From local to global influences of ecological and demographic factors on helping in a facultative cooperative breeder

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Abstract

The fitness consequences of cooperative breeding are increasingly well understood, but the ecological and demographic factors driving helping remain contentious. Comparative and single-species studies have identified factors that promote the evolution of helping, but analyses typically test single hypotheses so the relative importance of different factors, and the spatial scale of their influence, remain unknown. Our aim was to investigate multiple social and demographic drivers of helping decisions using 27 years of data from a facultative cooperative breeder, the long-tailed tit *Aegithalos caudatus*. We analysed the decisions to help or not by 1,338 failed breeders to investigate the influence of metrics related to predation pressure, population density, availability of relatives and timing of breeding. We also examined the scale at which these features acted (100-1000m from a failed nest). We found that the availability of nests at a broad spatial scale of 400-500m from the failed nest was higher around those failed breeders that decided to help than those that did not. Specifically, helpers of either sex were surrounded by lower predation pressure, while male helpers were surrounded by more breeding attempts, more active nests, and later nests. However, the most important factor driving helping, and from a very fine spatial scale (100+m), was kinship: future helpers were surrounded by more social first order kin than non-helpers. This effect held for males, but not females, when considering the genetic pedigree. Our findings highlight the interplay of multiple ecological, demographic and social factors, acting at different spatial scales, offering new insights into the drivers of sociality.

Keywords: Cooperative breeding, sociality, long-tailed tits *Aegithalos caudatus*, helping, cooperation, drivers, relatedness, kinship, kin selection

Introduction

The factors promoting the evolution of cooperative breeding have puzzled evolutionary ecologists for decades. While the ultimate functions of cooperation between helpers and breeders - the acquisition of direct and indirect fitness benefits via several processes - have been largely resolved in theoretical (1–3), and empirical studies (4, 5), the factors that drive the emergence of cooperative breeding as an adaptive strategy remain the subject of current debate (6).

Although initially neglected (7), the critical influence of phylogeny has become clear as knowledge of avian taxonomy and breeding systems improved (8–10). However, attempts to identify common ecological, demographic or social conditions underlying cooperative breeding have proved equivocal. The global pattern of a decreasing prevalence of cooperative breeding at northerly latitudes is well established (11, 12) and comparative analyses have linked cooperative breeding to climatic unpredictability (12–14), although others have found that cooperation evolves under stable conditions (15). ‘Slow’ life history traits (16) and mate fidelity (17) have also been implicated, as has the predation pressure to which a population is subjected (18). However, Cockburn (6) has recently argued that such analyses are subject to methodological and conceptual flaws, such as sampling biases, inadequate data, confounding relationships with latitude, and the testing of unitary hypotheses.

In birds, helping is generally facultative so an alternative approach is to identify social, demographic or ecological factors that promote cooperative behaviour within species, either by examining the prevalence of cooperation across individuals, years, or populations, or by experimental manipulation of specific factors. Such studies have identified the importance of population density (19, 20), food availability (21, 22), mate availability (23, 24) and predation (25) as drivers of helping. However, again there is a tendency to test single hypotheses rather than simultaneously test multiple factors. Such studies are also fraught with the problem of the spatial scale at which factors are measured. For example, an individual’s information about its social environment may be very local, while ecological factors are usually measured at a broad population-level scale (26). In addition, the behavioural decisions of whether to help or not are made by individuals, so ideally the social and ecological circumstances of each actor should be considered in order to understand the factors driving them to help.

The aim of this study was to identify the social and demographic drivers of helping decisions and the spatial scale at which they operate in the facultative cooperative breeding system of long-tailed tits *Aegithalos caudatus*. Long-tailed tits breed in kin neighbourhoods and exhibit redirected helping by failed breeders. Each year, all birds attempt initially to breed in independent monogamous pairs, but following failure of their own breeding attempts, some failed breeders become helpers, assisting another pair in raising their brood. Helping is kin-selected, with helpers preferring to help relatives and gaining indirect fitness by enhancing the productivity of helped broods. Previous studies have shown that the decision of a failed breeder to help or not is, at least in part, a function of its sex (27), phenology (28), and the presence of nearby relatives (29). However, analyses across years and populations found no effect of mean population relatedness on the prevalence of helping (26, 30). Instead, at the population level, the prevalence of helping was influenced by inter-year variation in predation rate, peaking at intermediate levels, and breeding season length, decreasing in longer seasons (26). These two factors were interpreted as determinants of the availability of potential helpers and recipients. Thus, the factors identified as promoters of cooperative behaviour in this system seem to vary according to the spatial scale at which they are investigated.

Here, we used long-term data to analyse the helping decisions of 1,338 failed breeders in relation to their social and demographic environment. Specific objectives were to determine whether helping was associated with: (1) the availability of nests to which care could be redirected, (2) the availability of relatives, and (3) timing of breeding because phenology is an important determinant of helping in this system. We analysed each factor at varying spatial scales around the nest of the failed breeders, allowing us to test the hypothesis that drivers of the decision to become a helper or not may operate at a range of spatial scales.

Material and methods

Study site and species monitoring

From 1995 to 2021, we studied a resident population of long-tailed tits in Rivelin Valley, Sheffield, UK (53°23′N, 1°34′W). The ca. 3 km² study site (Figure 1) encompasses diverse habitats, including woodland, hedgerows, fields, scrubland, and a golf course. The breeding population ranged from 17 to 82 pairs annually. During the non-breeding season, long-tailed tits form flocks of 10–20 individuals, foraging and roosting together (31). By early March, these flocks disband as individuals pair up and begin constructing domed nests, made of moss, fibres and lichens bound with spider silk and lined with feathers. Nest abandonment during building (sometimes after disturbance by predators) and total predation of clutches and broods are frequent in this species (28% and 52% on average, respectively; n = 1,991 breeding attempts in 1994-2021). Long-tailed tits are single-brooded, but after a failed attempt, pairs often re-nest, sometimes rebuilding up to five times in a single season. Therefore, following a nest failure we searched thoroughly for replacement nests in the vicinity of the last nesting site. Every year, we estimate that >95% of nests were found, the missed fraction being mostly short-lived attempts. Nest fate (abandoned, predated, successful) was closely monitored, as well as nest phenology (first egg, incubation, hatching and fledging dates), either through direct observations for low nests (<3m above ground, ~71% of the nests)(32) or by behavioural observations of the parents' nest attendance pattern for higher nests. Females usually lay 8-11 eggs and incubate them for ca. 15 days. Broods hatch synchronously and chicks fledge 16-18 days later. Extra-pair paternity is limited to 10% of nestlings in 27% of broods (33). See Hatchwell (34) for further details on the species' biology.

After early May, failed breeders stop attempting to re-nest and may instead help provision the nestlings of neighbouring pairs (28). Most helpers are males (81%)(29), with 38% and 9% of failed males and females, respectively, becoming helpers (30). To identify helpers, we observed nests with nestlings for one hour every other day (weather permitting), starting when the nestlings were two days old and continuing until fledging or nest failure.

Individuals were marked with a numbered metal ring from the British Trust for Ornithology (BTO) on one leg and a unique combination of two colour-rings on the other (under BTO licence), ca. 95% of breeding adults being individually identifiable every year.

Unringed adults were captured using mist-nets and nestlings from low nests were ringed when 11 days old. Upon capture, we collected blood samples by brachial venepuncture (under Home Office licence) and genotyped individuals at up to 19 microsatellite loci following standard protocols (35). Long-tailed tits being sexually monomorphic, we also used two microsatellite loci to sex them.

Long-tailed tits have a kin-directed helping system, individuals preferentially helping first order kin (parents, siblings, or offspring) (Leedale et al., 2018; Russell & Hatchwell, 2001). To identify individuals as first order kin (see *Drivers of helping, yi*), we estimated both (1) the social relatedness between individuals by reconstructing the social pedigree of the population using behavioural observations of nest attendance and the “pedigree” R package (37), and (2) the genetic relatedness between individuals using the microsatellite data and the “related” R package (38). For the latter, we used the Queller and Goodnight (39) coefficient of relatedness as this rendered the highest correlation between observed and expected relatedness (0.9). We used both metrics because, although they often provide very close approximations (40), the social and genetic relatedness metrics present technical pros and cons: the first is based on social pairs and is likely to most closely reflect the information on kinship available to the birds (41); the second allows us to account for relatedness of immigrants as well as recruits from high nests that could not be ringed before fledging, but is limited to individuals for which we successfully obtained genotypes.

Drivers of helping, y_i

We aimed to identify key ecological and demographic drivers of helping and the spatial scale at which they influenced helping decisions. We first identified failed breeders as those birds observed to breed but whose nests did not produce any fledglings that season. For each failed breeder, we considered the location of their last breeding attempt as the focal nest. We then calculated 10 potential drivers that could be associated with helping $y_{i,\alpha}$ at the vicinity of each focal nest. These included four metrics of nest availability that season for potential helpers:

- (1) the number of breeding attempts ***n.att***,
- (2) the number of still active nests ***n.act*** at the time of failure of the focal nest,
- (3) the number of predated nests ***n.pred***, and
- (4) the proportion of nests that were predated ***p.pred***.

As measures of opportunities to gain indirect fitness benefits by helping kin, we calculated:

- the number of first order kin breeders, determined either from (5) the social pedigree ***n.soc.kin***, or (6) the genetic pedigree, ***n.gen.kin***,
- the number of first order kin breeders at active nests at the time of failure of the focal nest, determined either from (7) the social pedigree, ***n.soc.kin.act***, or (8) the genetic pedigree, ***n.gen.kin.act***.

Finally, as measures of time available to help others and availability of other nests to help, we also calculated two metrics relating to phenology of the breeding season in the relevant year:

- (9) the mean first egg lay date, ***mean.lay***,
- (10) the standard deviation of first egg lay date, ***sd.lay***.

Count variables *n.x* (*n.att*, *n.act*, *n.pred*, *n.soc.kin*, *n.gen.kin*, *n.soc.kin.act*, *n.gen.kin.act*) were calculated for each focal nest *i* as the weighted sum of occurrences of events *O*:

$$n.x_{i,\alpha} \; = \; \sum_{j=1}^{N} w_{i,j,\alpha} \times O(j) \qquad \text{Eq. 1}$$

$O(j)$ being 1 when the condition was met (being respectively a breeding attempt, active nest, predated nest, first order kin, first order kin in active nest) and 0 when it was not met. We considered the influence of a nest *j* to exponentially decrease with its distance to the focal nest, d_{ij}, using a weighting coefficient $w_{i,j,\alpha}$ (as in 42):

$$w_{i,j,\alpha} = \exp\left(-\frac{d_{ij}}{\alpha}\right) \qquad \text{Eq. 2}$$

α being the spatial scale over which the response variable y_i is calculated. For small values of α, only nearby nests were considered when calculating $y_{i,\alpha}$ while the influence of more distant nests increased with increasing values of α (Figure S1). To determine whether some drivers $y_{i,\alpha}$ would be more influential in helping decisions at certain distances, we varied α from 100 to 1,000m (in 50m increments) in our models and determined which value of α led to the best fitted model (see *Statistical analyses* and Figure 1).

The proportion of predated nests around each focal nest *i* was calculated as the ratio between the number of predated nests and the weighted sum of nests available:

$$p.pred_{i,\alpha} \; = \frac{n.pred_{i,\alpha}}{\sum_{j=1}^{N} w_{i,j,\alpha}} \qquad \text{Eq. 3}$$

The mean and standard deviation of first egg lay date around each focal nest *i* were calculated as:

$$mean.lay_{i,\alpha} \; = \frac{\sum_{j=1}^{N} w_{i,j,\alpha} \times l_j}{\sum_{j=1}^{N} w_{i,j,\alpha}} \qquad \text{Eq. 4}$$

$$\text{and } sd.lay_{i,\alpha} \; = \frac{\sum_{j=1}^{N} w_{i,j,\alpha} \times (l_j - \underline{l})^2}{\sum_{j=1}^{N} w_{i,j,\alpha}} \qquad \text{Eq. 5}$$

l_j being the julian first egg lay date of the nest *j*, and l being the average julian first egg lay date that year. *N* was usually the total number of nests that season, except when considering predation events and laying dates, in which cases it was limited to nests available to predation (i.e. not formerly abandoned) and nests reaching egg stage respectively. The focal nest itself was always excluded from *N*.

One potential bias in our spatial approach is that nests closer to the edge of the study site (Figure 1) will have less chance of having other nests and kin detected near them. However, we do not believe this to be a problem for three reasons. First, failed breeders near the edge of the study site would have similarly lower chances to be detected helping at a nest because they may help outside the study area. Second, the whole study area is searched thoroughly for new nests, so there is no edge effect in nest detection, so no a priori bias in the $y_{i,\alpha}$ estimation with this definition. Finally, in many cases there are no helping options beyond the study site boundary because the study area is bounded on the north and south mostly by less suitable long-tailed tit breeding habitat (urban areas and open fields with stone walls; Figure 1).

Another potential bias is that failed nests close to each other will tend to have more similar estimates of variables $y_{i,\alpha}$ than failed breeders from focal nests further apart. However, we think that spatial autocorrelation is unlikely to be problematic. First, some variables are calculated using nest- or individual-specific criteria (e.g. the time of nest failure, helped or not) that are unlikely to covary spatially. Second, although nest density is to some extent dependent on spatial location within the study area, the success of breeding attempts is not (M Germain et al. unpublished) so breeders in certain areas are not more likely to become potential helpers. Third, as α values increase, the variance in $y_{i,\alpha}$ would be expected to decrease, but our weighting method prevents homogenisation of estimates by always giving more weight to closer nests (Eq. 2 and Figure S1).

Statistical analyses

To determine which driver $y_{i,\alpha}$ influenced the helping decision of the failed breeders, we fitted linear mixed effects models with each driver $y_{i,\alpha}$ as response variable, and the helping decisions as fixed factor (2 levels, helped or did not help, the latter being the reference group). As males are more likely to help than females, we expected their helping decisions to be influenced by different drivers. Therefore, each model was run separately for males and females.

To determine the spatial scale at which the neighbourhood around the nest of failed breeders influenced helping decisions, following Kivelä et al. (42), we varied the coefficient α from 100m to 1000m (every 50m) when calculating each $y_{i,\alpha}$ and fitted 19 versions of each model. We then estimated the fit of each model by calculating its R^2, defined as the proportion of variance explained by the fixed and random effects. Among the models with equivalent high R^2 ($R^2 > ¾ * \text{maximum } R^2$, as in Kivelä et al., (42)), we tested for the significance of the helping effect and determine the lowest value of α from which we detected such effect (hereafter, the influential α). Indeed, given that closer nests always have a stronger influence than more distant ones in the calculations of the $y_{i,\alpha}$ (Figure S1), when the helping effect differed from zero for a given value of α, it did so also for the higher values of α (Figure 2, Table S1). In total, we fitted 380 models (10 types of y_i variables, 19 values of α, 2 sexes).

All analyses were conducted in R v.4.4.2 (43). We fitted each of the $y_{i,\alpha}$ response variables with a Bayesian linear mixed effect model using “MCMCglmm” R package (44). All models included year as a continuous random term. For models fitting the number of kin (whether social or genetic, in active nests or overall), we used inverse Wishart priors (V = 1, nu = 0.002) for the residuals, expanded priors (V = 1, nu = 1, alpha.mu = 0, alpha.V = 1,000) for the fixed effects, 601,000 iterations, a burn-in period of 2,000 and a thinning interval of 300. For all other models, we used inverse Wishart priors for both residuals and fixed effects, 201,000 iterations, a burn-in period of 1,000 and a thin interval of 100. These parameters ensured an effective sample size greater than 1,500, autocorrelation values below 0.1, and model convergence (assessed visually and with Heidel tests).

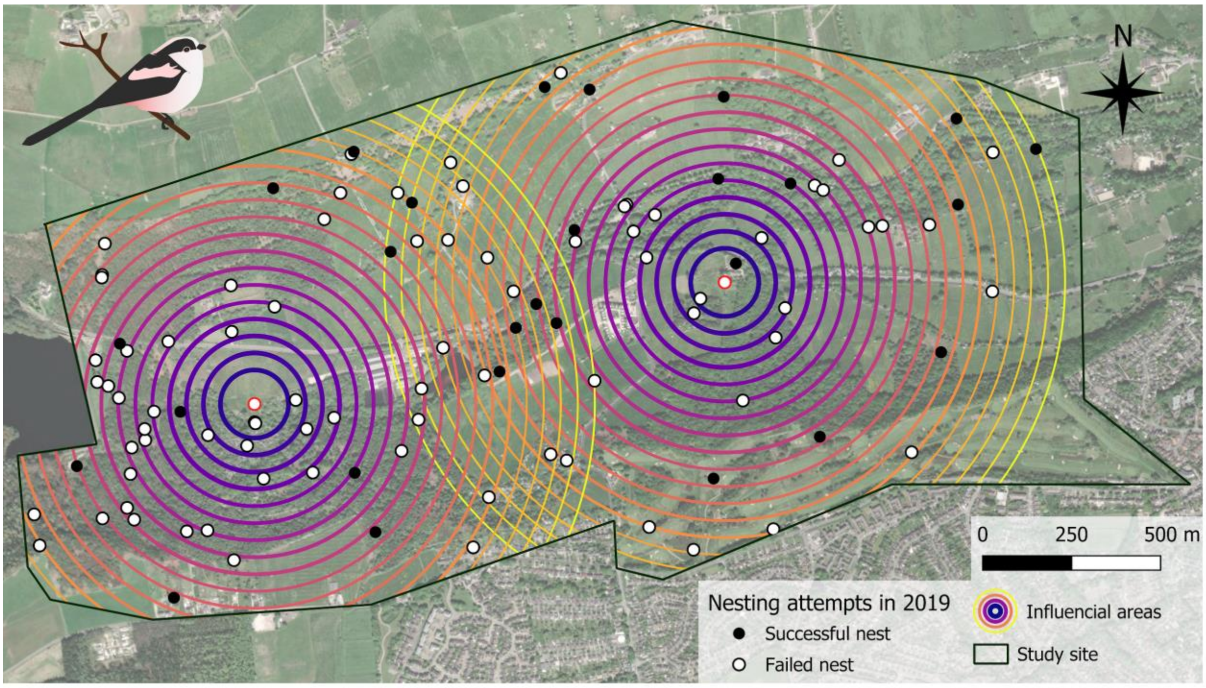

Figure 1. Map of the study area (black polygon) and all the nesting attempts detected in 2019 as an example. Successful and failed nests are denoted by black and white points respectively. Around two failed nests highlighted with red contour, we drew influential circles with radii from 100m (smaller one) to 1000m (larger one), every 50m. In the analyses, the influence of any surrounding nest on the focal failed nest was exponentially (and not linearly) related to the distance to the focal nest (see main text, Eq.2, and Figure S1). To visualise this specificity, closer circles (lower α values) are represented with thicker and darker coloured lines while outer circles (higher α values) are represented with thinner and lighter coloured lines.

Results

Between 1995 and 2021, we gathered helping decisions from 1,338 individually identifiable failed breeders, 237 (18%) of which became helpers. Of those failed breeders, 670 were males and 190 (28%) became helpers. Among the 623 female failed breeders, 43 (7%) became helpers. This confirms previous estimates showing that helping is male biased with > 80% of helpers being males.

Several proxies of nests available to be helped were found to be influential in helping decisions. The proportion of predated nests in the neighbourhood (~ 500m), but not the number of predated nests, differed for failed breeders that became helpers and those that did not, both for males and females (Figure 2, Table S1). More specifically, helpers experienced a lower local predation pressure than non-helpers, suggesting that predation was not high enough to cause a shortage of nests to help (Figure 3C). For male failed breeders, helpers bred at higher density than non-helpers (greater number of breeding attempts, within 550m; Figure 2, 3A) and were surrounded by more active nests (within 400m; Figure 2, 3B) and relatively late breeders (within ~300 m; Figure 2, 3D). For females, on the other hand, these other measures of nest availability (number of attempts, number of active nests and lay dates) were not significant influences on helping decisions (Figures 2 & 3).

The availability of first order kin in the immediate vicinity (100-200m) of a failed breeder seemed to play the most important role in helping decisions: helpers, whether males or females, were surrounded by more social first order kin than non-helpers (Figures 2 & 4A, Table S1). This relationship held for males when considering the genetic relatedness of failed breeders to their neighbours, but not for females (Figures 2 & 4C-D, Table S1). This relationship also held when considering either first order kin overall (Figure 4A,C), or only first order kin with active nests (Figure 4B,D).

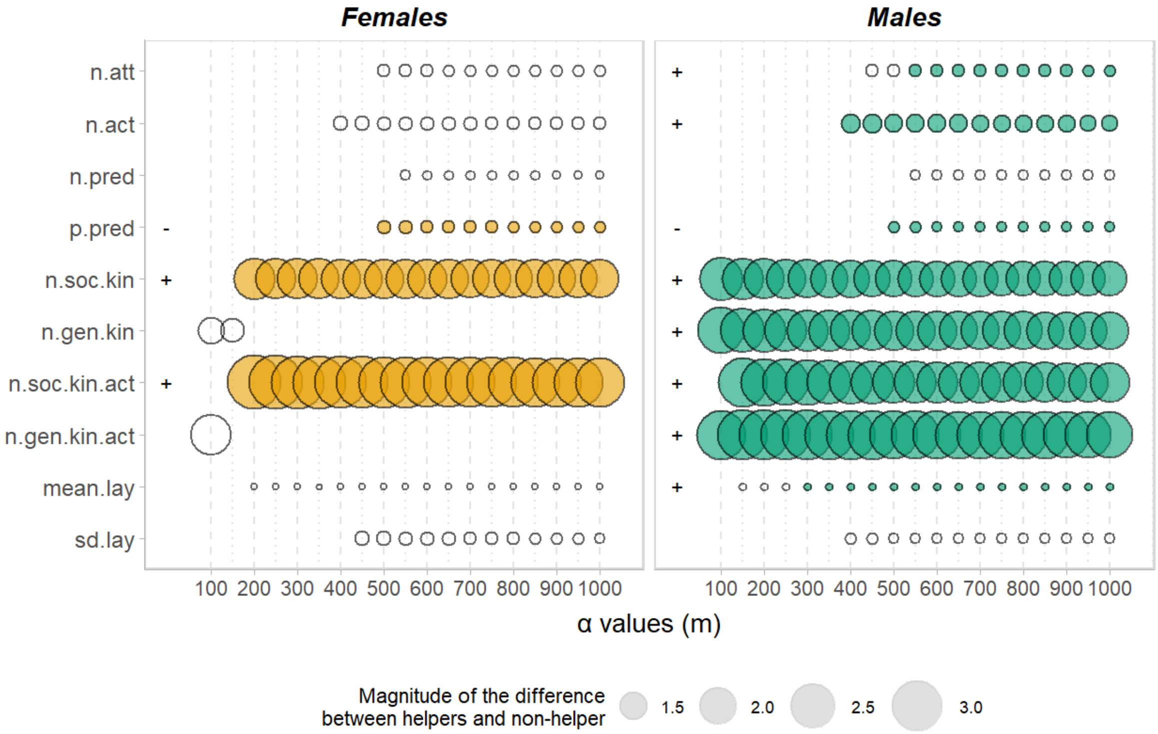

Figure 2. Effects of the ten tested drivers of helping $y_{i,\alpha}$, derived at all spatial scales. Circles are only represented for models which reach a high R^2 (within ¾ of the highest R^2). Full circles denote significant difference between future helpers and non-helpers, while empty circles denote an absence of significant difference. Symbols "+" and "-" on the left-hand side of each panel indicate whether the helping effect was positive (value for helper > non-helper) or negative respectively (see Table S1 and Figures 3 & 4). The sizes of the circles denote the absolute effect size of helping, calculated as the mean of the ratio between the posterior distributions of the $y_{i,\alpha}$ for helpers and non-helpers $\frac{intercept + helping\ "yes"}{intercept}$ if the helping effect is positive, and the inverse of that if the helping effect was negative. A positive magnitude of nearly 3 for the availability of kin near males thus means that male helpers were surrounded by 3 times more kin than male non-helpers. Colours refer to sex (yellow for females, green for males).

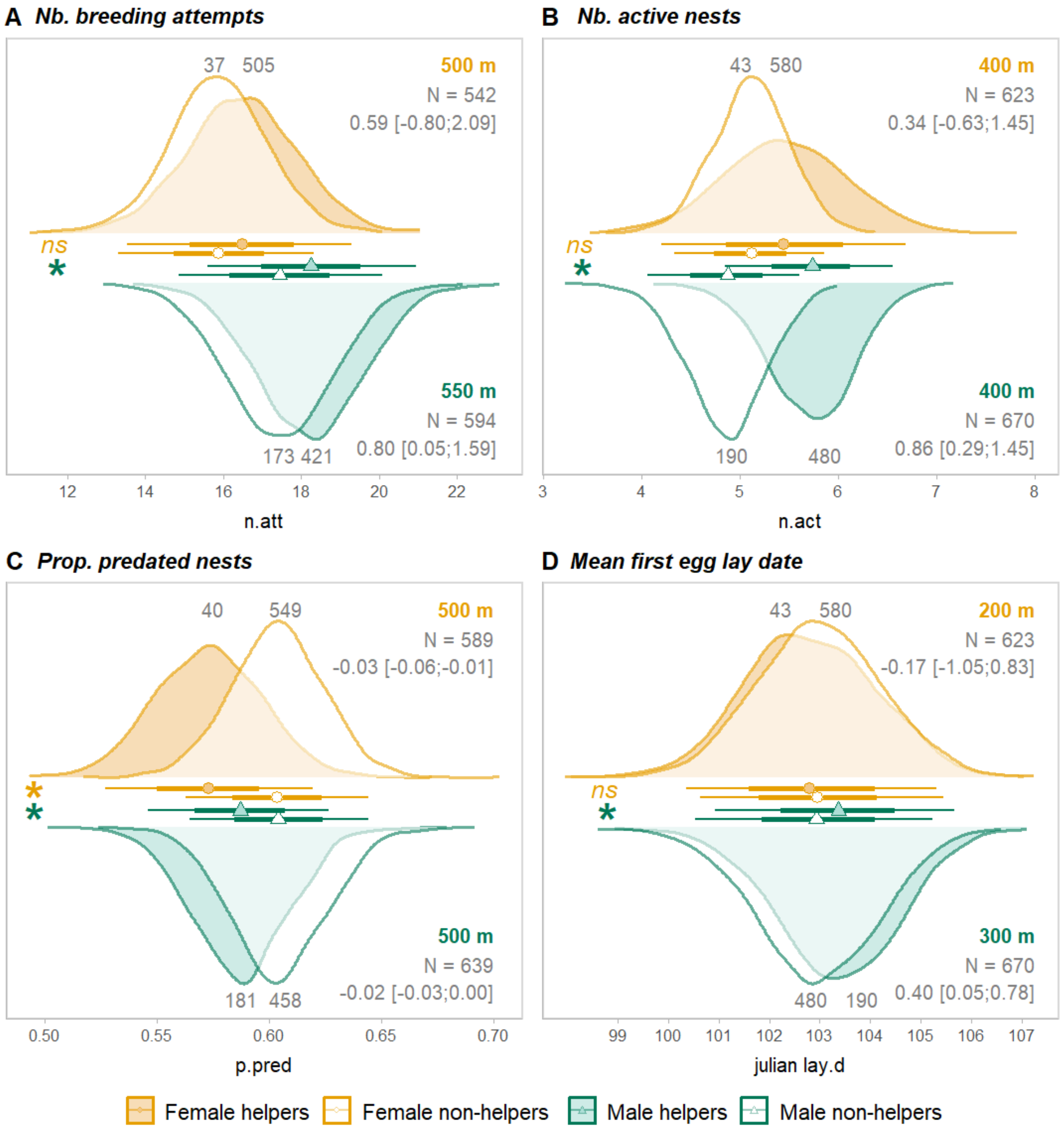

Figure 3. Distribution of the marginal means of four potential drivers of helping y_i, for helpers (filled) and non-helpers (empty). (A) number of breeding attempts, (B) number of active nests, (C) proportion of predated nests, and (D) mean first egg lay date. We present distributions for models on females (yellow) and males (green). The central points and bars indicate respectively the median, 50% and 95% quantiles of the distributions. *ns* and * indicate that the credible interval of the helping effect did and did not, respectively, overlap zero. All these results were derived from models with α set to its influential value, as indicated on the right-hand side of the graphs, together with overall sample sizes, posterior means and 95% Credible Intervals of the helping effect (see also Table S1). Numbers above/below each distribution are level-specific sample sizes.

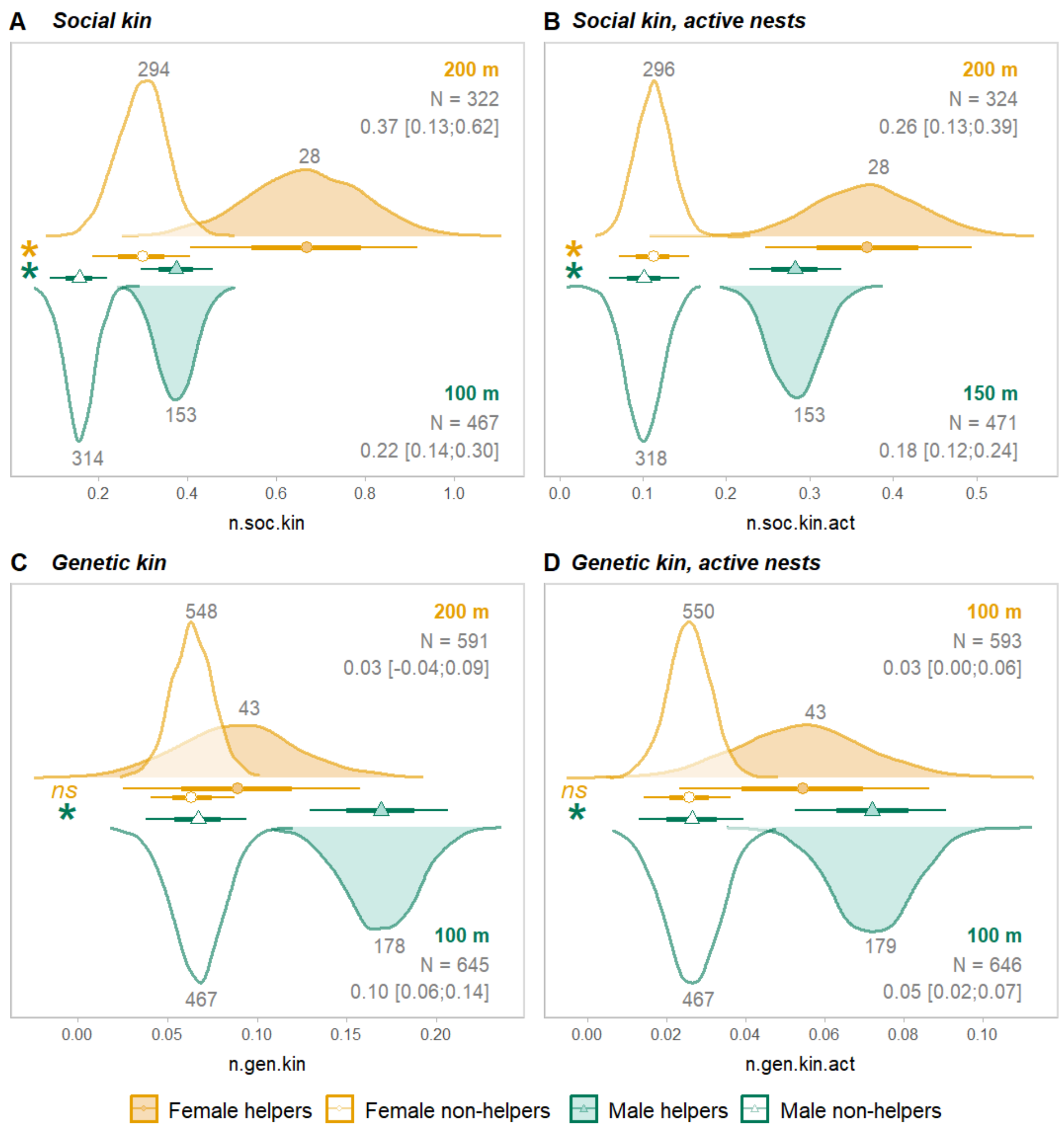

Figure 4. Distribution of the marginal means of the availability of first order kin, for helpers (filled) and non-helpers (empty). Models were derived based on the social pedigree (A-B) or genetic pedigree (C-D) and considering any nests (A, C) or only active nests at the time of failure of the focal nest (B, D). We present distributions for models on females (yellow) and males (green). The central points and bars indicate respectively the median, 50% and 95% quantiles of the distributions. *ns* and * indicate that the credible interval of the helping effect did and did not, respectively, overlap zero. All these results were derived from models with α set to its influential value, as indicated on the right-hand side of the graphs, together with overall sample sizes, posterior means and 95% Credible Intervals of the helping effect (see also Table S1). Numbers above/below each distribution are level-specific sample sizes.

Discussion

Using 27 years of data on helping decisions in a facultative cooperative breeder with redirected helping, we have shown that the availability of nests to help *globally* within the population and the availability of kin *nearby* influenced the propensity of failed breeders to help others in provisioning their nestlings. More specifically, nest density, nest predation probability and timing of breeding derived at broad spatial scales (~400-850m), played an important role in cooperative decisions. In contrast, social and genetic relatedness were influential in helping decisions at a fine spatial scale (~100-200m). Interestingly, the factors influencing the cooperative decisions differed between sexes, reflecting the different selection pressures on dispersal and fitness acquisition pathways for males and females. We discuss the implication of our results for the evolution of helping in cooperative breeders.

Predation and helping decisions

Predation has long been recognised as a key factor promoting group-living (45) because of grouping's positive effects on collective vigilance (46) and dilution of risk (47, 48). In cooperative breeders, Emlen's (49) ecological constraints hypothesis argued that high predation pressure could drive family group formation by acting as a constraint on dispersal, an idea supported by single-species studies (50–52) and comparative analyses (18). However, predation pressure does not constrain dispersal in long-tailed tits because although there are likely to be direct benefits of flock-living, dispersal between flocks is common (53) and independent breeding is not constrained. In some cooperative species, helpers cooperate not only in allofeeding but also in deterring nest predators (25, 54). This high predation pressure on breeding attempts may drive delayed dispersal and deferred reproduction, causing individuals to remain in family groups and help in predator defence. However, again this does not apply to long-tailed tits because there are no constraints on independent breeding and because they are unable to deter nest predators. Rather, it is the direct impact of nest predators on the success of breeding attempts by breeders that have already dispersed that promotes cooperation by creating a pool of failed breeders, i.e. potential helpers. Thus, predation plays a critical role in this system, but not in the manner envisaged by the constraints hypothesis.

On the other hand, our analysis showed that nest predation also limits opportunities for cooperation via its effect on the number of nests available to be helped. For both sexes, failed breeders that helped had a smaller proportion of depredated nests in their vicinity than non-helpers, and for males this translated into significantly fewer active nests. However, the number of available nests for males was not simply a function of predation, because males that became helpers also had more total breeding attempts in the vicinity of their nest, i.e. they bred at higher density. The discrepancy between males and females likely comes from the fact that females disperse further than males (32) and are thus less likely to have relatives in the population, regardless of the number of individuals breeding there. More broadly, this positive relationship between breeding density and helping is consistent with patterns observed in other cooperative breeders (23, 55), although in the long-tailed tit, the basis for this relationship is not increased constraints on dispersal at high density but rather increased helping opportunities.

These two consequences of nest predation, promoting cooperation by creating a pool of potential helpers, but limiting cooperation by influencing the number of nest available to be helped are consistent with Hatchwell et al.'s (26) finding that across years the prevalence of helping in the population peaked at intermediate predation rates. It is notable that Hatchwell et al. (26) found this effect of predation using population-level metrics, and here the effect of predation also acts at a large spatial scale (~500m) around the failed nest.

Nest predators can, therefore, be characterised as having an immediate impact on the availability of potential helpers and recipients. But, predation also plays another critical role in this system. Fecundity bias (56), i.e. high variance in fecundity, can result in a small effective population size that increases relatedness among recruits, enhancing opportunities for kin-selected helping (57). Beckerman et al. (58) used simulation modelling to demonstrate the positive impact of high nest predation rates on relatedness among recruits, contrasting the mortality regime of long-tailed tits with that of species with larger effective population size. Thus, the timing and intensity of predation are pivotal in the emergence of cooperative breeding in this species.

Phenology and helping decisions

Previous studies have revealed the importance of phenology for cooperation in long-tailed tits. The time of nest failure and remaining time available to breed independently is a critical factor when deciding to cooperate: beyond the end of April or early May, failed breeders no longer attempt to breed again and instead may help (28). The timing of this switch from breeding to helping is consistent with a change in the relative fitness pay-offs from the two strategies, helpers accruing a more assured and immediate indirect fitness return compared to the uncertain and delayed direct fitness benefit of attempting to breed again. These phenological patterns in fitness are most likely driven by a decline in prey availability following a peak in the abundance of defoliating caterpillars, an effect associated with temperature (59).

The only significant phenological driver recorded here was that male breeders that became helpers were surrounded by relatively late breeders, again indicating the importance of having nests available to help nearby. However, the effect size for the influence of lay date was small compared to other drivers. This is unsurprising because failing to breed successfully and becoming a helper are not necessarily tightly coupled events; a failed breeder may wait days or weeks for a brood to become available (i.e. hatch) to help. Such phenological patterns in helping are likely to be widespread in systems with redirected help (e.g. 60, 61), but they may also be important in more conventional cooperative breeding systems where there are seasonal patterns in food abundance that make the contributions of helpers more or less impactful on productivity (62, 63).

The decision to help was not influenced by the spread of lay dates at other nests. By contrast, Hatchwell et al. (26) found in a population-level analysis that the average number of helpers per helped nests was higher in short breeding seasons, the suggested reason being that during short seasons more individuals join the pool of potential helpers because of the limited opportunity to breed independently. These results illustrate the contrasting effects generated by analyses at different scales.

Kinship and helping decisions

Our results confirmed earlier findings that kinship plays a crucial role in helping decisions in this species (29, 36, 41). This kinship effect derived at the individual level was significant at a very short distance from the failed nest (100-200m), which is consistent with population kin structure and the fact that most helpers find a recipient nest within 300m of their last nest (29, 32). This local effect of relatedness contrasts with previous analyses at the population scale that revealed no relationship between helping and relatedness either within (26) or across (30) populations. Thus, analyses at a biologically inappropriate spatial scale runs a risk of masking kinship effects, as suggested by Hatchwell et al. (26) and Sharp et al. (30). Similarly, Clutton-Brock & Lukas (64) highlighted the importance of scale, arguing that ecological parameters influence social decisions at a broader scale than inbreeding avoidance, which, like kin-directed help, is often a function of local relatedness. Indeed, several studies in more conventional avian cooperative breeding systems have shown that helping decisions are contingent upon kinship within social groups (65).

Intriguingly, using the social pedigree, local kin availability positively influenced the decision to cooperate in both sexes, but genetic relatedness did so only in males (Figure 2). From a failed breeder’s perspective, regardless of their sex, previous studies indicate that they have access to social information about kinship, but not direct genetic information (29, 31, 41, 66). In this species, with monogamous pairs and low rates of extra-pair paternity, social pedigrees closely match genetic relatedness, but the information available to males and females on kinship may differ because of their respective dispersal strategies. Dispersal is female-biased, so resulting kin structure is stronger among males than among females (29). Moreover, social associations among related females within the population are weaker than among males (53), suggesting that females have fewer kin present and potentially poorer information about local kin, compared to males.

Conclusions

We have shown that two key drivers of helping decisions in this species, the availability of recipient nests and relatives, operate at different spatial scales. This explains why, for example, previous studies have sometimes failed to detect an effect of relatedness on the prevalence of cooperation, even though this is a kin-selected system with a strong kin preference in helping behaviour. The first general point to draw from this study is that it may be important to consider the effects of ecological, demographic and social factors at a range of scales when seeking correlates of sociality or other behaviours. Our results suggest that social effects may be more apparent at fine scales and ecological factors at large scale, as suggested by Clutton-Brock & Lukas (64). Secondly, we have shown that multiple factors influence helping decisions to varying degrees, and that their effects may be non-linear. Failure to recognise the range of such effects may create potential difficulties in comparative analyses that typically test single, uni-directional hypotheses (6). Finally, this analysis has revealed that associations between helping decisions and some demographic traits differed between males and females. Such sex-specificity may have to be considered in single species or comparative studies of the drivers of cooperative behaviour.

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Supplementary Information:

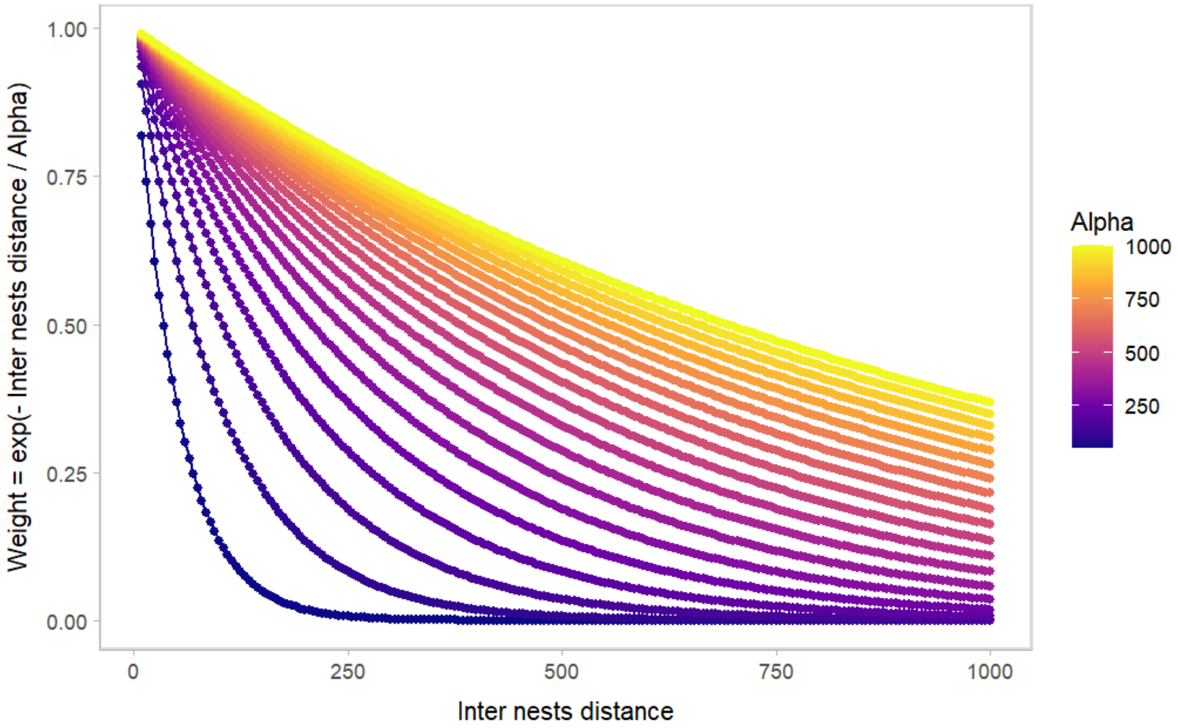

Figure S1. Values of the weight applied when calculating each y_i response variable, depending on the value of α and the distance between the focal failed nest and neighbouring nests. For all values of α, nests closer to the focal failed nest always have a higher weight in the calculation of the y_i than further nests, but this discrepancy decreases as the value of α increases.

Table S1. Values of R^2 and determination of the most influential α value for models with a significant effect on helping. The influential α was the lowest value of the range of α rendering equivalently high R^2, which intersects the range of α reaching significance of the helping effect. The value of R^2 corresponds to the highest one. An equivalently high R^2 was considered so if it exceeded ¾ of the highest R^2. We also provide the mean and 95% HPD interval of the effect of helping, a 2-level factor: “yes” (i.e. did become a helper) compared to the reference level “no” (i.e. did not become a helper). When this effect is above zero, it means that helpers presented higher values than non-helpers, and vice-versa for values below zero. Drivers presenting an effect of helping differing from zero are highlighted in bold and with a star. N is the sample size used for the model.

y_i	N	R^2	Range of α (m) with equivalent R^2		Range of α (m) reaching significance		Influencial α (m)	Effect of helping (yes vs. no)	
			min	max	min	max		mean	95% HPD interval
Females									
n.att	542	0.83	500	1000			500	0.59	[-0.80 ; 2.09]
n.act	623	0.29	400	1000			400	0.34	[-0.63 ; 1.45]
n.pred	589	0.79	550	1000			550	-0.15	[-1.10 ; 0.63]
* p.pred	589	0.85	500	1000	200	1000	**500**	**-0.03**	**[-0.06 ; -0.01]**
* n.soc.kin	322	0.13	200	1000	100	1000	**200**	**0.37**	**[0.14 ; 0.62]**
n.gen.kin	591	0.04	100	150			100	0.03	[-0.04 ; 0.09]
* n.soc.kin.act	324	0.09	200	1000	100	1000	**200**	**0.26**	**[0.13 ; 0.39]**
n.gen.kin.act	593	0.07	100	100			100	0.03	[-0.01 ; 0.06]
mean.lay	623	0.98	200	1000			200	-0.17	[-1.05 ; 0.83]
sd.lay	623	0.93	450	1000			450	-7.05	[-15.18 ; 1.99]
Males									
* n.att	594	0.83	450	1000	550	1000	**550**	**0.80**	**[0.05 ; 1.59]**
* n.act	670	0.30	400	1000	100	1000	**400**	**0.86**	**[0.29 ; 1.45]**
n.pred	639	0.80	550	1000			550	0.18	[-0.26 ; 0.64]
* p.pred	639	0.85	500	1000	150	1000	**500**	**-0.02**	**[-0.03 ; 0.00]**
* n.soc.kin	467	0.17	100	1000	100	1000	**100**	**0.22**	**[0.14 ; 0.30]**
* n.gen.kin	645	0.04	100	1000	100	1000	**100**	**0.10**	**[0.06 ; 0.14]**
* n.soc.kin.act	471	0.12	150	1000	100	1000	**150**	**0.18**	**[0.12 ; 0.24]**
* n.gen.kin.act	646	0.05	100	850	100	1000	**100**	**0.05**	**[0.02 ; 0.07]**
* mean.lay	670	0.98	150	1000	300	1000	**300**	**0.40**	**[0.05 ; 0.78]**
sd.lay	670	0.93	400	1000			400	2.65	[-2.17 ; 8.03]