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'Heritability' of dispersal propensity in a patchy population

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Although dispersal is often considered to be a plastic, condition-dependent trait with low heritability, growing evidence supports medium to high levels of dispersal heritability. Obtaining unbiased estimates of dispersal heritability in natural populations nevertheless remains crucial to understand the evolution of dispersal strategies and their population consequences. Here we show that dispersal propensity (i.e. the probability of dispersal between habitat patches) displays a significant heritability in the collared flycatcher *Ficedula albicollis*, as estimated by within-family resemblance when accounting for environmental factors. Offspring of dispersing mothers or fathers had a higher propensity to disperse to a new habitat patch themselves. The effect of parental dispersal status was additional to that of local habitat quality, as measured by local breeding population size and success, confirming previous results about condition-dependent dispersal in this population. The estimated levels of heritability varied between 0.30 ± 0.07 and 0.47 ± 0.10, depending on parent–offspring comparisons made and correcting for a significant assortative mating with respect to dispersal status. Siblings also displayed a significant resemblance in dispersal propensity. These results suggest that variation in between-patch natal dispersal in the collared flycatcher is partly genetically determined, and we discuss ways to quantify this genetic basis and its implications.

Keywords: assortative mating; between-patch dispersal; conditional dispersal; dispersal determinism; parent–offspring and sibling similarity; spatial constraints

1. INTRODUCTION

Dispersal, defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood & Harvey 1982), is a key life-history trait for evolutionary biology, ecology and conservation biology (Clobert *et al.* 2001; Kokko & López-Sepulcre 2006; Ronce 2007). In many species, individual dispersal decisions are strongly influenced by external factors (intraspecific competition, variability in habitat quality, etc.; reviews in Clobert *et al.* 2001, 2004; Bullock *et al.* 2002; Bowler & Benton 2005; Ronce 2007). Therefore, dispersal is generally considered as a highly plastic, condition-dependent behaviour, with a complex external multi-determinism and thus low heritability (Ims & Hjermann 2001).

However, a genetic basis of dispersal is required for dispersal strategies to respond to selection (Roff & Fairbairn 2001) and dispersal strategies can indeed evolve in response to selective pressures in the field (Thomas *et al.* 2001; Kokko & López-Sepulcre 2006; Duckworth & Badyaev 2007). Evidence for heritability of dispersal traits has been found mainly in plants and insects, in particular with selection experiments on seed or pollen dispersal structures or wing morphology (Roff & Fairbairn 2001; Ronce 2007). In vertebrates, the question of dispersal

heritability has recently received increased interest (e.g. Massot & Clobert 2000; Drent *et al.* 2003; Hansson *et al.* 2003; Pasinelli *et al.* 2004). Direct evidence supporting a genetic basis of dispersal traits in vertebrate species is rare, with only two well-documented examples so far (Trefilov *et al.* 2000; Sinervo & Clobert 2003), but indirect evidence includes (i) within-family (sibling and parent–offspring) resemblance in dispersal behaviour (reviews in Massot & Clobert 2000; Doligez & Pärt 2008; see also Massot *et al.* 2003; Sharp *et al.* 2008), (ii) correlation between dispersal behaviour and heritable traits (e.g. personality traits and behavioural syndromes; Dingemanse *et al.* 2003; see also Snoeijs *et al.* 2004), (iii) genetic differences between individuals of different dispersal status (Myers & Krebs 1971; although such differences may also be due to other processes, e.g. local adaptation) and (iv) responses of migratory, exploratory or movement traits to (rare) selection experiments (Roff & Fairbairn 2001; Dingemanse *et al.* 2002).

To predict evolutionary responses to environmental changes in terms of dispersal, it is crucial to obtain heritability estimates of realized dispersal events in natural populations over sufficiently large spatial and temporal scales. This can prove difficult because of the need to track an unbiased sample of parent and offspring movements (van Noordwijk 1984; Kokko & López-Sepulcre 2006; Doligez & Pärt 2008). It has been suggested that such unbiased estimates of dispersal heritability can only be obtained from data on dispersal between sub-populations

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(Hansson *et al.* 2003). In particular, when dispersal distances are used to compute heritability estimates (e.g. McCleery *et al.* 2004; Pasinelli *et al.* 2004), they may lead to biased estimates as soon as true (rather than observed) dispersal distance in the population is large compared with the size of the study area (see Doligez & Pärt 2008). This is due to constraints linked to the spatial configuration of the study area. Heritability estimates of dispersal distances may indeed be inflated by spatial heterogeneity in detecting long-distance dispersal events within the study area such that offspring dispersing longer distances are more likely to be detected for parents having themselves dispersed long distances within the area (as discussed in the case of the great tit *Parus major*; Greenwood *et al.* 1979; van Noordwijk 1984).

To reduce the problem of a constrained array of observable dispersal distances for each breeding site within a study area, we used dispersal propensity (i.e. the propensity to disperse to a new habitat patch) to estimate heritability in a patchy and unsaturated population of collared flycatchers *Ficedula albicollis*, where between-patch dispersal propensity should not be prone to biases due to spatial configuration constraints because settlement decisions at the patch scale should be relatively unconstrained. Furthermore, we investigated the influence of parental dispersal status on subsequent offspring natal dispersal probability while accounting for local habitat quality, which had previously been found to influence dispersal decisions in this population. Last, we report on sibling resemblance in natal dispersal propensity and assortative mating with respect to dispersal status of individuals.

2. MATERIAL AND METHODS

(a) *Study area, study species and definition of dispersal*

The collared flycatcher is a short-lived hole-nesting migratory passerine bird. Data have been collected between 1980 and 2005 in a spatially patchy population breeding on the island of Gotland, Southern Baltic (57°10′ N, 18°20′ E), where artificial nest-boxes have been regularly distributed in 14 discrete forest plots of varying size ('patches', see electronic supplementary material E1). Each year, adult flycatchers breeding in nest-boxes (and some in natural cavities) have been trapped, identified (with individually numbered aluminium rings) and aged based on their previous records in the population or morphological characteristics if unringed (yearlings versus older individuals). Breeding data have been monitored throughout the season and all nestlings in boxes have been ringed. For more details on the breeding ecology of the collared flycatcher and the study area see Gustafsson (1989), Pärt & Gustafsson (1989) and Pärt (1990).

Dispersal was defined as a change of plot between the years of birth and first breeding (natal dispersal) or between breeding years (breeding dispersal; see electronic supplementary material E2 for more details). This binary definition (dispersal versus philopatry) has been found to be biologically relevant in previous studies on this population (Doncaster *et al.* 1997; Doligez *et al.* 1999, 2002, 2004), although its simplifying categorical nature should lead to lower statistical power to detect effects (and thus conservative tests). Only adults whose natal or previous breeding site was known were included in the analyses: unringed immigrants in the

study area (on average, 35% of breeding adults each year; Doligez *et al.* 2004) were discarded because these birds include a mix of true immigrants and local birds previously born or breeding in natural holes or garden boxes within the study area. Because all breeding individuals could not be identified (on average 7.1 and 27.4% of breeding females and males, respectively, are missed each year; Doligez *et al.* 2004), dispersal status was in some cases determined with one (30.5%), two (7.4%) or three (1.3%) years of gap (see also Gustafsson & Pärt 1990 for non-breeders). Accounting for such gaps in the analyses did not qualitatively affect our results. All offspring involved in cross-fostering experiments during the course of the study period have been discarded from the analyses.

(b) *Statistical analyses of the influence of parental dispersal status*

We investigated the relationship between dispersal status (disperser versus philopatric individual) of male and female parents and their offspring using generalized linear mixed models (GLMMs; glimmix macro in SAS; Littell *et al.* 1996). Offspring dispersal status was determined upon first encounter of individuals as breeders (i.e. we analysed offspring natal dispersal). For parental dispersal status we used either the parents' status in the year of offspring birth, thus mixing parental natal and breeding dispersal events, or parental natal dispersal status only (i.e. in the year of offspring birth or before for older parents). Because extra-pair paternity was not determined routinely in this population, we used the dispersal status of the social father, despite 15 per cent of offspring in 33 per cent of nests having been found to be extra-pair (Sheldon & Ellegren 1999). Such levels of extra-pair paternity should however only slightly reduce our heritability estimates (see Charmantier & Réale 2005).

Offspring sex and local habitat quality, measured by breeding population size and mean number of fledglings per nest in a plot, were also included as explanatory variables because these variables have previously been shown to affect dispersal propensity in this population (for sex-biased dispersal, conspecific attraction and use of local reproductive success for emigration and immigration decisions, see Pärt & Gustafsson 1989; Pärt 1990; Doncaster *et al.* 1997; Doligez *et al.* 1999, 2002, 2004). Because plot area and number of boxes are strongly positively correlated to plot population size, using these variables instead of population size did not change the results (see electronic supplementary material E11). Furthermore, because 31 per cent of nests (303 out of 974) recruited more than one young, and 51 per cent of offspring (702 out of 1373) were therefore not independent, the models included nest of origin as a random variable to account for the non-independence of siblings (see also electronic supplementary material E3).

(c) *Computing dispersal 'heritability' estimates*

Estimates of heritability of dispersal propensity (binary variable) and associated standard errors were obtained using the threshold model, which assumes that the determination of the variation in a binary trait is the consequence of an underlying character (liability) that is itself continuously distributed (Falconer & Mackay 1996; see Roff 1997 and electronic supplementary material E4 for the equations linking the heritability values on the 0,1 scale and on the underlying scale). We computed two sets of heritability estimates using parent–offspring regressions, considering

(i) parental dispersal status in the year of offspring birth (i.e. mixing parental natal and breeding dispersal) and (ii) parental natal dispersal only, independent of the year when it occurred (i.e. whether parents were breeding for the first time or not). To account for sibling non-independence, we randomly selected one recruit for each breeding attempt that recruited several young, computed heritability values and repeated the operation 100 times. We present the mean values of heritability and standard error over the 100 repetitions. Because assortative mating biases the heritability estimate (Falconer & Mackay 1996), we checked whether assortative mating occurred with respect to dispersal status, and corrected the estimates obtained by the level of phenotypic correlation between parents (Roff 1997).

(d) Spatial constraints and detection of dispersal events

In spatially limited study areas, spatial constraints can artificially create a resemblance between parents and young in the absence of true resemblance, because of spatial heterogeneity in the detection of dispersal events and thus the distribution of dispersing individuals within the study area (van Noordwijk 1984). To test whether such spatial constraints could create parent–offspring resemblance in dispersal status in our population, we tested whether dispersal status of breeders (dispersing, philopatric and immigrant) depended on the location of the study plot within the study area and the location of the nest-box within the study plot. We categorized plots (and nest-boxes) as edge or central. The outer most seven plots of the study area were considered edge plots and the remaining seven were considered central (see detailed spatial configuration in electronic supplementary material E1). Within each plot, the two outer nest-box rows were considered edge boxes and the remaining were considered central, to divide boxes approximately equally between edge and central boxes (mean proportion of edge nest-boxes per plot: 0.61 ± 0.05 of all boxes in the plot). We analysed the proportion of dispersing, philopatric and immigrant individuals according to either plot or nest-box location category using GLMMs (glimmix macro in SAS; Littell *et al.* 1996), including sex and number of boxes in the plot as cofactors, and plot identity and year as random variables.

3. RESULTS

(a) Family resemblance in dispersal propensity

Dispersal status of both parents in the year of offspring birth significantly influenced offspring natal dispersal status in the subsequent year(s) (interaction between paternal and maternal dispersal status: $N = 1404$, $F_{1,404} = 9.30$, $p = 0.0024$; after accounting for offspring sex: $F_{1,404} = 19.35$, $p < 0.0001$). Offspring were more likely to disperse when either the mother ($F_{1,404} = 20.47$, $p < 0.0001$) or the father ($F_{1,404} = 14.10$, $p = 0.0002$) was a disperser in the year of offspring birth, but subsequent offspring dispersal propensity was the highest when both parents were dispersers (figure 1a), leading to the significant interaction between paternal and maternal dispersal status. Female offspring disperse at a higher rate than male offspring (adjusted offspring dispersal propensity, i.e. not constrained to be in a 0–1 scale, accounting for parental dispersal status: females, 0.981 ± 0.101; males, 0.462 ± 0.100).
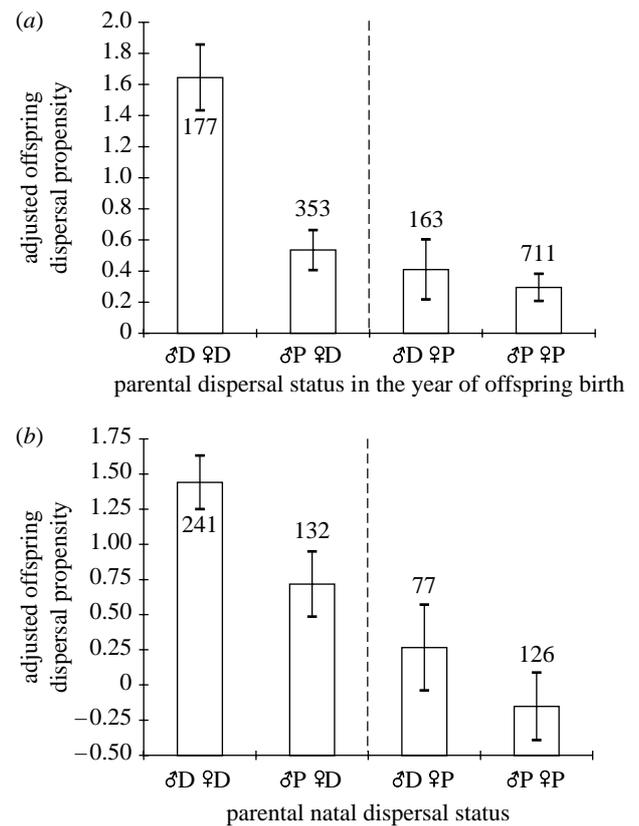
Figure 1. Offspring natal dispersal propensity (± 1 s.e.) according to the dispersal status of both parents (father first, mother second). (a) Parental dispersal status in the year of offspring birth (whether natal or breeding dispersal). (b) Parental natal dispersal status only (whether in the year of offspring birth or before). P, philopatric parent; D, dispersing parent. The *y*-axis represents the propensities adjusted for the significant effects of nest (random variable) and sex (i.e. least square means). Numbers are sample sizes.

The influence of parental dispersal status in the year of offspring birth on offspring dispersal propensity in the subsequent year(s) remained even when accounting for local habitat quality, as measured by local breeding density and mean local reproductive success in the year of offspring birth ($N = 1373$; interaction father × mother dispersal status: $F_{1,397} = 5.03$, $p = 0.025$; father dispersal status: $F_{1,397} = 7.09$, $p = 0.0081$; mother dispersal status: $F_{1,397} = 8.49$, $p = 0.0038$). In addition to the effect of parental dispersal status, offspring dispersal propensity decreased with increasing local habitat quality (breeding population size: $F_{1,397} = 49.25$, $p < 0.0001$, partial regression coefficient -0.025 ± 0.004; mean local success: $F_{1,397} = 10.87$, $p = 0.0011$, partial regression coefficient -0.269 ± 0.082). The effects of parental dispersal status and local habitat quality did not interact (all interaction terms: $p > 0.120$).

When considering parental natal dispersal status inclusive of dispersal before the year of offspring birth, natal dispersal status of both parents significantly influenced offspring dispersal status in the subsequent year(s): offspring were more likely to disperse when either the mother ($N = 576$, $F_{1,171} = 17.03$, $p < 0.0001$) or the father ($F_{1,171} = 6.61$, $p = 0.011$) were natal dispersers (figure 1b), after accounting for offspring sex ($F_{1,171} = 12.44$, $p = 0.0005$). Here, however, the interaction
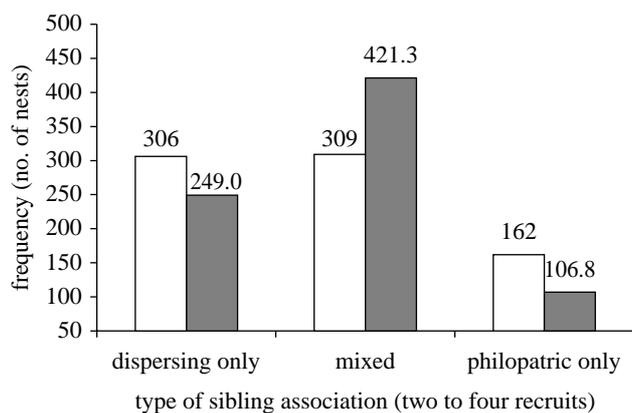
Figure 2. Resemblance between (social) siblings in natal dispersal propensity. Observed (white bars) and expected (grey bars) numbers of nests having recruited several offspring, depending on natal dispersal of siblings: either none or all of them having dispersed, or some having dispersed and others not ('mixed'). Expected numbers of nests are computed by accounting for sex-specific natal dispersal probabilities in the population for each combination of sibling association for two, three or four recruited siblings.

between father and mother natal dispersal status was not significant ($F_{1,171} = 0.39$, $p = 0.535$; figure 1b).

When several young recruited from a brood, the natal dispersal propensity of siblings was not independent. A total of 777 nests recruited between two and four young in the local breeding population, and the proportion of full (social) siblings sharing the same dispersal status (either all dispersing or all philopatric siblings) was higher than expected by chance ($\chi_2^2 = 71.47$, $p < 0.0001$; figure 2; see electronic supplementary material E7 for details).

In order to test for a genetic (and/or parental) origin of the observed within-family resemblance in dispersal propensity, we performed the same analyses again comparing dispersal status of (i) focal recruits and breeders of the nearest neighbouring box, and (ii) focal recruits with recruits of neighbouring boxes (with a maximal distance between boxes of 50 m in both cases); that is, we compared genetically unrelated individuals sharing similar small-scale environmental conditions (see detailed results in electronic supplementary material E9). Neither natal dispersal status of the neighbouring breeding male ($N = 105$, $F_{1,36} = 1.89$, $p = 0.178$) and female ($F_{1,36} = 1.28$, $p = 0.265$) nor dispersal status of the neighbouring male in the year of offspring birth ($N = 700$, $F_{1,202} = 0.51$, $p = 0.477$) were related to dispersal propensity of recruits, while dispersing neighbouring females in the year of offspring birth tended to associate with a higher dispersal propensity of recruits ($F_{1,195} = 3.87$, $p = 0.051$; accounting for population size and local reproductive success). Furthermore, pairs of recruits from neighbouring nests were not distributed randomly with respect to the dispersal status of recruits ($N = 273.4$, $\chi_2^2 = 6.94$, $p = 0.031$), but the bias was weaker than that in the case of pairs of siblings ($N = 596$, $\chi_2^2 = 39.63$, $p < 0.0001$). Pairs of philopatric recruits, but not pairs of dispersing recruits, were more numerous than expected by chance (59.4 versus 43.9 and 96.6 versus 98.2, respectively; see electronic supplementary material E9). These differences between analyses based on unrelated individuals and family members suggest

that genetic (and/or parental) effects explain a large part of the observed resemblance (see electronic supplementary material E9).

(b) *Heritability of dispersal propensity*
Breeders did not mate at random with respect to dispersal status, but were more likely to mate with a partner of the same dispersal status (table 1). This assortative mating by dispersal status was not due to assortative mating by age associated with higher dispersal rate in yearlings, because assortative mating by dispersal status remained significant within the different age categories (table 1). The heritability values were computed correcting for this assortative mating by dispersal status (phenotypic correlation coefficient between dispersal status of the male and the female within a pair, used to correct heritability estimates: $r = 0.193$ for the analysis of parental dispersal status in the year of offspring birth and $r = 0.223$ for the analysis of parental natal dispersal status; Roff 1997).

The estimated level of dispersal heritability is given in table 2 for mid-parent and one-parent regressions. For parental dispersal status in the year of offspring birth (i.e. mixing parental natal and breeding dispersal), estimated heritability level was 0.30 ± 0.07, and did not significantly differ between father–offspring and mother–offspring regressions ($F_{1,1} = 1.77$, $p = 0.410$; table 2a). For parental natal dispersal status, estimated heritability level was higher (0.47 ± 0.10) and, again, did not differ between father–offspring and mother–offspring regressions ($F_{1,1} = 2.23$, $p = 0.375$; table 2b).

(c) *Effect of spatial location on dispersal status and heritability estimates*
The proportion of dispersers and immigrants in a plot depended on the location of the plot within the study area. Edge plots had lower proportions of dispersers ($N = 597$, $F_{1,554} = 3.86$, $p = 0.049$) and higher proportions of immigrants ($N = 619$, $F_{1,576} = 5.56$, $p = 0.018$) than central plots, for both sexes (figure 3a). The proportion of philopatric breeders, however, did not depend on the location of the plot ($N = 597$, $F_{1,554} = 0.07$, $p = 0.792$; figure 3a). By contrast, the proportion of dispersers and immigrants was not associated with the location of the nest-box within the plot (all $p > 0.18$; figure 3b). Proportions of both dispersers and immigrants were always higher in females than in males (all $p < 0.001$; figure 3) and decreased with increasing plot size (number of boxes in the plot; all $p < 0.002$).

Importantly, the estimated heritability level based on parental dispersal status in the year of offspring birth did not differ between offspring of pairs breeding in the central plots ($N = 527$, $h^2 = 0.24 \pm 0.09$) and offspring of pairs breeding in the edge plots ($N = 473$, $h^2 = 0.20 \pm 0.12$; $F_{2,2} = 1.01$, $p = 0.497$) or in the whole study area ($F_{2,2} = 1.69$, $p = 0.372$). Similarly, no difference could be found between heritability estimates based on parental natal dispersal status for offspring of pairs in central plots ($N = 259$, $h^2 = 0.329 \pm 0.130$) and offspring of pairs in edge plots ($N = 145$, $h^2 = 0.578 \pm 0.166$; $F_{2,2} = 7.459$, $p = 0.118$) or in the whole study area ($F_{2,2} = 2.74$, $p = 0.267$).

In order to test whether dispersal outside the study area may bias our heritability estimates, we compared estimates based on offspring of pairs breeding in the central plots and recruiting either in the central plots

Table 1. Assortative mating by dispersal status, for all pairs and by age category: observed and expected (in parentheses) numbers of pairs according to male and female dispersal status. (In bold, observed values exceeding expected values. All χ^2 tests have 1 d.f. because they are computed line by line for a 2×2 table (two possible dispersal status for males and two for females) in each case. Assortative mating by age is strong in this population ($N = 7016$ matings where both male and female age were known, $\chi_1^2 = 313.4$, $p < 0.0001$). Furthermore, age-biased dispersal is also strong, with a higher proportion of dispersers among yearlings than older adults (females: 62.0 and 29.7% respectively, $N = 6022$; males: 55.3 and 15.7% respectively, $N = 5061$). We therefore detailed assortative mating by dispersal status by age category of each breeding pair member. Note that this analysis does not take environmental factors (plot population size or local reproductive success) into account. See electronic supplementary material E6 for details about computing expected values.)

	♂D ♀D	♂D ♀P	♂P ♀D	♂P ♀P	χ^2	p-value
all pairs	**343** (273.8)	339 (462.2)	744 (862.3)	**1628** (1455.7)	86.9	<0.0001
old ♂ and ♀	**119** (95.4)	158 (225.7)	466 (512.0)	**1302** (1215.4)	36.45	<0.0001
yearling ♂ and ♀	**81** (68.9)	29 (42.2)	38 (55.7)	**53** (34.1)	22.35	<0.0001
old ♂ and yearling ♀	**62** (39.6)	25 (24.3)	195 (212.7)	125 (130.4)	14.38	0.0002
yearling ♂ and old ♀	**80** (58.0)	123 (137.2)	33 (46.9)	**117** (110.9)	14.27	0.0002

Table 2. Estimates of heritability of dispersal propensity, based on random resampling of offspring for families having recruited several young (100 randomizations), for (*a*) parental dispersal status in the year of offspring birth and (*b*) parental natal dispersal status only. (In both cases, one-parent–offspring regressions did not account for the dispersal status of the other parent. Single-sex (i.e. mother–daughter and father–son) regressions gave similar heritability estimates (see the electronic supplementary material E10). $h_{0,1}^2$ (respectively h^2) is the heritability measured on the 0,1 scale (respectively underlying continuous scale), s.e. is the associated standard error, N disp is the average number of dispersing offspring over the 100 randomizations in the sample, N tot is the total number of offspring in the sample (1 offspring per family). For details, see electronic supplementary material E4. The average number of dispersing offspring in the population (whether dispersal status of parents is known or not) over the 100 randomizations is 1552, the total number of offspring (one per family) is 2584, and the proportion of dispersing offspring (*p*) is thus 0.60. The correlation coefficient between father and mother dispersal status is (*a*) 0.193 and (*b*) 0.223. For significance testing of differences between father–offspring and mother–offspring estimates, see the electronic supplementary material E5.)

relationship	$h_{0,1}^2$	s.e. ($h_{0,1}^2$)	N disp	N tot	h^2	s.e.(h^2)
(*a*) *all parental dispersal status (whether breeding or natal dispersal)*						
parent–offspring	0.186	0.044	615.7	999	0.298	0.070
mother–offspring	0.100	0.025	967.3	1544	0.276	0.057
father–offspring	0.154	0.029	915.6	1516	0.426	0.066
(*b*) *only parental natal dispersal status*						
parent–offspring	0.292	0.061	261.9	404	0.469	0.098
mother–offspring	0.125	0.033	597.7	946	0.330	0.074
father–offspring	0.174	0.030	619.1	985	0.458	0.069

only (thus ignoring dispersal within the study area but outside the central plots) or over the whole study area. Heritability estimates based on offspring recruiting into the central plots ($N = 379$, $h^2 = 0.310 \pm 0.109$ and $N = 182$, $h^2 = 0.402 \pm 0.155$ for parental dispersal status in the year of offspring birth and natal parental dispersal status, respectively) did not differ from those based on offspring recruiting in the whole study area (see above; $F_{2,2} = 1.15$, $p = 0.466$ and $F_{2,2} = 1.11$, $p = 0.473$, respectively). The absence of difference between these estimates thus suggests that undetected dispersal outside the study area is unlikely to bias our heritability estimates (see detailed results in electronic supplementary material E8).

4. DISCUSSION

Our results show high within-family (parent–offspring and sibling) resemblance and high estimated heritability level in between-patch dispersal propensity (i.e. propensity to disperse to a new habitat patch) in the collared flycatcher. Because we used dispersal propensity in an unsaturated population where most individuals should not be constrained in choosing their breeding plot, rather than dispersal distance, these results are unlikely to be due to

obvious spatial constraints inducing biases in the distribution of observed dispersal events (see van Noordwijk 1984). Accordingly, dispersers were not more likely to be found towards the edges of the study area and we found no significant effect of spatial location on heritability estimates. Actually, edge plots had a lower proportion of dispersers compared with central plots, probably because a larger fraction of dispersers from edge plots escaped detection by moving out from the study area (Doligez & Pärt 2008). This potentially reduced the number of parent–offspring dispersal observations at the edges, but did not affect our estimates (see electronic supplementary material E8). Our study therefore provides strong evidence for heritability of between-patch dispersal behaviour in this patchy population.

As suggested by our analyses comparing dispersal propensity between genetically unrelated individuals sharing similar environmental conditions (see electronic supplementary material E9), the observed heritability and within-family resemblance in dispersal propensity probably originate from a mixture of genetic, parental and environmental contributions. In uncontrolled field conditions, common environment effects can of course
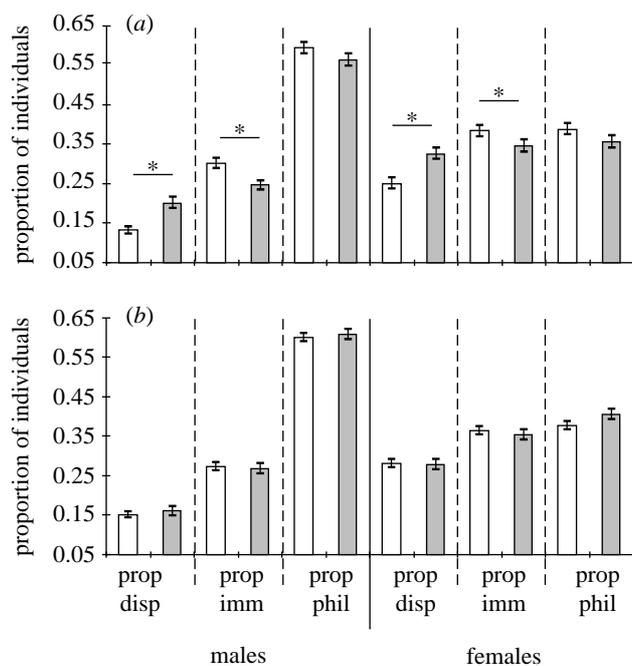
Figure 3. Mean proportion (± 1 s.e.) of dispersing (disp), immigrant (imm) and philopatric (phil) individuals among breeders of each sex depending on the location of (*a*) the study plot within the study area (edge versus central plots) and (*b*) the nest-box within the study plot (edge versus central nest-boxes). Asterisks indicate significant differences. White bars, edge; grey bars, centre. Sample sizes: (*a*) edge plots: $N=178$, central plots: $N=158$; (*b*) edge boxes: $N=332$, central boxes: $N=319$.

lead to true parent–offspring resemblance (e.g. by linking body condition, information about local habitat quality, competition and breeding site quality over generations; see examples in Clobert *et al.* 2001; Ronce 2007). Here, we found significant parent–offspring resemblance even after accounting for environmental factors known to affect between-patch dispersal decisions in this population (local habitat quality at the patch scale; Doligez *et al.* 2002, 2004), but no or weak resemblance between unrelated but neighbouring individuals. This both confirms previous results and supports the multifactorial nature of dispersal determinism in this population. The lower heritability estimates of dispersal propensity when considering both parental natal and breeding dispersal, as compared with when considering only parental natal dispersal, are probably due to the increasing influence of external information about habitat quality, and more particularly personal breeding experience, on dispersal decisions with increasing age (see Dufty *et al.* 2002). Such condition-dependent dispersal based on information about habitat quality is expected to be favoured over a fixed, 'blind' mechanism as soon as environmental variation is sufficiently predictable and information sufficiently cheap to acquire (Ronce 2007).

To quantitatively assess the relative contributions of genetic, parental and environmental components on dispersal propensity, more refined analyses based on quantitative genetics models using pedigrees to partition the variance between these factors ('animal breeding models'; Kruuk 2004) are needed. However, we did not use an animal breeding model here because the generalization of the estimation of variance components to the

analysis of binary traits, such as dispersal propensity, has not been fully implemented yet (but see Duckworth & Kruuk 2009). A further issue is that quantitative genetics models do not account for imperfect detection of individuals in the wild (Clobert 1995; Cam 2009), which occurs in our population, due in particular to early breeding failure and unchecked natural cavities or garden boxes (see Doligez *et al.* 2004). However, heterogeneity in detection probability with respect to phenotypic traits such as dispersal status may lead to biased inferences (for examples, see Gimenez *et al.* 2008), and should therefore be included in future work on dispersal heritability. Ideally, combining quantitative genetics and capture–mark–recapture methods (Lebreton *et al.* 1992) is required to fully understand the origin of within-family resemblance in between-patch dispersal behaviour, in this and other populations, and its implications for dispersal evolution, but such methodology has not been fully developed yet (Cam 2009; O. Gimenez 2008, personal communication).

Typical values for heritability of behavioural traits are 0.20–0.40, with a mean value of 0.30 ± 0.03 for traits linked to movement (see review in Stirling *et al.* 2002). Even when taking environmental effects into account, our estimates of heritability of dispersal propensity based on a large dataset are probably close to this general value and within the range of observed values recently obtained by other studies for dispersal traits (Hansson *et al.* 2003; McCleery *et al.* 2004; Pasinelli *et al.* 2004; review in Doligez & Pärt 2008). Such heritability values have implications regarding the relative fitness of dispersing and philopatric individuals, since heritability levels of 0.20 are typically associated with low proportions of fitness explained by the trait considered (less than 5%; e.g. Gustafsson 1986; Stirling *et al.* 2002; McCleery *et al.* 2004). If the genetic contribution to the observed dispersal heritability is sufficiently high, dispersal should therefore not be expected to have general lifetime fitness consequences, and observed fitness differences according to dispersal status may in fact be due to confounding effects (e.g. within-family resemblance in dispersal generating systematic underestimation of dispersers' fitness; Doligez & Pärt 2008). Actually, several of the studies reporting such fitness differences between dispersing and non-dispersing individuals also show a within-family resemblance in dispersal behaviour (reviews in Bélichon *et al.* 1996; Doligez & Pärt 2008). Observed fitness differences according to dispersal status may also be due to compensation between fitness components over individuals' lifetimes, since most studies investigate single or limited components rather than lifetime fitness (Bélichon *et al.* 1996).

Many classical models of dispersal evolution both consider a fixed, genetically determined dispersal rate and make (sometimes implicit) assumptions about the relative fitness of dispersing and non-dispersing individuals (Johnson & Gaines 1990; Clobert *et al.* 2001; Ronce 2007). Reconciling these two processes requires more knowledge about the genetic basis of dispersal traits and the inter- and intraspecific variations in dispersal determinism, in order to assess fitness consequences of dispersal at evolutionary time scales and to understand the patterns of fitness differences according to dispersal status in empirical studies (Bélichon *et al.* 1996;

Clobert *et al.* 2001). Beyond the mere genetic basis of dispersal as a binary response (dispersing versus non-dispersing), however, a crucial aspect is to investigate to what extent the sensitivity of individuals to environmental factors in their dispersal response (i.e. dispersal reaction norm) is genetically determined (Ronce 2007). This may prove more relevant (although more difficult) to understand how dispersal can be adaptive in environments heterogeneous at different spatial and temporal scales.

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