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Inclusive fitness consequences of dispersal decisions in a cooperatively-breeding bird, the long-tailed tit (*Aegithalos caudatus*)

Short title: Inclusive fitness consequences of dispersal

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Abstract

Natal dispersal is a demographic trait with profound evolutionary, ecological and behavioural consequences. However, our understanding of the adaptive value of dispersal patterns is severely hampered by the difficulty of measuring the relative fitness consequences of alternative dispersal strategies in natural populations. This is especially true in social species where natal philopatry allows kin selection to operate, so that both direct and indirect components of inclusive fitness have to be considered when evaluating selection on dispersal. Here, we use lifetime reproductive success data from a long-term study of a cooperative breeder, the long-tailed tit *Aegithalos caudatus*, to quantify the direct and indirect components of inclusive fitness. We show that dispersal has a negative effect on the accrual of indirect fitness, and hence inclusive fitness, by males. In contrast, the inclusive, predominantly direct, fitness of females increases with dispersal distance. We conclude that the conflicting fitness consequences of dispersal in this species result in sexually antagonistic selection on this key demographic parameter.

Significance statement

How far individuals disperse from their birth site has profound consequences for the genetic structure of populations and for individual fitness, affecting both the degree of gene flow between populations and the extent to which relatives and nonrelatives interact socially. Spatial clustering of kin arising from limited dispersal facilitates kin-selected cooperation and is considered an important step in the evolution of cooperative breeding. However, determining the fitness consequences of dispersal in wild populations has proved extremely challenging. Here, we use data from a long-term study of long-tailed tits to quantify the fitness payoffs of dispersal. We show that females’ reproductive success increases with dispersal distance, while for males, cooperation with kin generates fitness benefits that favour limited natal dispersal.

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Dispersal is of fundamental importance in behavioral and evolutionary ecology because it influences key processes such as local adaptation, gene flow and inbreeding (1-3). Dispersal is a particularly important process in social evolution theory because major evolutionary transitions in the history of life on earth are facilitated by social interaction among relatives, allowing kin selection to operate (4,5). This reasoning underpins theoretical and empirical explanations for the evolution of sociality in animals (6) and especially cooperative breeding in vertebrates (7-10). Empirical studies of dispersal in social species have generally focused on the environmental and social factors that either constrain or promote dispersal from natal groups (11). However, insights into the function of dispersal require knowledge of the fitness consequences of alternative dispersal strategies, and empirical study of such fitness effects have proved to be challenging. This is partly due to inherent difficulties in the study of dispersal in open systems (12-13), but more significantly because collection of empirical data to quantify inclusive fitness and relate it to specific dispersal strategies is extremely difficult for several reasons. Social species often have complex life histories, and are often long-lived (11), making the accumulation of data on lifetime reproductive success of many individuals impossible. Most crucially, to understand individual dispersal strategies, inclusive fitness must be partitioned into its direct and indirect components that can be directly related to specific dispersal decisions.

In this paper, we investigate the effect of natal dispersal decisions on the accrual of the direct and indirect components of inclusive fitness in a cooperatively breeding bird, the long-tailed tit *Aegithalos caudatus*. First, we quantify and describe the direct and indirect components of inclusive fitness using Lifetime Reproductive Success (LRS) data for a large sample of individuals derived from a long-term study (14). For each sex, we then determine the effect of categorical natal dispersal status on the accrual of direct and indirect fitness by comparing philopatric residents (hereafter, residents) and immigrants. Third, using data from resident birds only, we determine the effect of natal dispersal distance within the study site on the acquisition of direct and indirect fitness. These analyses allow us to test the hypothesis that sex-specific social interactions and their fitness consequences drive the divergent dispersal strategies of males and females.

Long-tailed tits have a relatively simple cooperative breeding system in which all helpers are failed breeders that redirect their care to assist other pairs raise their offspring by feeding nestlings and fledglings (14). Helping is costly, but these costs are outweighed by the indirect fitness benefits of helping to increase productivity of related broods and reduced reproductive costs of related male breeders (15). No significant direct benefits of helping have been detected (16). Long-tailed tits have a short lifespan compared to other cooperative breeders; all birds attempt to breed from their first year onwards and there is no discernible age effect on breeding or helping behaviour. This contrasts with most other cooperative species where long lives and age-related patterns of breeding and helping greatly complicate estimation of fitness (17). Therefore, rather than parametrizing demographic models (18-21) or using fitness components (22,23) to understand dispersal decisions, we were able to use LRS data to calculate the direct and indirect fractions of the inclusive fitness on an individual basis. Moreover, long-tailed tits have an atypical social structure in which helping is preferentially directed towards kin living within kin neighborhoods (24) that form via limited natal dispersal (25,26), coordinated dispersal of kin (27) and a small effective population size caused by depredation of broods (28). This social organization differs from the stable territorial structure that typifies most other cooperative breeders, so in addition to a categorical comparison of the fitness of philopatric and immigrant birds (18,20,21,23), we could also investigate the effect of fine-scale dispersal distance on individual fitness.

We studied a population of long-tailed tits from 1994 to 2016 in the Rivelin Valley, Sheffield, UK (52°23’N, 1°34’W) (14). Standard protocols were followed in each year of the study to monitor survival of adults, breeding attempts and helping behaviour. Birds were marked with unique combinations of colour bands either as adults when they first dispersed into the population, or as nestlings; >95% of adults were individually marked each year. Re-sighting probabilities for both sexes were high (83% for females and 92% for males based on capture-mark-recapture analysis of 985 individuals between 1994 and 2012 [29]), and our sample included only those individuals for whom we had complete life histories. Each individual was blood-sampled and genotyped at 19 microsatellite loci. Genotype data were used to assign parentage for ringed offspring, with extra-pair offspring assigned to their genetic father. Fitness metrics were calculated from individual life histories, using the number of recruits (i.e., offspring entering the adult population as breeders in the year after fledging) as the currency of fitness, using previously described methods (30) that follow Hamilton’s (4) definition of inclusive fitness. Briefly, direct fitness for individual breeders was obtained by first subtracting the fraction of recruits attributable to helpers (calculated using average population-level effects of helpers on productivity). The remaining fraction was then halved to reflect investment in recruit production by the breeding partners and then halved again to reflect an average parent-offspring relatedness of 0.5. Where extra-pair recruits were identified, the relevant fraction of direct fitness was stripped from social fathers and reassigned to genetic fathers. Indirect fitness for individual helpers was obtained by multiplying the fraction of recruits attributable to an individual helper (adjusted for the number of helpers at a nest) by its average relatedness to those recruits, estimated from the genotype data. For full details, see Methods.

Results

Inclusive fitness was estimated from the complete reproductive histories of 778 individuals that reached adulthood and recruited into the population as breeders (n = 393 males, 385 females). Of these birds, 37% produced at least one fledgling from their own nest in their life (37% of males, 36% of females), and 20% recruited at least one 1-year old offspring (19% of males, 21% of females) into the study population. The LRS of adults was strongly skewed, in terms of the production of both fledglings and recruits (SI Appendix, Fig. S1).

Fitness of residents versus immigrants

In our sample of birds with quantified fitness, more males (46%, n = 393) were philopatric residents than females (20%, n = 385; $\chi^2_1 = 61.97$, $P < 0.0001$), consistent with female-biased dispersal in long-tailed tits (25). Overall, residents were more likely to achieve indirect fitness than immigrants ($\chi^2_1 = 14.70$, $P = 0.0001$; SI Appendix, Table S1). Independently of dispersal status, males were more likely to achieve indirect fitness than females (14.5% *versus* 2.3%, respectively; $\chi^2_1 = 27.24$, $P < 0.0001$; Si Appendix, Table S1), a difference that arises not because males are more effective helpers, but simply because they are much more likely to help than females (31,32). Despite this sex difference in the likelihood of achieving indirect fitness, both males and females were more likely to gain indirect fitness as residents than as immigrants (sex x dispersal: $\chi^2_1 = 0.03$, $P = 0.87$).

In contrast, the probability of gaining direct fitness was not influenced by dispersal status ($\chi^2_1 = 0.34$, $P = 0.56$), sex ($\chi^2_1 = 0.37$, $P = 0.54$) or their interaction ($\chi^2_1 = 0.27$, $P = 0.60$; SI Appendix, Table S1). Likewise, there was no significant difference in the likelihood of accruing inclusive fitness between immigrants and residents ($\chi^2_1 = 1.83$, $P = 0.18$; dispersal status x sex: $\chi^2_1 = 1.81$, $P = 0.18$; SI Appendix, Table S1). There was, however, a tendency for a higher proportion of males (30.3%) to achieve some inclusive fitness than females (22.3%; $\chi^2_1 = 3.79$, $P = 0.05$; SI Appendix, Table S1), a consequence of the fact that males were more likely than females to achieve some indirect fitness (see above).

Similar results were obtained when analysing the amount of fitness gained with respect to dispersal status and sex (Fig. 1). For indirect fitness, males gained more than females (χ^2_1 = 24.92, $P < 0.0001$) and residents gained more than immigrants (χ^2_1 = 17.01, $P < 0.0001$), but there was no interaction between sex and dispersal status (χ^2_1 = 2.01, P = 0.16; Fig. 1a). The amount of direct fitness gained was not affected by dispersal status (χ^2_1 = 0.77, P = 0.38), sex (χ^2_1 = 0.70, P = 0.40) or their interaction (χ^2_1 = 0.28, P = 0.60; Fig. 1b). The amount of inclusive fitness gained did not differ significantly between immigrants and residents (χ^2_1 = 0.07, P = 0.79; dispersal status x sex: χ^2_1 = 0.63, P = 0.43; Fig. 1c), reflecting the fact that while the amount of fitness gained indirectly through helping was higher for residents, this component of fitness constitutes a relatively small proportion of inclusive fitness (Fig. 1). For the same reason, although males gained more indirect fitness than females, the relatively small contribution of indirect fitness to inclusive fitness (13.4% for males vs. 1.5% for females) and the absence of sex differences in direct fitness resulted in similar inclusive fitness gains for males and females (χ^2_1 = 0.08, P = 0.77; Fig. 1c). The same results were found when each sex was analysed separately (SI Appendix, Table S2).

Among those birds that achieved non-zero inclusive fitness, just 12 males (10.1%) and even fewer females (3 birds, 3.5%) achieved both direct and indirect fitness (SI Appendix, Table S1). For males, the observed number of cases was significantly lower than that expected if the probability of gaining fitness directly and indirectly were independent (χ^2_1 = 99.16, $P < 0.0001$), indicating that they tend to be mutually exclusive activities (too few females gained indirect fitness for an equivalent analysis). This makes intuitive sense because an individual long-tailed tit cannot gain both direct and indirect fitness (i.e., breed successfully and help) within the same season because helping is contingent on failed breeding, and the lifespan of long-tailed tits is short (annual adult survival rate is 0.55 [33]), with the result that around half of all birds experience only a single breeding season.

Fitness and dispersal distance of residents

For 235 resident birds (n = 75 females and 160 males) we were able to relate accrual of fitness to natal dispersal distance within the study site. For males, increasing dispersal distance was associated with a decline in both the probability of accruing indirect fitness (Fig. 2a) and the amount of indirect fitness accrued (Fig. 2b); too few females achieved indirect fitness to conduct an equivalent analysis. In contrast, the likelihood of accruing direct fitness was not influenced by dispersal distance (χ^2_1 = 0.20, P = 0.65), sex (χ^2_1 = 0.35, P = 0.56) or their interaction (χ^2_1 = 0.89, P = 0.35) and the same results were obtained when analysing the sexes separately (Fig. 2c,e). However, the amount of direct fitness gained was influenced by an interaction between sex and dispersal (χ^2_1 = 4.58, P = 0.03). When the sexes were analysed separately, females dispersing further from their natal nest gained more direct fitness, but this was not the case for males (Fig. 2d,f).

The combined effects of sex and dispersal had a significant influence on the likelihood of accruing inclusive fitness via an interaction (χ^2_1 = 4.62, P = 0.03). The effect of dispersal was not significant when the sexes were analysed separately, but contrasting trends were observed for males and females. For males, greater dispersal tended to be associated with a reduced probability of accruing inclusive fitness (Fig. 2g), driven by the decline in probability of accruing indirect fitness with dispersal distance (Fig. 2a). For females, however, the probability of gaining inclusive fitness tended to increase weakly with dispersal distance (Fig. 2i).

A significant interaction between sex and dispersal distance was also observed when analysing the amount of inclusive fitness gained by residents (χ^2_1 = 6.38, P = 0.01). The sexes were therefore analysed separately, with the regression slope in each case providing an estimate of the strength of linear (i.e. directional) selection on natal dispersal distance (see Methods). For females, the analysis revealed positive directional selection on dispersal distance (Fig. 2j) driven by the increase in the amount of direct fitness with dispersal distance (Fig. 2f). By contrast, for males the selection gradient, while negative, was nonsignificant (Fig. 2h). This again reflects the fact that indirect fitness constitutes only a small proportion of inclusive fitness (see above), resulting in a relatively small decrease in the magnitude of inclusive fitness gained as dispersal distance increased. There was no evidence for significant nonlinear selection on natal dispersal distance for either sex (see Methods).

Causes of differential direct and indirect fitness

Finally, we explore the reasons for the effects of dispersal and sex on fitness metrics. Indirect fitness was accrued by males but rarely by females reflecting the fact that helping in long-tailed tits is male-biased (85% of helpers are male [31]). The other clear pattern in acquisition of indirect fitness related to natal dispersal: males that dispersed further within our study site accrued less indirect fitness, as did immigrants relative to residents. A lower probability of helping as relatedness decreases has been reported in other cooperatively breeding birds (e.g. Galapagos mockingbirds *Nesomimus parvulus* [34] and white-fronted bee-eaters *Merops bullockoides* [35]), so these effects could result from males being less likely to help following nest failure the further they dispersed. Alternatively, given that the magnitude of indirect fitness gained by a helper depends on their relatedness to the recipient, the probability of helping may remain the same, but the relatedness between helper and recipient could decrease with dispersal distance and be lower for immigrants than for residents. Our results offer some support for both explanations: the probability of helping following nest failure was lower for immigrant males than for resident males (32% vs. 43%; $\chi^2_1 = 3.91$, $P = 0.05$), and the dyadic relatedness of helpers to recipients was lower for immigrants (mean ± SE = 0.10 ± 0.03) than for residents (0.26 ± 0.03; $L_1 = 12.86$, $P = 0.0003$). Among residents, the relatedness of helpers to recipients declined with natal dispersal distance ($L_1 = 8.16$, $P = 0.004$, Fig. 3), but there was no change in the probability of helping with dispersal distance ($\chi^2_1 = 0.45$, $P = 0.50$).

For direct fitness, differences in relation to sex or dispersal were less marked. Among males, no direct fitness benefit or cost of dispersal was detected, while among females, direct fitness, and hence inclusive fitness, increased with dispersal distance within the study site. Increased dispersal from the natal nest was not associated with the production of larger clutches ($L_1 = 1.27$, $P = 0.26$) or of more fledglings ($L_1 = 1.20$, $P = 0.27$). However, the proportion of fledglings that successfully recruited was higher for females dispersing greater distances ($\chi^2_1 = 16.57$, $P < 0.0001$; Fig. 4). Why this might be is unclear. One possibility is that both dispersal and reproductive success are dependent on quality, such that higher quality females are able to disperse further and succeed in producing more recruits. Alternatively, reproductive success may itself increase with dispersal distance if, for example, the risk of inbreeding declines with distance from the natal nest, a possibility we are currently exploring.

Discussion

Overall, our results indicate contrasting selection on the dispersal behaviour of males and females in a cooperatively breeding bird. Females achieve greater inclusive fitness, via increased direct fitness, the further they dispersed within the study site, a finding that is contrary to the general pattern of negative selection on dispersal observed across multiple species (e.g. 36-38). There are two important points about this relationship. First, Doligez & Pärt (13) pointed out that if dispersal behaviour is heritable, dispersers would have apparently low fitness because their offspring will also tend to disperse, which, if undetected, would generate a false negative relationship between fitness and dispersal. We have not yet investigated heritability of dispersal in long-tailed tits, but the fact that dispersal is associated with higher fitness indicates that there is no such confound in this case. Our observation that the proportion of fledglings that recruited increased with natal dispersal distance (Fig. 4) further supports this argument. Second, the positive effect of dispersal on fitness was evident among short distance dispersers, i.e. for philopatric females (Fig. 2e,f,i,j), but the difference in fitness between the categories of resident and immigrant females (Fig. 1) was not significant, even though the trend was clearly in the same direction. Most previous studies have used only the latter approach to investigate the fitness consequences and we suggest that more fine-grained analyses of dispersal consequences would be worthwhile.

In contrast, males tended to increase their probability of gaining inclusive fitness by limiting dispersal, allowing them to augment their inclusive fitness with the indirect fitness gained by helping relatives to raise their offspring. Male long-tailed tits are much more likely to help following the failure of their own breeding attempt than females and, as a consequence, gain considerably greater indirect fitness. This begs the question of why females do not help more often. One explanation is that females rarely have kin available to help due to kin-biased natal dispersal; alternatively, females may be inherently less likely to help than males even when the opportunity to help arises. Evidence supports the latter argument because our study population is kin-structured for females as well as males, albeit less strongly (26). Moreover, in another isolated study population, female dispersal was constrained by a lack of available breeding sites in the surrounding habitat so that they exhibited a similar degree of philopatry to males; nevertheless, the incidence of helping by females was not significantly higher than in the Rivelin Valley population (32). Why, then, might females spurn opportunities to accrue indirect fitness by helping? A likely explanation is that helping is costly (15) and the decision to help or not by failed breeders appears to depend on condition *inter alia* (16). During early phases of the reproductive cycle females invest substantially more than males. Mean clutch size is 10, each egg weighing *c.*1g so females (mean mass = 7.7g [39]) must produce *c.*130% of their own body mass in eggs during the 10-day laying period; once complete, the clutch is incubated by the female alone for 14-15 days which is also likely to be costly (40), while males undertake a major parenting role only when nestlings hatch. Therefore, females are probably in poor condition relative to males when nest failure occurs, and hence are less likely to help. Such conditional helping has been reported in other cooperatively breeding vertebrates (41-43).

Our findings have general implications for our understanding of the evolution of helping in birds and other taxa with kin-based cooperative groups. First, they imply that indirect fitness benefits alone can select for limited dispersal, i.e. there is no need to invoke direct fitness benefits of philopatry as a pathway towards or facilitator of social interaction with kin and subsequent helping behaviour (8, 10,44). This conclusion is consistent with previous studies of long-tailed tits that suggest no benefit of social interaction with kin except in the context of helping (16,45). In non-cooperative bird species, philopatry has often been reported to have direct fitness advantages for males (36-38). The absence of such an effect in this case may result from the fact that long-tailed tits are not territorial so there is no advantage of being able to claim a territory early by being philopatric.

The second general implication concerns the bet-hedging hypothesis, which argues that cooperative breeding evolved as a risk-averse strategy to reduce variance in fecundity (46). Our finding that indirect fitness is gained primarily by males that did not achieve direct fitness, thereby increasing the proportion of individuals achieving non-zero inclusive fitness, appears to support this hypothesis. However, the bet-hedging argument requires that variance in fitness is traded off against mean fitness, and here we found that the indirect fitness gained by males appears to augment rather than trade-off against direct fitness. Therefore, support for the bet-hedging hypothesis is currently equivocal and needs more detailed analysis of how direct and indirect fitness is acquired at the level of individual males.

In conclusion, using estimates of inclusive fitness partitioned into its direct and indirect components, we have shown that selection on the dispersal strategies of a cooperatively breeding bird, the long-tailed tit, is sexually antagonistic. The different fitness consequences of dispersal for each sex arise from females increasing their direct fitness via dispersal, the mechanism for which is as yet unknown, while males accrue kin-selected indirect fitness benefits by helping relatives, which also has the effect of increasing the proportion of males achieving non-zero inclusive fitness. The consequence is that there is positive selection for dispersal by females, while there tends to be negative selection on dispersal by males, driven in part by sex differences in social interactions. Thus, the potential for accruing fitness through both direct and indirect routes can have profound consequences for dispersal decisions and ultimately the structuring of populations.

Methods

Study population. A population of 25-72 pairs of long-tailed tits was studied between 1994 and 2016. The 2.5km^2 study site in the Rivelin Valley comprises deciduous woodland, farmland, scrub and gardens and is mostly surrounded by low-quality habitat. Each year, all nestlings were ringed with a unique colour-ring and a blood sample taken under Home Office License (PPL 7007834) for genetic analysis. In addition, we also succeeded in colourringing and blood-sampling >95% of all unringed adults in the population, either during nest-building or when they appeared as helpers at established nests. These adults were assumed to be immigrants born outside of the study site and to be one year of age, based on the observation that individuals tend to move relatively little following their first breeding season; specifically, very few individuals are missed (and therefore presumed to breed outside of the study site) in one breeding season only to reappear in the study site in a subsequent year (47). Individuals from whom blood samples were obtained were genotyped at 19 microsatellite loci (for details of the microsatellites used, see ref. 48). For further details of the field methods see ref 14.

We quantified lifetime fitness for a total of 778 birds (385 females and 393 males) that hatched between 1994 and 2014 and had died by 2016 and for whom we had precise information on offspring production in each year of life. This included a small number of birds whose breeding attempts in a particular year went undetected but who were later observed helping at other nests. Long-tailed tits in our population only help if their own breeding attempts fail, meaning that we could safely assume that individuals first observed as helpers had failed to fledge offspring in that year. Birds ringed as adults in the first year of the study (1994) were not included because we did not have information on breeding or helping in previous years.

Fitness calculations

Indirect fitness. In order to quantify indirect and direct fitness and combine these to obtain a measure of inclusive fitness, both fitness components were calculated as genetic offspring equivalents. Indirect fitness is the fitness that individuals accrue through helping relatives to reproduce – in this study, we calculated indirect fitness as the fraction of recruits from a brood that result from the brood being helped, multiplied by the average relatedness (r) between the helper and the recruits. The average effect of a given number of helpers on the probability of offspring recruitment was estimated using mixed-effects modelling (SI Appendix, section 1). For this and all subsequent analyses, we used R v. 3.2.3 in RStudio v. 1.0.136 (49). From this model, we estimated the average fraction of a recruit that is attributable to a helper for a given number of helpers at a nest. For each helping event, we then calculated the indirect fitness accrued through helping by multiplying this fraction by the relatedness between the helper and any offspring that successfully recruited (where multiple offspring recruited, the average relatedness between these and the helper was calculated). Pairwise relatedness between helpers and recruits was estimated from the genotype data using the method of Queller & Goodnight (50) in KINGROUP v. 2 (51). Helping events that did not lead to the production of recruits did not generate indirect fitness for the helper. Helpers also received no indirect fitness where their relatedness to recruits ≤ 0.

Direct fitness. Direct fitness is the fitness an individual accrues through the production of offspring, stripped of the effect of social partners (4). In this study, direct fitness measures were derived from the total number of recruits produced over an individual's lifetime and calculated in terms of genetic offspring equivalents. To do this, we first subtracted the fraction of recruits that was attributable to any helpers (see above). The remaining fraction was then halved to account for the contribution of the other breeding partner to recruit production. The resulting fraction was then halved a further time to reflect the average relatedness of 0.5 between parents and offspring.

Long-tailed tits are promiscuous, with estimates for our population indicating that 11% of offspring in 30% of nests are the product of extra-pair matings (SI Appendix, Table S5; note that this is somewhat higher than reported previously in ref. 52). We therefore checked paternity for all males in our data set, using the likelihood-based approach implemented in CERVUS v. 3.0.7 (53,54). For full details of the parentage assignment procedure, see SI Appendix, section 2. Where extra-pair recruits were identified, the fraction of direct fitness associated with their production was stripped from the social father and reassigned to the genetic father (where known). In a few cases (n = 5), extra-pair recruits were the genetic offspring of a male helper at their nest. In these cases, the direct fitness obtained by the helper was calculated as the number of extra-pair recruits multiplied by the fraction of recruit production attributable to helpers (see above) and then halved to reflect average parent-offspring relatedness of 0.5.

Analysis of fitness in relation to dispersal. The relationship between fitness (probability of accruing fitness or amount of fitness accrued) and either philopatric status (immigrant versus resident) or dispersal distance among residents was analyzed using mixed-effects models (for full details, see SI Appendix, section 3). We first analysed data from males and females together, fitting philopatric status/dispersal distance, sex and the interaction between philopatric status/dispersal distance and sex as fixed effects in the full model. We also split the data by sex to determine the effect of philopatric status/dispersal distance on the fitness accrued by males and females separately. The analyses comparing the fitness of immigrants and residents could be influenced by assortative pairing according to dispersal status, but we found no evidence for such an effect (χ^2_3 = 4.42, P = 0.22). From the analysis of the magnitude of inclusive fitness gains in relation to natal dispersal distance, we were able to quantify selection on natal dispersal for males and females. We initially included a quadratic term to test for nonlinear (γ) selection, but this was not significant for either sex (males: γ ± SE = 0.15 ± 0.44, χ^2_1 = 0.51, *P* = 0.48; females: 1.27 ± 1.87, χ^2_1 = 1.06, *P* = 0.30; values calculated according to ref. 55). Omitting the quadratic term from the model, univariate linear (β) selection gradients were estimated as the slope of the regression of dispersal distance on fitness (55).

A further set of analyses was performed to determine the factors driving the observed relationships between fitness gains and dispersal. For males, indirect fitness was lower for immigrants than for residents and among residents declined with increasing natal dispersal distance. We considered two possible explanations for these patterns: (1) that the probability of helping, and thus gaining indirect fitness, declines with dispersal and (2) that the average relatedness of males to broods to whom they provide alloparental care, which determines the amount of indirect fitness gained, declines with dispersal (note that these scenarios are not mutually exclusive). To investigate (1), we asked whether the probability of helping following brood loss differed between immigrants and residents (*n* = 179 and 154) and whether, among residents, the probability of helping following brood loss varied with natal dispersal distance (*n* = 132) using generalised linear models (GLMs) with a binomial error structure. Males were scored as having helped if they helped in at least one year of their lives, even if they suffered brood loss but did not help in another year. To control for the increased likelihood that older males would have helped in at least one year, lifespan was fitted as an additional fixed effect in both models. To investigate (2), we used mixed-effects models (SI Appendix, section 3) to test whether the mean relatedness of male helpers to recruits from the broods they helped differed between immigrants and residents (*n* = 37 and 44, respectively) and whether, among residents, relatedness of helpers to recruits varied with a helper's natal dispersal distance (*n* = 33).

Among resident females, our results revealed a significant positive association between natal dispersal distance and direct fitness. To investigate this further, we focused on broods that fledged successfully and tested for associations between maternal dispersal distance and (a) initial clutch size (n = 21 broods), (b) number of fledglings produced (n = 25 broods) and (c) proportion of fledglings successfully recruiting (n = 25 broods) using mixed-effects models (SI Appendix, section 3).

In all analyses, coefficients and standard errors for each predictor were taken from the full model, while test statistics (χ^2 values for GLM and GLMM and log-likelihood (L) ratios for LMM) and *P* values were calculated by comparing the full model to a second model without the predictor, having first removed any nonsignificant interaction terms. All analyses were two-tailed and effects were considered to be statistically significant if $P < 0.05$.

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Figure legends

Fig. 1. Mean ± SE (a) indirect fitness, (b) direct fitness, and (c) inclusive fitness accrued by female (dark grey) and male (light grey) long-tailed tits in relation to whether they were immigrants (IMM; *n* = 308 females and 211 males) or philopatric residents (RES; *n* = 77 females and 182 males) in the study population.

Fig. 2. Relationships between measures of fitness and natal dispersal distances for 75 female and 160 male long-tailed tits that recruited within our study site: (a) probability of gaining indirect fitness for males (β ± SE = -0.61 ± 0.25, χ^2_1 = 6.73, *P* = 0.009); (b) amount of indirect fitness for males (-0.97 ± 0.27, χ^2_1 = 14.60, *P* = 0.0001); (c) probability of gaining direct fitness for males (-0.02 ± 0.20, χ^2_1 = 0.01, *P* = 0.91); (d) amount of direct fitness for males (-0.15 ± 0.20, χ^2_1 = 0.57, *P* = 0.45); (e) probability of gaining direct fitness for females (0.32 ± 0.31, χ^2_1 = 1.06, *P* = 0.30); (f) amount of direct fitness for females (0.58 ± 0.27, χ^2_1 = 4.47, *P* = 0.03); (g) probability of gaining inclusive fitness for males (-0.32 ± 0.19, χ^2_1 = 2.94, *P* = 0.09); (h) amount of inclusive fitness for males (-0.25 ± 0.17, χ^2_1 = 2.28, *P* = 0.13); (i) probability of gaining inclusive fitness for females (0.43 ± 0.29, χ^2_1 = 2.20, *P* = 0.14); (j) amount of inclusive fitness for females (0.53 ± 0.27, χ^2_1 = 3.83, *P* = 0.05). In panels a, c, e, g and i, boxplots show dispersal distances for birds that do and do not gain fitness (central lines represent median values, outer lines of the box represent the first and third quartiles and horizontal lines represent approximately two standard deviations around the interquartile range (circles denote outliers). In panels b, d, f, h and j, dots show the raw data. In all cases, lines are predictions from generalized linear mixed-effects models (GLMMs) of fitness in relation to distance, averaging across cohort (see Methods and SI Appendix, section 3).

Fig. 3. Relationship between the mean relatedness of male helpers to the brood they cared for and their natal dispersal distance (*n* = 33). Points are raw data. Best-fit line and 95% Cis

are obtained from a linear mixed-effects model (LMM) of relatedness in relation to distance with male ID as a random factor (see Methods and SI Appendix, section 3).

Fig. 4. Relationship between the proportion of a female's fledglings that recruited into the study population and her natal dispersal distance (*n* = 25). Dots are raw data. Best-fit line and 95% CIs are obtained from a GLMM of recruitment success in relation to dispersal distance. For details of the model and full results, see SI Appendix, section 3 and Table S3.

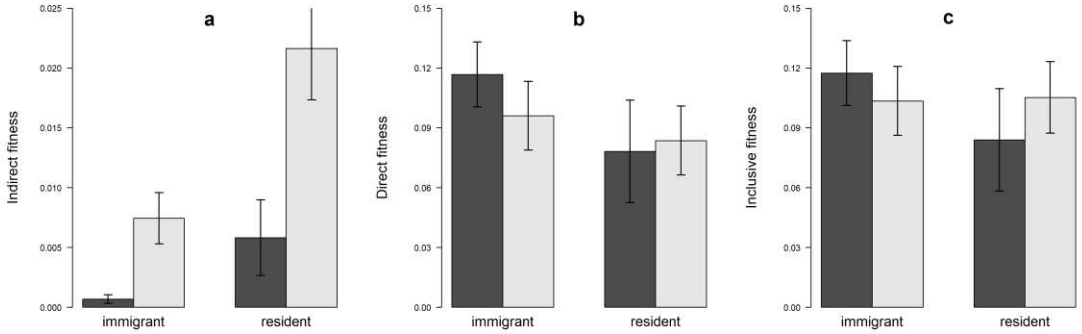
a
Indirect fitness
0.025
0.020
0.015
0.010
0.005
0.000
immigrant
resident
b
Direct fitness
0.15
0.12
0.09
0.06
0.03
0.00
immigrant
resident
c
Inclusive fitness
0.15
0.12
0.09
0.06
0.03
0.00
immigrant
resident

Figure 1

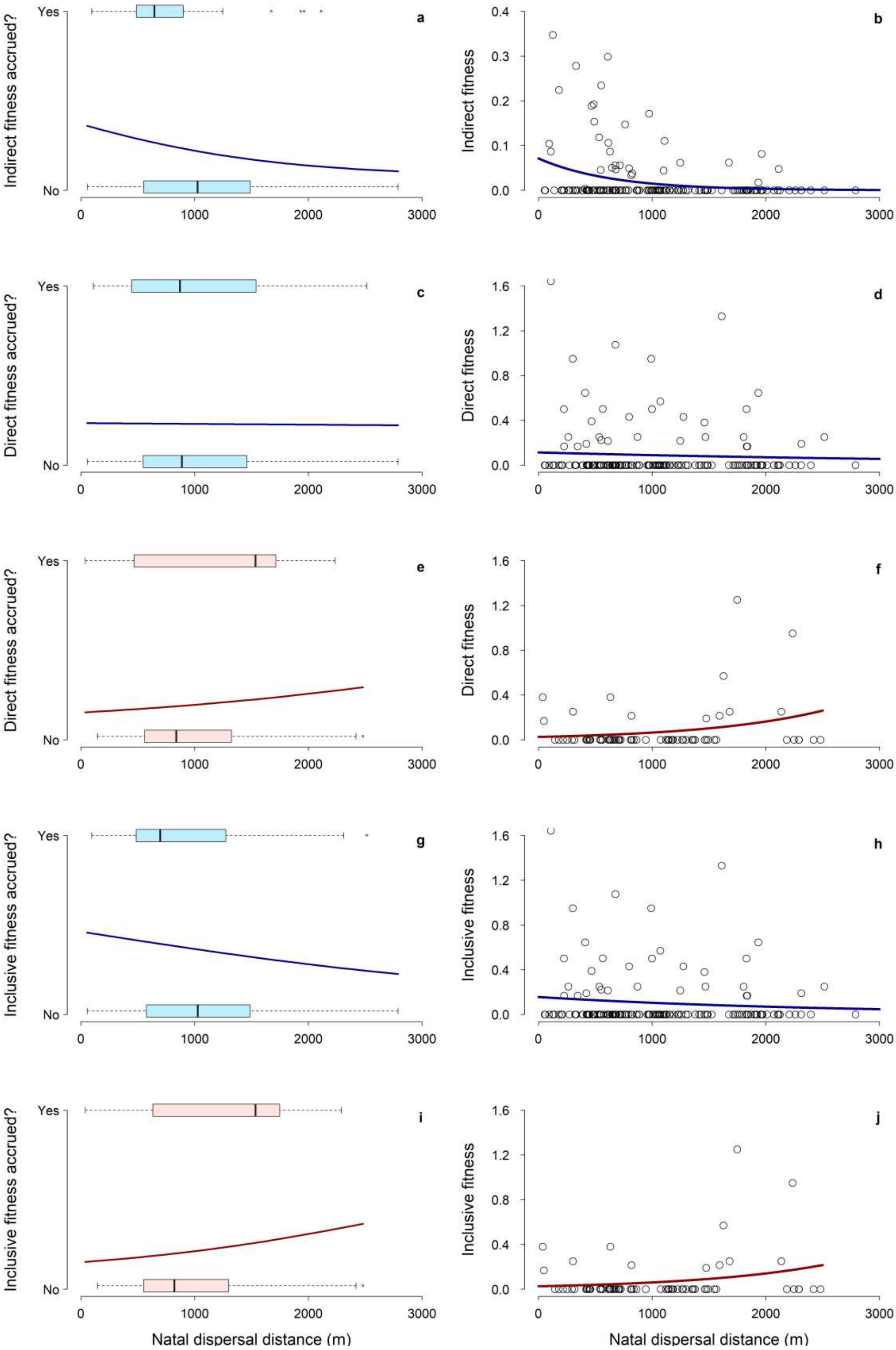
Indirect fitness accrued?
Yes
No
a
Indirect fitness
b
Direct fitness accrued?
c
Direct fitness
d
e
f
Inclusive fitness accrued?
g
Inclusive fitness
h
i
j
0.0
0.1
0.2
0.3
0.4
0.4
0.8
1.2
1.6
0
1000
2000
3000
Natal dispersal distance (m)
Natal dispersal distance (m)

Figure 2

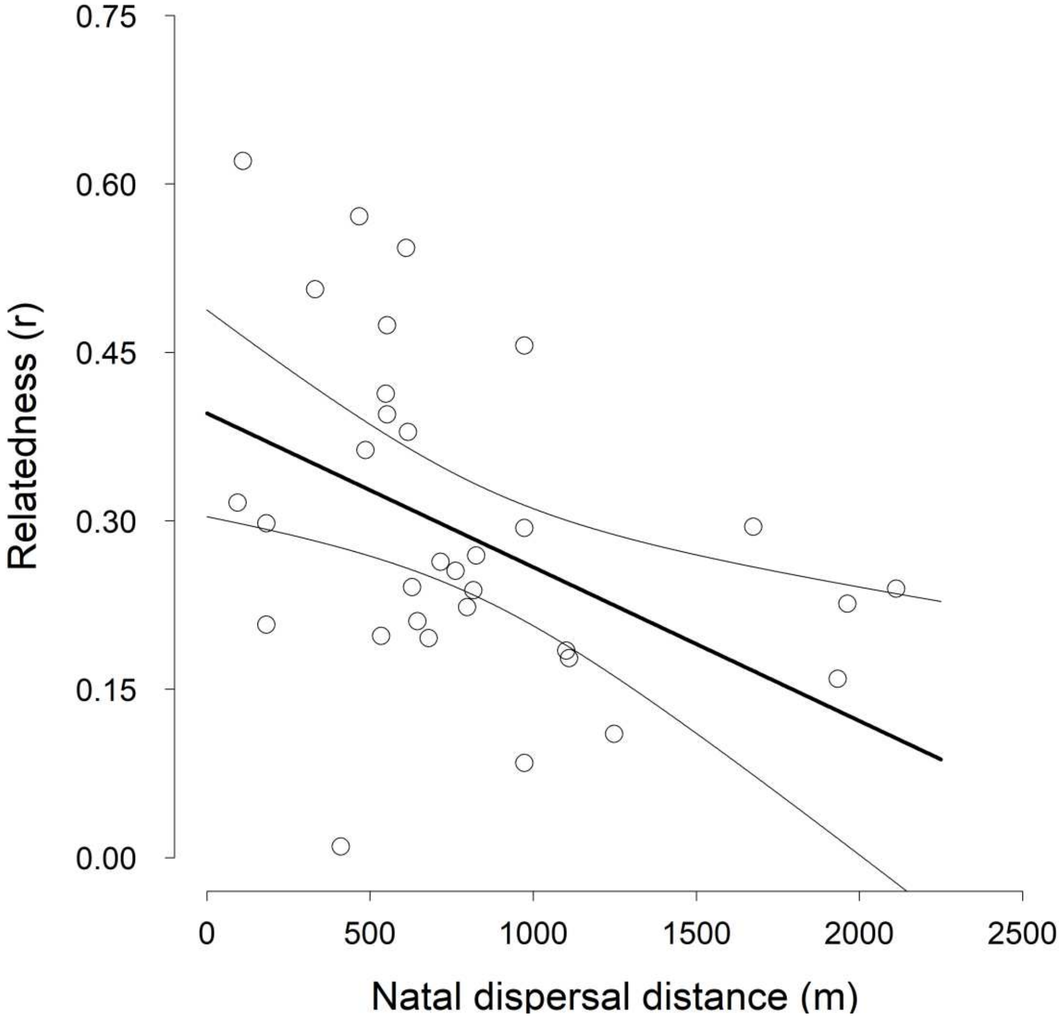
Relatedness (r)
0.75
0.60
0.45
0.30
0.15
0.00
0
500
1000
1500
2000
2500
Natal dispersal distance (m)

Figure 3

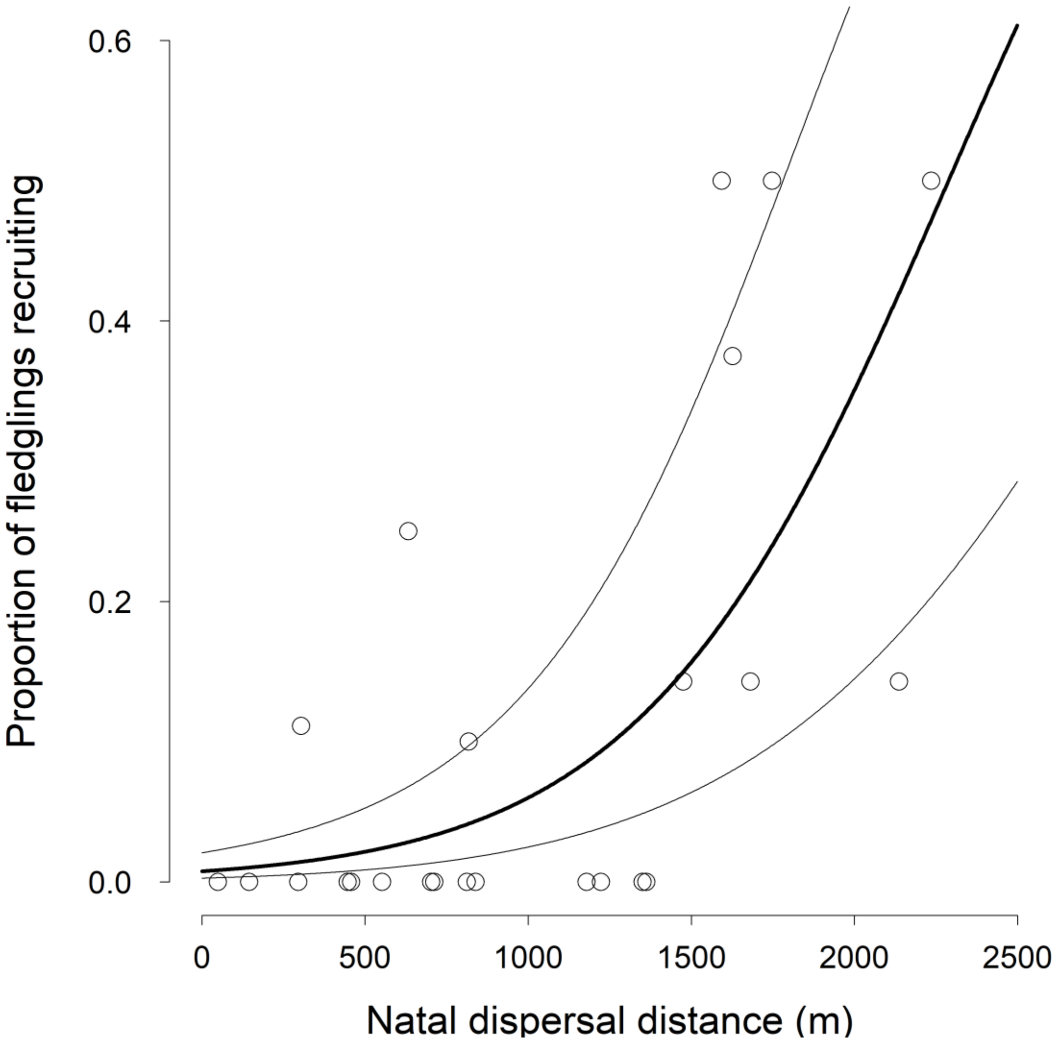
Proportion of fledglings recruiting
0.0
0.2
0.4
0.6
0
500
1000
1500
2000
2500
Natal dispersal distance (m)

Figure 4