

Natal dispersal and parental escorting predict relatedness between mates in a passerine bird

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Abstract

Although relatedness between mates is of considerable evolutionary and ecological significance, the way in which the level of relatedness is determined by different behavioural processes remains largely unknown. We investigated the role of behaviour in predicting mate relatedness in great tits using genotypic markers and detailed observations. We studied how mate relatedness is influenced by natal dispersal, inbreeding/outbreeding avoidance after natal dispersal and a behaviour not previously considered that influences membership to social aggregations, namely family escorting behaviour by parents. Among locally born individuals, the level of mate relatedness decreased with natal dispersal distance for females, but not for males. In contrast, mate relatedness was negatively related to the extent of family movements for males, but not for females. However, family movements did not predict dispersal distance for either sex. Local recruits were more related to their mates than immigrants, but this was only significant for females. No evidence was found for inbreeding/outbreeding avoidance after dispersal. Our results suggest that, in highly mobile species, mating options are spatially and/or socially limited, and that parents influence mating options of their offspring before dispersal.

Keywords: dispersal, inbreeding, mate choice, mate relatedness, microsatellite, *Parus major*

Received 17 October 2005; revision received 27 January 2006; accepted 17 February 2006

Introduction

In natural populations, the level of mate relatedness, i.e. relatedness between breeding mates, has important consequences for fitness due to inbreeding or outbreeding depression, and also for the maintenance of genetic variation, because it reflects the degree of nonrandom mating (Lynch 1991; Sugg *et al.* 1996; Keller & Waller 2002). Revealing the factors that cause different individuals to obtain mates with different relatedness is therefore an important issue for understanding evolution in, and conservation of, natural populations. Traditionally, two behaviours have been hypothesized to affect mate relatedness. Firstly, natal dispersal, the movement from the birth site to the first breeding site, is thought to determine mating options, i.e. the set of potential mates among which individuals choose a mate (Pusey & Wolf 1996; Wiley & Poston 1996; Keller & Arcese 1998). Second, active mate choice should allow individuals to avoid/prefer mating

with relatives among potential mates (Pusey & Wolf 1996; Wiley & Poston 1996; Keller & Arcese 1998). So far, the relative importance of these behaviours for shaping patterns of mate relatedness in natural populations remains unclear, for both methodological and conceptual reasons (Pärt 1996; Clobert *et al.* 2001).

Information about pairwise (i.e. among two individuals) relatedness values cannot easily be obtained, and some pairwise relatedness estimation methods are prone to systematic errors. For example, pedigree reconstructions based on observations of social parents yield underestimated pairwise relatedness estimates in descendants due to the presence of extra-pair parentage and immigration (Peacock & Ray 2001; Van de Castele *et al.* 2001). For other estimation methods, estimation bias may depend upon the true pairwise relatedness value (e.g. bandsharing coefficient, Lynch 1988). Applying these methods entails the risk that consequences of inbreeding/outbreeding avoidance and natal dispersal for mate relatedness are over- or underestimated. Even if unbiased pairwise relatedness estimates are available, natal dispersal is often studied at a spatial scale that is insufficiently large to span the spatial

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genetic structure of a population (Waser & Elliott 1991; Peacock & Ray 2001). This reduces the detectability of effects of natal dispersal on mate relatedness.

Apart from the aforementioned methodological problems, the hypothesis that dispersal affects mate relatedness rests implicitly on a number of assumptions about the behaviour of individuals in natural populations. First, the relative timing of mating and dispersal will determine to what extent mate relatedness is affected by the relatedness pattern near the birth area, as opposed to relatedness with conspecifics further away. Second, the extent to which conspecifics disperse nonindependently, either in a social context (e.g. in flocks) or in a purely spatial sense (e.g. common dispersal direction, Matthysen *et al.* 2005), will reduce the impact of dispersal on mate relatedness. Third, as the number of potential mates available after natal dispersal increases, the effect of dispersal on mate relatedness diminishes compared to the effects of other factors such as inbreeding/outbreeding avoidance after settlement. Typically, the existence of these socio-spatial constraints on patterns of mate relatedness has been ignored in studies of dispersal and mate choice. For example, studies testing inbreeding/outbreeding avoidance of relatives have made the assumption that mating options are unlimited or are restricted to individuals breeding in close proximity, and that they are determined after natal dispersal (Pärt 1996; Keller & Arcese 1998). This oversimplifies the complexity of many animal social systems where individuals participate in social aggregations that may limit their mating options (Sugg *et al.* 1996; Wiley & Poston 1996), and individuals may not disperse independently from and to such aggregations (Massot & Clobert 2000; Matthysen *et al.* 2005). Although it has been recognized that spatial behaviours other than natal dispersal could affect mate relatedness or mating patterns (Pusey & Wolf 1996; Wiley & Poston 1996), we know of no study that has investigated the role of behaviours either before or at the onset of natal dispersal in shaping patterns of mate relatedness.

The great tit, *Parus major* L., is a small (20 g), nonmigratory passerine bird with female-biased natal dispersal (Greenwood *et al.* 1979; Matthysen *et al.* 2001), which is typical of most bird species (Clarke & Saether 1997). The breeding system is territorial and socially monogamous, with the occurrence of extra-pair young. As in many bird species (Silver *et al.* 1985), parents feed and escort fledglings in stable family groups until they attain independence (up to 4 weeks after fledging, Cramp & Perrins 1985). Parents induce family movements using 'duple' calls (Cramp & Perrins 1985 and personal observation), suggesting that they control offspring movements before independence. After independence several families of juveniles merge to form summer flocks, and after a short peak of territorial behaviour by a percentage of the males in autumn, individuals participate in winter flocks that break up in spring

when breeding territories are established (Cramp & Perrins 1985 and personal observation; Drent 1983). The timing of pair formation is not well known but pairs are observed from January onwards suggesting that they are formed before the break-up of winter flocks.

Family movements are known to influence membership to summer flocks and the choice of the wintering area (Drent 1984; Cramp & Perrins 1985), which in turn has an influence on mating patterns (Dhondt *et al.* 1996). The natal dispersal phase lasts at least until autumn (Dingemanse *et al.* 2003 and personal observation). Although family movements predict the spatial distribution of individuals until winter (Drent 1984) their consequences for natal dispersal to the next breeding season have not been studied explicitly. We hypothesize that family movements may affect relatedness of offspring with their future mates in two possible ways. First, family movements could induce natal dispersal and thereby influence future mating options. Second, family movements could affect mate relatedness independently of natal dispersal by determining membership to social aggregations before the end of the dispersal phase.

We studied the consequences of natal dispersal, family movements and inbreeding/outbreeding avoidance after settlement, for the level of mate relatedness in a patchy population of great tits with a high degree of local recruitment (Matthysen *et al.* 2001). Pairwise relatedness was estimated using microsatellite markers that have been shown to give unbiased estimates of relatedness estimates (Van de Castele *et al.* 2001; Hansson 2004), although it has to be noted that molecular methods offer lower precision than pedigree data (Pemberton 2004). In this population, relatedness with the social mate predicts seasonal reproductive success (hatching rate, nestling survival and number of fledglings), but not lifetime reproductive success (lifetime number of fledglings and lifetime number of recruits) (Van de Castele *et al.* 2003). Natal dispersal was measured both at a small spatial scale within the study area, and at a larger spatial scale by comparing local recruits with immigrants, and is female-biased using either definition (Matthysen *et al.* 2001, unpublished). In this study we present evidence for the existence of a fine-scale genetic structure in the breeding population, and we show that both family movements and natal dispersal distances are correlated with relatedness with the future mate. We also show that there is no evidence for inbreeding/outbreeding avoidance after settlement.

Materials and methods

We studied great tits in a study area of approximately 4 × 3 km in northern Belgium ('Boshoeke': 51°08'N, 4°32'E). It consists of 13 deciduous (mainly mature oak, *Quercus robur*) woodlots ranging in size between 1 and 12 ha.

Woodlots are separated by 100–600 m in a landscape matrix of farmland, hedgerows, poplar (*Populus* sp.) stands and residential areas. Nest boxes (entrance diameter 32 mm) have been available in all woodlots at a constant density of about six per hectare since 1994. Breeding parameters have been recorded each year during weekly visits to all nest boxes (Van de Castelee *et al.* 2003). Parents were captured while feeding their 8-day-old young and labelled with uniquely numbered metal rings as well as coloured rings. Fifteen-day-old nestlings were labelled with a uniquely numbered metal ring and a brood-specific combination of coloured rings. Fledged broods accompanied by parents were traced upon hearing begging and/or 'duple' calls (Cramp & Perrins 1985) during at least weekly visits to five centrally located woodlots and the surrounding matrix, from 1996 to 1998. Parents and offspring were identified by reading their coloured rings with a telescope, and their locations were determined to the nearest 10 m by relating observations to aerial photographs and maps. Natal dispersal was defined as the distance in metres from the birth nest box to the breeding nest box the next year, and as a categorical variable indicating if an individual was ringed as a nestling in the study area ('local') or was captured as an unringed recruit ('immigrant'). The proportion of local recruits among first-year breeders was approximately 50% for males and 40% for females (Matthysen *et al.* 2001). It was assumed that the immigrant group consisted mostly of individuals that must have dispersed over a longer distance than locals, because (i) the breeding density in the matrix between woodlots is very low, and each year nestlings were systematically ringed in the few nest-boxes provided by the public; (ii) the density of birds breeding in natural cavities in the entire study area is very low (< 10% of all fledged broods, Matthysen *et al.* 2001); and (iii) only data for immigrants into the five centrally located woodlots are used.

Family movements were measured as the straight-line distance in metres between the location where a family was observed and the birth nest box. The median of all family movements was used for further analyses rather than the average because it is less sensitive to rare extreme observations. A total of 191 families were observed (number of observations per family: median = 6, range = 1–31).

In 1996 and 1997, breeding parents were blood-sampled and genotyped for nine microsatellite markers (Van de Castelee *et al.* 2001). Pairwise relatedness values were estimated from microsatellite genotypes using a weighted similarity index (Van de Castelee *et al.* 2001). This method is based on a measure of the similarity of alleles that two individuals carry. It yields unbiased pairwise relatedness estimates by correcting observed similarities for the fact that even under random mating some similarity is due to the limited number of alleles present in the population. For an individual pair, pairwise relatedness estimates may

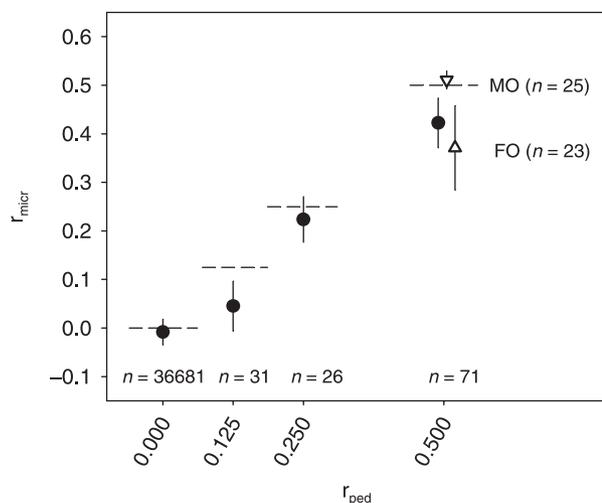


Fig. 1 Plot of microsatellite-based pairwise relatedness estimates (r_{micr}) against pairwise relatedness estimates obtained from pedigree reconstruction (r_{ped}). Sample means (black symbols), sample variances (error bars) and sample sizes for r_{micr} are shown for r_{ped} values equal to 0 (unrelated), 0.125 (first cousins, great-grandparent–great-grandchild), 0.25 (half-sibs, uncle/aunt–niece/nephew, grandparent–grandchild) and 0.5 (full-sibs and parent–offspring). For the latter category, separate sample means and variances are shown (white symbols) for mother–offspring (MO) and for father–offspring (FO) pairs. Dashed lines indicate the expected values of r_{micr} assuming the according r_{ped} value is correct. For $r_{ped} = 0$ the sample consists of all possible male–male, female–male and female–female pairs that could be constructed within one breeding season (1996 or 1997).

show values out of the range of theoretically possible pairwise relatedness values (by definition between 0 and 1). This occurs, for instance, when individuals either do not share very common allele(s), leading to negative estimates, or when they share very rare alleles, leading to estimates larger than 1 (Queller & Goodnight 1989). Because genotype frequencies deviated significantly from Hardy–Weinberg equilibrium for one locus (Ppi2, Van de Castelee *et al.* 2001), pairwise relatedness estimates were calculated from eight loci only (Gf4, Gf6, Mcy4, Pat43, Pk12, Pdo5, Pocc6 and Pocc8). A comparison of microsatellite-based pairwise relatedness estimates (r_{micr}), with relatedness values obtained from reconstruction of pedigrees up to the great-grandparent generation (r_{ped}), revealed lower values for the former (Fig. 1, Table 1). However, considering parent–offspring pairs, a significant difference between r_{micr} and r_{ped} was found for father–offspring but not for mother–offspring pairs (Table 1). This suggests that r_{ped} estimates are biased upward due to the occurrence of extra-pair paternity, and confirms patterns of extra-pair parentage in several other great tit populations (see References in Van de Castelee *et al.* 2003). The average of r_{micr} estimates for 'unrelated' pairs is very close to the expected value of zero (r_{micr} values

Table 1 Comparison of pedigree and microsatellite estimates of pairwise relatedness. r_{ped} : pedigree estimate. $r_{\text{micr}} - r_{\text{ped}}$: absolute difference between microsatellite and pedigree estimate \pm SE per r_{ped} category. For a given r_{ped} category, pairs include all combinations of same- or opposite-sex individuals for which r_{micr} estimates were available. FO, father–offspring pairs; MO, mother–offspring pairs

r_{ped}	$r_{\text{micr}} - r_{\text{ped}}$	N	P
0.0	-0.008 ± 0.001	36 681	< 0.0001
0.125	-0.080 ± 0.041	31	$= 0.06$
0.25	-0.027 ± 0.042	26	$= 0.54$
0.5	-0.078 ± 0.027	71	< 0.005
FO	-0.129 ± 0.061	23	< 0.05
MO	0.011 ± 0.027	25	$= 0.69$

for $r_{\text{ped}} = 0$ in Fig. 1, Table 1). It should be noted that the significance levels reported in Table 1 are only indicative because some individuals contribute to several pairwise relatedness estimates, thereby inducing pseudoreplication. This is particularly the case for the group of ‘unrelated’ pairs. The fact that for this group r_{micr} estimates do not appear to show a deviation from the expected values makes sense; for an unrelated pair in a population with a large fraction of unrelated individuals, extra-pair matings occurring in the pedigree will tend to have similar (and low) relatedness values as within-pair matings. We conclude that, in this study, the weighted similarity index is a more consistent estimator of true pairwise relatedness than the pedigree-based estimator, and therefore we have used only the former. Relatedness estimates for all possible pairs of individuals ranged from -0.59 to 0.91 .

When testing relationships between pairwise relatedness and metric distances, distances were transformed as $\log(x + 0.5)$. This was done because under isolation by distance in a two-dimensional space, relatedness is expected to decrease approximately linearly with the logarithm of spatial distance (Rousset 1997).

Statistical analyses were conducted with the SAS software, version 8.01. Analyses were conducted using general linear mixed models. Pseudoreplication within families was modelled by adding the nest of origin as a random factor. For F -tests, denominator degrees of freedom were determined from Satterthwaite’s formula (Littell *et al.* 1996).

Results

Family movements and natal dispersal distances

Median family movements covered distances similar to natal dispersal distances within the study area (Fig. 2). Several families did not respect territory boundaries and

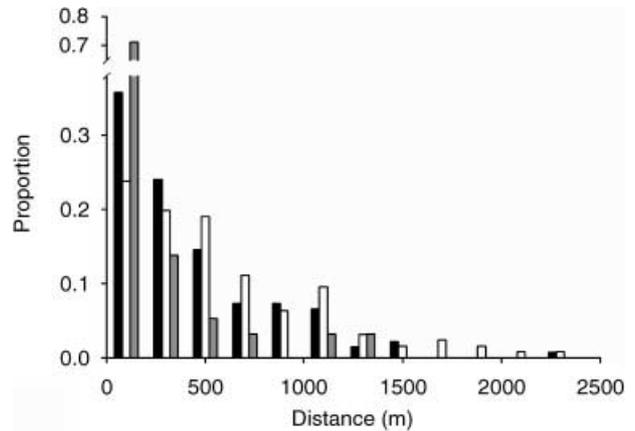


Fig. 2 Frequency distribution of natal dispersal distances and family movements. Black bars: natal dispersal distances (in metres) of males ($n = 137$, mean \pm SEM = 445.1 ± 34.2); white bars: natal dispersal distances (in metres) of females ($n = 126$, mean \pm SEM = 588.7 ± 43.1); grey bars: median family movements (in metres) per family ($n = 86$, mean \pm SEM = 247.0 ± 33.0). Data from years 1996–1998.

crossed stretches of unsuitable habitat up to 700 m wide (personal observation). Natal dispersal distances were larger for females than for males ($F_{1,254} = 7.91$, $P < 0.006$, Fig. 2). Recruits (i.e. nestlings captured as breeding birds) that had been observed with families ($n = 122$) and recruits that had not ($n = 141$) did not differ in dispersal distance ($F_{1,153} = 0.89$, $P = 0.35$). Recruits that had been observed with families ($n = 29$) and recruits that had not ($n = 17$) did not differ in mate relatedness ($F_{1,43} = 0.39$, $P = 0.54$, correcting for sex). This implies that there was no observation bias with respect to future natal dispersal and future mate relatedness.

Family movements were not correlated with offspring natal dispersal ($F_{1,82.3} = 0.24$, $P = 0.63$, correcting for sex), and this did not depend on the sex considered (Interaction Family Movement \times Sex: $F_{1,108} = 0.18$, $P = 0.67$).

Fine-scale genetic structure

We found evidence for fine-scale genetic structure because pairwise relatedness decreased significantly with the log-transformed distance between breeding locations of all pairwise combinations of same-sex individuals for males (Mantel’s test, Manly 1991: 1996: $r = -0.057$, $n = 96$, $P < 0.006$; 1997: $r = -0.046$, $n = 105$, $P < 0.015$), but not for females (1996: $r = -0.022$, $n = 93$, $P = 0.15$; 1997: $r = -0.022$, $n = 103$, $P = 0.13$). Hence, the maximum natal dispersal distances that could be detected in this study are larger than the spatial scale over which there is genetic structure, at least for males. The less pronounced fine-scale genetic structure among females is in line with the female-biased dispersal pattern.

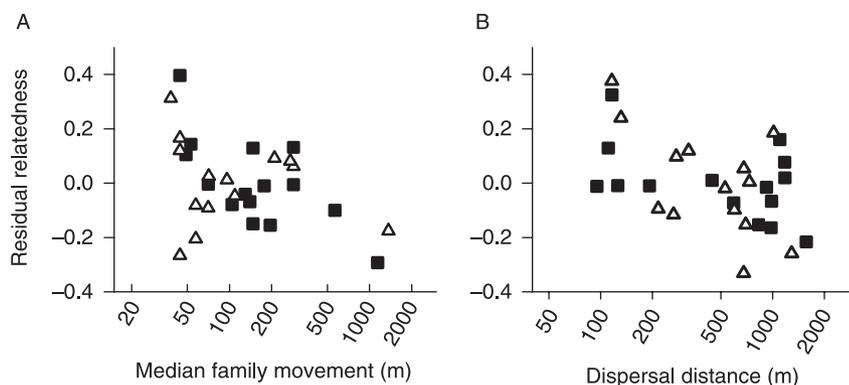


Fig. 3 Relationship of mate relatedness with family movement and natal dispersal, for males (black squares, $n = 15$) and for females (white triangles, $n = 14$). (A) Residual mate relatedness values (calculated from a model including natal dispersal) vs. median family movement (log-scale, in metres), for males (slope \pm SE = -0.12 ± 0.04) and for females (slope \pm SE = -0.03 ± 0.05). (B) Residual mate relatedness values (calculated from a model including family movement) vs. natal dispersal distance (log-scale, in metres), for males (slope \pm SE = -0.06 ± 0.03) and for females (slope \pm SE = -0.16 ± 0.06). Data used from breeding first year recruits in 1997.

Correlates of mate relatedness

We tested the prediction that natal dispersal and family movements influence mate relatedness using first-year breeders in 1997, for which all required data were available. Because family movements were not correlated with natal dispersal (see above), the effect of both variables on mate relatedness was tested in one statistical model. The analysis was done separately for females and males, to avoid pair members contributing data in the same analysis, and because spatial genetic structure appeared to be dependent on sex, as shown above. For females, mate relatedness was negatively related with natal dispersal distance (log-transformed: $F_{1,12} = 6.51$, $P < 0.0255$), but not the median family movement (log-transformed: $F_{1,11} = 0.44$, $P = 0.5204$) (Fig. 3). For males, mate relatedness was negatively related with the median family movement (log-transformed: $F_{1,13} = 7.74$, $P < 0.0157$), but there was only a tendency for a negative relation with the natal dispersal distance (log-transformed: $F_{1,10.1} = 3.47$, $P = 0.0917$) (Fig. 3). The relationship between mate relatedness and natal dispersal was confirmed at a large spatial scale (Fig. 4): immigrants had a lower mate relatedness than recruits born in the study area among females (data from 1996 and 1997: $n = 81$, $F_{1,79} = 5.66$, $P < 0.02$, difference \pm SE = -0.11 ± 0.05), but not among males ($n = 91$, $F_{1,89} = 0.61$, $P = 0.44$; difference \pm SE = -0.04 ± 0.05). Thus (future) mate relatedness decreased with natal dispersal in females, and decreased with family movements in males.

Inbreeding/outbreeding avoidance after settlement

We tested whether individuals avoid relatives as mates after settlement, by comparing the observed distribution of mate relatedness with a distribution obtained if individuals would have mated randomly with any breeding opposite-sex individual in the same breeding woodlot, or if they would have mated with their nearest neighbour. There was no significant difference for any of the comparisons

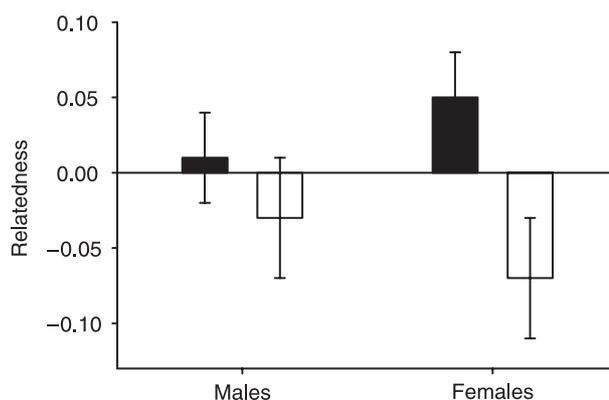


Fig. 4 Mate relatedness in relation to natal dispersal defined as a categorical variable for males ($n = 91$) and females ($n = 81$). Black bars: first year recruits born in the study area; white bars: first year recruits that immigrated. Bars indicate means \pm SE.

(Kolmogorov–Smirnov test for both sexes and years 1996 and 1997 separately: all $P > 0.18$), suggesting no inbreeding/outbreeding avoidance after settlement in a woodlot.

Discussion

In this study we showed that natal dispersal, a behaviour that has traditionally been hypothesized but has rarely been shown to influence relatedness patterns, predicts the level of relatedness with a mate, at least for females. In addition, a behaviour not previously considered, namely parental behaviour before the onset of offspring natal dispersal, was shown to influence relatedness between male offspring and their future mates.

A prerequisite for effects of spatial behaviours such as dispersal on mate relatedness is that there is a small-scale spatial genetic structure within the sexes. Such small-scale spatial genetic structure has recently been shown for several vertebrate species (Piertney *et al.* 1998; SurrIDGE *et al.* 1999; Shorey *et al.* 2000; Spong & Creel 2001; Coltman

et al. 2003; Foerster *et al.* 2003). However, other studies have not found any small (or large) scale genetic structure (e.g. Comer *et al.* 2005), or showed that it may change over time (Nussey *et al.* 2005). In this study we have detected a small-scale spatial genetic structure in a passerine bird species. In the same population we did not detect any genetic structure using a model-based clustering method (Pritchard *et al.* 2000), designed to detect the presence of genetically differentiated subpopulations (maximum number of clusters modelled was 12 = number of woodlots where genetic data were collected) (Van de Castele *et al.* 2003). This does not contradict the present results, but rather suggests that the spatial genetic structure of this population resembles an 'isolation-by-distance' model rather than an 'island' model (Rousset 1997). We found this pattern to be significant only in males, which is in line with their higher degree of philopatry. Another mechanism that might contribute to sex-specific genetic structure is sex-specific local adaptation. We have not studied that in this population, but recent studies on great tits have shown that local genetic differentiation can occur despite, or even driven by, substantial gene flow (Garant *et al.* 2005; Postma & van Noordwijk 2005).

The relationship between natal dispersal and mate relatedness appeared to be stronger in females than in males. In males, the relationship of mate relatedness with natal dispersal was not significant, irrespective of the scale on which natal dispersal was measured. In contrast, females dispersing over larger distances (including immigrants) ended up breeding with less-related males. The stronger pattern in females makes sense given the more pronounced fine-scale genetic structure among males, thus making the outcome for females, in terms of expected mate relatedness after dispersal, more predictable.

We also documented, for the first time, a relationship between mate relatedness and family movements during the dependent period. We showed that for a considerable proportion of broods (15%), median family movements extended beyond 300 m, which corresponds to the diameter of typical winter flock ranges (area 4–8 ha, Cramp & Perrins 1985). Moreover, the range of distances covered by family movements is comparable to the range of natal dispersal distances inside the study area. Thus, some individuals covered larger distances during family movements than other individuals in their lifetime. Nevertheless, family movements did not predict natal dispersal distances. This makes it unlikely that parents use family movements to disperse their offspring to resolve a parent–offspring conflict (Motro 1983) or to induce breeding habitat selection (Doligez *et al.* 2002). It also implies that most of the net natal dispersal distance is affected by offspring movements after independence. The fact that we established a relationship between future mate relatedness and family movements, but not dispersal distance for males, suggests that processes contributing to, or affecting, pair formation

are in operation before the onset of dispersal, and long before pairs are actually observed.

In the absence of behavioural observations between the period of family break-up and the establishment of territories and pairs in autumn, we can only speculate on the possible mechanisms underlying the relationship. First of all, family movements may influence membership to summer flocks by familiarizing offspring with particular areas outside the natal territory (Drent 1984; Matthysen 2002). We showed elsewhere that sibling great tits tend to disperse in similar directions but not over similar distances, suggesting that family movements may affect early stages of dispersal where movements are initiated in a certain direction, but that the final movement to the breeding site is affected by other processes (Matthysen *et al.* 2005). Second, family movements may affect future social status through prior residence effects (i.e. birds settling early acquire higher rank than latecomers in the same area), and through influencing the establishment of local dominance and dominance rank within flocks (Sandell & Smith 1991; Snell-Rood & Cristol 2005). Dominance in summer or winter flocks has been shown to affect mate choice in several other species; more specifically, dominant individuals may be preferred as mates (Choudhury & Black 1994; Otter & Radcliffe 1996) and mating may be assortative with respect to dominance (Matthysen 1990; Lahti *et al.* 1996). Third, early familiarization with a larger number of potential mates may facilitate discrimination between relatives and nonrelatives (Choudhury & Black 1994). Since we were unable to show inbreeding/outbreeding avoidance based on mating combinations within woodlots (see also further in this discussion), processes contributing to the observed pattern of mate relatedness are likely to operate at least partly through choice of settling areas rather than mate choice within sites. However, since this is a correlative study, we cannot draw strong conclusions about causality of any of the observed relationships. For instance, it could be possible that spatial environmental quality differences simultaneously affect genetic structure, parental escorting behaviour and natal dispersal.

As in most bird studies, we found no evidence that inbreeding/outbreeding avoidance after settlement determines mate relatedness. It has been noted that studies testing inbreeding/outbreeding avoidance in natural populations should not include particular inbreeding/outbreeding avoidance mechanisms, such as dispersal, in their null models (Pärt 1996). Lack of evidence for inbreeding/outbreeding avoidance could be due to a lack of power using the null models assumed, rather than an indication of the absence of inbreeding/outbreeding avoidance before, during or after natal dispersal. To overcome this problem, it has been suggested that the most promising approach is to study individual movements and mating preferences experimentally, in the presence and absence of relatives and nonrelatives (Pärt 1996). Our findings suggest that

such an experimental approach should integrate a social context as well. Ideally, inbreeding/outbreeding avoidance testing should be conditional on the social environment at the time of mate choice and pair formation.

In conclusion, our results suggest that in this population, behaviours affecting mating options are more important determinants of relatedness with a mate than inbreeding/outbreeding avoidance mechanisms after settlement. However, we cannot exclude the possibility that inbreeding/outbreeding avoidance drives natal dispersal and family movements. In any case, our results add a new mechanism to the ways in which individuals may reduce the fitness consequences of mating with relatives (Blomqvist *et al.* 2000; Van de Castele *et al.* 2003), i.e. the risk of mating with a relative can be reduced by associating with nonrelatives early after fledging. This may be a particularly interesting option for males who could obtain the benefits of philopatry (Greenwood 1980) and avoid the costs of inbreeding by participating in family movements, simultaneously. For females, the fitness consequences of postfledging movements in terms of the costs of inbreeding are less important, since by dispersing further this cost is reduced anyway. Of course, this does not preclude that there may be fitness benefits/costs associated with postfledging movements that were not studied here.

Our results may have important implications for understanding the co-evolution of natal dispersal and mate choice; they suggest that mating options (spatially or socially limited) are for a substantial part already determined before the onset of natal dispersal. This can be concluded from a combination of two pieces of information. First, family movements predict mate relatedness without influencing natal dispersal. Second, family movements are known to determine summer flock membership and wintering area where breeding pairs are formed (see Introduction). Thus, spatial and/or social limitations on mating options seem to exist in a highly mobile species, and matings are predetermined long before the first breeding season. Our results also suggest that the mating pattern is in part determined by the parents. This could indicate parental effects and raises the question whether variation in family movements reflects variation in parental effects or variation in environmental conditions that are not under control of the parents. Although many studies have revealed factors predicting natal dispersal (Clobert *et al.* 2001), we know of no study highlighting ecological factors that cause variation in family movements.

To conclude, our findings contrast with common assumptions of evolutionary models of natal dispersal that mating options are entirely determined after natal dispersal (Motro 1991, 1994; Olivieri & Gouyon 1997; Buse *et al.* 1999; Gandon & Rousset 1999; Perrin & Mazalov 2000), and that offspring control their own mating options (Motro 1994; Buse *et al.* 1999; Perrin & Mazalov 2000). Relaxation

of these assumptions will presumably lead to different evolutionary predictions, as it is well known that the presence of parental control affects the rate and outcome of the evolution of phenotypic traits (Mousseau & Fox 1998). More generally, our results stress the biological relevance of integrating socio-spatial constraints in evolutionary models of mate choice. This is important because evolutionary predictions may depend on the presence of constraints (Møller 1994).

Acknowledgements

We thank Frank Adriaensen, Jenny De Laet and Frans Fierens for help with fieldwork, and Tine Schenck and Peter Galbusera for microsatellite analyses. We thank Jean Clobert, André Dhondt, Laszlo Garamszegi, Vladimir Grosbois, Luc Lens, Raoul Van Damme, Tom Van Dooren and two anonymous referees for comments and discussion. This work was supported financially by a specialization grant of the IWT to T.V.D.C., and by research grant G0.166.00 of the FWO-Flanders to E.M.

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