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Inclusive Fitness May Explain Some but Not All Benefits Derived from Helping Behavior in a Cooperatively Breeding Bird

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ABSTRACT: In cooperative breeding systems, inclusive fitness theory predicts that nonbreeding helpers more closely related to the breeders should be more willing to provide costly alloparental care and thus have more impact on breeder fitness. In the red-cockaded woodpecker (*Dryobates borealis*), most helpers are the breeders' earlier offspring, but helpers do vary within groups in both relatedness to the breeders (some even being unrelated) and sex, and it can be difficult to parse their separate impacts on breeder fitness. Moreover, most support for inclusive fitness theory has been positive associations between relatedness and behavior rather than actual fitness consequences. We used functional linear models to evaluate the per capita effects of helpers of different relatedness on eight breeder fitness components measured for up to 41 years at three sites. In support of inclusive fitness theory, helpers more related to the breeding pair made greater contributions to six fitness components. However, male helpers made equal contributions to increasing prefledging survival regardless of relatedness. These findings suggest that both inclusive fitness benefits and other direct benefits may underlie helping behaviors in the red-cockaded woodpecker. Our results also demonstrate the application of an underused statistical approach to disentangle a complex ecological phenomenon.

Keywords: red-cockaded woodpecker, *Dryobates borealis*, kin selection, helpers, demography, functional linear models.

Introduction

In cooperatively breeding bird species, helpers often assist other individuals to rear their offspring before beginning to reproduce on their own. Cooperative breeding systems are often observed in harsh environments (Ridley et al. 2008; Jetz and Rubenstein 2011; Groenewoud et al. 2016; Cornwallis et al. 2017) or situations where high-quality breeding territories are limited (Emlen 1982; Walters et al. 1992) and/or dispersal costs are high (Stacey and Ligon 1991), all circumstances that discourage individuals from dispersing and breeding independently at an early age. Where high-quality breeding territories are limited, the best option is to remain on the natal territory as a nonbreeding helper and await opportunities to obtain a high-quality breeding position (why stay sensu Emlen 1982). Several possible mechanisms exist by which individuals could obtain direct fitness benefits by helping to rear offspring while remaining on a territory as nonbreeders (Kingma et al. 2011), or they might obtain indirect benefits (i.e., inclusive fitness) by helping to rear offspring closely related to them (Emlen et al. 1991; Bourke 2014; why help sensu Emlen 1982). In a number of cooperative breeding systems (Lennartz et al. 1987; Walters 1990; Khan and Walters 2002; Russell et al. 2007; Gusset and Macdonald 2010; Sparkman et al. 2011), helpers are known to increase breeder survival and reproductive success, a necessary condition for both indirect benefits and most direct benefits of helping to exist.

In reality, helpers often vary in their degree of genetic relatedness to the breeding pair whose offspring they help to rear (Dunn et al. 1995; Magrath and Whittingham 1997; Cockburn 1998; Clutton-Brock et al. 2000; Lukas et al. 2005; Riehl 2013). Moreover, when dispersal of juveniles from natal territories is sex biased (Greenwood 1980), the degree of relatedness between helpers and breeders will likely differ according to the sex of the helpers. For example, our study species, the red-cockaded woodpecker (*Dryobates borealis* L.), exhibits sex biases in both philopatry and dispersal, similar to many cooperatively breeding birds (Greenwood 1980). In this species, male offspring often remain as helpers, whereas female offspring more often disperse as juveniles. Breeding positions are inherited through the paternal line, so females

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that remain to help almost never inherit the breeding position in their natal territory (Walters et al. 1988; Walters 1990). Thus, male helpers typically assist a paternal relative of varying relatedness (e.g., father, uncle, brother, half brother) and either their mother or an unrelated female. Although some males disperse as juveniles and join nonnatal groups as unrelated helpers, this behavior is much more common among females (Walters and Garcia 2016). Thus, female helpers are often unrelated to either breeder, although some, similar to male helpers, remain in their natal territory and assist a male relative and either their mother or an unrelated female. On average, male helpers are more related to the breeding pair than are female helpers in this species.

When helpers differ by sex and relatedness to the breeders, an important question arises: do all helpers contribute equally to breeder fitness? According to Hamilton's (1964) law, altruism will be favored when $r \times B > C$, where (in the current context of alloparental care) B is the fitness benefit received by the offspring or breeder, $\mathbb{C}$ is the fitness cost paid by the helper, and r is the relatedness of the helper to the breeder or offspring the helper helps to rear. If the evolution of helping behavior is based on indirect fitness benefits, Hamilton's law predicts that helpers who are more closely related to the breeders should be willing to engage in more costly behaviors to provide benefits to the offspring they help to rear. Likewise, less related helpers should provide fewer, less costly benefits, and unrelated helpers should provide no benefits. Despite Hamilton proposing the theory of inclusive fitness more than 50 years ago, very few studies have tested the theory directly by measuring fitness costs and/or benefits (but see, e.g., Hatchwell et al. 2014). Instead, most evidence from natural populations supporting Hamilton's idea relies on the positive correlation between helper social behaviors (e.g., feeding frequency) and relatedness (Metcalf and Whitt 1977; Emlen and Wrege 1989; Hogendoorn and Leys 1993; Gadagkar 2001; Krakauer 2005; Bourke 2014; Green et al. 2016). However, such a correlation is incomplete support for Hamilton's idea, as social behaviors may not necessarily translate into fitness benefits (e.g., survival of breeders and offspring).

To quantify how often the relationship between fitness benefits and helper relatedness has been assessed, we classified published studies on helping in birds (tables 1, S1; tables S1–S4 are available online). The majority of studies quantified helper behaviors only and did not assess fitness consequences of helping. Those studies that did measure effects of helpers on breeder fitness either did not consider helper relatedness at all (comparing fitness in groups with and without helpers) or (in a few cases) considered only the average relatedness of helpers (Russell and Rowley 1988; Dickinson et al. 1996; Hatchwell et al. 2004, 2014; Green and Hatchwell 2018). We did not find any studies that considered the fitness effects of helpers that differed continuously in their relatedness to the breeders or offspring within the same social group.

Table 1: Contingency table summarizing ornithological literature on how articles quantified helper effects in social groups

	Article quantifies social behaviors of helpers only	Article quantifies helper effects on breeders' fitness components[a]
Article does not quantify helpers' relatedness to breeders or offspring	35	40
Article considers only average relatedness of helpers[b]	12	5
Article considers the consequences of variation in helpers' relatedness	22	0

Note: Articles were classified according to whether they quantified helper effects on either social behavior only (first column) or fitness components (second column). Then, articles were classified according to whether they did not consider relatedness of helpers (first row), considered average relatedness (second row), or considered multiple levels of relatedness of helpers (third row). Numbers are the total number of articles that fall under each category (refer to table S1). Relatedness of individuals could be either to the offspring or to the breeders separately.

[a] Fitness components may include breeder survival, offspring production, etc.

[b] Average relatedness also includes articles that consider only one class of related helpers, such as comparison between unrelated vs. related.

When breeding groups include multiple helpers that differ in relatedness to the breeders (as well as sex), it becomes challenging to disentangle their per capita effects. While one could imagine doing a multiple regression with the number of helpers in each relatedness and sex category as potential predictors of fitness, such complex models often pose a statistical challenge, since with an α level of .05, one of the 20 covariates is likely to be significant by chance alone. In ecology, the traditional approach for determining which possible drivers are influential is to either create a priori assumptions about which few drivers to include or use data-dredging approaches (Dalgleish et al. 2011; Crone et al. 2019), but these methods are prone to selecting spurious predictors (for details on model selection approaches, see Burnham and Anderson [2013] and James et al. [2013]).

However, recent developments in statistical modeling can reduce the chance that spurious predictors are included in the final model (Teller et al. 2016; Crone et al. 2019). One such approach is functional linear models (FLMs), which are a type of linear regression spline (Ramsay and Silverman 2005; Ramsay et al. 2009) that can reduce the dimensionality of the problem of multiple predictors (see Teller et al. 2016; Tenhumberg et al. 2018; Kerr et al. 2021). FLMs assume that the effect of some predictor (e.g., number of helpers) on a response (e.g., reproductive success of breeders) is a smooth function of some continuous attribute of the predictor (e.g., relatedness of the helpers). Therefore, FLMs avoid two problems that one may encounter when using many regression approaches: (1) the need to average relatedness of all helpers within groups to estimate their effects on group fitness (see table 1 for examples) and (2) model overparameterization when including all helpers separated by their relatedness, leading to potential spurious effects. Therefore, the advantage of FLMs is that they use fewer parameters to estimate fitness effects of helpers in relation to their relatedness and sex and thus reduce the likelihood of choosing spurious predictors.

Here, we used FLMs to delineate whether male and female helper effects on eight breeder fitness components vary according to their relatedness to breeders in the red-cockaded woodpecker. In doing so, we aim to test Hamilton's idea that more closely related helpers may provide more benefits (and presumably incur greater costs) to help raise offspring that are not their own. In the present context of helper behavior, rB is more likely to exceed $\mathbb{C}$ as r increases; thus, one expects the behaviors that affect fitness components to be more frequent and the resulting impact on fitness to be greater as r increases. We do not quantify helper behavior here but instead focus directly on effects of helpers on breeder fitness. First, we evaluated whether helpers bolster breeder fitness based on their relatedness to the offspring (or, equivalently, to the two breeders). Second, for the particular case of breeder survival where relatedness (and thus inclusive fitness benefits) can differ between the two breeders, we also evaluated whether helper effects vary according to their relationship to the male or female breeder rather than both, as, for example, conflicts over the breeding position may impact helper effects on survival of same-sex, but not opposite-sex, breeders.

Methods

Study Species

Red-cockaded woodpeckers (*Drybates borealis*) inhabit mature pine savannahs across the southeastern United States (Walters 1990; Jackson 2020). The species is legally protected throughout its range under the US Endangered Species Act, as its numbers are greatly diminished compared with its historical abundance as a result of conversion of pine savannahs to other uses, timber harvest, and fire suppression. Throughout the year, family groups defend territories that contain a set of cavities excavated in living pines. Helpers participate in territory defense against conspecifics, cavity excavation, feeding of nestlings and fledglings, and nest defense against predators. In contrast to many other cooperative breeders, helpers also incubate eggs (Walters et al. 1988), supported by the development of brood patches (Jackson 2020).

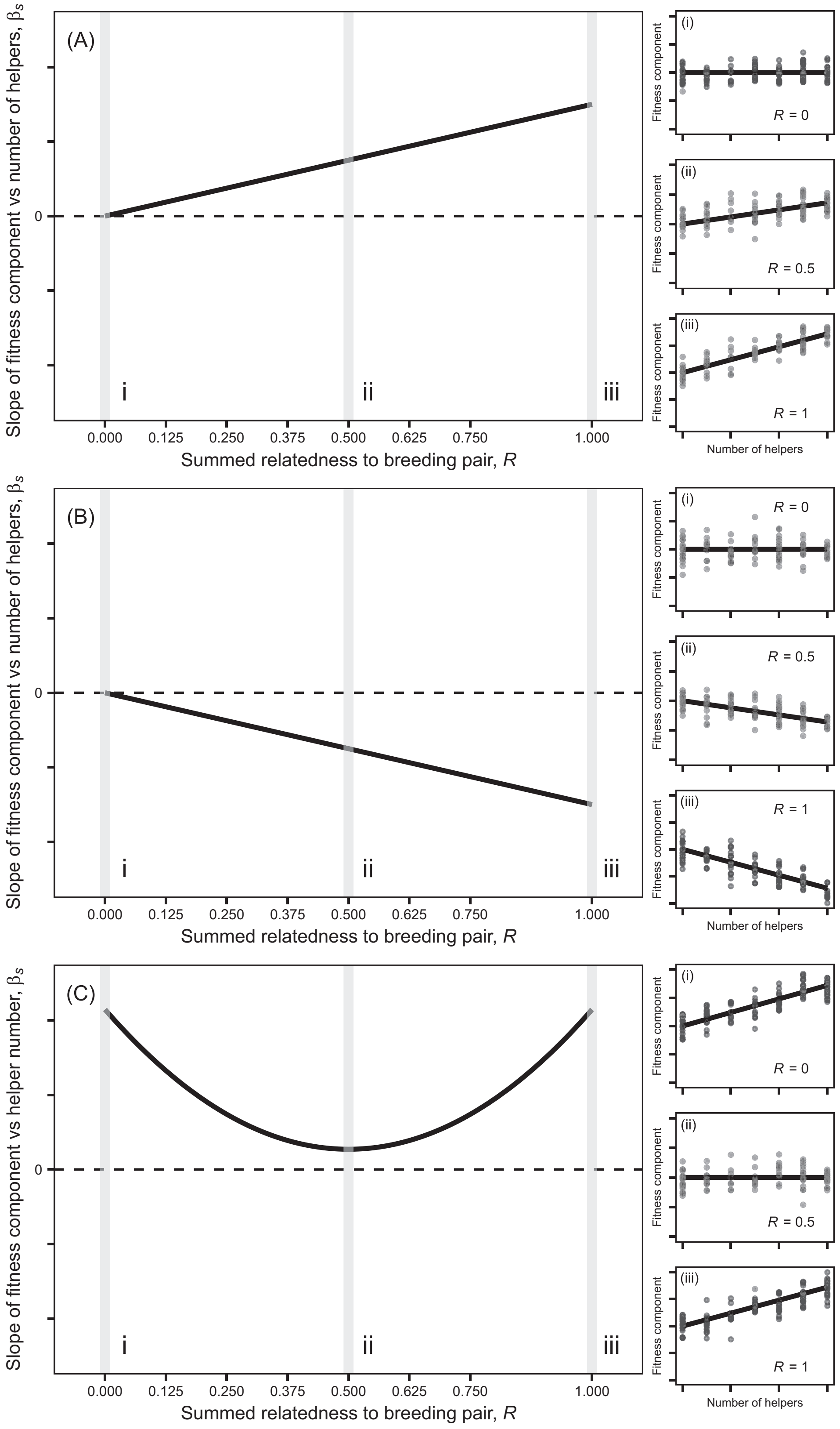
Data Collection

We used long-term demographic monitoring data collected over 28–41 consecutive years at three sites: the Sandhills region in south-central North Carolina (1980–2020), Marine Corps Base Camp Lejeune on the central coast of North Carolina (1986–2020), and Eglin Air Force Base in the western panhandle of Florida (1993–2020). Monitoring methods are described in detail by Walters et al. (1988; for more details on monitoring, see the supplemental PDF, sec. A). See Walters and Garcia (2016) for how individuals are assigned breeder and helper status.

Relatedness Calculations

We created a pedigree for each helper, extending back as far as its grandparents, and used it to determine that helper's relatedness to the two breeders each year (for the pedigree procedure, see fig. S1; for examples of common pedigrees with their associated relatedness values, see fig. S2). Determining relatedness based on a pedigree assumes no extrapair matings or intraspecific brood parasitism. Previous genetic work found no evidence of extrapair matings in this species (Haig et al. 1994), and the few enlarged clutches we observed (six to eight eggs, as opposed to the typical two to five eggs) often occurred in groups containing cobreeding females that laid together in the same nest, suggesting that brood parasitism rarely or never occurs. Cases of cobreeding were rare (~0.54% of groups) and excluded from these analyses.

We also summed the relatedness coefficients to the two breeders. While the literature often refers to relatedness to the offspring (e.g., Nam et al. 2010; Kramer et al. 2016; Dias et al. 2017; Vitikainen et al. 2017), a helper's relatedness to the offspring is simply one-half the summed relatedness to the breeders. By calculating relatedness in three different ways, we could assess whether helper effects on fitness components reflect relatedness to the offspring versus to each breeder independently. Given the extent of the pedigrees, relatedness r of helpers to each breeder separately had four


(A)
Slope of fitness component vs number of helpers, β_s
0
i
ii
iii
0.000
0.125
0.250
0.375
0.500
0.625
0.750
1.000
Summed relatedness to breeding pair, R
(i)
R = 0
(ii)
R = 0.5
(iii)
R = 1
Fitness component
Number of helpers
(B)
Slope of fitness component vs number of helpers, β_s
0
i
ii
iii
0.000
0.125
0.250
0.375
0.500
0.625
0.750
1.000
Summed relatedness to breeding pair, R
(i)
R = 0
(ii)
R = 0.5
(iii)
R = 1
Fitness component
Number of helpers
(C)
Slope of fitness component vs helper number, β_s
0
i
ii
iii
0.000
0.125
0.250
0.375
0.500
0.625
0.750
1.000
Summed relatedness to breeding pair, R
(i)
R = 0
(ii)
R = 0.5
(iii)
R = 1
Fitness component
Number of helpers

possible values (i.e., $r \in (0, 0.125, 0.25, 0.5)$) and summed relatedness R of helpers to both breeders had eight possible values (i.e., $R \in (0, 0.125, 0.25, 0.375, 0.5, 0.625, 0.75, 1)$). Although there could be additional inbreeding in the grandparental generation, including it would change the relatedness values only slightly. We included only group × year combinations in which (1) both breeders were known and (2) both parents of every helper were known. Consequently, our analysis includes only group × year combinations in which the relatedness of all helpers to both breeders was known (for a further breakdown of sample sizes, see table S2).

Breeder Fitness Components

We evaluated eight breeder fitness components (and thus components of the inclusive fitness of related helpers): the probability of attempting a nest in a year, clutch size, nest success at the egg stage, nest success at the nestling stage conditioned on nest success at the egg stage, the probability of an egg surviving to fledging (hereafter, "prefledging survival") conditioned on nest success at both stages, the probability of fledglings surviving to the next year (hereafter, "juvenile survival"), female breeder survival, and male breeder survival. Nest success at either stage indicates that the brood avoided both nest predation and abandonment by breeders and helpers (US Fish and Wildlife Service 2003). In contrast, prefledging survival less than one (but greater than zero) indicates partial brood loss, which is likely due to nestling starvation and hatch failure (note that hatching is asynchronous in this species) and is unlikely to be due to predation (LaBranche and Walters 1994; DeLotelle et al. 2004). We separated nest success between the two stages, since the mechanisms responsible for helper effects may differ between them. For example, predators of eggs and nestlings may differ, or a female helper competing for a breeding position might reduce egg success via egg ejection, which has been observed in other bird species (Moreno 2015).

All reproductive components were estimated using data from first nests in each year ($N = 7{,}742$ group × year combinations), as subsequent nest attempts are less common ($N = 618$ group × year combinations) and much less successful. Additionally, almost all subsequent nests are due to failure of the first nest ($N = 604$ of 618 group × year combinations).

Functional Linear Models

We used FLMs to quantify the per capita effects of helpers on breeder fitness components as a smooth function of helpers' relatedness to each breeder or the breeding pair (for simplicity, we show only summed relatedness, R, here). In simpler terms, FLMs calculate a slope of fitness versus helper number for each helper relatedness value and then describe how relatedness may influence these slopes (i.e., the slope of fitness vs. helper number becomes a nonlinear function of helper relatedness). The FLM expresses fitness component Y as

$$Y_i = \alpha_0 + \sum_{s,R} \beta_s(R) X_{i,s}(R), \tag{1}$$

where Y_i is the fitness component (on a link function scale) for breeding pair i in a given year, α_0 is the intercept plus potential additional terms not based on relatedness (e.g., fixed effects of breeder age, site, etc.), $X_{i,s}(R)$ is the number of helpers of sex s (i.e., male or female) and summed relatedness R to breeding pair i, $\beta_s(R)$ is the estimated slope of the fitness component with respect to helpers of sex s and relatedness R (referred to as the "smooth function" below), and the summation is over sexes and relatedness values. For male and female breeder survival, we compared (using Akaike information criterion [AIC]) models that evaluated whether helper effects were associated with their relatedness to the breeding pair (i.e., R ranging from 0 to 1) or relatedness to only that breeder (i.e., r ranging from 0 to 0.5; using bbmle::ICtab; Bolker and R Core Team 2016).

The per capita helper effects $\beta_s(R)$ in equation (1) as a smooth function of relatedness could have a variety of shapes (fig. 1). Where the function is positive, helpers of that relatedness increase the breeder fitness component (fig. 1*A*), and where it is negative, helpers of that relatedness decrease breeder fitness (fig. 1*B*). Differences in per capita effects based on relatedness to the breeding pair would result in a smooth function in which the slopes increase with relatedness (fig. 1*A*), decrease with relatedness (fig. 1*B*), or both over different ranges of relatedness (fig. 1*C*). Note that one limitation of FLMs is that the

Figure 1: Hypothetical results from functional linear models. *Left*, examples of possible smooth functions for per capita helper effects on breeder fitness components versus relatedness. *Right*, relationships between breeder fitness and the number of helpers at three particular values of relatedness (indicated by vertical lines and roman numerals) in the smooth functions on the left. *A*, Positive relatedness-based effects. *B*, Negative relatedness-based effects. *C*, Mixed relatedness-based effects. Horizontal dashed line represents no relatedness-based and no per capita effects of helpers (i.e., slope = 0 for all summed relatedness values). Relatedness is measured as the summed relatedness coefficient to the breeding pair R, whereby a son or daughter of both breeders would have $R = 1$.

function describing the covariate's effect (i.e., helper number) on the response (i.e., breeder fitness) is constrained to be a linear relationship; note that the effect of the attribute (i.e., helper relatedness) on these slopes can be nonlinear (i.e., smooth function).

We parameterized the smooth functions of the relatedness-specific slopes using generalized additive models (GAMs; using mgcv::gam function; Wood 2011) in R (R Core Team 2020). We used a cubic spline basis as the penalized smoother for our GAMs that sets the coefficient for a covariate with no real effects to zero (for a good introduction to GAMs and their terms, i.e., details on knots and spline penalties, see Zuur 2012). We constrained the number of knots to a maximum of five and rejected any nonunimodal function. We did this because GAMs are prone to overfitting (Wood 2011; Zuur 2012), nonunimodal functions would not be biologically plausible across the set of *R* values (refer to Kerr et al. 2021), and the number of discrete *R* values would not support models with many knots. Note that the mgcv package provides the effective degrees of freedom (edf), which indicates the magnitude of nonlinearity of the spline (e.g., $\mathrm{edf} = 0$ suggests no effect of relatedness, $\mathrm{edf} = 1$ suggests linearity, $\mathrm{edf} > 2$ suggests nonlinearity; Wood 2006; Zuur 2012; Hunsicker et al. 2016). We used a quasi-Poisson family for clutch size to account for underdispersed count data (clutch size ranging from one to six) and a binomial family for the remaining fitness components, all of which represented probabilities.

To account for known demographic and geographical effects independent of per capita helper relatedness (Walters 1990; DeMay and Walters 2019; Kappes et al. 2021), we included several covariates in the GAMs. Specifically, we included fixed parametric terms (incorporated into α_0 in eq. [1]) of study site, linear and quadratic effects of breeder age (age of both breeders for reproductive components and only breeder age of the respective sex for breeder survival), and sex (for juvenile survival) where appropriate. The majority of helpers remain on their natal territory as adults, but a small number of individuals disperse and join a nonnatal group as an unrelated helper. Both choosing to remain on the natal territory and choosing which group to join as an unrelated helper could be influenced by territory quality. Therefore, we also included random effects of year and territory to account for temporal variation in climate and spatial variation in habitat quality that often make it challenging to detect helper effects (Brouwer et al. 2020; Downing et al. 2020). Because habitat quality could also change over time in a particular territory cluster (e.g., because of better conservation management in some periods than others), we also compared models with random terms constructed by separating territories by management period (for details, see the supplemental PDF, sec. A). Since high-quality breeders or territories may produce helpers that remain in the group, resulting in higher relatedness to the breeding pair, we further investigated whether relatedness effects were confounded with either breeder quality or territory quality (see the supplemental PDF, sec. B). Note that these analyses specifically and results for covariates generally are not discussed further in the article but are presented in sections B and D of the supplemental PDF, respectively. Note also that we were unable to assess breeder quality because of low sample size for each unique breeder.

We used backward elimination to identify significant parametric terms (James et al. 2013), and the significance of smooth terms was evaluated using Wald-like tests (using stats::anova; R Core Team 2020) that compute the likelihood that the splines constituting the smooth functions are jointly zero. We used an effective *P* value threshold of .01, since *P* values for GAMs are only approximate (for details on effective *P* values for smooth components, see Wood 2013). We used generalized linear models (GLMs) to further explore fitness effects of helpers of certain relatedness values that the FLMs indicated had nonzero effects on fitness components (see the supplemental PDF, sec. C; tables S3, S4), since FLMs test the significance only of the overall spline. For example, this would be analogous to a post hoc test for an ANOVA to assess which group means differ, as statistical significance of the term indicates only that group means do differ but not which groups. Therefore, these GLMs were performed to determine whether helpers of different sex or summed relatedness values that had similar nonzero trends (i.e., all positive or all negative slope coefficients) had similar or dissimilar effects (e.g., did all of the helpers with positive effects have a similar magnitude of their effect?).

Results

Across 41 years and three sites, breeding pairs were more likely to have male helpers (45.1% of breeding pairs, $N = 4{,}293$ of 9,522 group × year combinations) than female helpers (7% of breeding pairs, $N = 666$ of 9,522 group × year combinations), including cases of unknown relatedness of helpers. Helper effects on breeder survival were better explained by helper relatedness to the breeding pair rather than to the respective breeder ($\Delta\mathrm{AIC}_{\text{breeder-pair}} = 2.4$ and 7.4 for female and male breeder survival, respectively), indicating that these effects are not specific to the breeder in the pair more related to the helpers. Hence, we describe the results of the models considering summed relatedness to the breeding pair for all fitness components. We point out cases where relatedness may be confounded with territory quality. Additional helper effects on juvenile survival emerged when we considered only high-quality territories; however, these are not discussed further (see the supplemental PDF, sec. D).

Reproductive Components

The average per capita effect of both male and female helpers on the probability of attempting a nest increased with their relatedness to the breeding pair (Wald test comparing models with and without smooth term; male: $\chi^2 = 32$, edf $= 1.9$, $P < .001$; female: $\chi^2 = 5.7$, edf $= 1$, $P = .008$). Male helpers moderately or highly related to one or both breeders ($R \geq 0.5$) had a positive per capita effect, with less related male helpers having no effect (fig. 2*A*). Similarly, only female helpers that are the daughters of the breeding pair ($R = 1$) had a positive per capita effect, with all other female helpers that are less related ($R < 1$) having no effect (fig. 2*B*). However, the number of highly related female helpers was confounded with territory quality (supplemental PDF, sec. B) and should be interpreted with caution.

The average per capita effect of male helpers on clutch size increased with their relatedness to the breeding pair (Wald test; $F = 10.7$, edf $= 2.7$, $P < .001$). Male helpers related to one or both breeders at a level of $R \geq 0.5$ had a positive per capita effect on clutch size, with male helpers less related having no effect (fig. 2*C*). Female helpers had no effect on clutch size regardless of their relatedness to the breeding pair (Wald test; $F = 1.4\mathrm{E}{-4}$, edf $= 8\mathrm{E}{-4}$, $P = .477$; fig. 2*D*).

The average per capita effects of male and female helpers on nest success at the egg stage increased with their relatedness to the breeding pair (Wald test; male: $\chi^2 = 52.5$, edf $= 1.6$, $P < .001$; female: $\chi^2 = 12.3$, edf $= 1.6$, $P < .001$), with less related male helpers ($R < 0.5$) and female helpers ($R < 0.75$) having no effect (fig. 2*E*, 2*F*). The average per capita effect of male helpers on nest success at the nestling stage increased with their relatedness to the breeding pair (Wald test; $\chi^2 = 19.8$, edf $= 1.7$, $P < .001$), with only unrelated male helpers ($R = 0$) having no effect (fig. 2*G*). However, the number of highly related male helpers was confounded with territory quality (supplemental PDF, sec. B), suggesting that this effect should be interpreted with caution. Female helpers had no effect on nest success at the nestling stage, regardless of their relatedness to the breeding pair (Wald test; $\chi^2 = 0.5$, edf $= 0.4$, $P = .232$; fig. 2*H*).

The positive per capita effect of male helpers on prefledging survival remained constant with their relatedness to the breeding pair (Wald test; $\chi^2 = 132$, edf $= 2.4$, $P < .001$; fig. 2*I*). Female helpers of any relatedness to the breeding pair had no effect on prefledging survival (Wald test; $\chi^2 = 2.8$, edf $= 1.7$, $P = .178$; fig. 2*J*).

Survival Components

Neither male helpers nor female helpers, regardless of their relatedness to the breeding pair, had an effect on juvenile survival (Wald test; male: $\chi^2 = 5.5\mathrm{E}{-4}$, edf $= 2\mathrm{E}{-3}$, $P = .567$; female: $\chi^2 = 4.2$, edf $= 2.6$, $P = .192$; fig. 3*A*, 3*B*). Male helpers of any relatedness had no per capita effect on female breeder survival (Wald test; $\chi^2 = 0.8$, edf $= 0.4$, $P = .181$). However, the average per capita effect of female helpers on female breeder survival slightly increased with their relatedness to the breeding pair (Wald test; $\chi^2 = 4.9$, edf $= 1.2$, $P = .023$). More specifically, only female helpers that are the daughters of the breeding pair ($R = 1$) had a slight positive per capita effect, with female helpers less related having no effect (fig. 3*D*).

The average per capita effect of male helpers on male breeder survival increased with their relatedness to the breeding pair (Wald test; $\chi^2 = 26.9$, edf $= 2.9$, $P < .001$), with highly related male helpers ($R \geq 0.75$) having positive effects and unrelated male helpers ($R = 0$) having a negative effect (fig. 3*E*; for GLM results, see the supplemental PDF, sec. C). Female helpers, regardless of their relatedness to the breeding pair, had no effect on male breeder survival (Wald test; $\chi^2 = 2.8\mathrm{E}{-5}$, edf $= 2\mathrm{E}{-3}$, $P = .955$; fig. 3*F*).

Discussion

Helpers had positive effects on seven of the eight breeder fitness components we analyzed, and male helpers had more positive effects (six components) than female helpers (three components). Our results are consistent with Hamilton's rule, in that the magnitude of these helper effects increased with the relatedness of the helpers to the breeders, with only one exception. Although the shape of the relationship between the magnitude of the helper effect and relatedness varied (figs. 2, 3), the general pattern was that the helper effect increased with relatedness, with less related (male and female effects on probability of nesting, male effect on clutch size, male and female effects on nest success at the egg stage, female effect on female breeder survival) or unrelated (male effect on nest success at the nestling stage) helpers having no significant effect or a negative effect (male effect on male breeder survival) on breeder fitness. In two of these cases (female effect on probability of nesting, male effect on nest success as the nestling stage), helper effects are potentially confounded with effects of territory quality. See section B of the supplemental PDF for details.

Inclusive fitness theory predicts that more related helpers should be more willing to provide benefits (even costly ones), since their gains in inclusive fitness would

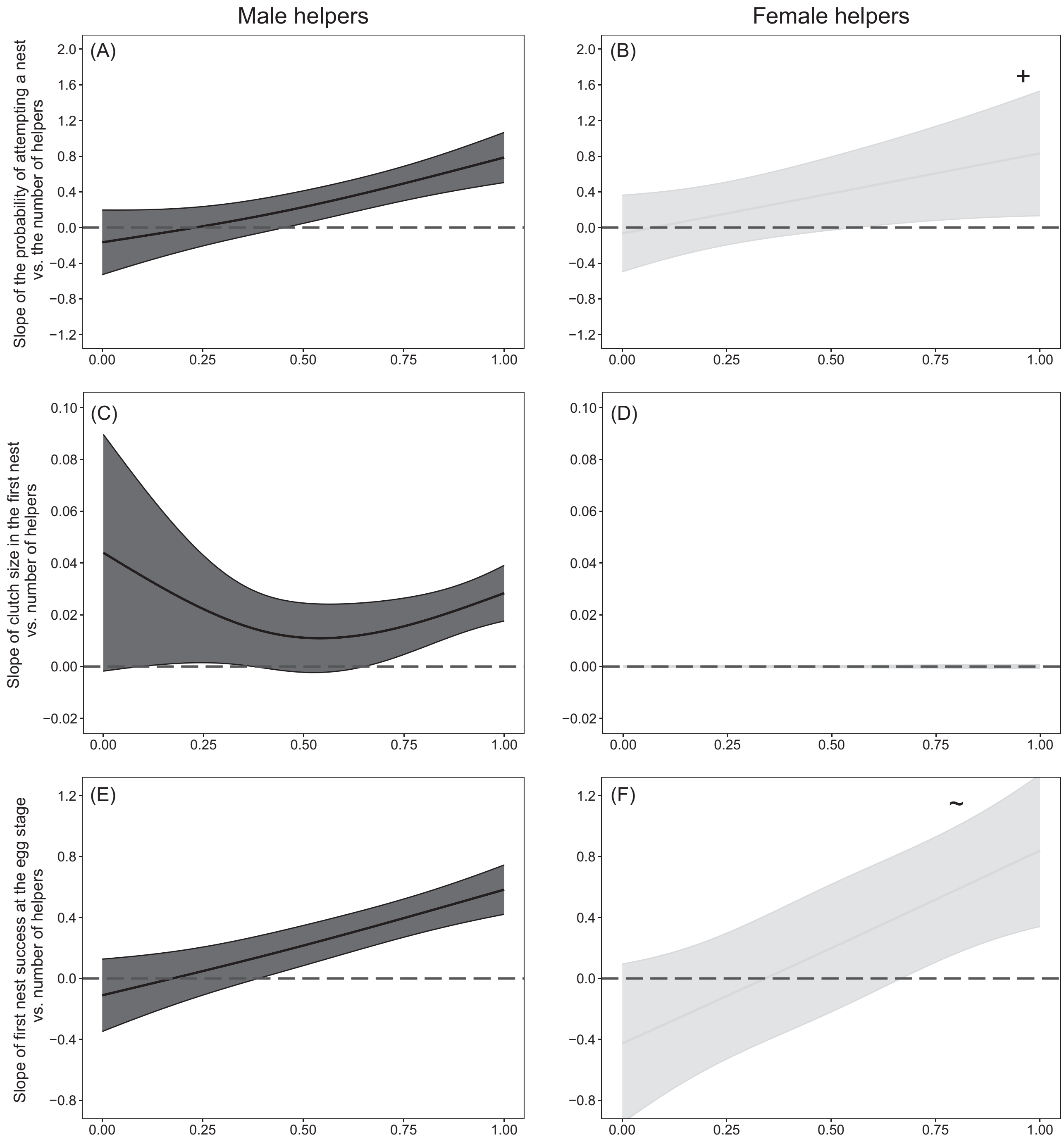


Figure 2: Relatedness-specific slopes from the functional linear models of five reproductive components of breeder fitness versus the number of male (*left*) and female (*right*) helpers. The five reproductive components are probability of attempting a nest (*A*, *B*), clutch size (*C*, *D*), nest success at the egg stage (*E*, *F*), nest success at the nestling stage (*G*, *H*), and prefledging survival (*I*, *J*). The shaded bands represent the best estimate ± standard error. Any value above the dashed line at zero has a positive per capita effect, whereas any value below the line has a negative per capita effect (refer to fig. 1). The plus sign indicates a potential spurious effect due to confounding with territory quality, whereas the sim symbol indicates weak evidence for spurious effects (for more details, see the supplemental PDF, sec. D). See figures S3 and S4 for histograms of sample sizes.

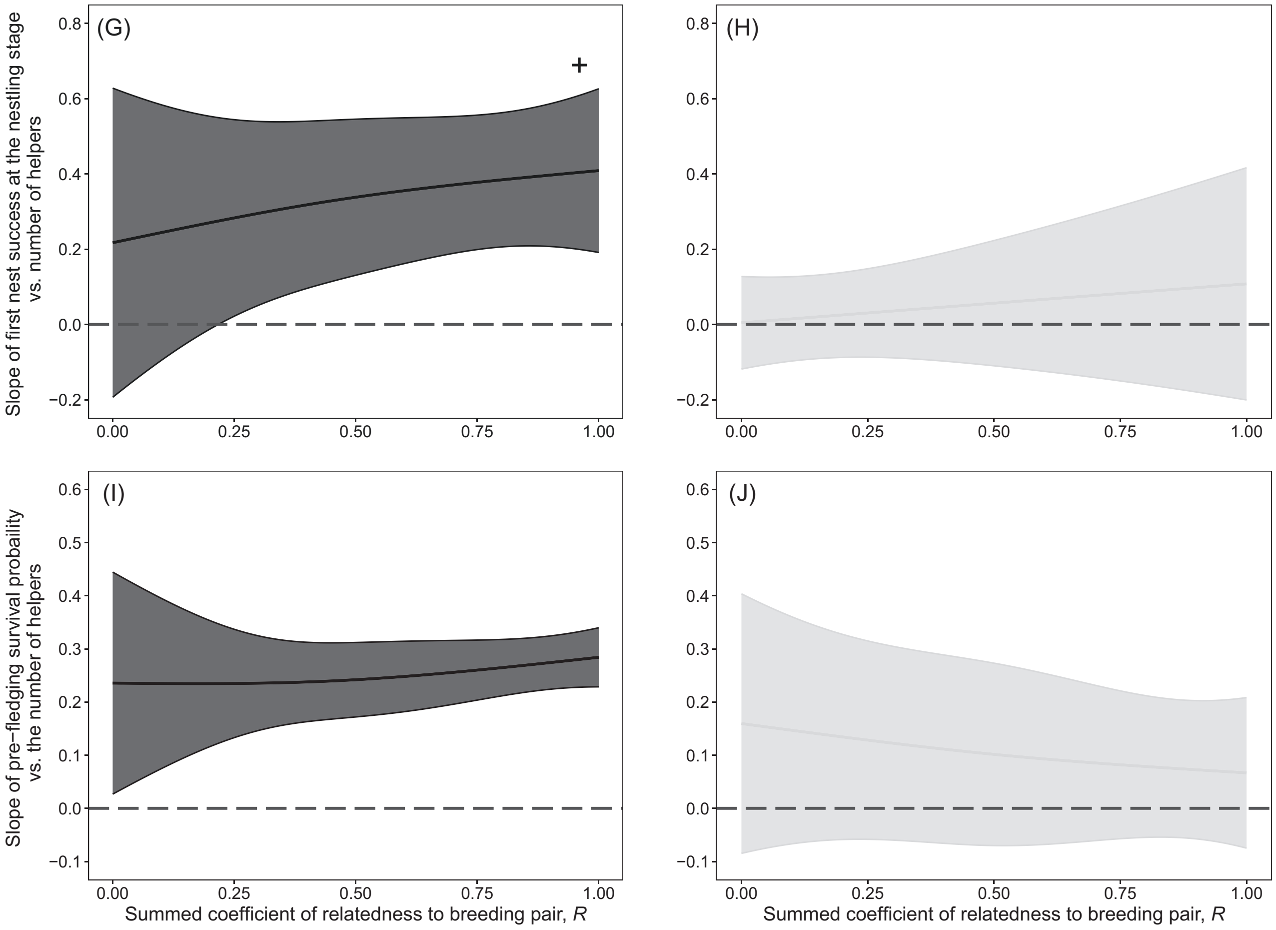


Figure 2: (*Continued*)

be greater (Hamilton 1964). Where costs and benefits of a particular beneficial act are fairly constant, one would expect a threshold effect, whereby only helpers above a particular relatedness gain indirect benefits from the act. Where costs and benefits of a particular act vary, one would expect circumstances where a helper gains indirect fitness benefits from the act to increase in frequency with relatedness. Most of the relationships between helper effects and relatedness we observed resemble the latter case, although a few (figs. 2*C*, 3*E*) resemble the former. Regardless, our principal contribution is to show that helper effects on breeder fitness scale with relatedness in the manner predicted by inclusive fitness theory.

Of course, a definitive test of Hamilton's rule would require identifying the acts involved and measuring costs and benefits. Hatchwell et al. (2014) and Emlen and Wrege (1989) provide the only such tests for cooperatively breeding birds that we are aware of (see also Bourke 2014). We did not measure any potentially relevant behavior or otherwise investigate what the mechanisms responsible for the helper effects we observed might be, but we can offer some insights based on what is known of helper behavior and the biology of the red-cockaded woodpecker to guide such research.

We have found no previous studies outlining a behavioral mechanism by which helpers could increase the probability of nesting or clutch size. Therefore, we suspect that these positive associations could be a result of changes in breeder behavior when in the presence of helpers rather than a result of helper behavior affecting these components. That is, in the presence of highly related helpers that will later have positive effects on nest success and prefledgling survival, breeding females may be more likely to nest and to lay larger clutches. Observed effects on nest success and prefledgling survival, on the other hand, could arise from helper behavior. Nest predation is a major cause of nest failure for red-cockaded woodpeckers (US Fish and Wildlife Service 2003). Hence, nest defense by helpers is a potential mechanism by which helpers could affect nest success and a behavior that one can imagine

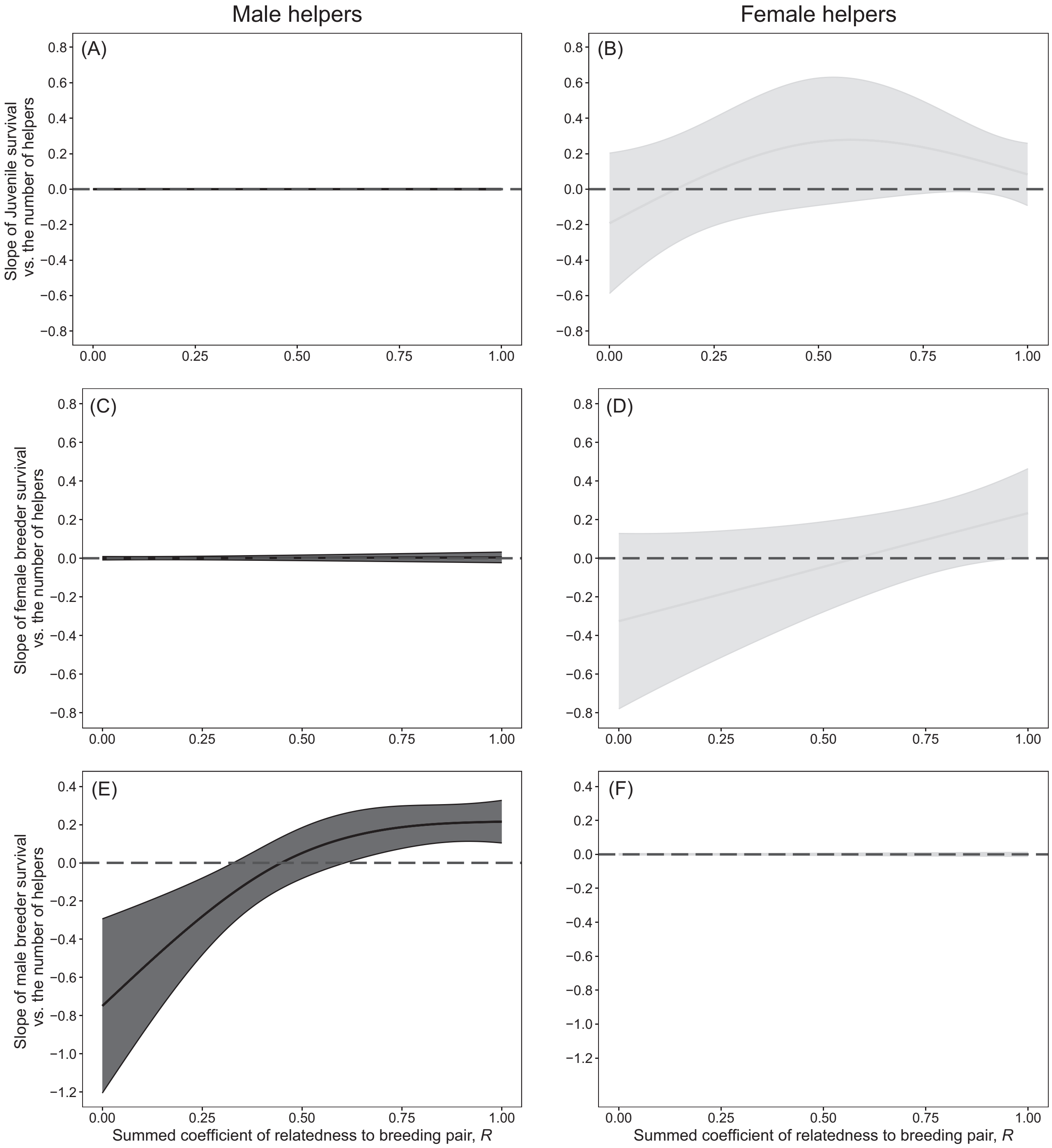


Figure 3: Relatedness-specific slopes from the functional linear models of three survival components of breeder fitness versus the number of male (*left*) and female (*right*) helpers: juvenile survival (*A*, *B*), female breeder survival (*C*, *D*), and male breeder survival (*E*, *F*). The shaded bands represent the best estimate ± the standard error. Any value above the dashed line at zero has a positive per capita effect, whereas any value below the line has a negative per capita effect (refer to fig. 1).

varies considerably in its potential benefit (i.e., chance of successful defense) and cost (i.e., mortality risk to the helper). In several cooperatively breeding species, individuals were more willing to engage in risky defense behaviors in social groups with kin than in those without kin (Hesse et al. 2015; Teunissen et al. 2021), which may be linked to increases in inclusive fitness. Helpers have been reported to reduce nest predation rates in several species of cooperatively breeding birds (Woolfenden and Fitzpatrick 1984; Mumme 1992; Schaub et al. 1992; Innes and Johnston 1996; Williams and Hale 2006), but none of these studies evaluate how relatedness of helpers may affect nest defense.

In the red-cockaded woodpecker, most partial brood loss occurs from eggs failing to hatch and nestlings starving in the first few days after hatching (DeLotelle and Epting 1992; LaBranche and Walters 1994) resulting in brood reduction (and not complete loss). Hence, incubation and feeding nestlings are two behaviors that could be responsible for helper effects on prefledgling survival. Red-cockaded woodpeckers are highly unusual among cooperative breeders in that helpers fully participate in incubation (Khan and Walters 2002). In contrast, provisioning of nestlings by helpers is almost universal among cooperatively breeding birds, and provisioning rates have been shown to be higher for helpers more closely related to offspring in several species (Reyer 1984; Curry 1988; Dunn et al. 1995; Magrath and Whittingham 1997; Nam et al. 2010; Wright et al. 2010; Doutrelant et al. 2011; Hatchwell et al. 2014; Green et al. 2016). This is the behavior Hatchwell et al. (2014) found to be consistent with Hamilton's rule in the long-tailed tit (*Aegithalos caudatus*). However, in our analyses, prefledgling survival was the sole exceptional case in which the positive effect of helpers (males, in this case) did not scale with their relatedness to the breeding pair. This is also the only case for which we have behavioral data, and it is consistent with this finding: preliminary evidence suggests that relatedness does not affect the frequency with which helpers feed young (or incubate eggs; M. Z. Khan and J. R. Walters, unpublished data). Thus, indirect fitness benefits cannot account for incubation and nestling provisioning behavior in red-cockaded woodpeckers.

Several direct benefits of helping behavior have been proposed (see summaries in Kingma et al. [2011] and the supplemental PDF, sec. E). Most of these hypotheses have very little empirical support generally and have been ruled out for the red-cockaded woodpecker specifically, with two exceptions: "pay to stay" (helpers must provide fitness benefits to the breeders to avoid being evicted from the group) and "passive group augmentation" (increasing group size through helping behavior results in survival benefits for helpers; supplemental PDF, sec. E). Neither hypothesis predicts that the effect of helpers on breeder fitness will scale with helper relatedness, and thus neither is competitive with indirect benefits as an explanation of most of the helper effects on breeder fitness we observed. The exception is helper effects on prefledging survival, which indirect benefits cannot account for. In this case, our results are consistent with Kingma's (2017) finding that in species in which territory inheritance is frequent (such as the red-cockaded woodpecker), helpers do not discriminate according to kinship when provisioning young, which he suggested might be explained by the direct benefits of pay to stay or passive group augmentation. Passive group augmentation is a particularly promising explanation in this case, as the presence of not only helpers but also fledglings has been shown to improve survival of breeders in the red-cockaded woodpeckers (Khan and Walters 2002), suggesting that survival rates increase with group size. However, it remains to be shown that an increase in group size improves helper survival specifically.

Helper effects on breeder survival are interesting in that they are sex specific and differ between related helpers and unrelated helpers. Breeder survival was positively related to the presence of related helpers, but only male helpers were associated with a positive effect on male breeder survival, and only female helpers were associated with a positive effect on female breeder survival. Previous work found that in many cooperative breeders, including the red-cockaded woodpecker (Khan and Walters 2002), breeders have higher survival in the presence of helpers (Hammers et al. 2019; Downing et al. 2021). Because the effects are sex specific, it seems unlikely that they would be driven by load lightening, that is, that compensatory feeding by helpers enables breeders to reduce their feeding effort, thereby enhancing their survival (Crick 1992; Hatchwell 1999). Alternatively, sex specificity could stem from sex- and status-specific differences in foraging locations. Males forage much more often on twigs and branches than females, whereas females forage much more often than males on the lower trunk below the limbs (Conner et al. 2001). The greater proximity of helpers to breeders of the same sex may promote interactions that somehow affect breeder fitness, for example, warning them of, or "shielding" them from, attacking predators.

In contrast, the presence of male helpers unrelated to either breeder ($R = 0$) was associated with decreased male breeder survival. This was the only negative effect of helpers on breeder fitness that we detected. Antagonistic effects of helpers on male breeder survival have been noted for the sociable weaver, *Philetairus socius* (Paquet et al. 2015), but whether this was based on relatedness was not examined. For unrelated helpers, reducing survival of breeders of the same sex results in no loss of indirect fitness benefits and likely increases their direct fitness, specifically their ability to acquire the breeding position. Therefore, unrelated helpers may behave in ways that are harmful to the breeders and that are not exhibited by related helpers, resulting in contrasting effects on breeder survival. The pay-to-stay hypothesis may explain why unrelated male helpers are tolerated by male breeders despite costs to their own survival. The only possible form of "payment"—that is, significant effect of unrelated helpers on breeder fitness—we detected was a positive effect on prefledgling survival.

The only fitness component that was unaffected by helpers was juvenile survival. It is interesting that although helpers have been known to affect juvenile (i.e., postfledging) survival in some species (Covas et al. 2011; Van de Loock et al. 2017), Woolfenden and Fitzpatrick (1984) found no such effect in Florida scrub jays (*Aphelocoma coerulescens*), a species with a social system extremely similar to that of the red-cockaded woodpecker.

That male helpers have more effects on breeder fitness than female helpers may relate to differences in their life history. As in many cooperatively breeding birds (Greenwood 1980), females are the dispersing sex in the red-cockaded woodpecker, and as a result, female helpers are often less related to group members (for red-cockaded woodpecker, see fig. S5; see also Barati et al. 2018). They likely are also more focused on seeking breeding positions elsewhere and less focused on assisting with brood rearing than male helpers. Indeed, female helpers foray to nearby territories frequently during the breeding season (Kesler et al. 2010), and they have a much higher annual probability of dispersal than male helpers (Walters and Garcia 2016), such that natal female helpers older than 3 years are rare, whereas male helpers up to age 7–8 years and beyond are common. Such a sex difference in helping is not surprising: in cooperatively breeding birds generally, the inclusive fitness benefits of helping are the same for both sexes given the same relatedness, yet the philopatric sex is more likely to help (Downing et al. 2018). Collectively, these findings suggest that for females, there may be opportunity costs of helping that do not apply to males that, in accordance with Hamilton's rule, make helping behavior less likely to evolve in females.

Through the use of FLMs we disentangled a complex phenomenon to evaluate how sex and relatedness of helpers in mixed breeding groups affected breeder fitness components in a cooperatively breeding bird and thus the helpers' inclusive fitness. Nevertheless, FLMs are still a correlative technique, and our results should be interpreted as such. Overall, FLMs are a good complement to other approaches (such as manipulative studies) that further assist with identifying the effects of complex drivers. Here, we were able to use this approach to provide one of the few tests of kin selection theory in a cooperatively breeding bird to date and show that helper effects on breeder fitness depended on relatedness of helpers to breeders in accordance with Hamilton's rule. For most breeder fitness components, indirect fitness benefits to helpers emerged as the best explanation of helping, and the direct benefit of passive group augmentation was the best explanation of the sole exception (Kingma 2017). Although kin selection has fallen out of favor as an explanation of helping behavior in cooperatively breeding birds (Nowak et al. 2010; Riehl 2013), we suggest that it remains the best explanation of helping in the majority of species.

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Statement of Authorship

N.Z.K. conceived the idea and designed methodology; J.R.W. collected the data; N.Z.K. and W.F.M. analyzed the data; and N.Z.K., W.F.M., and J.R.W. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data and Code Availability

Data and R code for running these functional linear models are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.3bk3j9kqs; Kerr et al. 2023).

Literature Cited

Barati, A., R. L. Andrew, J. C. Gorrell, F. Etezadifar, and P. G. McDonald. 2018. Genetic relatedness and sex predict helper provisioning effort in the cooperatively breeding noisy miner. Behavioral Ecology 29:1380–1389.

Bolker, B., and R Core Team. 2016. bbmle: tools for general maximum likelihood estimation, version 1.0.23. https://CRAN.R-project.org/package = bbmle.

Bourke, A. 2014. Hamilton's rule and the causes of social evolution. Philosophical Transactions of the Royal Society B 369:20130362.

Brouwer, L., A. Cockburn, and M. van de Pol. 2020. Integrating fitness components reveals that survival costs outweigh other benefits and costs of group living in two closely related species. American Naturalist 195:201–215.

Burnham, K. P., and D. R. Anderson. 2013. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Clutton-Brock, T. H., P. N. M. Brotherton, M. J. O'Riain, A. S. Griffin, D. Gaynor, L. Sharpe, R. Kansky, M. B. Manser, and G. M. McIlrath. 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. Proceedings of the Royal Society B 267:301–305.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. Annual Review of Ecology and Systematics 29:141–177.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker surviving in a fire-maintained ecosystem. University of Texas Press, Austin.

Cornwallis, C. K., C. A. Botero, D. R. Rubenstein, P. A. Downing, S. A. West, and A. S. Griffin. 2017. Cooperation facilitates the colonization of harsh environments. Nature Ecology and Evolution 1:0057.

Covas, R., A.-S. Deville, C. Doutrelant, C. N. Spottiswoode, and A. Grégoire. 2011. The effect of helpers on the postfledging period in a cooperatively breeding bird, the sociable weaver. Animal Behaviour 81:121–126.

Crick, H. Q. P. 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. Ibis 134:56–61.

Crone, E. E., E. M. Pelton, L. M. Brown, C. C. Thomas, and C. B. Schultz. 2019. Why are monarch butterflies declining in the West? understanding the importance of multiple correlated drivers. Ecological Applications 29:e01975.

Curry, R. L. 1988. Influence of kinship on helping behavior in Galápagos mockingbirds. Behavioral Ecology and Sociobiology 22:141–152.

Dalgleish, H. J., D. N. Koons, M. B. Hooten, C. A. Moffet, and P. B. Adler. 2011. Climate influences the demography of three dominant sagebrush steppe plants. Ecology 92:75–85.

DeLotelle, R. S., and R. J. Epting. 1992. Reproduction of the red-cockaded woodpecker in central Florida. Wilson Bulletin 104: 285–294.

DeLotelle, R. S., D. Leonard Jr., and R. Epting. 2004. Hatch failure and brood reduction in 3 central Florida red-cockaded woodpecker populations. Pages 616–623 *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, WA.

DeMay, S. M., and J. R. Walters. 2019. Variable effects of a changing climate on lay dates and productivity across the range of the red-cockaded woodpecker. Condor 121:duz048.

Dias, R. I., M. S. Webster, and R. H. Macedo. 2017. Parental and alloparental investment in campo flickers (*Colaptes campestris*): when relatedness comes first. Behavioral Ecology and Sociobiology 71:139.

Dickinson, J. L., W. D. Koenig, and F. A. Pitelka. 1996. Fitness consequences of helping behavior in the western bluebird. Behavioral Ecology 7:168–177.

Doutrelant, C., A. Dalecky, and R. Covas. 2011. Age and relatedness have an interactive effect on the feeding behaviour of helpers in cooperatively breeding sociable weavers. Behaviour 148:1399–1417.

Downing, P. A., A. S. Griffin, and C. K. Cornwallis. 2018. Sex differences in helping effort reveal the effect of future reproduction on cooperative behaviour in birds. Proceedings of the Royal Society B 285:20181164.

———. 2020. The benefits of help in cooperative birds: nonexistent or difficult to detect? American Naturalist 195:1085–1091.

———. 2021. Hard-working helpers contribute to long breeder lifespans in cooperative birds. Philosophical Transactions of the Royal Society B 376:20190742.

Dunn, P. O., A. Cockburn, and R. A. Mulder. 1995. Fairy-wren helpers often care for young to which they are unrelated. Proceedings of the Royal Society B 259:339–343.

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. American Naturalist 119:29–39.

Emlen, S. T., H. K. Reeve, P. W. Sherman, P. H. Wrege, L. W. R. Francis, and J. Shellman-Reeve. 1991. Adaptive versus nonadaptive explanations of behavior: the case of alloparental helping. American Naturalist 138:259–270.

Emlen, S. T., and P. H. Wrege. 1989. A test of alternate hypotheses for helping behavior in white-fronted bee-eaters of Kenya. Behavioral Ecology and Sociobiology 25:303–319.

Gadagkar, R. 2001. The social biology of *Ropalidia marginata*: towards understanding the evolution of eusociality. Harvard University Press, Cambridge, MA.

Green, J. P., R. P. Freckleton, and B. J. Hatchwell. 2016. Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton's rule. Nature Communications 7:12663.

Green, J. P., and B. J. Hatchwell. 2018. Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). Proceedings of the National Academy of Sciences of the USA 115:12011.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Groenewoud, F., J. G. Frommen, D. Josi, H. Tanaka, A. Jungwirth, and M. Taborsky. 2016. Predation risk drives social complexity in cooperative breeders. Proceedings of the National Academy of Sciences of the USA 113:4104–4109.

Gusset, M., and D. W. Macdonald. 2010. Group size effects in cooperatively breeding African wild dogs. Animal Behaviour 79:425–428.

Haig, S. M., J. R. Walters, and J. H. Plissner. 1994. Genetic evidence for monogamy in the cooperatively breeding red-cockaded woodpecker. Behavioral Ecology Sociobiology 43:295–303.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. Journal of Theoretical Biology 7:1–16.

Hammers, M., S. A. Kingma, L. G. Spurgin, K. Bebbington, H. L. Dugdale, T. Burke, J. Komdeur, and D. S. Richardson. 2019. Breeders that receive help age more slowly in a cooperatively breeding bird. Nature Communications 10:1301.

Hatchwell, B. J. 1999. Investment strategies of breeders in avian cooperative breeding systems. American Naturalist 154:205–219.

Hatchwell, B. J., P. R. Gullett, and M. J. Adams. 2014. Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. Philosophical Transactions of the Royal Society B 369:20130565.

Hatchwell, B. J., A. F. Russell, A. D. C. MacColl, D. J. Ross, M. K. Fowlie, and A. McGowan. 2004. Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. Behavioral Ecology 15:1–10.

Hesse, S., J. M. Anaya-Rojas, J. G. Frommen, and T. Thünken. 2015. Kinship reinforces cooperative predator inspection in a cichlid fish. Journal of Evolutionary Biology 28:2088–2096.

Hogendoorn, K., and R. Leys. 1993. The superseded female's dilemma: ultimate and proximate factors that influence guarding behaviour of the carpenter bee *Xylocopa pubescens*. Behavioral Ecology and Sociobiology 33:371–381.

Hunsicker, M. E., C. V. Kappel, K. A. Selkoe, B. S. Halpern, C. Scarborough, L. Mease, and A. Amrhein. 2016. Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management. Ecological Applications 26:651–663.

Innes, K. E., and R. E. Johnston. 1996. Cooperative breeding in the white-throated magpie-jay: how do auxiliaries influence nesting success? Animal Behaviour 51:519–533.

Jackson, J. A. 2020. Red-cockaded woodpecker (*Picoides borealis*). *In* A. Poole and F. Gill, eds. Birds of the world. Cornell Lab of Ornithology, Ithaca, NY. https://doi.org/10.2173/bow.recwoo.01.

James, G., D. Witten, T. Hastie, and R. Tibshirani. 2013. An introduction to statistical learning with applications in R. Springer, New York.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Kappes, J. J., Jr., S. A. Lauerman, R. Costa, and J. Raglin. 2021. Breeder age, group size, and fledgling production in the cooperatively breeding red-cockaded woodpecker (*Dryobates borealis*). Wilson Journal of Ornithology 132:495–512.

Kerr, N. Z., R. L. Malfi, N. M. Williams, and E. E. Crone. 2021. Larger workers outperform smaller workers across resource environments: an evaluation of demographic data using functional linear models. Ecology and Evolution 11:2814–2827. https://doi.org/10.1002/ece3.7239.

Kerr, N. Z., W. F. Morris, and J. R. Walters. 2023. Data from: Long-term demographic data on the red-cockaded woodpecker. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.3bk3j9kqs.

Kesler, D. C., J. R. Walters, and J. J. Kappes Jr. 2010. Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers. Behavioral Ecology 21:1337–1343.

Khan, M. Z., and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 51:336–344.

Kingma, S. A. 2017. Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. Nature Communications 8:1094.

Kingma, S. A., M. L. Hall, and A. Peters. 2011. Multiple benefits drive helping behavior in a cooperatively breeding bird: an integrated analysis. American Naturalist 177:486–495.

Krakauer, A. H. 2005. Kin selection and cooperative courtship in wild turkeys. Nature 434:69–72.

Kramer, J., N. Klauke, M. Bauer, and H. M. Schaefer. 2016. No evidence for enforced alloparental care in a cooperatively breeding parrot. Ethology 122:389–398.

LaBranche, M., and J. R. Walters. 1994. Patterns of mortality in nests of red-cockaded woodpeckers in the sandhills of south-central North Carolina. Wilson Journal of Ornithology 106: 258–271.

Lennartz, M. R., R. G. Hooper, and R. F. Harlow. 1987. Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. Behavioral Ecology and Sociobiology 20:77–88.

Lukas, D., V. Reynolds, C. Boesch, and L. Vigilant. 2005. To what extent does living in a group mean living with kin? Molecular Ecology 14:2181–2196.

Magrath, R. D., and L. A. Whittingham. 1997. Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. Behavioral Ecology and Sociobiology 41:185–192.

Metcalf, R. A., and G. S. Whitt. 1977. Relative inclusive fitness in the social wasp *Polistes metricus*. Behavioral Ecology and Sociobiology 2:353–360.

Moreno, J. 2015. The incidence of clutch replacements in the pied flycatcher *Ficedula hypoleuca* is related to nest-box availability: evidence of female-female competition? Ardeola 62:67–80.

Mumme, R. L. 1992. Do helpers increase reproductive success? Behavioral Ecology and Sociobiology 31:319–328.

Nam, K.-B., M. Simeoni, S. P. Sharp, and B. J. Hatchwell. 2010. Kinship affects investment by helpers in a cooperatively breeding bird. Proceedings of the Royal Society B 277:3299–3306.

Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. Nature 466:1057.

Paquet, M., C. Doutrelant, B. J. Hatchwell, C. N. Spottiswoode, and R. Covas. 2015. Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. Journal of Animal Ecology 84:1354–1362.

Ramsay, J. O., G. Hooker, and S. Graves. 2009. Functional data analysis with R and Matlab. Springer, New York.

Ramsay, J. O., and B. W. Silverman. 2005. Functional data analysis. Springer, New York.

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

Reyer, H.-U. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). Animal Behaviour 32:1163–1178.

Ridley, A. R., N. J. Raihani, and M. J. Nelson-Flower. 2008. The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. Journal of Avian Biology 39:389–392.

Riehl, C. 2013. Evolutionary routes to non-kin cooperative breeding in birds. Proceedings of the Royal Society B 280:20132245.

Russell, A. F., A. J. Young, G. Spong, N. R. Jordan, and T. H. Clutton-Brock. 2007. Helpers increase the reproductive potential of offspring in cooperative meerkats. Proceedings of the Royal Society B 274:513–520.

Russell, E., and I. Rowley. 1988. Helper contributions to reproductive success in the splendid fairy-wren (*Malurus splendens*). Behavioral Ecology and Sociobiology 22:131–140.

Schaub, R., R. L. Mumme, and G. E. Woolfenden. 1992. Predation on the eggs and nestlings of Florida scrub jays. Auk 109:585–593.

Sparkman, A. M., J. Adams, A. Beyer, T. D. Steury, L. Waits, and D. L. Murray. 2011. Helper effects on pup lifetime fitness in the cooperatively breeding red wolf (*Canis rufus*). Proceedings of the Royal Society B 278:1381–1389.

Stacey, P. B., and J. D. Ligon. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. American Naturalist 137:831–846.

Teller, B. J., P. B. Adler, C. B. Edwards, G. Hooker, and S. P. Ellner. 2016. Linking demography with drivers: climate and competition. Methods in Ecology and Evolution 7:171–183.

Tenhumberg, B., E. E. Crone, S. Ramula, and A. J. Tyre. 2018. Time-lagged effects of weather on plant demography: drought and *Astragalus scaphoides*. Ecology 99:915–925.

Teunissen, N., S. A. Kingma, M. Fan, M. J. Roast, and A. Peters. 2021. Context-dependent social benefits drive cooperative predator defense in a bird. Current Biology 31:4120–4126.

US Fish and Wildlife Service. 2003. Red-cockaded woodpecker (*Picoides borealis*) recovery plan. 2nd rev. US Fish and Wildlife Service, Atlanta.

Van de Loock, D., D. Strubbe, L. De Neve, M. Githiru, E. Matthysen, and L. Lens. 2017. Cooperative breeding shapes post-fledging survival in an Afrotropical forest bird. Ecology and Evolution 7:3489–3493.

Vitikainen, E. I. K., H. H. Marshall, F. J. Thompson, J. L. Sanderson, M. B. V. Bell, J. S. Gilchrist, S. J. Hodge, H. J. Nichols, and M. A. Cant. 2017. Biased escorts: offspring sex, not relatedness explains alloparental care patterns in a cooperative breeder. Proceedings of the Royal Society B 284:20162384.

Walters, J. R. 1990. Red-cockaded woodpeckers: a "primitive" cooperative breeder. Pages 67–101 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Walters, J. R., C. K. Copeyon, and J. H. Carter III. 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. Auk 109:90–97.

Walters, J. R., P. D. Doerr, and J. H. Carter III. 1988. The cooperative breeding system of the red-cockaded woodpecker. Ethology 78:275–305.

Walters, J. R., and V. Garcia. 2016. Red-cockaded woodpeckers: alternative pathways to breeding success. Pages 58–76 *in* W. D. Koenig and J. L. Dickinson, eds. Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press, London.

Williams, D. A., and A. M. Hale. 2006. Helper effects on offspring production in cooperatively breeding brown jays (*Cyanocorax Morio*). Auk 123:847–857.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL.

———. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society B 73:3–36.

———. 2013. On *p*-values for smooth components of an extended generalized additive model. Biometrika 100:221–228.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida scrub jay. Princeton University Press, Princeton, NJ.

Wright, J., P. G. McDonald, L. te Marvelde, A. J. N. Kazem, and C. M. Bishop. 2010. Helping effort increases with relatedness in bell miners, but "unrelated" helpers of both sexes still provide substantial care. Proceedings of the Royal Society B 277:437–445.

Zuur, A. F. 2012. A beginner's guide to generalized additive models with R. Highland Statistics, Newburgh, UK.

References Cited Only in the Online Enhancements

Arnold, K. E., I. P. F. Owens, and A. W. Goldizen. 2005. Division of labour within cooperatively breeding groups. Behaviour 142:1577–1590.

Austad, S. N., and K. N. Rabenold. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren. Behavioral Ecology and Sociobiology 17:19–27.

Barati, A., R. L. Andrew, and P. G. McDonald. 2021. Nestling sex does not influence provisioning effort of parents or helpers in a cooperative bird with a male-biased helper contingent. Behavioral Ecology and Sociobiology 75:94.

Blackmore, C. J., and R. Heinsohn. 2007. Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler. Journal of Zoology 273:326–332.

Boland, C., R. J. Heinsohn, and A. Cockburn. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. Journal of Animal Ecology 66:683–691.

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

Brown, J. L. 1987. Helping and communal breeding in birds: ecology and evolution. Princeton University Press, Princeton, NJ.

Brown, J. L., E. R. Brown, S. D. Brown, and D. D. Dow. 1982. Helpers: effects of experimental removal on reproductive success. Science 215:421.

Browning, L. E., S. C. Patrick, L. A. Rollins, S. C. Griffith, and A. F. Russell. 2012. Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. Proceedings of the Royal Society B 279:3861–3869.

Caffrey, C. 2000. Correlates of reproductive success in cooperatively breeding Western American crows: if helpers help, it's not by much. Condor 102:333–341.

Canestrari, D., E. Chiarati, J. M. Marcos, J. Ekman, and V. Baglione. 2008. Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows. Animal Behaviour 76:943–949.

Canestrari, D., J. M. Marcos, and V. Baglione. 2007. Costs of chick provisioning in cooperatively breeding crows: an experimental study. Animal Behaviour 73:349–357.

———. 2011. Helpers at the nest compensate for reduced maternal investment in egg size in carrion crows. Journal of Evolutionary Biology 24:1870–1878.

Capilla-Lasheras, P., X. Harrison, E. M. Wood, A. J. Wilson, and A. J. Young. 2021. Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird. Science Advances 7:eabe8980.

Capilla-Lasheras, P., A. J. Wilson, and A. J. Young. 2021. Mothers front-load their investment to the egg stage when helped in a wild cooperative bird. bioRxiv, https://doi.org/10.1101/2021.11.11.468195.

Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. Nature 462:51–57.

Cornwallis, C. K., S. A. West, and A. S. Griffin. 2009. Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. Journal of Evolutionary Biology 22:2445–2457.

Covas, R., M. A. du Plessis, and C. Doutrelant. 2008. Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. Behavioral Ecology and Sociobiology 63:103–112.

Cusick, J. A., M. de Villa, E. H. DuVal, and J. A. Cox. 2018. How do helpers help? helper contributions throughout the nesting cycle in the cooperatively breeding brown-headed nuthatch. Behavioral Ecology and Sociobiology 72:43.

de la Cruz, C., M. Expósito-Granados, and J. Valencia. 2019. Distribution of the parental care in the Iberian magpie *Cyanopica cooki*: worker males but lazy helpers? Behaviour 156:79–107.

Dias, R. I., M. S. Webster, and R. H. Macedo. 2015. Helping enhances productivity in campo flicker (*Colaptes campestris*) cooperative groups. Science of Nature 102:31.

Dickinson, J. L. 2004. Facultative sex ratio adjustment by western bluebird mothers with stay-at-home helpers-at-the-nest. Animal Behaviour 68:373–380.

Doutrelant, C., R. Covas, A. Caizergues, and M. du Plessis. 2004. Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not. Behavioral Ecology and Sociobiology 56:149–154.

Eguchi, K., S. Yamagishi, S. Asai, H. Nagata, and T. Hino. 2002. Helping does not enhance reproductive success of cooperatively breeding *Rufous vanga* in Madagascar. Journal of Animal Ecology 71:123–130.

Emlen, S. T., and P. H. Wrege. 1988. The role of kinship in helping decisions among white-fronted bee-eaters. Behavioral Ecology and Sociobiology 23:305–315.

Fortuna, R., M. Paquet, A. C. Ferreira, L. R. Silva, F. Theron, C. Doutrelant, and R. Covas. 2021. Maternal allocation in relation to weather, predation and social factors in a colonial cooperative bird. Journal of Animal Ecology 90:1122–1133.

Fox, J., and S. Weisberg. 2019. An companion to applied regression. Sage, Thousand Oaks, CA.

Gaston, A. J. 1978. The evolution of group territorial behavior and cooperative breeding. American Naturalist 112:1091–1100.

Green D. J., A. Cockburn, M. L. Hall, H. Osmond, and P. O. Dunn. 1995. Increased opportunities for cuckoldry may be why dominant male fairy-wrens tolerate helpers. Proceedings of the Royal Society B 262:297–303.

Guindre-Parker, S., and D. R. Rubenstein. 2018. Multiple benefits of alloparental care in a fluctuating environment. Royal Society Open Science 5:172406.

Haig, S. M., J. R. Belthoff, and D. H. Allen. 1993. Population viability analysis for a small population of red-cockaded woodpeckers and an evaluation of enhancement strategies. Conservation Biology 7:289–301.

Hajduk, G. K., A. Cockburn, H. L. Osmond, and L. E. B. Kruuk. 2021. Complex effects of helper relatedness on female extrapair reproduction in a cooperative breeder. Behavioral Ecology 32:386–394.

Hammers, M., S. A. Kingma, L. A. van Boheemen, A. M. Sparks, T. Burke, H. L. Dugdale, D. S. Richardson, and J. Komdeur. 2021. Helpers compensate for age-related declines in parental care and offspring survival in a cooperatively breeding bird. Evolution Letters 5:143–153.

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 B 263:83–88.

Hatchwell, B. J., S. P. Sharp, A. P. Beckerman, and J. Meade. 2013. Ecological and demographic correlates of helping behaviour in a cooperatively breeding bird. Journal of Animal Ecology 82:486–494.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. Journal of Wildlife Management 58:479–487.

Hewett Ragheb, E. L., and J. R. Walters. 2011. Favouritism or intrabrood competition? access to food and the benefits of philopatry for red-cockaded woodpeckers. Animal Behaviour 82:329–338.

Hunter, L. A. 1987. Acquisition of territories by floaters in cooperatively breeding purple gallinules. Animal Behaviour 35:402–410.

Kaiser, S. A., T. E. Martin, J. C. Oteyza, J. E. Danner, C. E. Armstad, and R. C. Fleischer. 2019. Within-group relatedness and patterns of reproductive sharing and cooperation in the tropical chestnut-crested yuhina. Animal Behaviour 158:89–99.

Khan, M. Z., and J. R. Walters. 1997. Is helping a beneficial learning experience for red-cockaded woodpecker (*Picoides borealis*) helpers? Behavioral Ecology and Sociobiology 41:69–73.

———. 2000. An analysis of reciprocal exchange of helping behavior in the red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 47:376–381.

Kingma, S. A., M. L. Hall, E. Arriero, and A. Peters. 2010. Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? Journal of Animal Ecology 79:757–768.

Kingma, S. A., P. Santema, M. Taborsky, and J. Komdeur. 2014. Group augmentation and the evolution of cooperation. Trends in Ecology and Evolution 29:476–484.

Klauke, N., G. Segelbacher, and H. M. Schaefer. 2013. Reproductive success depends on the quality of helpers in the endangered, cooperative El Oro parakeet (*Pyrrhura orcesi*). Molecular Ecology 22:2011–2027.

Koenig, W. D., and E. L. Walters. 2011. Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses. Animal Behaviour 82:437–444.

———. 2012. Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. Behavioral Ecology 23:181–190.

———. 2016. Provisioning patterns in the cooperatively breeding acorn woodpecker: does feeding behaviour serve as a signal? Animal Behaviour 119:125–134.

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.

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.

Kokko, H., R. A. Johnstone, and T. H. Clutton-Brock. 2001. The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society B 268:187–196.

Komdeur, J. 1994. The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). Proceedings of the Royal Society B 256:47–52.

Komdeur, J., D. S. Richardson, and T. Burke. 2004. Experimental evidence that kin discrimination in the Seychelles warbler is based on association and not on genetic relatedness. Proceedings of the Royal Society B 271:963–969.

Leedale, A. E., R. F. Lachlan, E. J. H. Robinson, and B. J. Hatchwell. 2020. Helping decisions and kin recognition in long-tailed tits: is call similarity used to direct help towards kin? Philosophical Transactions of the Royal Society B 375:20190565.

Leedale, A. E., S. P. Sharp, M. Simeoni, E. J. H. Robinson, and B. J. Hatchwell. 2018. Fine-scale genetic structure and helping decisions in a cooperatively breeding bird. Molecular Ecology 27:1714–1726.

Legge, S. 2000. Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. Animal Behaviour 59:1009–1018.

Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. Auk 87:255–278.

Luck, G. W. 2001. The demography and cooperative breeding behaviour of the rufous treecreeper, *Climacteris rufa*. Australian Journal of Zoology 49:515–537.

Magrath, R. D. 2001. Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? Journal of Animal Ecology 70:370–385.

McDonald, P. G., J. G. Ewen, and J. Wright. 2010. Brood sex ratio does not affect helper effort in a cooperative bird, despite extreme sex-biased dispersal. Animal Behaviour 79:243–250.

McDonald, P. G., A. J. N. Kazem, M. F. Clarke, and J. Wright. 2008. Helping as a signal: does removal of potential audiences alter helper behavior in the bell miner? Behavioral Ecology 19:1047–1055.

McDonald, P. G., A. J. N. Kazem, and J. Wright. 2009. Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. Animal Behaviour 77:369–376.

McDonald, P. G., and J. Wright. 2011. Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. Proceedings of the Royal Society B 278:3403–3411.

Meade, J., K.-B. Nam, A. P. Beckerman, and B. J. Hatchwell. 2010. Consequences of "load-lightening" for future indirect fitness gains by helpers in a cooperatively breeding bird. Journal of Animal Ecology 79:529–537.

Mulder, R. A., and N. E. Langmore. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. Animal Behaviour 45:830–833.

Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1988. Costs and benefits of joint nesting in the acorn woodpecker. American Naturalist 131:654–677.

Naef, J., and M. Taborsky. 2020. Punishment controls helper defence against egg predators but not fish predators in cooperatively breeding cichlids. Animal Behaviour 168:137–147.

Nam, K.-B., J. Meade, and B. J. Hatchwell. 2011. Do parents and helpers adjust their provisioning effort in relation to nestling sex in a cooperatively breeding bird? Animal Behaviour 82:303–309.

Nomano, F. Y., L. E. Browning, J. L. Savage, L. A. Rollins, S. C. Griffith, and A. F. Russell. 2015. Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowed babblers. Behavioral Ecology 26:986–995.

Pacheco, M. L., P. G. McDonald, J. Wright, A. J. N. Kazem, and M. F. Clarke. 2008. Helper contributions to antiparasite behavior in the cooperatively breeding bell miner. Behavioral Ecology 19:558–566.

Pike, K. N., B. J. Ashton, K. V. Morgan, and A. R. Ridley. 2019. Social and individual factors influence variation in offspring care in the cooperatively breeding Western Australian magpie. Frontiers in Ecology and Evolution 7:92.

Preston, S. A. J., J. V. Briskie, and B. J. Hatchwell. 2016. Adult helpers increase the recruitment of closely related offspring in the cooperatively breeding rifleman. Behavioral Ecology 27:1617–1626.

Rabenold, P. P., K. N. Rabenold, W. H. Piper, J. Haydock, and S. W. Zack. 1990. Shared paternity revealed by genetic analysis in cooperatively breeding tropical wrens. Nature 348:538–540.

Raihani, N. J., M. J. Nelson-Flower, K. Moyes, L. E. Browning, and A. R. Ridley. 2010. Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. Journal of Animal Ecology 79:44–52.

Raihani, N. J., and A. R. Ridley. 2007. Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers. Animal Behaviour 74:1303–1309.

Reed, J. M., and J. R. Walters. 1996. Helper effects on variance components of fitness in the cooperatively breeding red-cockaded woodpecker. Auk 113:608–616.

Ridley, A. R. 2007. Factors affecting offspring survival and development in a cooperative bird: social, maternal and environmental effects. Journal of Animal Ecology 76:750–760.

Ridley, A. R., and N. J. Raihani. 2007*a*. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. Behavioral Ecology 18:324–330.

———. 2007*b*. Variable postfledging care in a cooperative bird: causes and consequences. Behavioral Ecology 18:994–1000.

———. 2008. Task partitioning increases reproductive output in a cooperative bird. Behavioral Ecology 19:1136–1142.

Rudolph, D. C., R. N. Conner, and J. R. Walters. 2004. Red-cockaded woodpecker recovery: an integrated strategy. Pages 70–76 *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, WA.

Russell, A. F., and B. J. Hatchwell. 2001. Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. Proceedings of the Royal Society B 268:2169–2174.

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.

Sharp, S. P., M. Simeoni, A. McGowan, K.-B. Nam, and B. J. Hatchwell. 2011. Patterns of recruitment, relatedness and cooperative breeding in two populations of long-tailed tits. Animal Behaviour 81:843–849.

Skutch, A. F. 1961. Helpers among birds. Condor 63:198–226.

te Marvelde, L., P. G. McDonald, A. J. N. Kazem, and J. Wright. 2009. Do helpers really help? provisioning biomass and prey type effects on nestling growth in the cooperative bell miner. Animal Behaviour 77:727–735.

Teunissen, N., S. A. Kingma, and A. Peters. 2020*a*. Nest defence and offspring provisioning in a cooperative bird: individual subordinates vary in total contribution, but no division of tasks among breeders and subordinates. Behavioral Ecology and Sociobiology 74:94.

———. 2020*b*. Predator defense is shaped by risk, brood value and social group benefits in a cooperative breeder. Behavioral Ecology 31:761–771.

Trapote, E., D. Canestrari, and V. Baglione. 2021. Female helpers signal their contribution to chick provisioning in a cooperatively breeding bird. Animal Behaviour 172:113–120.

Valencia, J., C. de la Cruz, J. Carranza, and C. Mateos. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. Animal Behaviour 71:1021–1028.

Valencia, J., C. Mateos, C. de la Cruz, and J. Carranza. 2017. Maternal allocation in eggs when counting on helpers in a cooperatively breeding bird. Journal of Avian Biology 48:536–543.

van Boheemen, L. A., M. Hammers, S. A. Kingma, D. S. Richardson, T. Burke, J. Komdeur, and H. L. Dugdale. 2019. Compensatory and additive helper effects in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). Ecology and Evolution 9:2986–2995.

van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within-versus between-subject effects using mixed models. Animal Behaviour 77:753.

Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. Annual Review of Ecology and Systematics 22:505–523.

———. 2004. Unusual dynamics in a rapidly increasing population of red-cockaded woodpeckers at Camp Lejeune, North Carolina. Pages 256–257 *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, WA.

Walters, J. R., K. E. Gault, B. W. Hagedorn, C. J. Petrick, L. F. Phillips Jr., J. Tomcho Jr., and A. Butler. 2004. Effectiveness of recruitment clusters and intrapopulation translocation in promoting growth of the red-cockaded woodpecker population in Eglin Air Force Base, Florida. Pages 325–334 *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, WA.

Wiley, E. M., and A. R. Ridley. 2016. The effects of temperature on offspring provisioning in a cooperative breeder. Animal Behaviour 117:187–195.

Wiley, R. H., and K. N. Rabenold. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. Evolution 38:609–621.

Williams, D. A., and A. M. Hale. 2007. Female-biased helping in a cooperatively breeding bird: female benefits or male costs? Ethology 113:534–542.

———. 2008. Investment in nesting activities and patterns of extra- and within-group genetic paternity in a cooperatively breeding bird. Condor 110:13–23.

Woxvold, I. A., and M. J. L. Magrath. 2005. Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. Journal of Animal Ecology 74:1039–1050.

Woxvold, I. A., R. A. Mulder, and M. J. L. Magrath. 2006. Contributions to care vary with age, sex, breeding status and group size in the cooperatively breeding apostlebird. Animal Behaviour 72:63–73.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behavioral Ecology and Sociobiology 42:423–429.

Wright, J., P. G. Parker, and K. J. Lundy. 1999. Relatedness and chick-feeding effort in the cooperatively breeding Arabian babbler. Animal Behaviour 58:779–785.

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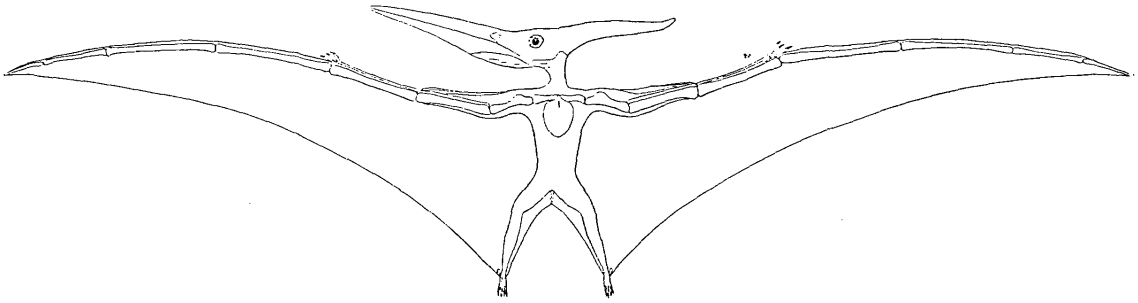

“The number of digits is probably five as there are two bones articulating with the distal carpal on the inner side of the wrist which Marsh (’82, p. 254) interprets as the metacarpal and first phalanx of the first digit. The phalanx, which he calls the ‘pteroid bone,’ formed part of the support for the prepatagium, being directed inward toward the shoulder. Others have interpreted this bone as an ossified tendon. If Marsh is correct the number of digits would be five, the fifth being the wing finger.” Figured: “*Pteranodon* sp. Modified from Eaton.” From “Volant Adaptation in Vertebrates” by Richard S. Lull (*The American Naturalist*, 1906, 40:537–566).