Article:

Sturrock, N.J., Hatchwell, B.J., Firth, J.A. et al. (2022) Who to help? Helping decisions in a cooperatively breeding bird with redirected care. Behavioral Ecology and Sociobiology, 76 (6). 83. ISSN: 0340-5443

https://doi.org/10.1007/s00265-022-03190-w

Behavioral Ecology and Sociobiology (2022) 76:83
https://doi.org/10.1007/s00265-022-03190-w

ORIGINAL ARTICLE

Who to help? Helping decisions in a cooperatively breeding bird with redirected care

Nicole J. Sturrock[1] · Ben J. Hatchwell[2] · Josh A. Firth[1] · Jonathan P. Green[1]

Received: 15 February 2022 / Revised: 1 June 2022 / Accepted: 3 June 2022

Abstract

Cooperative breeding sometimes occurs when adult breeders form groups following natal dispersal and mating. In such cases, individuals typically face a choice of social partner with whom to cooperate. Selecting appropriate social partners is crucial to maximising the fitness payoffs from cooperation, but our understanding of the criteria guiding partner choice is limited. Here, we analyse helping decisions by long-tailed tits (*Aegithalos caudatus*), which may redirect their care to assist breeders in raising offspring following the failure of their own nests. In this species, helpers prefer to help relatives at nearby nests, but it is unclear whether other criteria that may affect helper fitness also influence helping decisions. When choosing among broods of equivalent kinship, we found that helpers did not prefer those broods that offered the greatest indirect fitness returns. Further analyses revealed that helpers did not choose nests on the basis of brood size or age, but were more likely to help broods that were closer to their own failed nests and that were already being cared for by other helpers. Both effects likely reflect the limited choice available to helpers: although individuals breed close to relatives within kin neighbourhoods, a high rate of nest predation constrains helpers' choice of broods. In other species where cooperatively breeding groups form after natal dispersal, a greater range of options may be available and here detailed analysis of group formation will be helpful for determining the decision rules that underpin partner choice and permit stable cooperation in the face of alternative options.

Significance statement

Cooperative breeding occurs most frequently when offspring delay dispersal from their natal site and help to care for their younger siblings. In some species, however, individuals first disperse and then come together as adults to cooperate in rearing young. In the latter case, multiple social partners may be available — what then determines which partner is helped? We studied partner choice in long-tailed tits, which may help to feed other broods if their own brood fails. When multiple related broods were available, individuals were more likely to help those close by but showed no preference for broods offering the greatest indirect fitness returns. One explanation for this result is that helping options for most individuals are limited by high levels of nest predation, favouring a simpler decision-making process based on identifying close relatives breeding in close proximity.

Keywords Altruism · Cooperation · Help · Long-tailed tit · Partner choice · Group formation

Introduction

Cooperation is widespread among organisms, with individuals of many species expressing behaviours that increase the fitness of conspecifics and heterospecifics (West et al. 2021). Cooperative breeding is a conspicuous and well-studied form of cooperation that occurs in a range of invertebrate and vertebrate taxa and is characterised by the presence of alloparental care, i.e. care for non-descendant offspring (Choe and Crespi 1997; Koenig and Dickinson 2016). Given that alloparental care is often costly (Heinsohn and Legge 1999),

---

Communicated by D. Rubenstein

✉ Jonathan P. Green
jonathan.green@zoo.ox.ac.uk

[1] Department of Zoology, University of Oxford, 11a Mansfield Road, Oxford OX1 3SZ, UK

[2] School of Biosciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK

much research has focused on quantifying the benefits of this investment (e.g. Hatchwell et al. 2004; Cockburn et al. 2008; Downing et al. 2020) and understanding the factors that influence an individual's propensity to engage in alloparental care (e.g. Emlen and Wrege 1988; Field and Foster 1999; Covas et al. 2004), as well as the amount of care provided (e.g. Field and Cant 2006; Green et al. 2016; Kingma 2017).

The most common route to cooperative breeding is through the delayed dispersal of individuals from their natal territory, delayed dispersers then assuming the role of helpers, assisting the breeders on the territory (typically their parents) with care of their offspring (Koenig et al. 1992; Clutton-Brock 2009; Hatchwell 2009). An alternative route, however, is through the formation of groups among adults following natal dispersal (Lin and Michener 1972; Hatchwell 2009). Reproduction may then either be shared among group members, with all individuals contributing to the care of a combined brood, or else monopolised by one or a few individuals, with other group members investing exclusively in alloparental care (Hager and Jones 2009). Just as for species exhibiting delayed dispersal, the decision of adults to cooperate following dispersal is shaped to a large extent by constraints on breeding. In some cases, the success of solitary breeders is so low as to effectively render group-living obligate (Leadbeater et al. 2011; Riehl 2011). In other cases, however, solitary breeding may be a viable strategy, with cooperative breeding contingent on the presence of kin (Harrison et al. 2018), or else favoured by individuals in poor condition that would have low success if attempting to reproduce independently (Ferrari et al. 2019). Indeed, in a minority of species, all individuals initially attempt to breed independently, with some individuals providing alloparental care to broods in other nests while simultaneously caring for their own offspring or after their own reproductive attempts have failed (e.g. Emlen 1981; Preston et al. 2013; Hatchwell 2016).

When opportunities for alloparental care arise following natal dispersal, potential helpers are frequently faced with the choice of helping multiple recipients and so must actively locate desirable social partners. In such cases, selection is expected to favour information-gathering and decision-making strategies that enable cooperation to be targeted in a way that maximises the inclusive fitness payoffs to the actor. Knowledge of these strategies and the processes by which cooperatively breeding groups form following natal dispersal remains limited, but kinship is often important, with cooperation among kin facilitated by the existence of kin neighbourhoods (Dickinson and Hatchwell 2004). Kin neighbourhoods form when limited dispersal causes kin to be spatially clustered but not segregated from non-kin (Harrison et al. 2018; Parsons et al. 2019), requiring active discrimination of kin through familiarity (Seppä et al. 2012; Weidt et al. 2014) or phenotype matching (Green et al. 2015) for selection of the best social partner. However, the payoffs of cooperation can also be enhanced through selection of partners based on criteria other than kinship. Where cooperation results in direct fitness gains through offspring production, individuals may select social partners from whom they are able to extract the greatest productivity benefit, either through monopolising reproduction (Nonacs and Reeve 1995; Öst et al. 2003) or by maximising the competitive advantage of own offspring over other offspring in the group (Harrison et al. 2018). In the contrasting case where cooperation entails a net loss of direct fitness (i.e. where helping is altruistic), criteria other than kinship could in principle also be used to identify recipients that would enjoy the greatest productivity benefit as a result of being helped (Sumner et al. 2007; Kennedy et al. 2021). Collectively, analyses of group formation in these systems point to the importance of choosing appropriate partners for maximising the inclusive fitness payoffs of cooperation and suggest that both kinship and other factors play a role in partner choice.

A major problem in understanding choices of social partner is that assumptions must be made about the options available to an individual actor. In laboratory experiments, options can be effectively manipulated to isolate specific factors on which choices are made (e.g. Weidt et al. 2008; Green et al. 2015). However, in field studies, these options are typically much harder to define, making decisions on social association harder to study. In this study, we investigate the criteria guiding selection of cooperative partners in the long-tailed tit (*Aegithalos caudatus*), a species that exhibits redirected care, whereby individuals that fail to breed may then choose to assist a successful breeder in provisioning its young (MacColl and Hatchwell 2002; Hatchwell 2016). Among failed breeders, the decision to help appears to be condition-dependent, with help provided only by those in good condition (Meade and Hatchwell 2010). Approximately 15% of failed breeders become helpers, with approximately 40% of nests attracting helpers during the nestling stage (Hatchwell et al. 2004). Helpers do not influence survival of nestlings to fledging but improve downstream survival of offspring, with fledglings from helped nests more likely to recruit into the adult population in the following year (Hatchwell et al. 2004; Roper et al. 2022). This enhanced productivity of helped broods not only results in direct fitness benefits for breeders but also generates indirect fitness benefits for helpers because their care is typically directed towards related social partners (Hatchwell et al. 2014; Leedale et al. 2018). In contrast, alloparental care does not generate any direct reproductive or survival benefits for helpers (Meade and Hatchwell 2010). Long-tailed tits exhibit significant population structure (Leedale et al. 2018), with limited dispersal (Sharp et al. 2008a) and coordinated dispersal of kin (Sharp et al. 2008b) giving rise to kin neighbourhoods. The genetic structuring of populations is further reinforced by high rates of whole-brood predation (72% of nests are predated before offspring fledge; Hatchwell 2016) accompanied by very low rates of partial brood mortality through starvation (< 3% broods; Hatchwell et al. 2004), which results in recruitment of sibling groups from a small number of successful nests, i.e. a small effective population size (Beckerman et al. 2011). Despite the existence of kin neighbourhoods, kin-biased helping in long-tailed tits does not arise passively from helping nearest neighbours. Rather, individuals actively seek out social partners to help (Russell and Hatchwell 2001), with a preference for first-order relatives likely underpinned by familial imprinting on family-specific vocal cues during the nestling phase (Sharp et al. 2005; Leedale et al. 2020).

The kin neighbourhood structure of long-tailed tit populations (Leedale et al. 2018) means that although helpers assist only one breeding pair at a time, they may be faced with a choice of multiple close relatives with active broods at the time that the helper's own breeding attempt fails. What factors may influence their choice of social partner in these circumstances? The proximity of nests (Leedale et al. 2018) and the familiarity of potential recipients (Napper and Hatchwell 2016) are known to influence helping decisions, but helpers could also seek to maximise the fitness payoff by choosing broods that would deliver the greatest return for the additional investment that they provide. Here, for helpers with the choice of multiple close relatives, we estimate the indirect fitness payoffs available from helping each brood and ask whether help is preferentially given to those broods that offer the greatest fitness return. In addition, we decompose this fitness payoff into separate components — brood size, brood age, and the number of other helpers at the nest — to determine whether brood selection is made on the basis of one or more of these factors. First, with respect to brood size, we predict that helpers will prefer to assist breeders with larger broods, since the amount of indirect fitness accrued through helping will increase with the number of (related) offspring that successfully recruit into the breeding population. Note that this prediction holds only if the effect of help on per capita recruitment success does not diminish as brood size increases, which could occur if the additional food provided by helpers is outweighed by increased competition for food within large broods. Under such a scenario, the effect of help on number of recruiting offspring, and thus the indirect benefit to helpers, may be greatest at smaller brood sizes. Therefore, to test this assumption, we examine the effect of help on recruitment success across varying brood sizes. Second, with respect to brood age, the high and constant risk of brood predation (Hatchwell et al. 2004) may cause helpers to favour older broods since these are more likely to survive to fledging age, thereby maximising the chance that helpers see some return on their investment. On the other hand, previous studies suggest that the effect of helpers on offspring recruitment results from the increased investment that nestlings receive prior to fledging and that fledglings receive after fledging until nutritional independence (Hatchwell et al. 2004). Effects of helpers beyond independence are less likely because flock membership is dynamic from soon after fledging (Napper and Hatchwell 2016). Thus, in theory, if broods are helped from a younger age, this should result in greater benefits in terms of higher offspring recruitment success. Third, we asked whether the choice of recipients was based on the number of other helpers already in attendance at a nest. The effect of additional helpers on recruitment appears to be more or less additive (Hatchwell et al. 2004, 2014), at least over the normal range of helper numbers, so we make no strong prediction about the direction of any effect of current helpers on choice of social partner.

Methods

Study site and study population

Data were collected between 1994 and 2019 as part of a long-term study of a population of long-tailed tits in the Rivelin Valley, Sheffield, UK (53°23′N 1°34′W). The study site consists of approximately 160 ha of interconnected patches of deciduous woodland, scrub, farmland and gardens, and is surrounded by low-quality habitat that is largely unsuitable for long-tailed tits. Each year, nestlings from almost all broods are ringed with a British Trust for Ornithology ring and unique combination of colour rings, and blood samples are taken under UK Home Office licence for genetic analysis. Unringed adults present at the start of the breeding season are also colour-ringed and blood-sampled; these are assumed to be 1-year old immigrants born outside of the study site. Approximately 95% of the adult population is individually marked each breeding season. Standard protocols are followed each year to monitor breeding and helping by all adults in the population, with nests checked every 2–3 days throughout the breeding season, with daily checks around the expected date of hatching. Consequently, the timing of brood hatching is typically known to within 1 day, and the timing of breeding failure through predation or abandonment is typically known to within 2 days. Nests containing nestlings are watched every other day from day 2 (hatching day = day 0) to fledging/nest failure to identify all adults provisioning the nest, allowing us to determine the number and identity of all helpers, as well as the date at which they began to help (within two days). Broods usually fledge on day 16–18. For more details of the study population and monitoring, see Hatchwell (2016).

Helping options

We identified instances of helping behaviour where the helper had one or more alternative helping options. These were other breeding pairs in the population that were (a) caring for nestlings on the day that the helper began to help its chosen nest and (b) were of equivalent or higher relatedness to the helper than the pair that it chose to help. Relatedness of helpers to both the breeders they chose to help and to other breeders they could have helped was determined primarily by reference to the social pedigree. For individuals that migrated into the population as adults and for which, consequently, a full social pedigree was unavailable, we performed sibship reconstructions to search for full siblings among birds migrating into the population in the same year (Sharp et al. 2008b), which then allowed us to identify other first- and second-order relatives in the population. Sibship reconstructions were performed in KINGROUP v. 2 (Konovalov et al. 2004) using genotypes for 19 microsatellite loci with a primary hypothesis of full sibling versus a null hypothesis of non-relative (for full details see Green and Hatchwell 2018). Of the 22 helpers included in our analysis, 16 helped a first-order relative (sibling, parent or offspring), four helped a second-order relative (aunt or uncle) and two helped a non-relative (in one case, the sibling of the helper's breeding partner), reflecting the preference for helping first-order relatives seen across the population as a whole (Hatchwell 2016; Leedale et al. 2020). All individuals helping a first-order relative had at least one other first-order relative in the population that was able to receive help. At least one first-order relative was also available to help in two cases when individuals helped second-order relatives; in the other two cases, an alternative second-order relative was available. Finally, in both cases when individuals helped non-relatives, a first-order relative was also available to help. Of the 22 helpers, 17 (77%) were male, which closely matches the sex ratio of helpers in the population as a whole (84%; Sharp et al. 2011).

For both the nest that was helped and nests that could have received help, we gathered data on the size and age of broods and the number of other helpers present, which were then used to calculate the indirect fitness payoff available from helping each brood (see below). Brood size was measured as the number of nestlings in the nest on day 11, while the age of broods was calculated as the number of days from hatching to the appearance of the helper at its chosen nest. Finally, because the likelihood of helping at a nest is known to decline with increasing distance from the helper's own nesting attempt (Leedale et al. 2018), we also recorded the distance of nests from the helper's final, failed nesting attempt. It was not possible to record data blind because our study involved focal animals in the field.

Statistical analysis

Estimating indirect fitness payoffs

To obtain the indirect fitness payoff available from helping each brood, we first estimated the effect of help on offspring recruitment, following the approach of Hatchwell et al. (2004, 2014), Green and Hatchwell (2018), and Roper et al. (2022), We modelled individual recruitment success for 1861 ringed individuals that fledged from a nest within the study site from 1994 to 2018 (individuals that fledged in 2000 were omitted from the analysis due to poor coverage of the study site in 2001). Whether an individual recruited into the study population in the following year (yes/no) was fitted as a binary response variable in a generalised linear mixed-effects model (GLMM) with a binomial error structure. The number of helpers at the natal nest was fitted as a fixed effect, together with the sex of the individual and the date that it fledged (relative to the median date in each year). These fixed effects account for the fact that males are more philopatric than females (Green and Hatchwell 2018) so there is a greater probability of detecting male recruits than female recruits, and that offspring fledging earlier in the season have a greater probability of recruitment (MacColl and Hatchwell 2002). As we note above, the prediction that individuals should prefer to help larger broods holds only if the effect of help on *per capita* recruitment success does not decline with increasing brood size. We tested this assumption by including brood size (number of nestlings on day 11) as a fixed effect and fitting an interaction between brood size and helper number. Finally, nest ID and year were included in the model as random effects to account for brood and cohort effects on recruitment.

Using the relationship between helper number and recruitment success from the above analysis, we calculated the contribution of a single helper to an offspring's probability of recruitment for a given number of helpers at a nest. For each nest available to help, we then multiplied this fraction by the size of the brood (number of nestlings at day 11) to calculate the marginal productivity benefit available to an individual helper, while accounting for the number of other helpers already in attendance. This value was then multiplied by the average relatedness of the helper to the brood. Finally, this value was weighted by the probability that the brood survives to fledging. Gullett et al. (2015) previously estimated a daily survival rate for broods during the nestling period of 96.7%. We therefore calculated survival probability as 0.967^n, where n equals the difference in number of days between day 17 (when fledging most frequently occurs) and the day on which helping decisions were made. To illustrate, consider the payoff available to a helper assisting a full sibling in rearing a brood of 10 nestlings (nieces and nephews, average $r = 0.25$), having begun helping on day 13 when one other helper was already in attendance. On average, when two helpers are present, the above analysis shows that a single helper is responsible for 14% of recruits produced by a brood that survives to fledging. The indirect fitness payoff for this helper is thus:

$$0.14 \times 10 \times 0.25 \times 0.967^4 = 0.306$$

Note that while this calculation accounts for whole-brood mortality during the nestling period, it assumes that all offspring that survive to fledging have an equal probability of recruiting into the adult population. Therefore, the indirect fitness payoff we calculate here represents the *maximum* payoff available to a helper from helping at a given nest. Note also that we are making the simplifying assumptions that the effect of help is the same for all helpers and does not vary with the length of time that helpers care for a brood prior to fledging. In the absence of evidence that offspring recruitment is positively correlated with the duration of pre-fledging help and given that the period of post-fledging care can match or exceed that provided prior to fledging, this latter assumption appears reasonable. However, if recruitment success does increase with helper investment prior to fledging, we would expect this to bias the preference of helpers towards helping younger broods, a preference we should then detect in our analysis of helping decisions.

Helping decisions

To analyse helping decisions, we used GLMMs with a binomial error structure and set the model response variable as the decision to help or not at a given nest. In the indirect fitness analysis, we asked whether helping decisions were sensitive to the indirect fitness payoffs available from helping at a particular nest by fitting this payoff as a fixed effect, together with the distance of the nest from the helper's own final breeding attempt. In the fitness component analysis, we considered the separate factors that may influence helping decisions by fitting brood size, brood age, and number of other helpers at the nest as fixed effects, again fitting distance as an additional fixed effect. In both models, the ID of the helper was included as a random effect to account for the fact each helper had multiple broods that they could help. Modelling the data in this way does not, however, overcome the non-independence that arises from the fact that long-tailed tits do not help at multiple nests simultaneously, meaning that if an individual chooses to help at a particular nest, it is consequently unavailable to help at other nests. Permutation tests can be a useful tool for considering the potential for non-independence (and other structural aspects of the dataset) alone to generate significant results under the models used (Whitehead 2008). Therefore, along with reporting the significance calculated from the standard models, we also tested the significance of each fixed effect in turn by running the analysis 1000 times, each time randomly reassigning values for the fixed effect of interest among the different nests available to each individual to help, while holding the values of the other fixed effects and the response constant. The significance of each effect was then determined by calculating the proportion of simulated test statistics (denoted P_{null}) that were more extreme (in either direction) than the observed test statistic obtained when the model was run with the true (i.e. unrandomised) values, whereby a value of $P_{\mathrm{null}} < 0.05$ would indicate that the observed test statistic falls outside of the 95% range expected under the randomised permutations alone. If structural aspects of the dataset (non-independence, sample size, distributions) alone drive significance of particular factors, then effects of the same magnitude as found in the real observed dataset will also be found in randomisations of the dataset, but if the observed effects are larger or smaller than those found in the model outputs using a randomised dataset, then the permutation tests will show the observed model parameters are statistically different from the null range that is expected by chance alone given the data/model structure (Whitehead 2008).

All analyses were performed in R v. 4.0.3 (R Core Team 2020). GLMMs were performed using the glmmadmb function in the glmmADMB package (Fournier et al. 2012). Coefficients and standard errors for fixed effects were obtained from the full model, while χ^2 and P values were obtained by comparing the full model to a second model without the fixed effect of interest, having first removed any non-significant interaction terms. All analyses were two-tailed, and effects were considered to be statistically significant at $P < 0.05$. For the analysis of helping decisions, P_{null} is reported for each fixed effect alongside the P value obtained from the GLMM analysis.

Results

Of a total of 521 recorded helping events, we identified 33 cases where helpers had the option of helping one or more breeding pairs of equal or higher relatedness to them than the pair they chose to help (total helping options across all individuals = 79, mean ± SD number of alternative options per individual = 1.39 ± 0.61, range = 1–3, $n = 33$). For 22 helpers, we had information on the size and age of broods, number of other helpers in attendance, and inter-nest distances for all available helping options (total = 54).

Analysis of *per capita* recruitment success confirmed a positive effect of the number of helpers on recruitment (coefficient ± SE = 0.31 ± 0.10, $\chi^2 = 9.55$, $P = 0.002$). However, the magnitude of this effect did not depend on the size of the helped brood (helper number × brood size: $\chi^2 = 0.09$, $P = 0.76$). As expected, measured recruitment was higher in males ($\chi^2 = 53.80$, $P < 0.0001$) and in individuals that fledged early in the season (-0.28 ± 0.10, $\chi^2 = 7.41$, $P = 0.006$). The analysis also revealed that individuals in smaller broods had a higher probability of recruiting (-0.22 ± 0.09, $\chi^2 = 5.97$, $P = 0.01$). Despite this, total productivity (number of fledglings × probability of recruitment) increased with brood size, plateauing at broods of five or more nestlings (Fig. 1). Larger broods thus offer greater fitness returns to helpers, yet we found no difference in size between helped and non-helped broods (0.25 ± 0.34, $\chi^2 = 0.53$, $P = 0.47$, $P_{\text{null}} = 0.49$; Fig. 2a). There was also no significant difference between helped and non-helped broods in the age of nestlings (− 0.53 ± 0.34, $\chi^2 = 2.53$, $P = 0.11$, $P_{\text{null}} = 0.13$; Fig. 2b). We did, however, find a difference in helper attendance, with individuals more likely to help at nests where a greater number of helpers were already in attendance (0.80 ± 0.38, $\chi^2 = 5.50$, $P = 0.02$, $P_{\text{null}} = 0.03$; Fig. 2c). Helped broods also tended to be closer to the helper's own final nesting attempt than non-helped broods (− 1.03 ± 0.49, $\chi^2 = 7.10$, $P = 0.008$, $P_{\text{null}} = 0.01$; Fig. 2d), but this result was strongly influenced by three non-helped nests located far (> 2000 m) from the helper's own nest. The difference in distance between helped and non-helped nests remained significant when the data were winsorised by setting values greater than the 95th percentile to the 95th percentile (− 0.82 ± 0.39, $\chi^2 = 5.63$, $P = 0.02$, $P_{\text{null}} = 0.01$) but was no longer significant when these three helping decisions were removed from the analysis (− 0.36 ± 0.36, $\chi^2 = 1.07$, $P = 0.30$, $P_{\text{null}} = 0.49$, $N = 19$ helping decisions). When removing these three helping decisions, differences in brood age and size between helped and non-helped nests remained non-significant (age: $\chi^2 = 1.93$, $P = 0.17$, $P_{\text{null}} = 0.09$; size: $\chi^2 = 0.70$, $P = 0.40$, $P_{\text{null}} = 0.27$).

When combining information about helper number, brood age, and brood size to estimate indirect fitness payoffs of helping, we found that helpers did not prefer to help at nests that offered the greatest fitness gains (− 0.27 ± 0.29, $\chi^2 = 0.86$, $P = 0.35$, $P_{\text{null}} = 0.36$; Fig. 3). This result remained unchanged when excluding the three individuals whose helping options included nests located > 2000 m from their own nesting attempt ($\chi^2 = 0.00$, $P = 0.97$, $P_{\text{null}} = 0.92$).

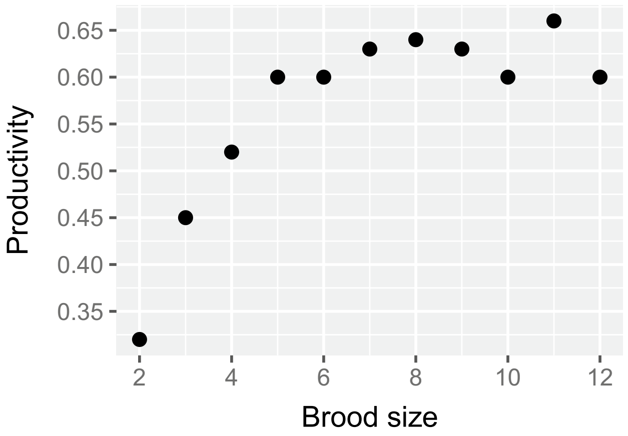

Fig. 1 The relationship between the size of fledged broods and productivity. Productivity at each brood size was calculated as the number of fledglings multiplied by the *per capita* recruitment probability, estimated from a GLMM that had brood size, presence of helpers, sex, and fledge date as fixed effects and year (1994–2018, excluding 2000) and nest ID ($n = 238$ nests) as random effects

Discussion

In long-tailed tits, cooperation occurs following natal dispersal, with individuals that have failed to breed successfully sometimes opting to redirect their effort towards caring for a brood belonging to another breeding pair, to which they are typically related. This redirected care is altruistic, with helpers gaining indirect fitness by enhancing the productivity of breeders (Hatchwell et al. 2014). Limited dispersal coupled with coordinated dispersal among siblings and a small effective population size results in significant kin structure within the population, with relatives living in close proximity (Leedale et al. 2018). Within these kin neighbourhoods, helpers actively discriminate among breeders, preferentially helping those to whom they are most closely related (Russell and Hatchwell 2001; Leedale et al. 2020). In this study, we asked whether helping decisions are also sensitive to other factors that influence the indirect fitness payoff of helping. To do this, we identified cases across the 26-year study period where helpers had the opportunity to help broods of equal or greater relatedness than those they elected to help. Statistical analysis of social partner choice is potentially complicated in species such as the long-tailed tit where help is given to only one partner at a time, since help given to one partner then necessarily precludes help being given to others. To address this source of non-independence in the data, we performed simulations to generate a null distribution of values for each predictor based on random reassignment of an individual's choice among the set of nests available for it to help. In all cases, however, the P values we obtained using this approach very closely matched those from the GLMM analysis of the raw data, indicating that the non-independence within an individual's helping options had little influence on the statistical significance of the predictors that we analysed. Contrary to our expectation, these analyses showed that helpers did not choose nests that offered the greatest indirect fitness returns. In addition to the relatedness between helpers and broods, our estimate of indirect fitness payoffs incorporated information about the size and age of broods and the number of helpers at the nest. Below we consider the role of each of these factors in turn in guiding nest choice by helpers.

We expected that helpers should preferentially help larger broods based on the indirect fitness benefits that accrue through offspring recruitment. We first tested the assumption underlying this prediction that the effect of helpers on recruitment probability did not diminish at larger brood sizes, finding that helpers should indeed prefer to help larger

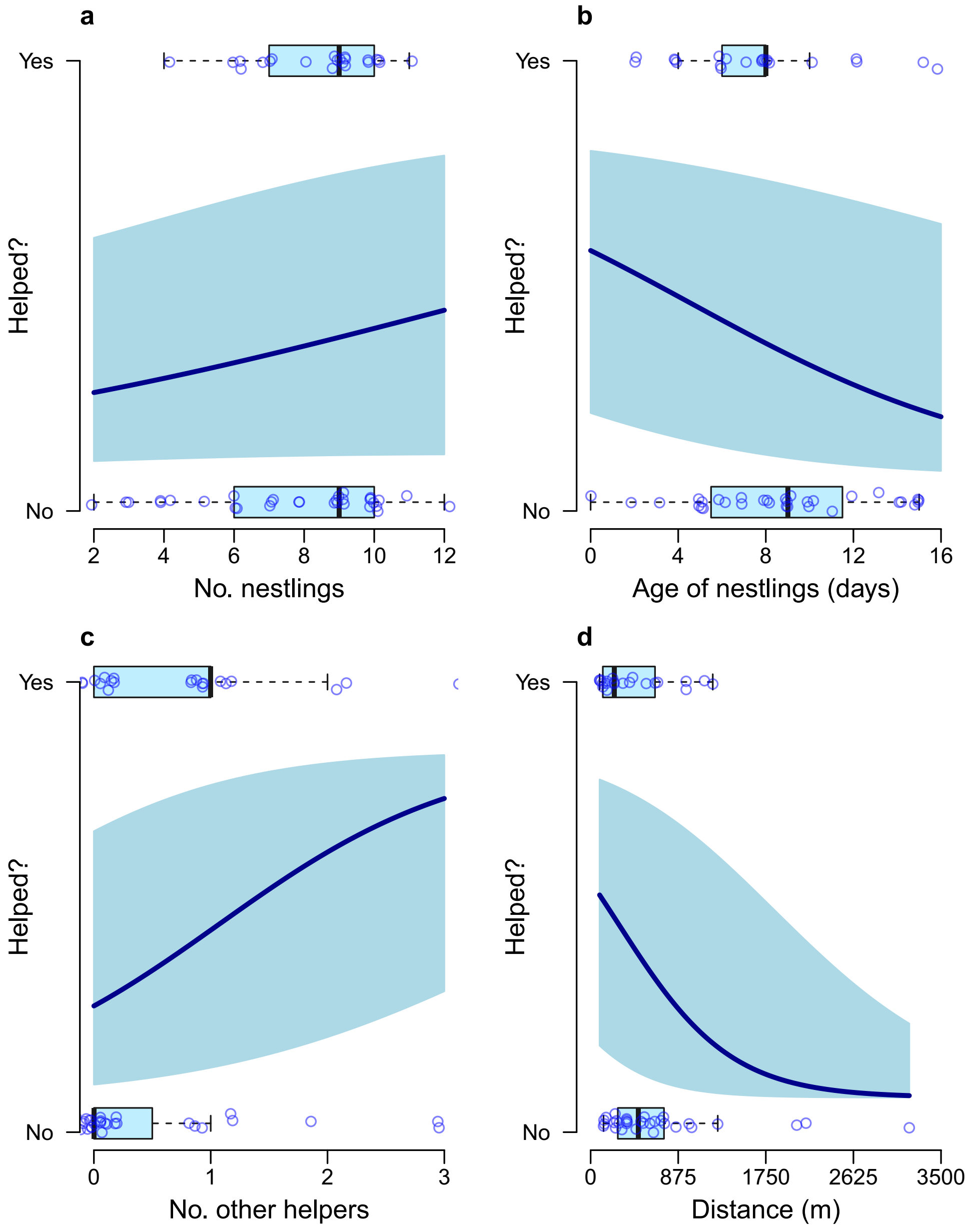

Fig. 2 The probability that a nest is helped as a function of **a** the number of nestlings, **b** the age of nestlings (in days), **c** the number of other helpers at the nest, and **d** distance from the helper's breeding attempt. Lines are predictions from GLMMs, controlling for other fixed effects and helper ID, and the shaded area denotes the standard error. Boxplots show values for helped and non-helped nests. Central lines represent median values, outer lines of the box represent the first and third quartiles, and horizontal lines represent approximately 2 SD around the interquartile range. Points are raw data

broods. Helped broods were, however, neither significantly larger nor smaller than non-helped broods. One explanation for this result is that brood size is difficult for helpers to assess. Long-tailed tits build domed nests, and it is possible that this architecture hinders visual assessment of brood size; however, the fact that helpers adjust their provisioning effort according to the number of nestlings they are feeding (Nam et al. 2010) suggests that helpers are able to gather information about brood size, possibly via nestling vocalisations or via the provisioning rates of other carers (Meade et al. 2011). Alternatively, the lack of preference for large brood sizes may reflect the limited variation in brood size in this species, a consequence of low rates of partial brood mortality (see Introduction). Among nests in this study, brood sizes ranged from 2 to 12 nestlings, but the interquartile range was narrower, spanning 6–10 nestlings, with a median brood size of 9 nestlings. With limited variation in brood size, selection for discrimination among broods by helpers on the basis of nestling number is then likely to be weak.

In addition to brood size, we also considered the possibility that brood age may influence the fitness payoff that individuals receive from helping. The high rate of whole-nest predation experienced by the population may favour helping at nests with older broods, since these have a greater likelihood of surviving to fledging, maximising the chances that the helper secures some return on its investment. Alternatively, younger broods may be favoured if the duration of help positively correlates with offspring quality and

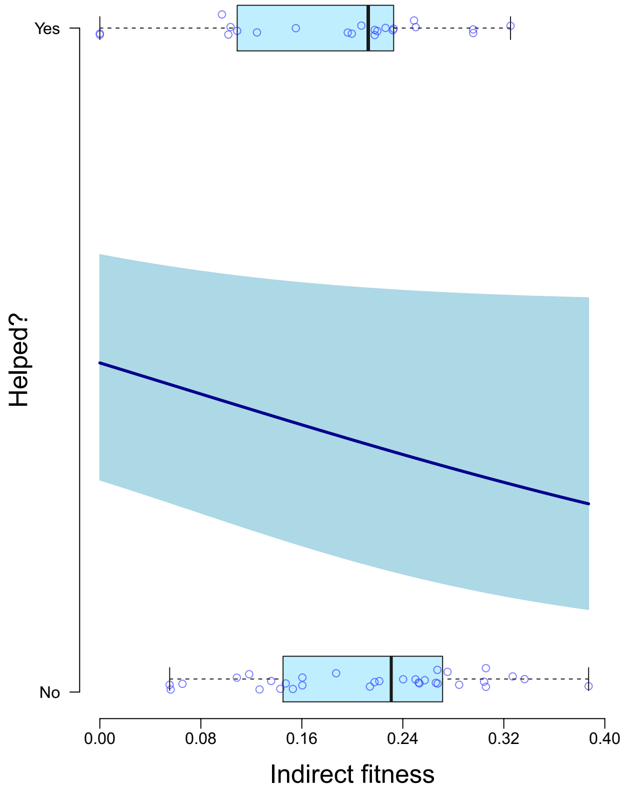

Fig. 3 The probability that a nest is helped as a function of the indirect fitness payoff that a helper stands to receive from caring for the brood. The line is predicted from a GLMM, controlling for distance from the helper's breeding attempt and helper ID, and the shaded area denotes the standard error. Boxplots show values for helped and non-helped nests. Central lines represent median values, outer lines of the box represent the first and third quartiles, and horizontal lines represent approximately 2 SD around the interquartile range. Points are raw data

recruitment success. Helped broods did not, however, differ significantly in age from non-helped broods. Again, it is unlikely that this reflects a failure to respond to cues of nestling age, since helpers are also known to increase their provisioning effort as broods age (MacColl and Hatchwell 2003; Nam et al. 2010). It is also unlikely that the lack of a clear preference for broods of a particular age reflects limited variation in the age of nestlings among broods available to help: the rate of nest predation across the population is high but predation occurs largely at random and breeders that lose their first nest may attempt to reproduce a second or even third time. As a result, on any given day the age of nestlings among nests is expected to vary considerably — among nests in this study, the mean age of nestlings ranged from 0 to 16 days (mean ± SD = 8.3 ± 3.9 days), which spans the entire nestling period.

An alternative explanation for why we found no preference for nests based on the size or age of broods or the estimated indirect fitness returns available is that there is simply not much opportunity for individuals to exercise choice about which broods to help. The preference shown for helping at the nests of first-order relatives reduces the pool of potential recipients available to help, yet as a consequence of low-within brood mortality and high whole-brood mortality caused by depredation of entire nests (Hatchwell et al. 2004; Beckerman et al. 2011) individuals born in the study site that succeed in recruiting into the adult population will often do so in the company of one or more siblings (66% with ≥ 1 siblings versus 40% with ≥ 2 siblings, $N = 154$ fledged broods; JPG and BJH, unpublished data). To this pool may be added any surviving parents (adult survival across breeding seasons = 52%; Hatchwell 2016) and, after the first breeding year, any offspring that succeed in recruiting into the breeding population (average recruitment probability = 14%; Sharp et al. 2011). Immigration is also frequently coordinated among kin, with the majority of individuals that migrate into the study site as adults doing so with one or more siblings (Sharp et al. 2008b). It might thus be expected that failed breeders regularly have the option of helping two or more first-order relatives, yet across 521 helping events recorded in 26 years, we identified only 33 cases (6.3%) where helpers could have helped at one or more broods of equal or higher relatedness to the brood they chose to help; of these, 22 (67%) involved a single alternative option, while in only 11 cases (33%) a helper had two or three alternative options. The most likely explanation for the paucity of options is the high level of nest predation which, as already discussed, appears largely stochastic, with the result that the survival of a given breeder's offspring is highly unpredictable. Given that a lack of choice appears to be common, only weak selection for choice of the kind investigated here would be expected. Instead, individuals may be favoured to help the first related breeder they encounter, with the result that helpers typically end up helping relatives whose nests are close to their own nesting attempt without searching over greater distances for other options. In this regard, the situation is somewhat analogous to mate selection in species that experience high mortality, where high rates of divorce between breeding seasons reflect, in part, the low probability that the partner of an individual surviving to the next breeding season will also have survived (Jeschke and Kokko 2008).

This scenario is consistent with our finding that helpers tended to help at nests closer to the site of their own final, failed nesting attempt. This result was, however, contingent on the inclusion of three non-helped nests in the analysis located > 2000 m from the helper's own final reproductive attempt, which exceeds the maximum distance that long-tailed tits are known to travel to a nest they then choose to help (1800 m; Leedale et al. 2018). Indeed, the majority of helpers travel within 600 m, with a median distance travelled of 278 m (Leedale et al. 2018), which is similar to the median distance for the sample of birds included in this study (235 m for helped nests versus 478 m for non-helped nests). The existence of kin neighbourhoods arising from limited dispersal ensures that helpers travelling within this distance from their own failed breeding attempt are likely to encounter any close relatives still caring for nestlings. This effect is, however, stronger for males than for females, which tend to disperse further from their natal nests and are also less likely to help (Green and Hatchwell 2018). Indeed, it is notable that the greatest distance between a helper's own nest and a non-helped nest (3183 m) was for a mother-daughter pair, with the younger female instead helping at the nest of her partner's sibling, to whom she was unrelated.

Within a kin neighbourhood, a successful breeder is likely to represent the nearest helping opportunity for multiple individuals living in close proximity whose own nesting attempts have been depredated. The spatial clustering of kin in long-tailed tits, in combination with high nest failure rates, probably explains our finding that individuals were more likely to help at nests where other helpers were already in attendance. We consider the alternative explanation that individuals actively prefer to help at nests that are already receiving help, to be unlikely. While in some species there are synergistic benefits to cooperative breeding, with the combined help provided by helpers exceeding the sum of each helper's individual contribution (Powers and Lehmann 2017), in long-tailed tits, the contribution to offspring recruitment by each helper is largely independent of the total number of helpers (Hatchwell et al. 2014), with only a small decrease in *per capita* marginal productivity with an increasing number of helpers (e.g. 16% increase in recruitment with a single helper versus 14% when two helpers are present; this study). Therefore, targeting nests where helpers are already in attendance does not substantially increase or decrease the indirect fitness payoff the helper receives from helping. Direct benefits of associating with other helpers, in the breeding season or beyond, are also unlikely to explain the frequent co-occurrence of helpers at the same nest because investment in helping does not improve an individual's survival or future reproductive success in this species (Meade and Hatchwell 2010).

In long-tailed tits, where cooperation is maintained exclusively through the indirect benefits that helpers accrue from assisting related breeders, our analysis of helping decisions provides no evidence that helpers increase their indirect fitness payoff by targeting nests where the effect of their help on offspring recruitment is most strongly felt. To date, evidence for such behaviour appears to be limited to the wasp *Polistes canadensis*, in which non-reproductive subordinates are observed to undertake frequent visits to nests other than their natal nest (Sumner et al. 2007). Here, the tendency to help additional nests that are relatively small in size has been interpreted as an attempt to target help towards those broods that would benefit most from the additional investment. However, it remains unclear whether the indirect fitness gains of helping are in fact maximised by this behaviour, since the benefits experienced by these smaller colonies are potentially offset by the reduced relatedness of the subordinates to broods on these nests (Sumner et al. 2007).

Among species in which investment in alloparental care yields direct benefits, there is also evidence that individuals target social partners from whom they can extract the greatest direct fitness payoff from cooperation. In the wasp *P. dominula*, for example, subordinate females may abandon groups to attempt to usurp the dominant egg-layer in smaller, more vulnerable groups (Nonacs and Reeve 1995), while in house mice (*Mus musculus domesticus*), females show a weak preference for combining their newborn litters with other litters of a similar age (Harrison et al. 2018), thereby maximising the relative competitive ability of their own offspring within the communal nest and reducing the risk of offspring loss through infanticide (Schmidt et al. 2015). In these and other taxa, however, cooperation among kin also yields significant indirect benefits, which can complicate attempts to disentangle the different factors governing partner selection. To this end, increased focus on species in which cooperation occurs routinely or exclusively among non-kin may help to determine criteria other than kinship that are used to select social partners. Such evidence for discrimination among unrelated partners comes from eider ducks (*Somateria mollissima*), where females in good condition prefer to nest alongside females in poor condition, which may reflect an attempt to maximise the benefits of communal nesting while minimising costs of competition (Öst et al. 2003). Occasional nest-switching by breeding pairs of greater anis (*Crotophaga major*), as reported by Riehl (2011), is also suggestive of some form of assessment of social partners, which are typically unrelated, but the criteria that underpin this assessment and the fitness consequences of movement between groups remain unknown.

In cooperatively breeding systems where individuals can choose among multiple social partners, the stage may be set for market forces to influence the payoffs that partners obtain from cooperation (Noë and Hammerstein 1994). It is difficult to see how such forces could operate in species such as the long-tailed tit where help is altruistic and the payoff of cooperating depends entirely on the effort put in by partners. In contrast, when cooperation involves an exchange of resources that generate direct fitness benefits, an individual's outside options (the benefits it would gain from cooperating with different partners, in addition to not cooperating) may influence the magnitude of the benefit that is given to ensure cooperation (e.g. Grinsted and Field 2017a, b). Further research is needed on cooperatively breeding species where individuals have the option of cooperating with multiple recipients to identify both the factors other than relatedness that drive partner choice and the scope for market forces to shape the payoffs of cooperation.

Acknowledgements Molecular analyses were conducted at the Natural Environment Research Council (NERC) Biomolecular Analysis Facility at the University of Sheffield, with support from Terry Burke and Deborah Dawson. We are grateful to all field researchers who have contributed to the long-tailed tit project, and thank Sheffield City Council, Yorkshire Water, Hallamshire Golf Club, and private landowners of the Rivelin Valley for access to their land. Finally, we also thank the Editor and two anonymous reviewers for helpful feedback on the manuscript.

Author contribution BJH managed the field study and collected data on which analyses are based over 25 years. NJS, JAF, and JPG analysed data. JPG wrote the first version of the manuscript, and along with BJH, NJS and JAF revised and edited the manuscript.

Funding Fieldwork was funded by the NERC, UK (recent awards: NE/I027118/1 and NE/R001669/1).

Data availability The datasets analysed during the current study have been deposited in the DRYAD repository (https://doi.org/10.5061/dryad.mw6m905z7).

Declarations

Ethics approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. The animal study was reviewed and approved by University of Sheffield Ethical Review Committee (Project Applications and Amendments Sub-Committee), and a project license is held for taking blood samples from the UK Home Office (PPL 70/8434).

Consent for publication All authors approved the submitted draft of this manuscript and agree to be responsible for their contributions to this publication.

Competing interests The authors declare no competing interests.

References

Beckerman AP, Sharp SP, Hatchwell BJ (2011) Predation and kin-structured populations: an empirical perspective on the evolution of cooperation. Behav Ecol 22:1294–1303

Choe JC, Crespi BJ (1997) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge

Clutton-Brock T (2009) Structure and function in mammalian societies. Phil Trans R Soc B 364:3229–3242

Cockburn A, Sims RA, Osmond HL, Green DJ, Double MC, Mulder RA (2008) Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? J Anim Ecol 77:430–438

Covas R, Doutrelant C, du Plessis MA (2004) Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. Proc R Soc Lond B 271:827–832

Dickinson JL, Hatchwell BJ (2004) Fitness consequences of helping. In: Koenig WD, Dickinson JL (eds) Ecology and evolution of cooperative breeding in birds. Cambridge University Press, Cambridge, pp 48–66

Downing PA, Griffin AS, Cornwallis CK (2020) The benefits of help in cooperative birds: nonexistent or difficult to detect? Am Nat 195:1085–1091

Emlen ST (1981) Altruism, kinship, and reciprocity in the White fronted bee-eater. In: Alexander RD, Tinkle D (eds) Natural selection and social behaviour: recent research and new theory. Chiron Press, New York, pp 217–230

Emlen ST, Wrege PH (1988) The role of kinship in helping decisions among white-fronted bee-eaters. Behav Ecol Sociobiol 23:305–315

Ferrari M, Lindholm AK, König B (2019) Fitness consequences of female alternative reproductive tactics in house mice (*Mus musculus domesticus*) Am Nat 193:106–124

Field J, Cant MA (2006) Helping effort in primitively eusocial wasps. Ann Zool Fenn 43:481–487

Field J, Foster W (1999) Helping behaviour in facultatively eusocial hover wasps: an experimental test of the subfertility hypothesis. Anim Behav 57:633–636

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterised complex nonlinear models. Optim Methods Softw 27:233–249

Grinsted L, Field J (2017) Biological markets in cooperative breeders: quantifying outside options. Proc R Soc B 284:20170904

Green JP, Freckleton RP, Hatchwell BJ (2016) Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton's Rule. Nat Commun 7:12663

Green JP, Hatchwell BJ (2018) Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). P Natl Acad Sci USA 115:12011–12016

Green JP, Holmes AM, Davidson AJ, Paterson S, Stockley P, Beynon RJ, Hurst JL (2015) The genetic basis of kin recognition in a cooperatively breeding mammal. Curr Biol 25:2631–2641

Grinsted L, Field J (2017b) Market forces influence helping behaviour in cooperatively breeding paper wasps. Nat Commun 8:13750

Gullett PR, Hatchwell BJ, Robinson RA, Evans KL (2015) Breeding season weather determines long-tailed tit reproductive success through impacts on recruitment. J Avian Biol 46:441–451

Hager R, Jones CB (2009) Reproductive skew in vertebrates: proximate and ultimate causes. Cambridge University Press, Cambridge

Harrison N, Lindholm AK, Dobay A, Halloran O, Manser A, König B (2018) Female nursing partner choice in a population of wild house mice (*Mus musculus domesticus*). Front Zool 15:4

Hatchwell BJ (2009) The evolution of cooperative breeding in birds: kinship, dispersal and life history. Phil Trans R Soc B 364:3217–3227

Hatchwell BJ (2016) Long-tailed tits: ecological causes and fitness consequences of redirected helping. In: Koenig WD, Dickinson JL (eds) Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press, Cambridge, pp 39–57

Hatchwell BJ, Gullett PR, Adams MJ (2014) Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. Phil Trans R Soc B 369:20130565

Hatchwell BJ, Russell AF, MacColl AD, Ross DJ, Fowlie MK, McGowan A (2004) Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. Behav Ecol 15:1–10

Heinsohn R, Legge S (1999) The cost of helping. Trends Ecol Evol 14:53–57

Jeschke JM, Kokko H (2008) Mortality and other determinants of bird divorce rate. Behav Ecol Sociobiol 63:1–9

Kennedy P, Sumner S, Botha P, Welton NJ, Higginson AD, Radford AN (2021) Diminishing returns drive altruists to help extended family. Nat Ecol Evol 5:468–479

Kingma SA (2017) Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. Nat Commun 8:1094

Koenig WD, Dickinson JL (2016) Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press, Cambridge

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150

Konovalov DA, Manning C, Henshaw MT (2004) KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. Mol Ecol Notes 4:779–782

Leadbeater E, Carruthers JM, Green JP, Rosser NS, Field J (2011) Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. Science 333:874–876

Leedale AE, Lachlan RF, Robinson EJ, Hatchwell BJ (2020) Helping decisions and kin recognition in long-tailed tits: is call similarity used to direct help towards kin? Phil Trans R Soc B 375:20190565

Leedale AE, Sharp SP, Simeoni M, Robinson EJ, Hatchwell BJ (2018) Fine-scale genetic structure and helping decisions in a cooperatively breeding bird. Mol Ecol 27:1714–1726

Lin N, Michener CD (1972) Evolution of sociality in insects. Q Rev Biol 47:131–159

MacColl AD, Hatchwell BJ (2002) Temporal variation in fitness payoffs promotes cooperative breeding in long-tailed tits *Aegithalos caudatus*. Am Nat 160:186–194

MacColl AD, Hatchwell BJ (2003) Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. Anim Behav 66:955–964

Meade J, Hatchwell BJ (2010) No direct fitness benefits of helping in a cooperative breeder despite higher survival of helpers. Behav Ecol 21:1186–1194

Meade J, Nam KB, Lee JW, Hatchwell BJ (2011) An experimental test of the information model for negotiation of biparental care. PLoS One 6:e19684

Nam KB, Simeoni M, Sharp SP, Hatchwell BJ (2010) Kinship affects investment by helpers in a cooperatively breeding bird. Proc R Soc Lond B 277:3299–3306

Napper CJ, Hatchwell BJ (2016) Social dynamics in nonbreeding flocks of a cooperatively breeding bird: causes and consequences of kin associations. Anim Behav 122:23–35

Noë R, Hammerstein P (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav Ecol Sociobiol 35:1–11

Nonacs P, Reeve HK (1995) The ecology of cooperation in wasps: causes and consequences of alternative reproductive decisions. Ecology 76:953–967

Öst M, Ydenberg R, Kilpi M, Lindström K (2003) Condition and coalition formation by brood-rearing common eider females. Behav Ecol 14:311–317

Parsons PJ, Grinsted L, Field J (2019) Partner choice correlates with fine scale kin structuring in the paper wasp *Polistes dominula*. PLoS ONE 14:e0221701

Powers ST, Lehmann L (2017) When is bigger better? The effects of group size on the evolution of helping behaviours. Biol Rev 92:902–920

Preston SA, Briskie JV, Burke T, Hatchwell BJ (2013) Genetic analysis reveals diverse kin-directed routes to helping in the rifleman *Acanthisitta chloris*. Mol Ecol 22:5027–5039

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Riehl C (2011) Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. Proc R Soc Lond B 278:1728–1735

Roper MA, Sturrock NJ, Hatchwell BJ, Green JP (2022) Individual variation explains aging patterns in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). J Anim Ecol (published online, https://doi.org/10.1111/1365-2656.13741)

Russell AF, Hatchwell BJ (2001) Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. Proc R Soc Lond B 268:2169–2174

Schmidt J, Kosztolányi A, Tökölyi J, Hugyecz B, Illés I, Király R, Barta Z (2015) Reproductive asynchrony and infanticide in house mice breeding communally. Anim Behav 101:201–211

Seppä P, Queller DC, Strassmann JE (2012) Why wasp foundresses change nests: relatedness, dominance, and nest quality. PLoS ONE 7:e45386

Sharp SP, Baker MB, Hadfield JD, Simeoni M, Hatchwell BJ (2008) Natal dispersal and recruitment in a cooperatively breeding bird. Oikos 117:1371–1379

Sharp SP, McGowan A, Wood MJ, Hatchwell BJ (2005) Learned kin recognition cues in a social bird. Nature 434:1127–1130

Sharp SP, Simeoni M, McGowan A, Nam KB, Hatchwell BJ (2011) Patterns of recruitment, relatedness and cooperative breeding in two populations of long-tailed tits. Anim Behav 81:843–849

Sharp SP, Simeoni M, Hatchwell BJ (2008) Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. Proc R Soc Lond B 275:2125–2130

Sumner S, Lucas E, Barker J, Isaac N (2007) Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. Curr Biol 17:140–145

Weidt A, Hofmann SE, König B (2008) Not only mate choice matters: fitness consequences of social partner choice in female house mice. Anim Behav 75:801–808

Weidt A, Lindholm AK, König B (2014) Communal nursing in wild house mice is not a by-product of group living: females choose. Naturwissenschaften 101:73–76

West SA, Cooper GA, Ghoul MB, Griffin AS (2021) Ten recent insights for our understanding of cooperation. Nat Ecol Evol 5:419–430

Whitehead H (2008) Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago