Ecological, demographic and social factors shape helping decisions at different spatial scales in a facultative cooperative breeder

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Short title: Drivers of helping & their spatial scale

Abstract

Species-specific and comparative studies have identified multiple ecological and demographic factors promoting the evolution of helping in cooperative breeding systems. However, analyses typically employ univariate analyses, the relative importance of different factors remaining unknown. Moreover, the potential for factors to operate at different spatial scales is virtually unexplored. We aimed to investigate multiple ecological and demographic drivers of sex-specific helping decisions in the long-tailed tit *Aegithalos caudatus*, a cooperatively breeding species in which failed breeders may redirect their care to raise another pair's brood. We investigated the influence of breeding density, availability of relatives, predation pressure on nests and timing of breeding on 1,580 helping decisions by males and females collected over 26 years, examining the spatial scale at which each driver operated. In univariate analyses, decisions to help were positively associated with local breeding density (males), presence of relatives (both sexes) and time of breeding (males), but negatively associated with predation pressure (both sexes). Thus, the decisions made by males and females were driven by different combinations of drivers. Moreover, the spatial scale at which each driver was influential varied from local (100m) to global (750m and beyond) in population terms. In a multivariate analysis, the relative contribution of each driver to helping decisions was approximately equal. In conclusion, our results highlight the importance of considering the interplay of multiple ecological and demographic factors in driving cooperative decisions, and demonstrate that the influence of each driver may differ according to sex and the spatial scale investigated.

Introduction

The factors promoting the evolution of cooperative breeding have puzzled evolutionary ecologists for decades. While the ultimate function of the cooperative behaviour exhibited by helpers - the acquisition of direct and/or indirect fitness benefits via several potential routes - have been largely resolved, the proximate factors that drive the emergence of cooperative breeding as an adaptive strategy remain the subject of current debate (Rubenstein and Abbot 2017; Cockburn 2020). Comparative analyses have identified correlates of cooperative breeding, especially unpredictable or harsh environments (Jetz and Rubenstein 2011; Cornwallis et al. 2017, p. 207; Lukas and Clutton-Brock 2017), but also stable environments (Gonzalez et al. 2013), life history traits (Lukas and Clutton-Brock 2012; Downing et al. 2015; Satoh et al. 2026), predator diversity (Bliard et al. 2024), and mate fidelity (Cornwallis et al. 2010), among others. These studies reveal a strong phylogenetic signal in the distribution of helping, but there are clearly multiple potential drivers and no consensus on their relative influence has emerged. One explanation for this is that all hypothesised drivers apply so that each analysis captures some of the variance in sociality seen across species. However, as pointed out by Cockburn (2020), virtually all such studies test a single hypothesis rather than evaluating support for the influence of multiple ecological, demographic or social drivers in the same analysis.

The same difficulty applies to identifying general patterns from single-species studies. Many detailed, long-term investigations of social vertebrates have successfully identified ecological, demographic and social drivers of cooperative breeding behaviour in specific systems, a frequent approach being to correlate the prevalence of cooperation with annual variation in key variables (Stacey and Koenig 1990; Koenig and Dickinson 2016). Such intensively-studied species have also lent themselves to experimental manipulation of key resources to test specific hypotheses (e.g. Pruett-Jones and Lewis 1990; Walters et al. 1992). These observational and experimental studies have, unsurprisingly, identified multiple drivers of cooperative behaviour, including shortages of mates (Pruett-Jones and Lewis 1990; Dickinson 2004), high quality territories (Komdeur 1992; Dickinson and McGowan 2005; Baglione et al. 2006), nest-sites (Walters et al. 1992) and food (Covas et al. 2004), or harsh environmental conditions (Faulkes and Bennett 2016), predation pressure (Groenewoud et al. 2016; Tanaka et al. 2016; Brouwer and Cockburn 2020), inbreeding avoidance (O'Riain et al. 2000) and reproductive suppression (Young et al. 2006; Cant et al. 2010). Many of these diverse factors may be characterised as examples of access to key resources being constrained,

but whether each constraint acts in concert or in isolation and their relative importance in determining whether individuals become helpers or not typically remains untested.

This focus on individual factors as drivers of behavioural decisions with far-reaching fitness consequences is potentially misleading because such decisions are likely to result from a variety of influences and cues that differ in importance. Therefore, behaviours may neither be fully nor accurately explained by single drivers. The exceptions to the general pattern of univariate analyses illustrate this point very nicely. For example, using long-term data and field experiments, Johnson & Pruett-Jones (2025) argued that ecological constraints (lack of breeding vacancies), benefits of philopatry (increased survival) and life history traits (sex differences) all played a role in shaping dispersal of splendid fairy-wrens *Malurus splendens*. Similarly, Nelson-Flower et al. (2018) showed that the predictions of multiple hypotheses were supported by the dispersal behaviour of pied babblers *Turdoides bicolor*. These studies show that analysis of a combination of factors affecting an individual's social circumstances provides a more complete explanation of the decision to delay dispersal and cooperate in vertebrates.

Another major problem in analyses of the ecological or demographic drivers of cooperative behaviours is identification of the spatial scale at which they act. Consideration of spatial scales is central to movement ecology (Potts and Börger 2023), yet the effects of scale on the key factors influencing social behaviours are rarely considered (Webber et al. 2023). This is despite the fact that spatial effects are likely to vary widely, with some factors applying in the immediate proximity of the decision-maker, while other influences may be population-wide. For example, experimental studies typically focus on an individual's response to manipulation of its local social or ecological environment, such as mate presence/absence (e.g. Pruett-Jones and Lewis 1990) or food supply (e.g. Covas et al. 2004; Baglione et al. 2006), whereas inter-annual comparisons of helper prevalence and a putative driver more typically focus on population-level metrics, such as population density (e.g. Komdeur et al. 2016) or ecological conditions (e.g. Rubenstein 2016). Moreover, the relevant scale for analysis might vary with a species' social organisation, ecology or life history. In species with highly structured social groups with low turnover that occupy stable territories, local factors may dominate decision-making, especially if inheritance of breeder status in the same group is a primary route to fitness or when dispersal is very limited, e.g. in Florida scrub-jays *Aphelocoma coerulescens* (Fitzpatrick and Bowman 2016) and stripe-backed wrens *Campylo-rhynchus nuchalis* (Rabenold et al. 1990). If, on the other hand, long distance dispersal from a natal territory provides better fitness returns, then broad population-level factors may be a more appropriate level of analysis, e.g. purple-crowned fairy-wrens *Malurus coronatus* (Teunissen

et al. 2025). Moreover, such dispersal decisions will often be sex-specific (Downing et al. 2018; Green and Hatchwell 2018) suggesting that the spatial scale of the factors driving them should be treated separately.

The aim of this study was to identify the spatial scale at which key drivers of cooperation were influential, and quantify their relative contribution to individual helping decisions. To achieve this, we used helping decisions in a facultative cooperative breeder, the long-tailed tit *Aegithalos caudatus*. Long-tailed tits have an unusual redirected helping system that is ideally suited to dissection of decision-making by individuals when faced with the option of cooperating or not (Hatchwell 2016). Nearly all adults in a population attempt to breed in pairs each year, but most pairs fail to breed successfully due to nest predation. Beyond a certain date in the season, failed breeders abandon breeding for that year and may then choose to redirect their care to help at another pair's nest, feeding their young until independence (MacColl and Hatchwell 2002). Several factors are known to influence the decision by failed breeders to help at another nest or not, including: the sex of the potential helper ((males > females; Hatchwell et al. 2004), the relatedness of potential recipients (helpers prefer close kin; Russell and Hatchwell 2001; Leedale et al. 2018), the distance from the failed breeder's last attempt (helpers care at relatively close nests; Leedale et al. 2018; Sturrock et al. 2022), and the rate of nest predation and breeding phenology in that year (which determine nest availability; Hatchwell et al. 2013). However, those previous studies have analysed the drivers of helping decisions at various levels ranging from individuals to populations, and the influence of each specific factor is not necessarily consistent across scales. For example, while helpers strongly prefer to assist kin in their neighbourhood (Russell and Hatchwell 2001), population-level measures of relatedness do not predict the prevalence of helping (Sharp et al. 2011; Hatchwell et al. 2013). Furthermore, in prior studies each factor has, in common with studies of other species, been analysed as separate drivers rather than in a manner that allows comparison of the relative importance of each factor in decision-making.

Here, we used long-term data to analyse multiple drivers of 1,580 decisions to help or not by 1,091 individual long-tailed tits. From previous univariate studies, we expected helping to increase with: (1) the number of active nests to which care could be redirected, (2) lower predation pressure on nests, (3) later breeding seasons, and (4) the availability of relatives. First, we investigated each factor independently at a range of spatial scales from immediately around the failed nest of a focal individual to population-wide, allowing us to test the hypothesis that drivers of decisions may operate at a range of spatial scales. We analysed the helping decisions of males and females separately because males are more likely to help and

travel less far to do so than females (Leedale et al. 2018). Secondly, having identified the scale at which each driver influenced helping decisions for each sex, we investigated the relative importance of each driver in a multivariate analysis that included all factors at their influential scale, again conducting separate analyses for males and females. Here, we anticipated that relatedness would play the most important role in determining whether an individual helped or not because long-tailed tits have a kin-selected cooperative breeding system in which only indirect fitness benefits of helping have been identified (Meade et al. 2010; Hatchwell et al. 2014). Kinship was also expected to act at a relatively fine scale given that long-tailed tits usually help at nearby nests. Finally, we discuss the implications of our findings for the maintenance of variation in cooperation in plastic systems.

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). We excluded from the analyses data from 2001 when study site access was limited due to an outbreak of foot and mouth disease. The ca. 2.5 km² study site (Figure 1a) encompasses diverse habitats, including woodland, hedgerows, fields, scrubland, and a golf course. The breeding population ranged from 26 to 88 pairs. During the non-breeding season, long-tailed tits form flocks of ca. 10–20 individuals, foraging and roosting together (Hatchwell et al. 2001). 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 1995-2021). 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, hatch and fledge dates), either through direct observations for low nests (<3m above ground, ~71% of the nests; Morinay et al. 2025) 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 (Morinay et al. 2025). See Hatchwell (2016) for further details on the species' biology.

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), 92% 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 (Simeoni et al. 2007). Long-tailed tits being sexually monomorphic, we also used two microsatellite loci (P2P8 and Z002A) to sex them.

Helping

After early May, the payoff from helping exceeds that of initiating a new breeding attempt and we observe a behavioural switch between these two strategies, with failed breeders ceasing attempts to re-nest and some deciding to help (MacColl and Hatchwell 2002). The mean first egg lay-date of the final clutch in a given season is 10 May (± 8 days SD, N=26 years, 1995-2021, excluding 2001). Helping behaviour in this population consists primarily of provisioning nestlings at a nearby nest and, if successful, fledglings until ca. 3 weeks after fledging, but they also assist with mobbing of nest predators and on rare occasions feed incubating females (Hatchwell et al. 2004). Most helpers are males (81%; Leedale et al. 2018), with 38% and 9% of failed males and females, respectively, becoming helpers (Sharp et al. 2011). 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 (day 16-18) or nest failure. This provided us with two metrics: (i) the helping decision (2-level factor, yes vs. no), which we then used as response variable in our statistical models, and (ii) the helping distance for each sex, i.e. the distance between the nest where male and female helpers failed in their last breeding attempt and the nest they helped (Figure 1b).

Kinship

Long-tailed tits have a kin-directed helping system, helpers preferentially caring at a nest belonging to a first order relative, i.e. a parent, sibling or offspring (Russell and Hatchwell

2001; Sharp et al. 2005; Leedale et al. 2018). To identify first order kin (see Drivers of helping), we estimated the genetic relatedness between individuals using the microsatellite data and the "related" R package (Pew et al. 2015). For the latter, we used the Queller and Goodnight (1989) coefficient of relatedness r_{QG} as this rendered the highest correlation between observed and expected relatedness (0.9). We could then determine the number of first order kin (r_{QG}>0.25) each failed breeder has in the population. If genetic relatedness was not available for a failed breeder (no blood sample), we used instead the social pedigree to count the number of first-order kin (r_{PED} = 0.5).

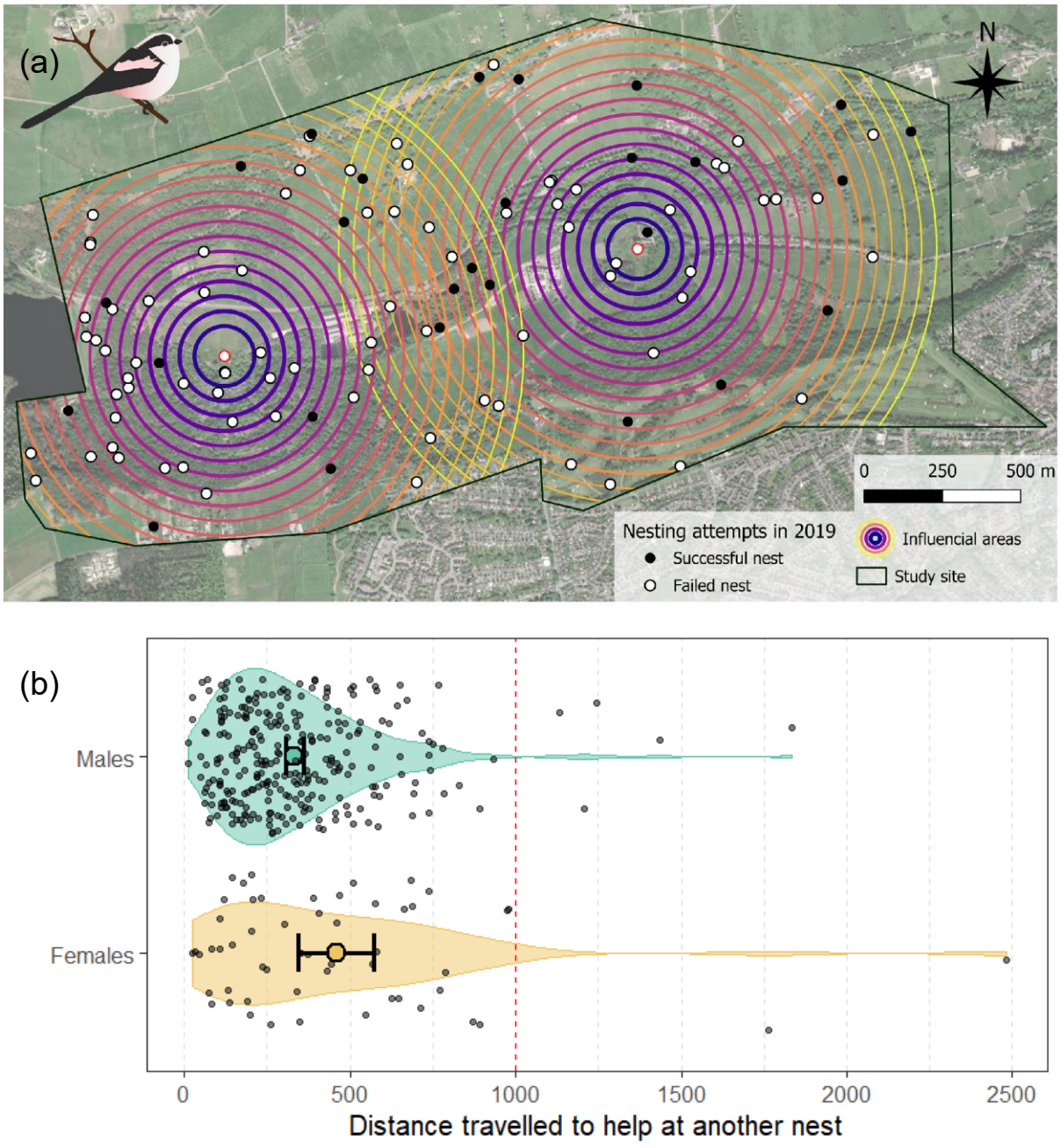


Figure 1. (a) Map of the study area (black polygon) and all the nesting attempts detected in 2019 as an example. Successful and failed nests are denoted by black and white points

respectively. Around two failed nests highlighted with a red circle, we drew influential circles with radii from 100m (smaller one) to 1000m (larger one), every 50m. (b) Distribution of the distances between the last failed nest of helpers and the nest at which they decided to help, in meters, for each sex.

Drivers of helping

We aimed to identify key ecological and demographic drivers of helping as well as 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 four potential drivers $x_{i,\alpha}$ that could be associated with helping in the vicinity of each focal nest, based on previous evidence (see Introduction) as follows:

(1) The number of still active nests ***n.act*** at the time of failure of the focal nest. This quantifies the availability of nests at which a failed breeder could redirect their help within specified distances from the focal nest; this is likely to be a function of breeding density and also the failure rate of breeding attempts. We predicted that the likelihood of helping should increase with the number of active nests.

(2) The proportion of nests that were predated ***p.pred***. This is a key determinant of nest availability and, additionally, could reflect the likelihood that a helped nest will succeed, and also a failed breeder's past investment in breeding that season. Although nest predation is important for generating potential helpers, we predicted that when predation pressure is more intense, helping would be less prevalent because of the shortage of available nests. Having both these metrics *n.act* and *p.pred* allows us to disentangle the potential effect of nest availability vs. predation pressure *per se*.

(3) The mean first egg lay date of all nests, ***mean.lay***. Phenology, i.e. the timing of breeding in a given year, is a potential driver of helping decisions via two routes. The length of the breeding season and hence the opportunity for a pair to raise their own brood is reduced when breeding is relatively late (Gullett et al. 2013; Hatchwell et al. 2013). In addition, failed breeders can become helpers only if there are late nests available to be helped. Therefore, we predicted that the probability of helping would be higher when the mean lay date was later because the probability of raising a brood independently would be lower and the number of nests available to help in the vicinity of a focal nest would be higher.

(4) The number of breeders that were first order kin ***n.kin***, determined from the genetic pedigree. This measures the opportunity to gain indirect fitness benefits by helping kin. Naturally, we predicted that failed breeders would be more prone to help when they have close kin nearby because of the kin preference in helping (Russell and Hatchwell 2001; Leedale et al. 2018) and because only indirect fitness benefits of helping have been identified in this species (Meade and Hatchwell 2010; Meade et al. 2010; Hatchwell et al. 2014). The distance travelled to help differs significantly for males and females (Figure 1b), so we also predicted that kinship would influence helping decisions of each sex at different scales.

To estimate the number of still active nests *n.act* and the number of first order kin *n.kin*, we considered the total number of neighbouring nests that year. In contrast, to estimate the proportion of predated nests *p.pred* and mean laying date *lay.d*, we considered only nests available to predation (i.e. not formerly abandoned) and nests reaching egg stage respectively. The focal nest itself was always excluded from the calculations of all drivers because we wanted to disentangle the environment that failed breeders faced when making their decisions from their own personal experience. All four drivers were non-collinear (Figure S1, Table S1).

Models to detect the influential scale for each driver

To determine the distance at which each of these drivers was influential in helping decisions, we estimated each driver $x_{i,\alpha}$ considering only nests within a certain distance from the focal failed nest and varied this distance limit α from 100 to 1,000m (in 50m increments) (Figure 1a). We chose 1000m because it encompasses most of the study area for most nests (Figure 1a), most helpers move less than 1000m to help (Figure 1b), and this is also the distance after which all drivers' variation became negligible (Figure S2 for the distribution of each driver across these scales).

We fitted Generalized Linear Mixed effects Models with the helping decision as response variable (1 became a helper, 0 did not help), one scaled driver $x_{i,\alpha}$ as covariate, and both year and individual ID as random factors:

$$Became.helper\ 0/1_i \sim scale(x_{i,\alpha}) + (1|Individual\ i) + (1|Year) \qquad \text{Eq. 1}$$

$x_{i,\alpha}$ being either *n.act*, *p.pred*, *lay.d* or *n.kin*.

To determine the spatial scale at which the neighbourhood around the nest of failed breeders influenced helping decisions, we fitted 19 versions of each model, one for each value of α. We then compared the 95% Credible Intervals around the effects of $x_{i,\alpha}$ for each α and determined the lowest value of α above which we consistently observed such an effect

(hereafter, the influential α). As females are less likely to help and travel further to help than males, we expected their helping decisions to be influenced by different drivers and at different spatial scales. Therefore, each model was run separately for males and females. In total, we fitted 152 models (4 types of $x_{i,\alpha}$ variables, 19 values of α, 2 sexes).

Models with all drivers combined, at their respective influential scale

We tested the relative contribution of each driver to helping decisions by fitting two models (one for males, one for females), with the helping decision as response variable, as above, and each driver estimated at their respective influential $\alpha_{1\text{-}4}$.

$$Became.helper\ 0/1_i \sim scale(n.act_{i,\alpha1}) + scale(p.pred_{i,\alpha2}) + scale(lay.d_{i,\alpha3}) + scale(n.kin_{i,\alpha4}) + (1|Individual\ i) + (1|Year) \quad \text{Eq. 2}$$

If a driver proved not to have a significant effect on the helping decision for one sex, we still included its estimation at the same influential distance as for the other sex, for comparability with the other drivers and across sexes. We then compared the predicted posterior distribution of each of these scaled drivers (Figures 3 & 4).

Controlling for methodological biases

We investigated two biases that could potentially have arisen from our approach. First, we ensured that all drivers $x_{i,\alpha}$ were only weakly correlated at each given distance (Figure S1), and were non-collinear when considering them at the respective influential α (Table S1). Second, with our approach nests closer to the edge of the study site (Figure 1) could have less chance of having other nests and kin detected near them. We therefore repeated the analyses considering only nests of failed breeders that were within the core of the study area, i.e. removing breeders from nests with the 5% lowest and 5% highest values of latitude and longitude. Results remained qualitatively similar despite the lower sample size and wider confidence intervals (Figures S3-S4). This is both reassuring and not surprising 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 $x_{i,\alpha}$ 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 1a).

Statistical details

All analyses were conducted in R v.4.5.2 (R Core Team 2024). We fitted all models (with future helping decisions as response variable: yes 1, no 0) as GLMMs. More specifically, to account for repeated measures across individuals while handling a highly sparse data structure (1,091 unique birds across 1,580 observations), we fitted our models using Bayesian Regression Models using 'Stan' with the *brms* package (Bernoulli family; Bürkner 2017). While frequentist approximations overfit sparse binary data by inflating random intercept variances, the weakly informative default priors in *brms* provided stable regularisation, allowing us to explicitly control for individual identity and year without biasing our fixed effect estimates. We used *cmdstanr* as the backend package for fitting the Stan model (Gabry et al. 2025). We fitted 4 chains, using 4 CPU to speed up sampling, and 4,000 iterations. Due to highly structured posterior geometries for the random terms, initial sampling runs exhibited divergent transitions and exceeded default step limits. To resolve these sampling issues and ensure robust posterior exploration and valid inferences, the MCMC control parameters were adjusted to a target acceptance probability (adapt_delta) of 0.999 and a maximum tree depth (max_treedepth) of 15. Model convergence was confirmed by ensuring a good mixing of the chains, verifying that all Gelman-Rubin diagnostics ($\hat{R}$) was close to 1.00, that no divergent transitions remained, and that bulk and tail effective sample sizes (ESS) exceeded 500 per parameter (lower values for estimates related to the random terms, but always exceeding 3100 for estimates of the effect of the driver). We ensure low collinearity among the drivers from the male and female models including all drivers, using the *performance* package (Lüdecke et al. 2021; see Table S1 for all Variance Inflation Factors estimates close to 1).

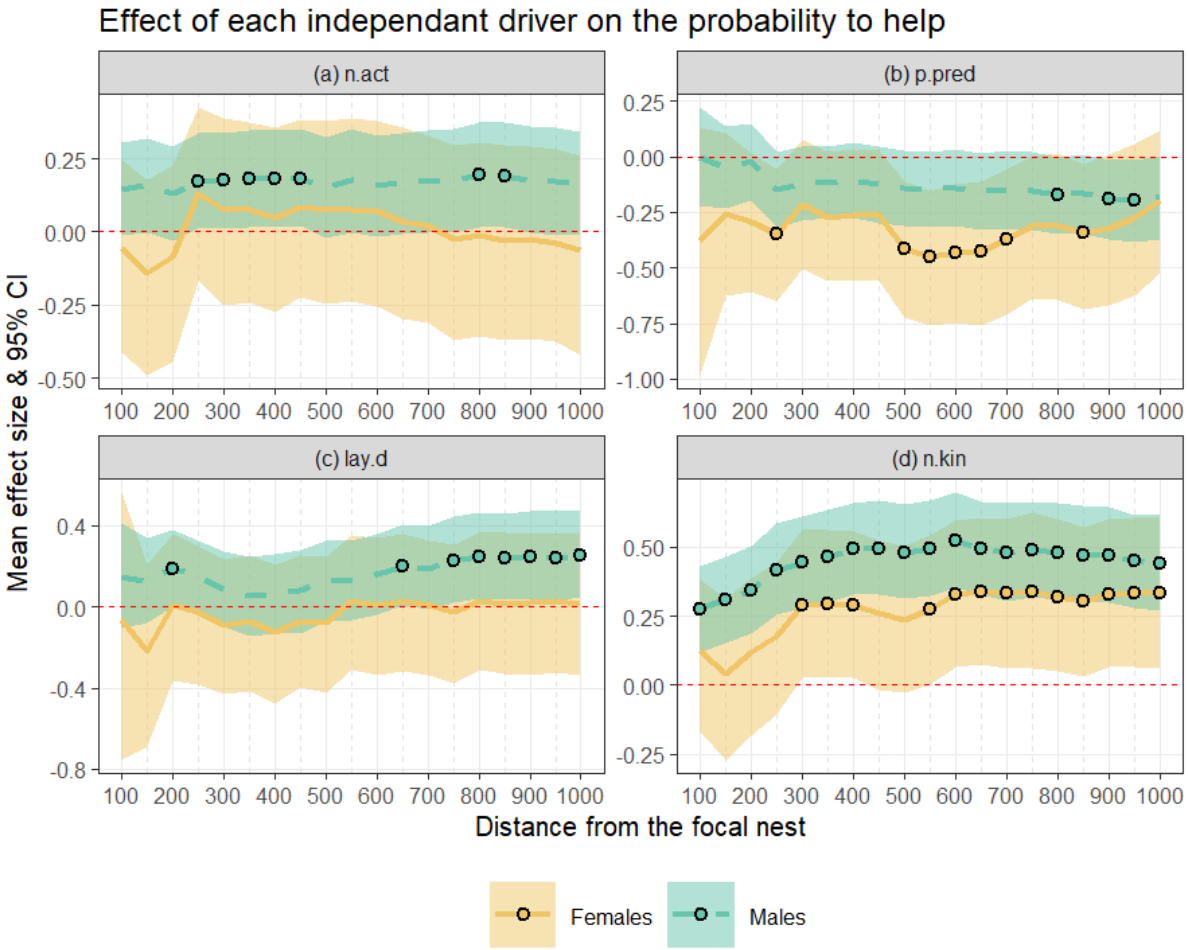


Figure 2. Effect of each independent driver on the probability of helping. We present the mean posterior estimate (lines) and 95% Credible Intervals (ribbon) of the effect of each driver, derived from models fitting the probability of helping with only one driver at a time (Eq. 1), for all possible values of influential distance to the focal nest α on the x-axis. Estimates for females are shown in yellow (solid line) and estimates for males are in green (dashed line). The horizontal red dashed line indicates zero (no effect on the probability of helping). *n.act, p.pred, lay.d*, and *n.kin* stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin.

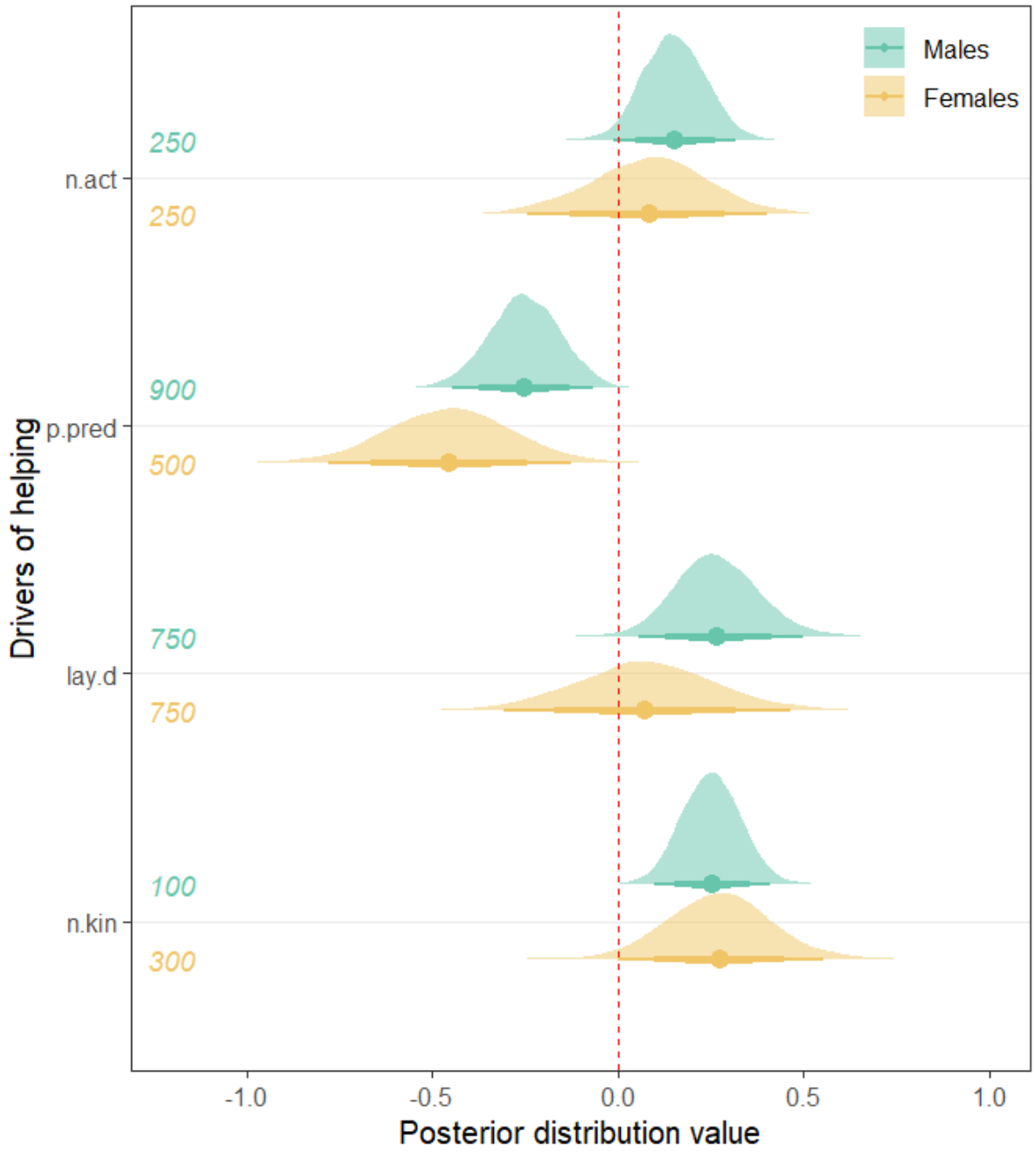


Figure 3. Posterior distribution of the effect of each driver on the probability of becoming a helper, for females (yellow, bottom graphs) and males (green, top graphs). These distributions are derived from a model including all drivers together, at their influential distance α (numbers indicated on the left-hand side of each distribution) as described in Eq.2. The mean, 50%, 80%, and 95% Credible Intervals around the mean are represented at the bottom of each distribution. The vertical dashed red line indicates zero, i.e. an absence of effect on the probability of helping. *n.act, p.pred, lay.d*, and *n.kin* stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin.

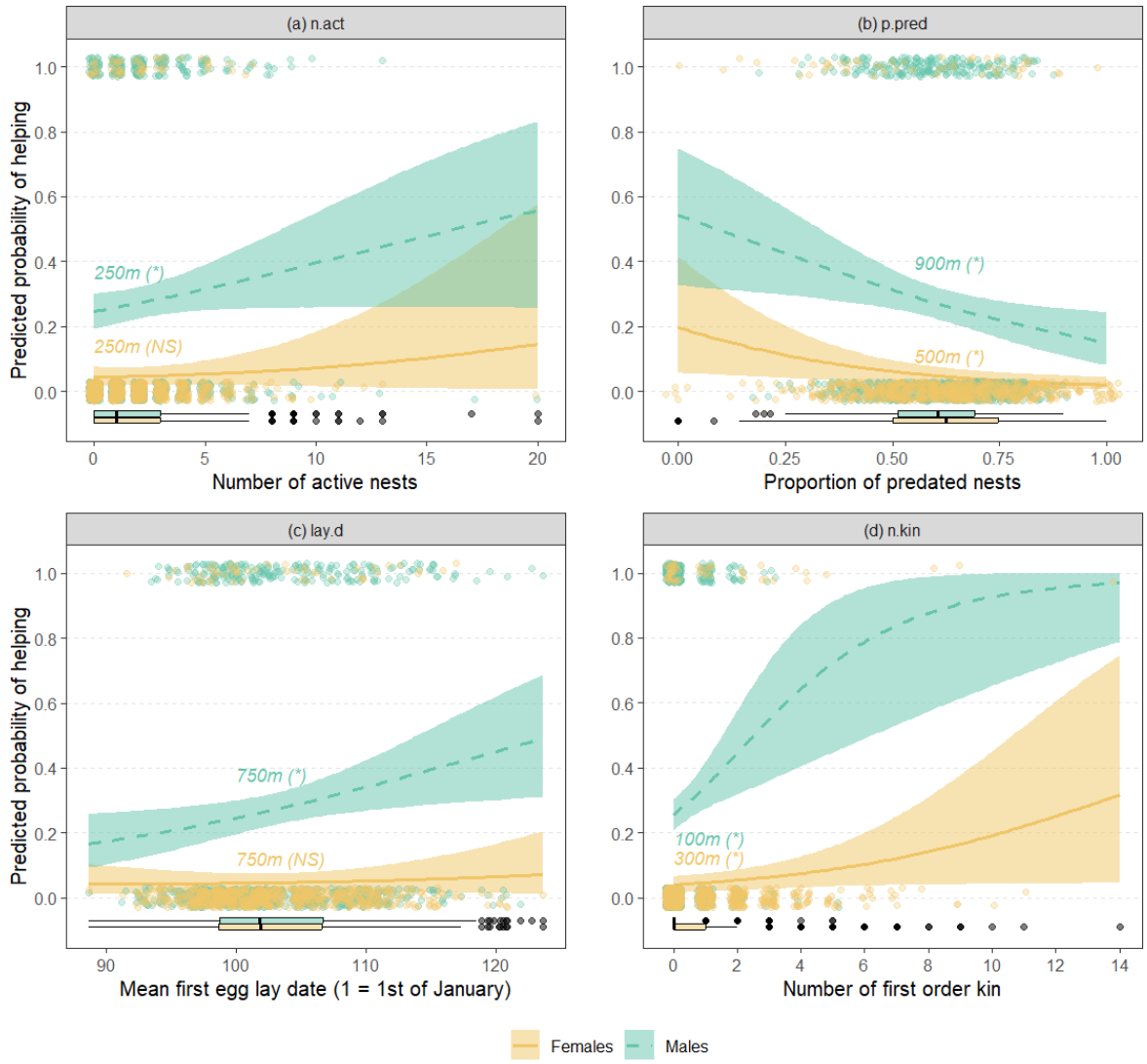


Figure 4. Effect of each driver, estimated at their influential distance, on the probability of becoming a helper, for females (yellow, solid lines) and males (green, dashed lines). We indicate on the graph the influential distance for each driver. When a driver had no effect on the probability of helping, we show the estimate at the same spatial scale as for the other sex. The star and NS in parentheses respectively indicate whether the 95% Credible Interval around the driver's mean estimate overlapped zero or not. Dots are raw data and their distribution is summarized by sex with the box plot below each graph. *n.act, p.pred, lay.d*, and *n.kin* stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin. See also Figure S5 for the same effect shown at the median distance where these drivers were influential, rather than the minimal distance.

Results

Helping decisions

Between 1995 and 2021, we accumulated 1,580 helping decisions from 1,091 individually identifiable failed breeders. Among those 1,580 helping decisions, 283 (18%) were to help. Of the 817 decisions made by failed males, 232 (28%) helped, while among the 763 decisions made by failed females, 51 (7%) helped. This confirms previous results showing that helping is male-biased with >80% of helpers being males. The discrepancy between the number of failed males and females in our dataset arises because identifiable breeders were sometimes paired with an unidentifiable mate (i.e. without colour rings), and those unidentified birds were more likely to be immigrants and hence more often females.

On average, male helpers helped at a nest located 332m from their own last failed nest (range: 11m to 1,835m, SD=234, n=280 nests helped by males) while the equivalent distance for females was 459m (range: 25m to 2,481m, SD=428, n=54 nests helped by females; Figure 1b).

Drivers of helping

The decision to help was influenced by multiple drivers at variable distances, their effects differing for males and females (Figures 2-4; see Tables S2-S3 for all models' estimates). Males were more likely to become helpers when the number of active nests within 250m to 450m of their failed nest was high, while females' decision to help was not significantly associated with this driver at any distance (Figure 2a). The availability of active nests for a potential helper is likely to be a function of predation pressure and, as expected, the helping propensity of both sexes decreased as the proportion of nests depredated increased; this effect was significant from 500m and 900m around the failed nests of females and males, respectively (Figure 2b). Similarly, males' helping decisions (but not those of females) were influenced by the timing of breeding: males were more likely to become helpers if nests from 750m around them onwards were breeding relatively late (Figure 2c), again as expected. Finally, the helping decisions of both sexes were strongly influenced by the availability of nearby kin. The availability of first order kin greatly increased the likelihood of helping for males, from 100m onwards around their failed nest, while this driver was influential only from 300m around the nest of failed females (Figure 2d).

When comparing all drivers at their influential scale in a single model, all trends identified for drivers analysed separately were confirmed (Figures 3 & 4). Importantly, the effect sizes of all significant drivers were of the similar orders of magnitude, indicating that there was not one dominant driver, but rather that each contributed more or less equally to the helping decision (Figure 3; Table S3). The relationships between the predicted probability of helping and each of the four drivers at their influential distance illustrate the general finding that females are less likely to help than males (Figure 4). Figure 4d also shows that the local availability of kin has a particularly sharp effect on the helping propensity of males, the presence of each additional kin increasing by nearly 10% the probability of helping when the number of kin is limited (0-5, the vast majority of cases).

Discussion

Using 26 years of data on helping decisions in a facultative cooperative breeder with redirected helping, we have shown that multiple factors jointly, and fairly equally, influenced the propensity to help, and that the scale at which each of them acts varies across factors and between the sexes. More specifically, nest predation probability and timing of breeding derived at broad spatial scales (>500m) had a significant influence on cooperative decisions, while the number of active nests and availability of relatives were influential in helping decisions at a finer spatial scale (~100-300m). Importantly, the factors influencing helping decisions differed between the sexes. Males were more likely to help when there were more available nests, predation was lower, breeding was relatively late and when there were more kin in local proximity. For females, on the other hand, only low predation and the presence of kin enhanced the probability of helping. Finally, the effect size for each of these factors was broadly similar, although the slope of the kinship effect is steepest, demonstrating its pivotal effect in helping decisions, especially for males.

First, we discuss the effects of different drivers on helping behaviour and the ecological scale at which they act. The availability of active nests (for males) and close relatedness of breeders to focal birds (both sexes) were positive drivers of helping decisions at fine spatial scales. These results confirm earlier findings that failed breeders preferentially choose close relatives that live nearby when deciding to become helpers (Russell and Hatchwell 2001; Sharp et al. 2005; Leedale et al. 2018). The kinship effect, derived individually for each failed breeder, was significant from a relatively short distance from the failed nest for males (100m) and females (300m), which is consistent with population kin structure, the fact that a large majority of helpers find a recipient nest within 500m of their last nest (Leedale et al. 2018; Morinay et al. 2025) and that helping distance differs for males (332m on average) and females (459m on average; Figure 1b and *Results*). The positive effect of relatedness persisted from the immediate vicinity of a failed breeder to the maximum distance considered (1000m) because most close relatives live nearby and hence are still influential even though mean kinship is diluted at the broader spatial scale. This finding contrasts with analyses conducted at the population level that revealed no relationship between the annual metrics of helping and mean annual dyadic relatedness of members of the population across years (Hatchwell et al. 2013) or study sites (Sharp et al. 2011). Thus, analyses at a biologically inappropriate spatial scale run a risk of masking kinship effects. A likely explanation for this is that a potential helper's knowledge about the availability of kin in the population may be incomplete if they are familiar only with

their immediate neighbourhood. Relatives living farther afield with whom they have limited social association may not be recognised as such. For example, Russell & Hatchwell (2001) found that failed breeders did not help at the nests of relatives that had spent the previous winter in a different flock. Similarly, Sturrock et al. (2022) showed that when faced with a choice of helping broods of equal relatedness the preference was for the closest brood, and Napper & Hatchwell (2016) found that helpers were more likely to help familiar relatives. However, familiarity may often be difficult to quantify in natural systems (Leedale et al. 2020) and, at present, our understanding of the influence of prior social association on the effectiveness of mechanisms for discrimination of kin is incomplete. But, if familiarity with neighbours plays a role in breeding site selection, and if kin recognition is localised to an individual's immediate vicinity, this may reduce the importance of kinship within the population relative to other factors that determine the availability of potential recipients, as suggested by Sharp et al. (2011) and Hatchwell et al. (2013). More generally, it is important to know the information that animals have when making decisions about who to interact with; if knowledge of the broader social environment is limited, for example in socially or spatially structured populations, then recognition errors are likely and adaptive decision-making may be constrained (Reeve 1989; Sherman et al. 1997).

The other two potential drivers of helping decisions, the proportion of nests depredated and breeding phenology, were both influential at relatively broad spatial scales. It is important to stress that although both factors are likely to impact the number of active nests available to failed breeders, their influence was independent of that metric (Figure 3) and generally occurred at different scales (Figure 2), hence requiring a separate explanation.

Predation has long been recognised as a factor promoting sociality (Hamilton 1971; Pulliam 1973; Alexander 1974; Foster and Treherne 1981) and Emlen's (1982) ecological constraints hypothesis argued that high predation pressure could drive the evolution of cooperative breeding by constraining dispersal or independent reproduction, an idea supported by single-species studies (Griesser et al. 2006; Sorato et al. 2012; Groenewoud et al. 2016; Tanaka et al. 2016; Hoppe et al. 2025) and comparative analyses (Bliard et al. 2024). However, predation pressure does not constrain dispersal in long-tailed tits because short- and long-distance dispersive movements are frequent (Sharp et al. 2008; Napper and Hatchwell 2016; Morinay et al. 2025) and virtually all adults attempt independent breeding each year. So how does broad scale predation pressure influence helping decisions? One clue is the fact that the negative effect of predation probability on helping decisions was more severe on females than on males (Figures 2 & 3). We suggest that this may be linked to condition. Females are less

likely to help than males even when the opportunity arises and Morinay et al. (2025) argued that this was because females bear a greater cost of reproduction than males. Both sexes contribute to nest-building, but females must lay a large clutch (8-11 eggs) that cumulatively weighs ca. 120% of body mass and then incubate alone for ca. 15 days. This disproportionate investment in reproduction by females is exacerbated by high predation rates because predation of early nests induces repeat nesting attempts (MacColl and Hatchwell 2002) and hence even greater female investment. Males, by contrast, invest relatively little until the nestling period and may be less impacted physiologically by multiple breeding attempts. This suggestion is supported by Roper et al.'s (2022) analysis of age-related fitness in long-tailed tits that found that helping was positively associated with body condition; we are currently investigating the effect of condition on helping by both sexes in more detail.

Thus, predation pressure plays a critical role in this system, but not in the manner described by the ecological constraints hypothesis. First, there is a direct impact of nest predators on the success of breeding attempts by breeders that promotes cooperation by creating a pool of failed breeders, i.e. potential helpers. Second, nest predation limits helping opportunities via its effect on the number of active nests available to be helped. These two consequences of nests predation, promoting cooperation by creating a pool of potential helper, but limiting cooperation by influencing the number of nest available to be helped, are consistent with Hatchwell et al.'s (2013) finding that across years the prevalence of helping in the population peaked at intermediate predation rates. Third, predation rates may dictate prior investment in breeding, especially by females, influencing helping decisions via body condition. Finally, predation induces fecundity bias (Lehmann and Balloux 2007), i.e. high variance in fecundity, that results in a small effective population size and increases relatedness among recruits, thereby enhancing opportunities for kin-selected helping (Lehmann and Rousset 2010; Beckerman et al. 2011). Therefore, the intensity of nest predation is pivotal in the emergence of cooperative breeding in this species.

The final factor influencing the availability of nests for potential helpers in our study was phenology: male failed breeders that helped were surrounded by pairs that bred relatively late, at a broad spatial scale (> 750m; Figure 2). As noted above, this effect was independent of the influence of the number of active nests on helping (Figure 3) and was consistently significant only for males, the predominant helping sex, at a distance beyond that normally moved for helping. Previous analyses have revealed the importance of phenology for cooperation in long-tailed tits, the time of nest failure being a key trigger for helping (MacColl and Hatchwell 2002), and shorter breeding seasons being associated with a greater prevalence

of helping (Hatchwell et al. 2013). The latter effect is probably most relevant here, although across the years sampled for this analysis there was no correlation between the mid-80%, mid-90% or total spread of laying and mean lay date (Pearson's product-moment correlation, all $P>0.30$), as also found by Gullett et al. (2013). In other species, average phenological indices, such as mean lay date, do not necessarily capture critical phenological events or the distribution of breeding attempts within a breeding season (Halupka and Halupka 2017; Tarwater and Arcese 2018; Solís et al. 2023). This makes interpretation of any effect of phenology challenging because how the start, end and length of breeding seasons relate to mean lay date is extremely variable (Halupka and Halupka 2017). Therefore, while the positive effect of mean lay date on helping probability in male long-tailed tits matches our prediction, the reason for this relationship at broader spatial scales remains speculative due to the complex relationship between phenological indices (Gullett et al. 2013).

More generally, phenological influences on cooperative breeding have received little attention except in species with redirected helping, where the switch from a breeding to helping strategy is typically related to the stage of the season (Emlen 1990; Preston et al. 2013; Dickinson et al. 2016). However, they may also be important in conventional cooperative breeding systems where there are seasonal or annual patterns in food abundance that make the contributions of helpers more or less impactful on productivity (Baglione et al. 2006; Covas et al. 2008). Such variation in the impact of helpers within or between years is intrinsic to the bet-hedging hypothesis for cooperative breeding (Rubenstein 2011; Kennedy et al. 2018), a neglected idea (but see Koenig and Walters 2015; Capilla-Lasheras et al. 2021) that deserves greater attention at a time of rapid environmental change.

Finally, the multivariate analysis of helping decisions, incorporating each driver at the smallest spatial scale at which it had a consistently significant effect on helping decisions, revealed that for males, the main helping sex, each of the four drivers investigated had broadly similar effects, even though the spatial scale at which they acted varied. This was contrary to the expectation that kinship would be the dominant factor, given that helping is kin-selected in long-tailed tits (Hatchwell et al. 2014) and that their short lifespan means that the accrual of indirect fitness through helping is typically an alternative route to fitness rather than being supplementary to direct fitness (MacColl and Hatchwell 2004; Green and Hatchwell 2018). Therefore, if birds fail to reproduce themselves, seeking relatives to help should be paramount. Nevertheless, the fact that our analysis identified four drivers of helping is consistent with the studies of Nelson-Flower et al. (2018) and Johnson & Pruett-Jones (2025) – see introduction –

and suggests that similar analyses, whether of single species or comparisons across phylogenies, should consider multiple factors where possible. Moreover, our analysis demonstrates the importance of spatial scale when investigating social, demographic or ecological correlates of behavioural decisions. As noted above, such considerations have often been neglected in studies of social species, a notable exception being Clutton-Brock & Lukas's review (2012). They highlighted the importance of scale when analysing animal movements, arguing that inbreeding avoidance, like kin-directed help, is a function of local relatedness, while dispersal is a function of broader ecological parameters. The interesting distinction is that in our analysis we found that a single decision (to help or not) was a function of multiple drivers that impact across different spatial scales.

Conclusions

We have identified multiple co-occurring drivers of helping decisions in long-tailed tits, the importance of each varying with sex and the scale at which it is analysed. 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 (kinship, breeding density) may be more apparent at fine scales and ecological factors (phenology, predation pressure) at broader scales, as suggested by Clutton-Brock & Lukas (2012). Secondly, we have shown that multiple factors influence helping decisions to varying degrees, emphasising the importance of inclusive approaches when testing hypotheses on social evolution (Cockburn 2020). Finally, this analysis has revealed that associations between helping decisions and demographic traits differed strikingly between males and females. Such sex-specificity should not be neglected in single species or comparative studies of the drivers of cooperative behaviour.

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Supplementary Material for

Ecological, demographic and social factors shape helping decisions at different spatial scales in a facultative cooperative breeder

This Supplementary material is composed of two documents:

- Supplementary Material 1 below with Figures S1, S2, S3, S4, S5, Table S1, and Table S3
- Supplementary Material 2 with Table S2 in a .csv format.

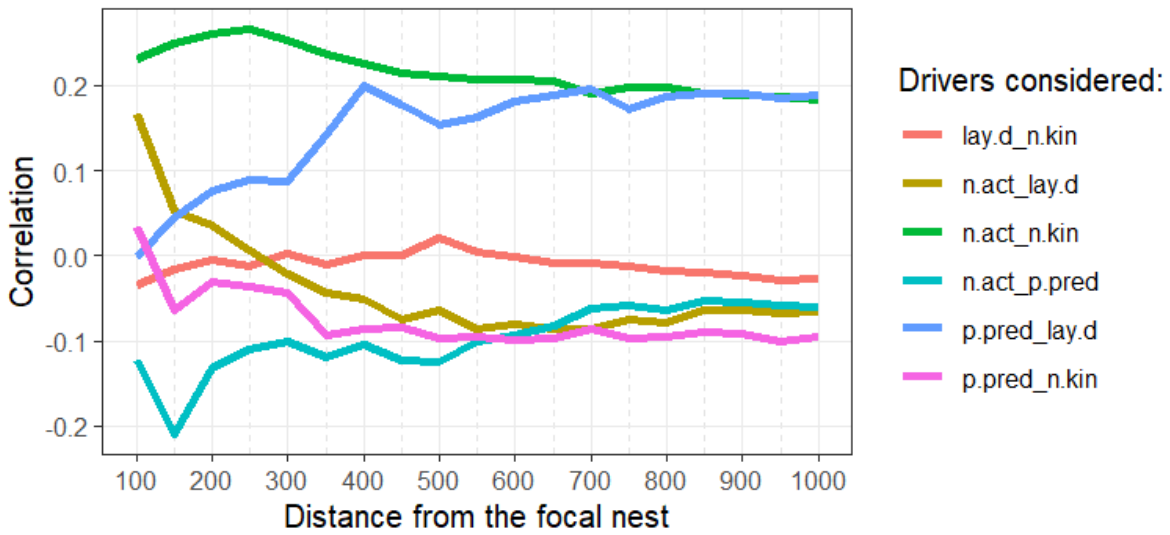


Figure S1. Estimates of Spearman correlation coefficient among all drivers, derived at all tested distances from the focal nest. There is no general increase or decrease of coefficient, but correlations reach a plateau as the distance increases, similarly to the estimates of the drivers themselves (Figure S2).

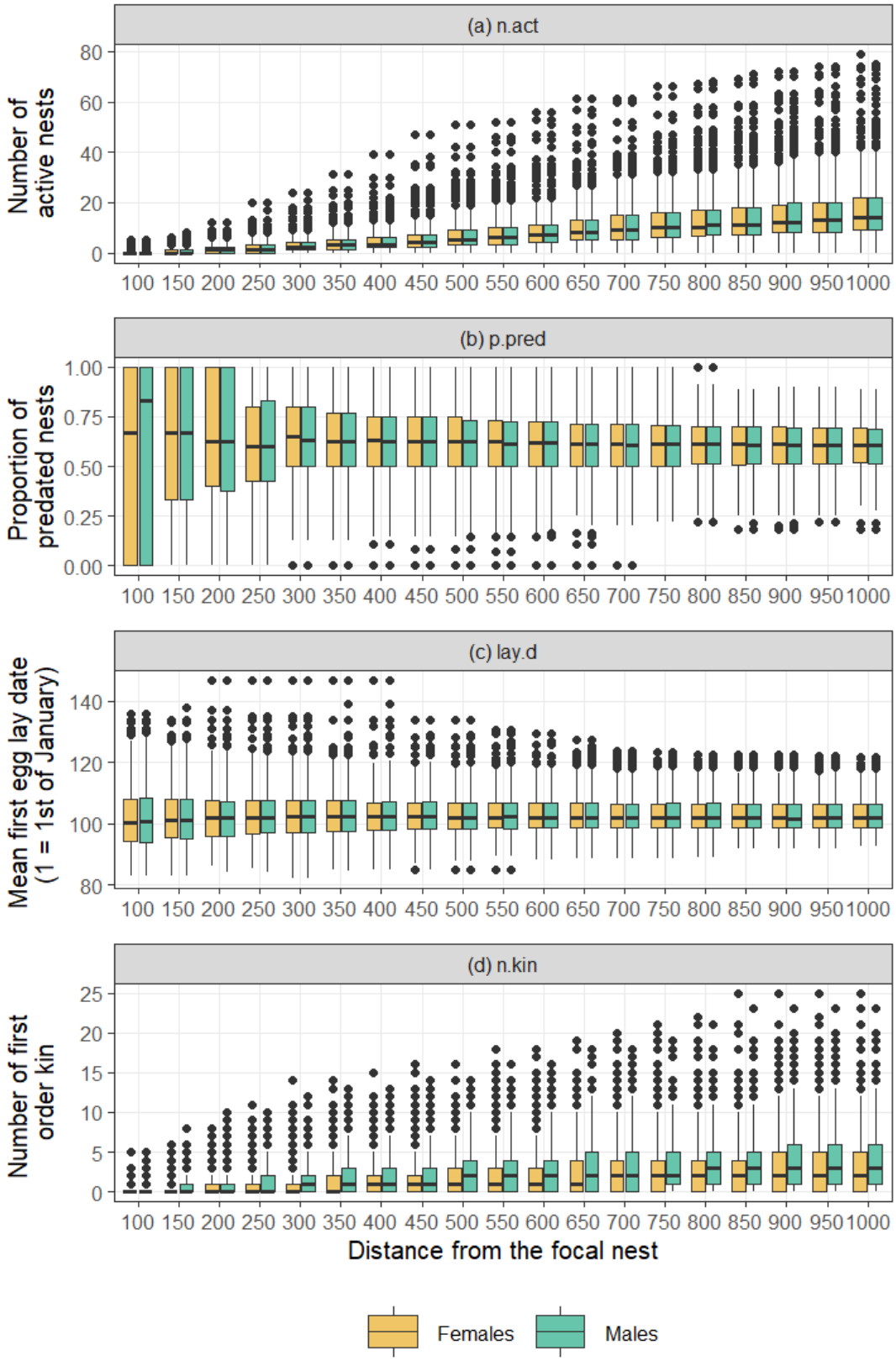


Figure S2. Distribution of the raw data for each driver, assorted by sex and distance from the focal nest.

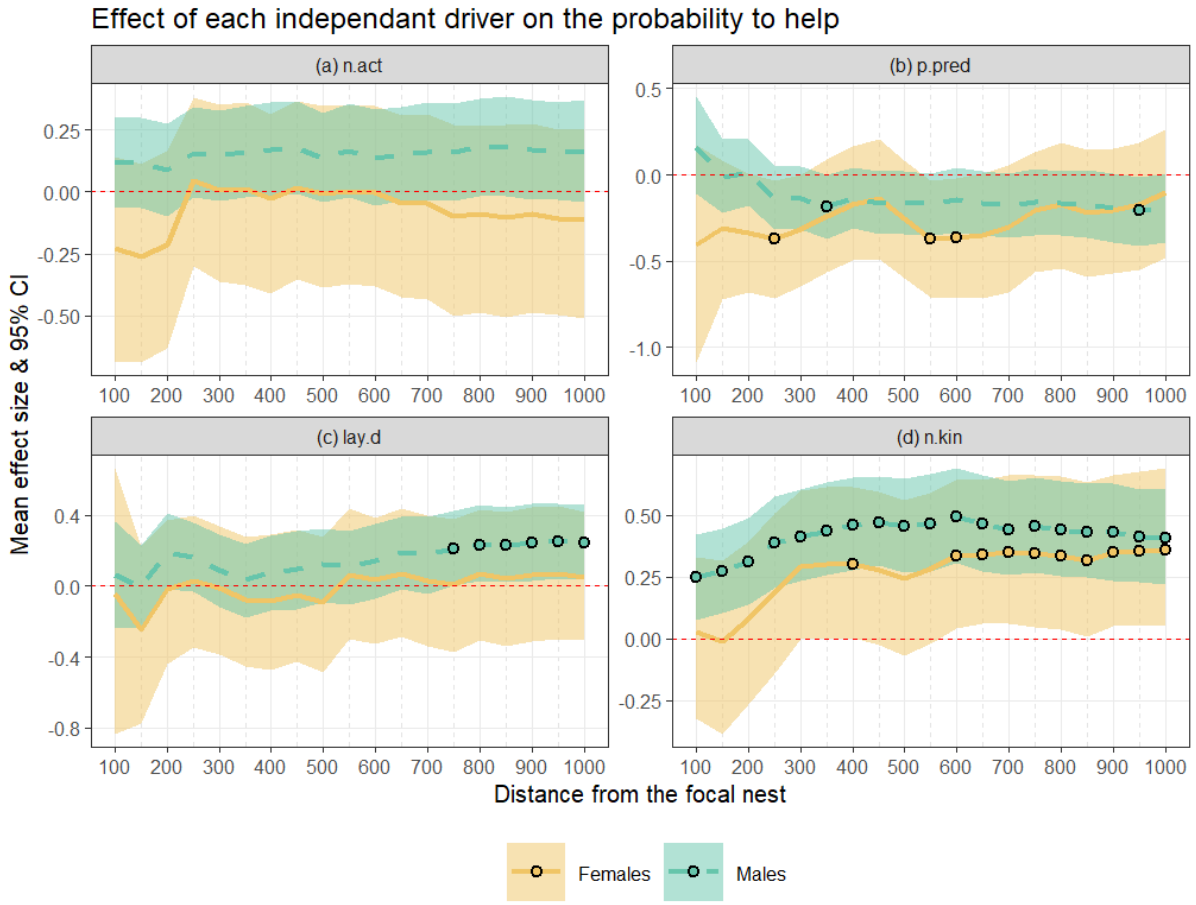


Figure S3. Duplication of Figure 2 from the main text, when removing individuals whose last nest was located outside the 90% inner values for either latitude or longitude. Effect of each independent driver on the probability of helping. We present the mean posterior estimate (lines) and 95% Credible Intervals (ribbon) of the effect of each driver, derived from models fitting the probability of helping with only one driver at a time (Eq. 1), for all possible values of influential distance to the focal nest α on the x-axis. Estimates for females are shown in yellow (solid line) and estimates for males are in green (dashed line). The horizontal red dashed line indicates zero (no effect on the probability of helping). *n.act, p.pred, lay.d*, and *n.kin* stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin.

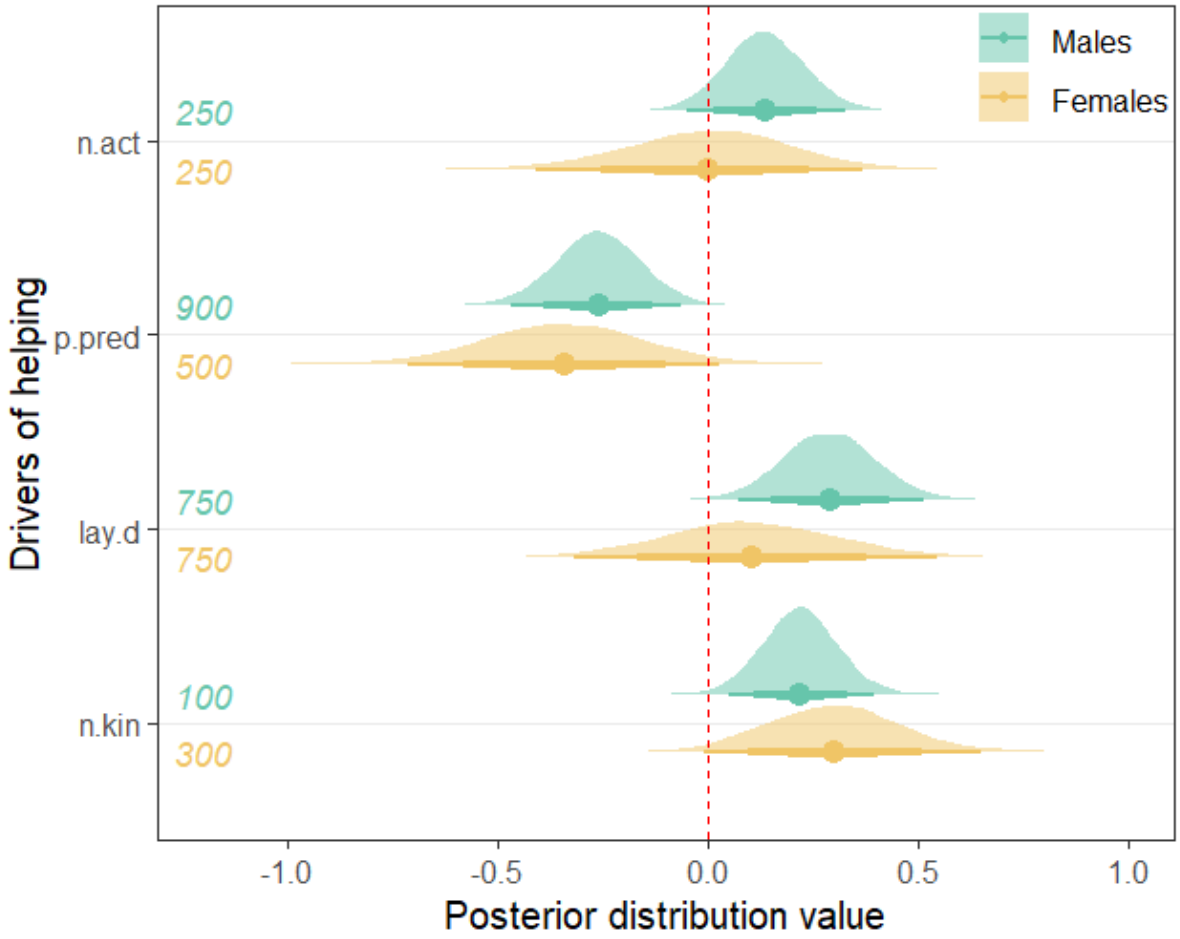


Figure S4. Duplication of Figure 3 from the main text, when removing individuals whose last nest was located outside the 90% inner values for either latitude or longitude. Posterior distribution of the effect of each driver on the probability of becoming a helper, for females (yellow, bottom graphs) and males (green, top graphs). These distributions are derived from a model including all drivers together, at their influential distance α (numbers indicated on the left-hand side of each distribution) as described in Eq.2. The mean, 50%, 80%, and 95% Credible Intervals around the mean are represented at the bottom of each distribution. The vertical dashed red line indicates zero, i.e. an absence of effect on the probability of helping. n.act, p.pred, lay.d, and n.kin stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin.

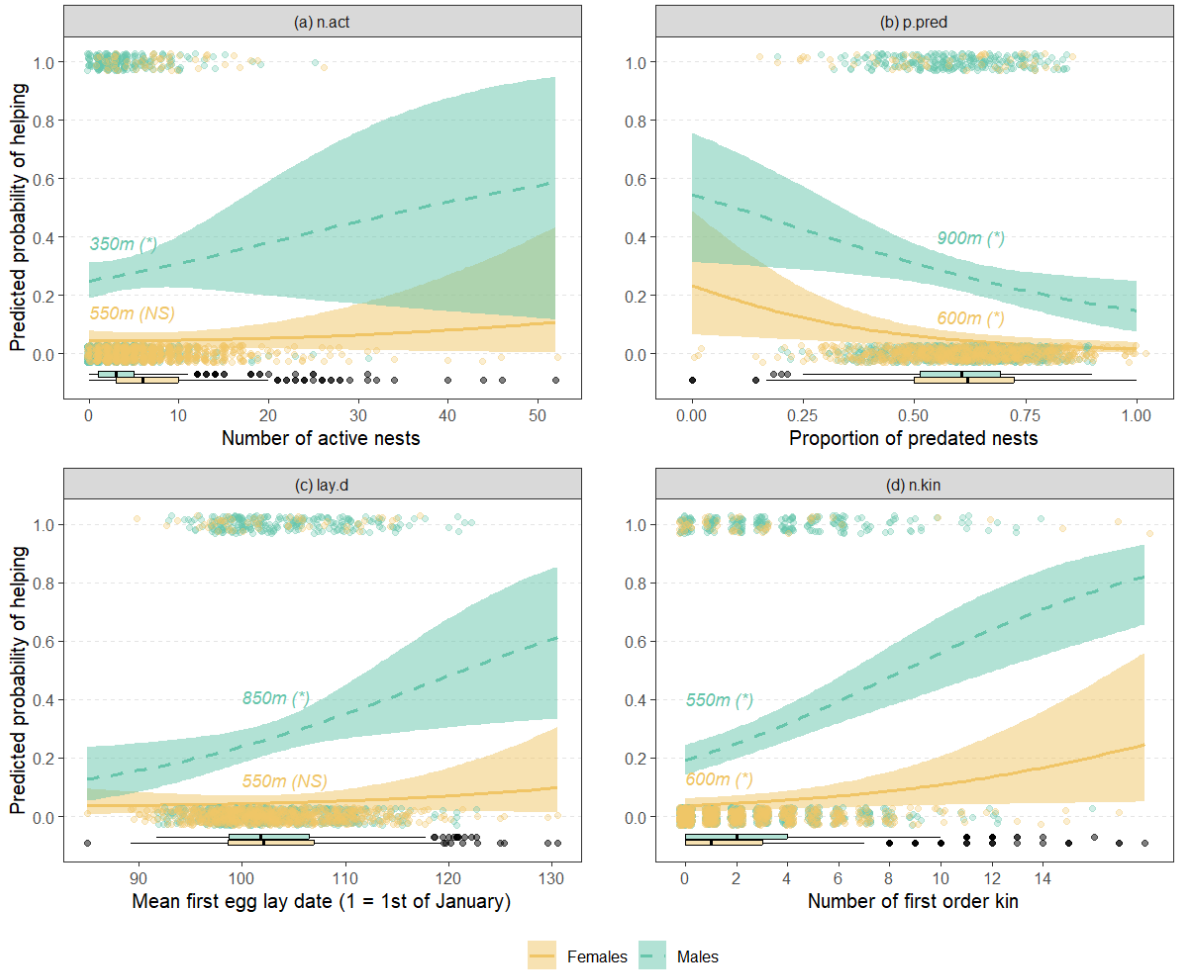


Figure S5. Effect of each driver on the probability of becoming a helper, estimated at their intermediate influential distance as indicated on the graphs, rather than the minimal distance at which they start to be influential in Figure 4. We present estimates for females (yellow, solid lines) and males (green, dashed lines). When a driver had no effect on the probability of helping, we show the estimate at the same spatial scale as for the other sex. The star and NS in parentheses respectively indicate whether the 95% Credible Interval around the driver's mean estimate overlapped zero or not. Dots are raw data and their distribution is summarized by sex with the box plot below each graph. *n.act, p.pred, lay.d*, and *n.kin* stand for number of active nests, proportion of predated nests, first egg lay date, and number of first order kin.

Table S1. Absence of collinearity among predictors for the models incorporating all scaled drivers together.

	Predictor	Variance Inflation Factor (VIF)			SE Factor	Tolerance		
	Variable	Estimate	95% CI Lower	95% CI Upper	Multiplier	Estimate	95% CI Lower	95% CI Upper
Females	n.act_250	1.06	1.04	1.08	1.03	0.94	0.93	0.96
	p.pred_500	1.05	1.03	1.07	1.02	0.95	0.93	0.97
	lay.d_750	1.03	1.02	1.06	1.02	0.97	0.95	0.98
	n.kin_300	1.05	1.03	1.07	1.02	0.96	0.94	0.97
Males	n.act_250	1.03	1.01	1.06	1.01	0.97	0.94	0.99
	p.pred_900	1.05	1.04	1.08	1.03	0.95	0.93	0.97
	lay.d_750	1.04	1.03	1.07	1.02	0.96	0.93	0.98
	n.kin_100	1.02	1.01	1.06	1.01	0.98	0.95	0.99

Table S2. Summaries of the models fitting the probability to become a helper, given one single driver. We provide results for each sex and each distance from the focal nest considered. As Table S2 comprises 608 rows, it is available in a .csv format.
[Please ask the corresponding author]

Table S3. Summaries of the model fitting the probability to become a helper, given all drivers estimated at their influential distance and scaled.

		Posterior Summary				Convergence
	Parameter	Estimate	SD (Error)	95% CI Lower	95% CI Upper	Rhat
Females	Intercept	-3.07	0.37	-3.97	-2.53	1.00
	n.act_250	0.08	0.16	-0.24	0.40	1.00
	p.pred_500	-0.45	0.17	-0.78	-0.13	1.00
	lay.d_750	0.08	0.19	-0.30	0.47	1.00
	n.kin_300	0.27	0.14	0.00	0.56	1.00
	(1|BirdID)	0.61	0.44	0.03	1.64	1.00
	(1|Year)	0.63	0.30	0.07	1.27	1.00
Males	Intercept	-0.99	0.13	-1.24	-0.74	1.00
	n.act_250	0.15	0.08	-0.01	0.32	1.00
	p.pred_900	-0.25	0.10	-0.44	-0.06	1.00
	lay.d_750	0.27	0.11	0.06	0.50	1.00
	n.kin_100	0.25	0.08	0.10	0.41	1.00
	(1|BirdID)	0.30	0.21	0.01	0.76	1.00
	(1|Year)	0.42	0.16	0.11	0.74	1.00