breeder survival was positively correlated with mean family size in the Atlantic coast populations, although it is not yet known if this relationship is the result of helper benefits or favorable site conditions leading both to survival and increased helper retention (Breininger et al. 2022). For Florida Scrub-Jays, the length of the breeding lifespan is one of the most important components of total lifetime reproductive success, accounting for 30% of variance, and is considerably more important than annual fledgling production (Fitzpatrick et al. 1988). Future research evaluating whether load-lightening by helpers results in increased female breeder survival and productivity could help clarify whether helpers increase or decrease increased lifetime reproductive success. The benefits of translocating helpers to other populations must be weighed against the potential, still understudied long-term consequences of helper removal on the donor population.

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LITERATURE CITED

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178. https://doi.org/10.2193/2009-367

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48. https://doi.org/10.18637/jss.v067.i01

Bennett, V. A., V. A. Doerr, E. D. Doerr, A. D. Manning, D. B. Lindenmayer, and H. J. Yoon. 2013. Causes of reintroduction failure of the Brown Treecreeper: implications for ecosystem restoration. Austral Ecology 38:700-712. https://doi.org/10.1111/aec.12017

Boland, C. R., R. Heinsohn, and A. Cockburn. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding White-winged Choughs. Journal of Animal Ecology 66(5):683-691. https://doi.org/10.2307/5921

Bolker, B. 2014. Logistic regression, accounting for differences in exposure: version 2014-09-30 19:33:20.

Bolker, B. 2020. emdbook: ecological models and data in R; R package version 1.3.12.

Breininger, D. R., G. M. Carter, S. A Legare, W. V. Payne, E. D. Stolen, D. J. Breininger, and J. E. Lyon. 2022. Multistate modeling of Florida Scrub-Jay adult survival and breeding transitions. Ecosphere 13:e3991. https://doi.org/10.1002/ecs2.3991

Breininger, D. R., E. D. Stolen, G. M. Carter, S. A Legare, W. V. Payne, D. J. Breininger, J. E. Lyon, and C. D. Schumann. 2023. Territory and population attributes affect Florida scrub-jay fecundity in fire-adapted ecosystems. Ecology and Evolution 13: e9704. https://doi.org/10.1002/ece3.9704

Brooks M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9:378-400. https://doi.org/10.32614/RJ-2017-066

Brown, J. L. 1978. Avian communal breeding systems. Annual Review of Ecology and Systematics 9:123-155. https://doi.org/10.1146/annurev.es.09.110178.001011

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Carrie, N. R., R. N. Conner, D. C. Rudolph, and D. K. Carrie. 1999. Reintroduction and postrelease movements of Red-cockaded Woodpecker groups in eastern Texas. Journal of Wildlife Management 63:824-832. https://doi.org/10.2307/3802795

Clarke, R. H., R. L. Boulton, and M. F. Clarke. 2002. Translocation of the socially complex Black-eared Miner (Manorina melanotis): a trial using hard and soft release techniques. Pacific Conservation Biology 8:223-234. https://doi.org/10.1071/PC030223

Cockburn, A., R. A. Sims, H. L. Osmond, D. J. Green, M. C. Double, and R. A. Mulder. 2008. Can we measure the benefits of help in cooperatively breeding birds: the case of Superb Fairy-wrens Malurus cyaneus? Journal of Animal Ecology 77:430-438. https://doi.org/10.1111/j.1365-2656.2007.01351.x

Cox, J. A. 1984. Distribution, habitat, and social organization of the Florida Scrub-Jay, with a discussion of the evolution of cooperative breeding in New World jays. Dissertation, University of Florida, Gainesville, Florida, USA.

Downing, P. A., A. S. Griffin, and C. K. Cornwallis. 2020. The benefits of help in cooperative birds: nonexistent or difficult to detect? American Naturalist 195:1085-1091. https://doi.org/10.1086/708515

Eden, S. F. 1987. When do helpers help? Food availability and helping in the moorhen, Gallinula chloropus. Behavioral Ecology and Sociobiology 21:191-195. https://doi.org/10.1007/BF00303210

Fitzpatrick, J. W., and R. Bowman. 2016. Florida scrub-jays: oversized territories and group defense in a fire-maintained habitat. Pages 77-96 in W. D. Koenig and J. L. Dickinson, editors.

Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9781107338357.006

Fitzpatrick, J. W., G. E. Woolfenden, and K. J. McGowan. 1988. Sources of variance in lifetime fitness of Florida Scrub Jays. Acta: XIX Congressus Internationalis Ornithologici, Ottawa, Canada 22-29 VI .1986 19:876-891.

Florida Fish and Wildlife Conservation Commission (FWC). 2019. Scrub habitat management guidelines. Tallahassee, Florida, USA.

Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida: 2010 edition. Florida Natural Areas Inventory, Tallahassee, Florida, USA.

Fox J., and S. Weisberg. 2019. An R companion to applied regression. Third edition. Sage, Thousand Oaks, California, USA.

Franzreb, K. E. 2007. Reproductive success and nest depredation of the Florida Scrub-Jay. Wilson Journal of Ornithology 119:162-169. https://doi.org/10.1676/05-075.1

Grubb, T. C. Jr., G. E. Woolfenden, and J. W. Fitzpatrick. 1998. Factors affecting nutritional condition of fledgling Florida Scrub-Jays: a ptilochronology approach. Condor 100:753-756. https://doi.org/10.2307/1369761

Hartig, F., and M. F. Hartig. 2017. Package 'DHARMa.'

Hatchwell, B. 1999. Investment strategies of breeders in avian cooperative breeding systems. The American Naturalist 154:205-219. https://doi.org/10.1086/303227

Hatchwell, B. J., and A. F. Russell. 1996. Provisioning rules in cooperatively breeding Long-tailed Tits (Aegithalos caudatus): an experimental study. Proceedings of the Royal Society of London. Series B: Biological Sciences 263:83-88. https://doi.org/10.1098/rspb.1996.0014

Hinchee, J. K., and J. O. Garcia. 2017. Sand pine and Florida Scrub-Jays: an example of integrated adaptive management in a rare ecosystem. Journal of Forestry 115:230-237. https://doi.org/10.5849/jof.15-150

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. The reintroduction and invasive species specialist groups' task force on moving plants and animals for conservation purposes. IUCN Species Survival Commission, Gland, Switzerland.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72-78. https://doi.org/10.1016/j.cub.2010.11.075

Johnstone, R. A. 2011. Load lightening and negotiation over offspring care in cooperative breeders. Behavioral Ecology 22:436-444. https://doi.org/10.1093/beheco/arq190

Koenig, W. D., E. L. Walters, and S. Barve. 2019. Does helping-at-the-nest help? The case of the Acorn Woodpecker. Frontiers in Ecology and Evolution 7:272. https://doi.org/10.3389/fevo.2019.00272

Koenig, W. D., E. L. Walters, and J. Haydock. 2011. Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the Acorn Woodpecker. American Naturalist. 178:145-158. https://doi.org/10.1086/660832

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.

McGowan, K. J. 1987. Social development in young Florida Scrub Jays (Aphelocoma c. coerulescens). Ph.D. Dissertation, University of South Florida, Tampa, Florida, USA.

McGowan, K. J., and G. E. Wolfenden. 1990. Contributions to fledgling feeding in the Florida Scrub-Jay. Journal of Animal Ecology 59:691-707. https://doi.org/10.2307/4889

Menges, E. S., and D. R. Gordon. 2010. Should mechanical treatments and herbicides be used as fire surrogates to manage Florida's uplands? A review. Florida Scientist 73:147-174.

Miller, K. E., C. A. Faulhaber, and J. O. Garcia. 2015. Accuracy assessment of a Jay Watch post-reproductive survey of Florida Scrub-jays (Aphelocoma coerulescens). Florida Field Naturalist 43:4:139-147.

Miller, K. E., R. Risch, and J. O. Garcia. 2021. Long-distance dispersal in a sedentary species, Aphelocoma coerulescens (Florida Scrub-Jay), in Northern Florida. Southeastern Naturalist, 20:37-41. https://doi.org/10.1656/058.020.0118

Miller, K. E., and C. P. Shea. 2021. Characterizing suitable habitat for the largest remaining population of the threatened Florida Scrub-Jay Aphelocoma coerulescens. Endangered Species Research 45:99-107. https://doi.org/10.3354/esr01128

Miller, K. E., C. P. Shea, and M. A. Barrett. 2023. Florida Scrub-Jay population estimate for Ocala National Forest under different management scenarios. Final report, Florida Fish and Wildlife Conservation Commission, Gainesville, Florida, USA.

Mumme, R. L. 1992. Do helpers increase reproductive success - an experimental-analysis in the Florida Scrub Jay. Behavioral Ecology and Sociobiology 31:319-328. https://doi.org/10.1007/BF00177772

Mumme, R. L., and T. H. Below. 1999. Evaluation of translocation for the threatened Florida Scrub-Jay. Journal of Wildlife Management 63:833-842. https://doi.org/10.2307/3802796

Mumme, R. L., R. Bowman, M. S. Pruett, and J. W. Fitzpatrick. 2015. Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub-Jay. Auk: Ornithological Advances 132:634-646. https://doi.org/10.1642/AUK-14-258.1

Myers, R. L. 1990. Scrub and high pine. Pages 150-193 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rensel, M. A., T. E. Wilcoxen, and S. J. Schoech. 2010. The influence of nest attendance and provisioning on nestling stress physiology in the Florida Scrub-Jay. Hormones and Behavior 57:162-168. https://doi.org/10.1016/j.yhbeh.2009.10.009

Reynolds, S. J., S. J. Schoech, and R. Bowman. 2003. Diet quality during pre-laying and nestling periods influences growth and survival of Florida Scrub-Jay (Aphelocoma coerulescens) chicks. Journal of Zoology 261:217-226. https://doi.org/10.1017/S0952836903004023

Russell, A. F., N. E. Langmore, A. Cockburn, L. B. Astheimer, and R. M. Kilner. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. Science 317:941-944. https://doi.org/10.1126/science.1146037

Russell, A. F., N. E. Langmore, J. L. Gardner, and R. M. Kilner. 2008. Maternal investment tactics in superb fairy-wrens. Proceedings of the Royal Society B: Biological Sciences, 275:29-36. https://doi.org/10.1098/rspb.2007.0821

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540. https://www.jstor.org/stable/4090416

Stacey, P. B., and W. D. Koenig, editors. 1990. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9780511752452

Stallcup, J. A., and G. E. Woolfenden. 1978. Family status and contributions to breeding by Florida Scrub Jays. Animal Behaviour 26:1144-1156. https://doi.org/10.1016/0003-3472(78)90104-5

U.S. Fish and Wildlife Service (USFWS). 1987. Endangered and threatened wildlife and plants; threatened status for the Florida scrub-jay. 50 CFR Part 17. Federal Register Vol 52, No. 106, Proposed Rules, May 21, 1986. USFWS, Jacksonville, Florida, USA.

U.S. Fish and Wildlife Service (USFWS). 2007. Florida Scrub-Jay (Aphelocoma coerulescens) 5-year review: summary and evaluation. USFWS, Jacksonville, Florida, USA.

U.S. Fish and Wildlife Service (USFWS). 2019. Draft revised recovery plan for the Florida Scrub-Jay (Aphelocoma coerulescens). U.S. Fish and Wildlife Service. Atlanta, Georgia, USA. https://ecos.fws.gov/docs/recovery_plan/Florida%20Scrub-Jay%20Draft%20Revised%20Recovery%20Plan.pdf

Venables W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA. https://doi.org/10.1007/978-0-387-21706-2

Weekley, C. W., E. S. Menges, A. L. Craddock, and R. Yahr. 2013. Logging as a pretreatment or surrogate for fire in restoring Florida scrub. Castanea 78:15-27. https://doi.org/10.2179/12-030

Woolfenden, G. E. 1975. Florida Scrub Jay helpers at the nest. Auk 92:1-15. https://doi.org/10.2307/4084414

Woolfenden, G. E. 1978. Growth and survival of young Florida Scrub Jays. Wilson Bulletin 90:1-18.

Woolfenden, G. E., and J. W. Fitzpatrick. 1977. Dominance in the Florida Scrub Jay. Condor 79:1-12. https://doi.org/10.2307/1367524

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Monographs in population biology, volume 20. Princeton University Press, Princeton, New Jersey, USA.

Woolfenden, G. E., and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), version 2.0, in A. F. Poole and F. B. Gill, editors. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.228

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Appendix 1. Sample sizes used in provisioning, nestling mass, nest survival, and productivity analyses grouped by year and treatment (helpers, no helpers, and helpers experimentally removed). For all analyses with a 2-level helper effect, groups with no helpers and groups where helpers were experimentally removed were pooled.

	2018			2019			
Analysis	Helpers	No Helpers	Helpers Removed	Helpers	No Helpers	Helpers Removed	Total
Provisioning rates							
Total nests	3	10	2	9	7	2	33
Female breeders	3	6	2	6	4	2	23
Male breeders	3	6	2	6	4	2	23
Helpers	3	-	-	8	-	-	11
Nestling mass							
Nestlings	15	44	2	21	18	4	104
Broods	5	16	2	8	7	2	40
Nest survival							
Nests	22	41	6	24	32	6	131
Productivity							
Nests	22	39	6	23	32	6	128
Successful nests	9	20	2	10	4	2	47

Appendix 2. Florida Scrub-Jay family groups monitored in 2018 and 2019 in Ocala National Forest, Florida, USA, with the sex and age of banded helpers. Age categories include second-year (SY; hatched the previous breeding season), after-second year (ASY; banded as adults but hatch year unknown), third-year (TY; hatched two breeding seasons ago), and fourth-year (4Y; hatched three breeding seasons ago).

	2018	2019
Family groups	56	55
Helpers removed	6	4
0 helpers	33	30
1 helper	13	18
2 helpers	3	2[ab]
3 helpers	1[c]	1
Mean group size	2.39	2.47
Banded male helpers	9	14
SY	4	14
ASY	2	0
TY	2	0
4Y	1	0
Banded female helpers	4	4
SY	2	3
ASY	2	1
Banded helpers (sex unknown)	1	0
SY	1	0

[a]This territory had two helpers on the first nest attempt and one helper on the second attempt.
[b]One of these territories had three different helpers across three nest attempts with a maximum of two helpers at one nest.
[c]This territory had one helper for the first and second nest attempt and three helpers on the third nest attempt.

Appendix 3. Raw nestling provisioning rate (feeds/hr) for Florida Scrub-Jay adults in family groups with (gray) or without (white) helpers from Ocala National Forest, Florida, USA (2018-2019). Boxplots represent median values (bold line), first and third quartiles (box), 95% confidence intervals (whiskers), and outliers (dots).