

# Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird

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Kin selection is a major force in social evolution, but dispersal is often assumed to reduce its impact by diluting kinship. In most cooperatively breeding vertebrates, in which more than two individuals care for young, juveniles delay dispersal and become helpers in family groups. In long-tailed tits (*Aegithalos caudatus*), however, offspring disperse to breed and helpers are failed breeders that preferentially aid kin. Helping also occurs among immigrants, but their origins are unknown and cooperation in these cases is poorly understood. Here, we combine long-term demographic and genetic data from our study population to investigate immigration and helping in this species. We first used a novel application of parentage analysis to discriminate between immigrants and unknown philopatric recruits. We then cross-checked sibship reconstruction with pairwise relatedness estimates to show that immigrants disperse in sibling coalitions and helping among them is kin biased. These results indicate that dispersal need not preclude sociality, and dispersal of kin coalitions may help maintain kin-selected cooperation in the absence of delayed dispersal.

**Keywords:** *Aegithalos caudatus*; cooperative breeding; dispersal; immigration; kin selection; long-tailed tit

## 1. INTRODUCTION

Kin selection plays a key role in the evolution of social behaviour (Hamilton 1964; Maynard Smith 1964; Emlen 1997), although the generality of its importance has been the source of much debate (Cockburn 1998; Clutton-Brock 2002; Griffin & West 2003). One ubiquitous biological process that may reduce the potential influence of kin selection is dispersal, which is often assumed to inhibit sociality by diluting kinship (Emlen 1997; Perrin & Goudet 2001; Ross 2001; Gardner & West 2006). However, evidence suggests that in several social species, relatives may disperse together in coalitions (Packer & Pusey 1993; Heinsohn *et al.* 2000; Koenig *et al.* 2000; Williams & Rabenold 2005; Bradley *et al.* 2007), a process that must have a strong impact on population kin structure and therefore selection for social behaviour (Johnson & Gaines 1990; Ross 2001; Walters *et al.* 2004; Gardner & West 2006). Surprisingly, precise estimation of the prevalence of dispersal in kin coalitions and its consequences have rarely been investigated, and the relationship between dispersal, kinship and sociality remains poorly understood (Ekman *et al.* 2004; Walters *et al.* 2004).

Cooperative breeding systems, in which helpers assist breeders in caring for their offspring, are an excellent model for studying these processes (Stacey & Koenig 1990; Emlen 1997; Griffin & West 2003). In most cooperative vertebrates, offspring delay dispersal and become helpers in family groups; in many species, however, helping also occurs among dispersing individuals. For example, long-term

population studies of various cooperatively breeding birds have revealed that immigrants regularly become helpers (Stacey & Koenig 1990). Unfortunately, the origins of these individuals are usually unknown. Furthermore, the suggestion that cohorts of immigrants may comprise groups of relatives is confounded by the difficulty of distinguishing between true immigrants and philopatric recruits that for some reason are not marked.

Recently developed molecular procedures have provided powerful tools for studying dispersal and sociality beyond the well-documented limits of observational data (Koenig *et al.* 1996; Ross 2001; Blouin 2003). In this study, we combine these techniques with long-term demographic data in order to investigate helping among immigrants in cooperatively breeding long-tailed tits (*Aegithalos caudatus*). Unusually among cooperative birds, offspring in this species do not delay dispersal or breeding and all helpers are failed breeders, with help consisting almost exclusively of nestling provisioning (Hatchwell *et al.* 2004). Helpers use vocal cues to recognize and preferentially aid close relatives in the absence of spatial cues to kinship (Hatchwell *et al.* 2001a; Russell & Hatchwell 2001; Sharp *et al.* 2005), gaining indirect fitness benefits by increasing the productivity of helped broods (Hatchwell *et al.* 2004; MacColl & Hatchwell 2004); no significant direct fitness benefits of helping have been identified (McGowan *et al.* 2003; Hatchwell & Sharp 2006). Such strong evidence for the importance of kin selection in this system is potentially undermined by relatively high immigration rates (Russell 2001). On average, immigrants make up approximately 44% of our study population (S. P. Sharp & B. J. Hatchwell 2006, unpublished data), but the frequent occurrence of helping among these birds has hitherto remained

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unexplained. Here, we (i) use a novel application of parentage analysis to discriminate between immigrants and unknown philopatric recruits, (ii) use genetic data to determine the relatedness of confirmed immigrants, and (iii) analyse the pattern of helping among these birds in order to test the hypothesis that dispersal inhibits kin-selected cooperation.

## 2. MATERIAL AND METHODS

### (a) Study population

We studied a marked population of 17–72 pairs of long-tailed tits in the Rivelin Valley, Sheffield, UK (53°23' N 1°34' W) from 1994 to 2005. The breeding attempts of all individuals were closely monitored every year, and nestlings were given unique colour ring combinations. Any unringed birds present at the start of each breeding season were trapped using mist nets and also colour ringed. Previously, it was assumed that all such birds were immigrants (Hatchwell & Sharp 2006). However, 0–3 pairs with inaccessible nests are known to fledge unringed young each year, and successful nests in the study site on average fledge  $7.94 \pm 2.25$  (mean  $\pm$  s.d.) chicks; any philopatric recruits from inaccessible nests will thus have been mistakenly classified and this would clearly bias any analysis of relatedness among birds assumed to be immigrants. Therefore, in this study, we initially classified all of these individuals as putative immigrants only.

Blood samples were taken from all nestlings and putative immigrants caught (under Home Office licence), and through this samples were available for  $80.3 \pm 10.3\%$  of individuals in the breeding population each year, including  $74.1 \pm 9.0\%$  of putative immigrants. In order to detect and identify helpers, all nests were observed for a minimum of 30 min but usually 1 h on alternate days of the nestling period from hatching until fledging or failure of the breeding attempt. For more details of the study system and general methods, see Hatchwell *et al.* (2004) and Hatchwell & Sharp (2006).

### (b) Genetic analysis

Genomic DNA was extracted from blood and amplified as previously described (Simeoni *et al.* 2007). All sampled individuals were sexed using standard techniques (Griffiths *et al.* 1998) and genotyped at nine microsatellite loci. The following loci were selected from a recently characterized set of 20 (Simeoni *et al.* 2007) according to their degree of polymorphism and avoiding deviations from Hardy–Weinberg equilibrium, null alleles, linkage disequilibrium and sex linkage: Ase18; Ase37; Ase64; Hru2; Hru6; LOX1; Pca3; Pma22 and Ppi2. Wherever appropriate, the long-term pedigree established for our study population was used to guide the application of molecular procedures and the interpretation of results as described below; integrating pedigree and genetic data in this way provides one of the most powerful methods of investigating evolutionary processes in wild populations (Kruuk & Hill 2008; Pemberton 2008).

### (c) Parentage analysis

We used the new likelihood approach in CERVUS v. 3.0 (Kalinowski *et al.* 2007) to determine whether parentage assignments could be made for any genotyped putative immigrants that appeared in the population from 1997 to 2005; analysis was done on a year by year basis, and 1994–1996 were excluded due to inadequate sampling and pedigree data early in the project. Allele frequencies were

generated using all genotyped individuals from all years to maximize accuracy in estimating the frequency of rare alleles and to ensure a non-zero frequency for all alleles in the dataset. For each year, CERVUS was run with the following simulation parameters: 100 000 offspring, the true number and sampled proportion of candidate parents (see below), 0.92 of loci typed (calculated from the allele frequency data), 5 as the minimum number of typed loci and a mistyping rate of 0.01. The latter value is conservative, as previous analyses have shown that the true error rate is less than 1% (M. Simeoni, S. P. Sharp & B. J. Hatchwell 2007, unpublished data). We classed putative immigrants as ‘offspring’ and all breeders from the population in the previous year as ‘candidate parents’; at one or two nests per year neither parent was sampled, but none of these nests were known to produce fledglings. We then carried out parent pair analysis with known sexes (but no prior information about how parents were paired) using critical LOD scores for 99% confidence derived from the simulations. The critical LOD scores for assigning a mother alone, father alone and parent pair averaged across years were  $3.91 \pm 0.53$ ,  $2.99 \pm 0.82$  and  $11.39 \pm 0.93$ , respectively.

### (d) Sibship reconstruction

Long-tailed tits disperse in their first year and rarely thereafter (McGowan *et al.* 2003), so all immigrants in a given year are likely to be from the same generation. Furthermore, extra-pair paternity is rare in this species (Hatchwell *et al.* 2002), so half-siblings are unlikely to occur. In order to determine whether cohorts of confirmed immigrants contained groups of close relatives, we therefore tested for the presence of full siblings among the confirmed immigrants in each year using sibship reconstruction algorithms. Various methods are available, but few have been adequately tested or applied to field data (Blouin 2003; Butler *et al.* 2004; Berger-Wolf *et al.* 2007). We applied two of the most widely used procedures, the ‘Descending Ratio’ algorithm implemented in KINGROUP v. 2 (Konovalov *et al.* 2004) and Wang’s (2004) algorithm in COLONY v. 1.2. We first tested and compared the two methods by applying each to our established pedigree and trying to assign philopatric recruits to their correct sibling groups (i.e. natal nests); the methods were then used to identify sibships among the confirmed immigrants. The allele frequencies calculated for the parentage analysis were used for sibship reconstruction of both philopatric recruits and confirmed immigrants. In both KINGROUP and COLONY, a primary hypothesis of full siblings was tested against a null hypothesis of unrelated pairs; separate analyses were carried out for each year from 1997 to 2005. In COLONY, we incorporated a genotyping error rate of 0.01 for each locus; this is conservative as discussed previously.

Having identified sibships among each cohort of confirmed immigrants, we compared the results with those derived from pairwise relatedness estimates calculated for each possible pair of immigrants; cross-checking like this is often recommended and has recently been successfully applied elsewhere (Blouin 2003; Langmore *et al.* 2007). The performance of different pairwise relatedness measures varies (Blouin 2003; Csillery *et al.* 2006), but we used KINGROUP to test for full-sibling relationships using likelihood ratio tests based on Queller and Goodnight’s *r* (Queller & Goodnight 1989; Goodnight & Queller 1999; Konovalov *et al.* 2004), which was found to be reliable when tested using our pedigree (M. Simeoni, S. P. Sharp & B. J. Hatchwell 2007, unpublished data). The

primary and null hypotheses from the sibship reconstruction were again used and 10 000 simulations were carried out. The results from the sibship reconstruction were considered to match those from likelihood ratio tests if individuals in a dyad with a significant likelihood ratio ( $p < 0.05$ ) were placed in the same sibling group or if those in a dyad with a non-significant likelihood ratio were placed in different groups.

#### (e) Analysis of helping

In the Rivelin Valley, failed breeders usually re-nest early in the season but later on will either abandon independent breeding until the following year or become helpers; this switch from re-nesting to helping occurs at the beginning of May (MacColl & Hatchwell 2002), with very few nesting attempts started after 30 April. It was therefore possible to identify pairs of individuals between which helping could potentially have occurred. From the confirmed immigrant siblings for which complete nesting histories were available, we identified those dyads in which one individual failed on or after 30 April and the other had a nest with chicks at or later than this time. We then examined all cases of helping and calculated the proportion of immigrants with the opportunity to help a sibling that did so. Similarly, for those individuals that dispersed into the population alone and for which complete histories were available, we identified individuals that failed on or after 30 April; these birds had no known sibling in the population and thus no opportunity to help close kin. We therefore calculated the proportion that became helpers and the number of these that helped a relative ( $r \geq 0.25$ ) according to Queller & Goodnight's (1989)  $r$ .

### 3. RESULTS

#### (a) Parentage analysis

Of 244 putative immigrants over 9 years ( $27.11 \pm 9.56$  per year), we found parental matches from the previous year's breeding population for 41 (16.8%;  $4.56 \pm 3.84$  per year). Of these, 16 (39.0%) cases were easily explained because the individuals were assigned to parents with inaccessible nests that were known to fledge unringed chicks, either to both members of the pair (eight cases) or to one parent with an unknown or unsampled partner (eight cases), thus providing independent evidence that our application of parentage analysis was successful. In the remaining 25 (61.0%) cases, individuals were assigned to parents whose nests in the previous year either failed or fledged ringed young; these individuals may have been born to their assigned parents in a previous year, either at an unknown nest or a nest just outside the study site boundary, or they may have been assigned to relatives of their true parents (Marshall *et al.* 1998). However, in order to be conservative all 41 individuals were excluded from any further analyses. This left 203 confirmed immigrants ( $22.56 \pm 8.50$  per year), 127 (62.6%) of which were female; this is a significant bias (Binomial test with normal approximation:  $Z = 3.58$ ,  $p < 0.001$ ).

#### (b) Sibship reconstruction

When applied to our pedigree of philopatric recruits, KINGROUP and COLONY produced identical results except for one individual that was known to be an extra-pair offspring (M. Simeoni, S. P. Sharp & B. J. Hatchwell 2007, unpublished data); KINGROUP assigned this bird to its paternal half siblings and COLONY to its maternal half

siblings. Each programme assigned 140/148 (94.6%) individuals to the correct sibling group, indicating that both methods could be reliably applied to the confirmed immigrants alongside likelihood ratio tests for each possible pair ( $n = 2477$  dyads). The results of these tests matched the output of KINGROUP marginally more closely than that of COLONY (matched results for 2353 dyads (95.0%) versus 2339 (94.4%), respectively); the results from KINGROUP were thus used for subsequent analyses and are presented here.

A significant proportion of immigrants in any given year belonged to groups of full siblings, with 107/203 (52.7%) belonging to sibships of between two and seven individuals (mean group size  $2.89 \pm 1.13$  siblings; figure 1). Out of 37, 28 (75.7%) of the sibling groups identified were sex biased (19 female biased, 9 male biased), with 18 (48.7%) consisting entirely of one sex (14 females, 4 males). To test the significance of these sex biases, we first calculated the absolute deviation of the sex ratio from 0.5 for each sibling group, and then tested these values against a null value of zero. Across all groups, sex ratio deviations from 0.5 were highly significant (Wilcoxon signed-rank test:  $n = 37$ ,  $W = 406.0$ ,  $p < 0.001$ ); groups containing an odd number of siblings cannot have a sex ratio of 0.5, but the result still held when all such groups were excluded from the analysis (Wilcoxon signed-rank test:  $n = 22$ ,  $W = 91.0$ ,  $p = 0.002$ ).

#### (c) Analysis of helping

Across all of the kin groups identified, there were 90 sibling dyads and complete nesting histories were available for both individuals in 54 (60.0%) of them. Of the failed breeders that had the opportunity to help at least one sibling ( $n = 22$ ), seven (31.8%) did help a sibling; only two (9.1%) helped other birds and the rest did not become helpers (figure 2). Pedigree and genetic data were unavailable for those helped birds that were not siblings, but they may have been related in some other way; importantly, no individual helped a known non-relative. Complete histories were available for 70/96 (72.9%) of those individuals that did not disperse in sibling groups. Of the failed breeders ( $n = 34$ ), only four (11.8%) became helpers and in no case where genetic data were available (5/8 possible dyads) did one of these helpers aid a relative.

### 4. DISCUSSION

To our knowledge, this is the first time parentage analysis has been used to discriminate between true immigrants and unknown philopatric recruits. The results strongly suggest that this procedure was successful and may be a useful technique for other study populations with incomplete sampling. The significant predominance of females among the confirmed immigrants supports previous findings that dispersal is female biased in long-tailed tits (Russell 2001; Sharp *et al.* 2008), just as it is in the majority of bird species (Greenwood 1980; Clarke *et al.* 1997). Sex-biased dispersal is widely thought to have evolved at least in part as an inbreeding avoidance mechanism, especially in kin-structured populations such as those of social species (Pusey 1987; Perrin & Goudet 2001). The causes and consequences of female-biased dispersal in long-tailed tits are discussed in greater detail elsewhere (Russell 2001; Sharp *et al.* 2008).



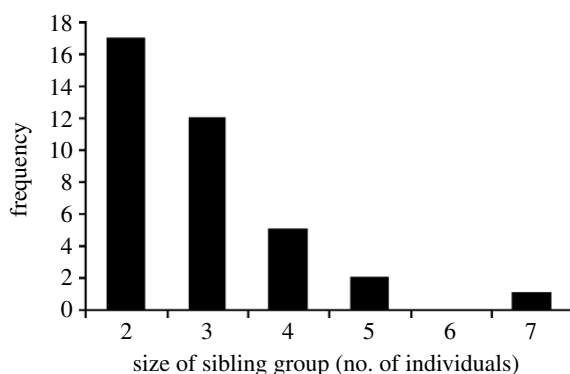


Figure 1. The size of all sibling groups identified among confirmed immigrants using KINGROUP.

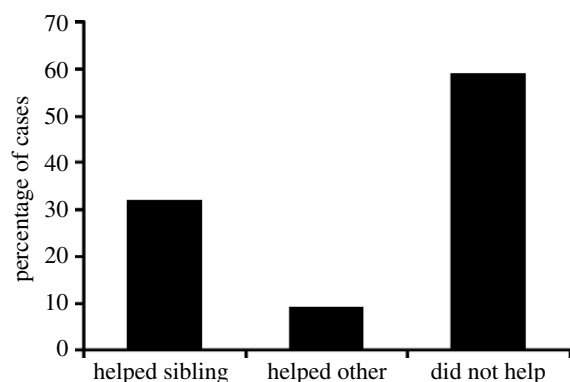


Figure 2. The outcome of all cases where an immigrant failed breeder had the opportunity to help a sibling.

The results of the sibship reconstruction show that groups of immigrant siblings enter the population together. A previous study of the same population showed that philopatric siblings tend to disperse similar distances and in similar directions, even after controlling for study site boundary effects (Sharp *et al.* 2008). The prolonged period of post-fledging association in this species is conducive to siblings remaining together during dispersal (Gaston 1973; Hatchwell *et al.* 2001b), but the appearance of sibling immigrants in a population may result at least in part from the predominance of short-distance natal dispersal movements. However, much of the habitat on the edge of the study site is unsuitable for breeding long-tailed tits (Hatchwell *et al.* 2001b), and many of the individuals that do breed just outside the site have been genotyped, so their offspring would probably have been excluded from our analyses after assigning parentage. The results therefore provide strong evidence that immigrant long-tailed tits often disperse in sibling coalitions.

Dispersal coalitions have been reported in other social species; the majority are mammals and in particular primates and social carnivores (Packer & Pusey 1993; Lambin *et al.* 2001; Bradley *et al.* 2007), but there are several examples in cooperatively breeding birds (Heinsohn *et al.* 2000; Koenig *et al.* 2000; Williams & Rabenold 2005). In the majority of species, these coalitions are composed of a single sex only; in this study, however, coalitions were found to be sex biased but some were female biased and some male biased. Thus, despite the overall female bias in dispersal reported here and elsewhere, males still disperse in sufficient numbers such that brothers may do so in groups. Dispersal in sex-biased sibling coalitions may minimize the risk of

inbreeding in kin-structured populations while maintaining a high degree of relatedness among members of each sex (Pusey 1987; Lambin *et al.* 2001; Perrin & Goudet 2001). This impact on population kin structure potentially facilitates the evolution and maintenance of social behaviour (Johnson & Gaines 1990; Ross 2001; Walters *et al.* 2004), and the results from this and other studies together suggest that dispersal patterns in long-tailed tits are indeed reflected by the pattern of helping in this species (Russell 2001; Sharp *et al.* 2008).

If the dispersal of sibling coalitions promotes kin-biased cooperation, helping should at least sometimes occur among immigrant siblings, which we have shown to be the case here. In fact, the pattern of helping among confirmed immigrants is comparable with that of philopatric recruits: most helping occurs between siblings, but more than half of all failed breeders, including many that have the opportunity to help a relative, do not become helpers; this is perhaps because they never encounter their close kin (Hatchwell *et al.* 2001a; Russell & Hatchwell 2001; Hatchwell *et al.* 2004). Helping also occurs occasionally among non-kin, which is thought to result from kin recognition errors (Hatchwell *et al.* 2001a; Sharp *et al.* 2005). Regardless, kin-directed helping occurs among members of immigrant sibling groups, thereby enabling these dispersers to gain indirect fitness through kin selection when their own reproductive attempts fail, just as philopatric recruits do (MacColl & Hatchwell 2004).

In conclusion, the dispersal of immigrants in sibling coalitions provides the opportunity for kin-biased helping in the absence of delayed dispersal. These results offer some of the first empirical support for theoretical evidence that dispersal in kin coalitions can play a key role in the evolution of cooperative behaviour (Gardner & West 2006). There is probably strong selection pressure maintaining this dispersal pattern in long-tailed tits, because for many individuals helping provides the sole source of fitness (MacColl & Hatchwell 2004). It is possible that there is a heritable component to dispersal behaviour as has been suggested in other species (Hansson *et al.* 2003; Pasinelli *et al.* 2004), but this has not yet been explored. The results presented here demonstrate the value of integrating molecular data, pedigrees and field observations for understanding the relationship between dispersal, kinship and sociality. Future studies of this kind may reveal that kin associations and kin-biased social behaviour are more common among dispersing individuals than is generally recognized.

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