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Estimation and comparison of heritability and parent–offspring resemblance in dispersal probability from capture–recapture data using different methods: the Collared Flycatcher as a case study

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Abstract Understanding the evolution of a trait requires analysing its genetic basis. Many studies have therefore estimated heritability values of different traits in wild populations using quantitative genetic approaches on capture–recapture data of individuals with known parentage. However, these models assume perfect individual detection probability, a hidden hypothesis that is rarely met in natural populations. To what extent ignoring imperfect detection may bias heritability estimates in wild populations needs specific investigation. We give a first insight into this question using dispersal probability in a patchy population of Collared Flycatchers *Ficedula albicollis* as an example. We estimate and compare heritability and parent–offspring resemblance in dispersal obtained from (1) quantitative genetic approaches ("classical" parent–offspring regressions and more recent animal models) and (2) multi-state capture–recapture models accounting for individual detection probability. Unfortunately, current capture–recapture models do not provide heritability estimates, preventing a full comparison of results between models at this stage. However, in the study population, detection probability may be expected to be lower for dispersing compared to philopatric individuals because of lower mating/breeding success and/or higher temporary emigration, making the use of capture–recapture models particularly relevant. We show significant parent–offspring resemblance and heritable component of between-patch dispersal probability in this population. Accounting for imperfect detection does however not seem to influence the observed pattern of parent–offspring resemblance in dispersal probability, although detection probability is both sensibly lower than 1 and heterogeneous among individuals according to dispersal status. We discuss the problems encountered, the information that can be derived from, and the constraints linked to, each method. To obtain unbiased heritability estimates, combining quantitative genetic and capture–recapture models is needed, which should be one of the main developments of capture–recapture models in the near future.

Keywords Capture–recapture models · Family effects · Individual detection probability · Mixed models · Quantitative genetics

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Introduction

The response of a trait to evolutionary pressures directly depends on its heritability and the strength of the selective pressures acting on this trait. Understanding the evolution of a trait in natural populations therefore involves analyzing (1) the variation in this trait among individuals, (2) the relationship between this trait and individual fitness, and (3) the genetic basis of the trait (Fairbairn and Reeve 2001; Kruuk et al. 2008). Based on capture–recapture data collected over generations, many evolutionary studies have used quantitative genetic models to estimate heritability of morphological, physiological, behavioral and life-history traits and address related evolutionary questions in natural populations (reviews in, e.g., Kruuk et al. 2008; Stirling et al. 2002). In particular, the use of generalized linear mixed models ("animal models") in this context, which allow partitioning the total observed phenotypic variance among individuals between genetic, environmental and other factors by incorporating pedigree information of marked individuals in a population (Kruuk 2004), has recently expanded over classical regressions between close relatives.

However, current quantitative genetic models, developed for captive animal populations, rely on the hidden assumptions that detection and/or capture of individuals is perfect and thus that phenotypic variance is identical among marked and unmarked individuals (Cam 2009). Both hypotheses are unlikely to be met in natural populations (Cam 2009; Clobert 1995; Lebreton et al. 1992), where detection and/or capture probability often depends on individual phenotype such as morphology, behavior (e.g., breeding behavior: Gustafsson and Pärt 1990; or personality: Biro and Dingemanse 2009), health status (e.g., Hawley et al. 2007), etc. Violating the hypothesis of a perfect individual detection can, however, not only lead to biased estimates of the demographical parameters of interest but also to flawed inferences on the biological processes revealed by relationships between these estimates and other factors, as shown for survival patterns (see, e.g., Gimenez et al. 2008; Martin et al. 1995). This issue can therefore not be ignored (Cam 2009). Capture–recapture (CMR) methods have been specifically developed to account for imperfect individual detection and its heterogeneity among individuals, but they remain largely ignored in the context of estimating trait heritability (Cam 2009). However, classical CMR models do not currently allow random effects, which could include genetic effects from pedigree information, to be tested and therefore cannot directly estimate heritability levels. Building the required CMR mixed models (Cam 2009) or "capture–recapture animal models" (O'Hara et al. 2008; Papaïx et al. 2010) by integrating random effects while accounting for imperfect detection has only been undertaken very recently (Papaïx et al. 2010; Royle 2008).

Until CMR mixed models become fully available, the question remains to what extent ignoring imperfect individual detection probability may bias heritability estimates in wild populations. In order to explore this question, we attempted here to compare measures of heritability (i.e., the fraction of additive genetic variance in the total observed phenotypic variance for a trait) or parent–offspring resemblance (i.e., the degree by which offspring trait is affected by parental trait) obtained via methods accounting (CMR models) and not accounting (quantitative genetic models) for imperfect detection for a given behavioral trait. As an example, we used on the one hand classical parent–offspring regressions and animal models, and on the other hand CMR models to estimate heritability of, or parent–offspring resemblance in, dispersal probability in a patchy population, in order to highlight the constraints linked to each method. Dispersal, defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood and Harvey 1982), is a key life-history trait for evolutionary biology, ecology and conservation biology (Clobert et al. 2001; Kokko and López-Sepulcre 2006; Ronce 2007). Dispersal strategies have been found to evolve in response to selective pressures in the wild (Duckworth and Badyaev 2007; Kokko and López-Sepulcre 2006; Thomas et al. 2001), suggesting a genetic basis of dispersal. 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 and Fairbairn 2001; Ronce 2007). In vertebrates, direct evidence supporting a genetic basis of dispersal traits is rare (Sinervo and Clobert 2003; Trefilov et al. 2000; see also Dingemanse et al. 2002; Roff and Fairbairn 2001 for selection experiments on exploratory or movement traits), but indirect evidence is accumulating in the form of within-family (sibling and parent–offspring) resemblance in dispersal behavior (reviews in Doligez and Pärt 2008; Massot and Clobert 2000; see also Massot et al. 2003; Sharp et al. 2008).

However, all studies providing estimates of dispersal heritability in natural populations so far have completely ignored the issue of imperfect individual detection probability, even when the observed number of recruits was explicitly noted to be much lower than expected (see, e.g., Hansson et al. 2003, in which the authors estimate that 37% of expected recruits were not detected). To what extent these dispersal heritability estimates may be biased thus needs to be explored. Strong biases may be expected because detection probability is likely to differ between dispersing and non-dispersing individuals due in particular to differences in (1) future dispersal probability, and thus

chances to temporarily leave the study area (Doligez and Pärt 2008), and/or (2) breeding status, in particular mating success (e.g., Bensch et al. 1998; Pärt 1994). Accordingly, dispersing individuals may be expected to show lower detection probability, and estimations of dispersal heritability may be affected not only by imperfect individual detection but also by the heterogeneity of detection probability among individuals depending on the trait of interest, here dispersal status, and other traits linked to dispersal (e.g., sex and age; Greenwood and Harvey 1982).

Using dispersal probability, i.e., the probability to disperse to a new habitat patch, we obtained measures of dispersal heritability and parent–offspring resemblance in dispersal in a patchy and unsaturated population of Collared Flycatchers *Ficedula albicollis*, and we compared the results obtained using the same data with different methods. In a first step, we estimated parent–offspring resemblance in between-patch dispersal propensity and heritability using quantitative genetic methods (parent–offspring regressions and animal models). In a second step, we used a multi-state CMR approach to estimate the level of parent–offspring resemblance in between-patch dispersal propensity. In this case, using parental dispersal status as individual initial state (i.e., at age 0), parent–offspring resemblance was estimated via the transition probability between states from age 0 to 1. A full comparison of the three currently available methods is difficult because they yield different kinds of estimates: current CMR models estimate offspring dispersal probability according to parental dispersal status but provide no heritability estimate, while the reverse is true for animal models. The two types of estimates are of course linked (the higher the heritability level, the higher the parent–offspring resemblance) but cannot be directly compared as such. Results from CMR and animal models were therefore both compared to parent–offspring regressions. We discuss the constraints of each method and stress the need for developing CMR mixed models that can be used to estimate heritability of many quantitative and discrete traits in the wild (see O'Hara et al. 2008).

Methods

Study area and study species

The Collared Flycatcher is a short-lived hole-nesting migratory passerine bird. The data were 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 were erected in 14 discrete forest plots of varying size (patches) (see Doligez et al. 2009 and Appendix for more details). Each year, adult flycatchers breeding in nest boxes were trapped (females during incubation, males during nestling feeding), identified with individually numbered aluminium rings, and aged (yearlings versus older individuals; Doligez et al. 2009). Breeding data were monitored throughout the season and all nestlings in boxes were ringed. For more details on the study population and study area, see Doligez et al. 2009; Gustafsson 1989; Pärt 1990; Pärt and Gustafsson 1989.

Definition of dispersal, dispersal variables and individual detection probability

Dispersal was defined as an observed change of patch between the years of birth and first breeding (natal dispersal) or between breeding years (breeding dispersal) (Doligez et al. 2009). This binary definition (dispersal versus philopatry) minimizes methodological problems compared to a continuous variable such as dispersal distance, since the array of observable dispersal distances is strongly constrained in this patchy population with respect to settlement decisions at the patch scale (Doligez and Pärt 2008; Doligez et al. 2004; Appendix). Furthermore, this binary variable was found to respond to many social and environmental factors in previous studies on this population (Doligez et al. 1999, 2002, 2004; Doncaster et al. 1997). 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 missed. All recruits involved in cross-fostering experiments were discarded from the analyses. Because we focused in this study on comparing the results obtained using different methods rather than obtaining the most precise heritability estimates, we ignored all maternal and environmental factors potentially affecting dispersal in order to keep results fully comparable between methods.

We used for parental dispersal status either the parents' status in the year of offspring birth whatever parents' age (i.e., mixing natal dispersal for first-time breeders and breeding dispersal for older parents) or parental natal dispersal status only (i.e., in the year of offspring birth for first-time breeders or before for older parents). Approximately 15% of nestlings distributed over 33% of nests are extra-pair in this population (Sheldon and Ellegren 1999). Because extra-pair paternity was not determined routinely in this population, and because such levels of extra-pair paternity were shown to have little impact on heritability estimates both using parent–offspring regressions and animal models (Charmantier and Réale 2005; Merilä et al. 1998), we used the dispersal status of the social father.

In this population, the capture of adults is tightly linked to their sex, breeding status and success (see Appendix). As a consequence, dispersal status was in some cases determined with one (30.5%), two (7.4%) or three (1.3%) years of gap (Doligez et al. 2009). In the study population, earlier results suggested that dispersing individuals achieved lower mating and breeding success (Pärt 1991, 1994) and were more likely to subsequently disperse out of the study area (Doligez et al. 1999; Pärt and Gustafsson 1989) than philopatric individuals. Thus, they may be expected to show lower individual detection probability.

Parent–offspring regressions

We first investigated the relationship between dispersal status (disperser versus philopatric individual) of male and female parents and their offspring, controlling for offspring sex, using generalized linear mixed models (GLMMs with binomial error structure and logit link; glimmix macro in SAS; Littell et al. 1996). Offspring dispersal status was determined upon first encounter of individuals as breeders, i.e., we analyzed offspring natal dispersal. Furthermore, because 31% of nests (303 of 974) recruited more than one young, and 51% of recruited offspring (702 of 1,373) were therefore not independent, the models included nest of origin as a random variable to account for the non-independence of siblings.

The heritability (h^2) of a given trait is computed as the ratio of additive genetic variance (σ_A^2) over total phenotypic variance (σ_P^2), and can be estimated by the slope (b) of the corresponding parent–offspring regression (Falconer and Mackay 1996). Estimates of heritability of dispersal probability (binary variable) and associated standard errors were obtained here using the threshold model (Falconer and Mackay 1996). This model assumes that the determination of the variation in a binary trait is the consequence of an underlying character (liability) that is itself continuously distributed. Individuals for which the liability character is below (with respect to above) a threshold value will develop the first (with respect to the second) morph of the dimorphic trait. Because the liability is continuously distributed, the threshold model allows obtaining heritability estimates using the usual linear approach, by linking the heritability measured on a binary (0,1) scale ($h_{0,1}^2$) to the heritability on the underlying continuous scale (h^2) (see Roff 1997; Doligez et al. 2009 for more details). We computed two sets of heritability estimates using parent–offspring regressions considering (1) parental dispersal status in the year of offspring birth, and (2) parental natal dispersal only, independently of the year when it occurred. To account for sibling non-independence in these estimations, we randomly selected one recruit for each breeding attempt that recruited several young, computed heritability estimates on the data subset, and repeated the operation 100 times to obtain mean values of heritability and standard error over the 100 repetitions. Heritability estimates were corrected by the level of phenotypic correlation of dispersal status between parents (Falconer and Mackay 1996; Roff 1997; see Doligez et al. 2009).

Animal models

Animal models are mixed models partitioning the observed total phenotypic variance in a trait (σ_P^2) into additive genetic, parental and environmental components of variance, using information about the degree of relatedness between individuals contained in their pedigree (Kruuk 2004 and references therein). These models consider additive genetic value of individuals as a random effect because they aim at providing an estimate of the variance of this effect rather than one parameter for each individual (Kruuk 2004). In the simplest form of animal models, the phenotype y of individual i can be written as: $y_i = \mu + a_i + e_i$, where μ is the population mean, a_i is the additive genetic value of individual i and e_i is a random residual error (μ is thus the only fixed effect). Random effects a_i and e_i are assumed to have a zero mean and unknown variance to be estimated, σ_A^2 (the additive genetic variance) and σ_R^2 (the residual variance), respectively. If the only random effect in the model is the additive genetic effect, the total phenotypic variance for the trait y is: $\sigma_P^2 = \sigma_A^2 + \sigma_R^2$. Variance components are estimated by fitting the respective random effects in a generalized linear mixed model, and the heritability of trait y is computed as $h^2 = \sigma_A^2/(\sigma_A^2 + \sigma_R^2)$ (Kruuk 2004). In addition to the additive genetic variance (random effect), we included sex and age (fixed effects) in our animal models. In a first analysis, the estimation of heritability of dispersal probability included all dispersal events, thus mixing natal and breeding dispersal events. In a second analysis, only natal dispersal events were analyzed, thus estimating heritability of natal dispersal probability. In the study population, the pedigree depth (i.e., maximum possible number of ancestor generations for an individual) is 25 generations since individuals can start breeding at age 1 (parentage relationships between individuals were unknown in the first year of the study as none were ringed).

The models were run using MCMCglmm, a recently issued R package for fitting generalized linear mixed models using Monte Carlo Markov chain techniques (Hadfield 2010). The model was fitted as if the dispersal variable was normally distributed and thus heritability values were obtained using the threshold model again to transform heritability on the binary (0,1) scale ($h_{0,1}^2$) given by the MCMCglmm package into heritability on the underlying continuous scale (h^2) as above (further work is

needed to run a model fitting directly binary variables using MCMCglmm). Based on the results obtained with parent–offspring regressions, a prior of 0.4 was used for heritability to start with. To compute the posterior mode, the 15,000 first iterations were discarded and 1 iteration was kept every 50 iterations over the next 50,000 iterations (i.e., 1,000 iterations were used in total), in order to reduce autocorrelation between iterations used. The trace and densities of fixed and random effects and residuals were checked. The estimates obtained were similar for different priors tested, indicating that they were not sensitive to the prior chosen. MCMCglmm provides 95% credible interval around each estimate of variance, heritability and fixed effects, allowing testing the significance of these parameters.

Multi-state capture–recapture models: capture histories, effects modeled and notations

Individual capture histories were built using three different events (Pradel 2005): 0, not encountered; 1, philopatric status (i.e., encountered in the same patch as previously); and 2, dispersing status (i.e., encountered in a different patch). Since only individuals born on the study area were included, the first encounter for each individual always corresponded to age 0. Since individual dispersal status was not defined at age 0, the corresponding event was the dispersal status of the same-sex parent. Subsequent events were defined by the dispersal status of the individual. Individual sex and dispersal status of the opposite-sex parent were coded as groups (i.e., 4 groups). Capture histories contained 25 events corresponding to the 26 years of the study considered, excluding the first year for which parental dispersal status was unknown for all individuals. We used E-SURGE (Choquet et al. 2009; Pradel 2005) to estimate survival (*S*), capture (*P*) and between-state transition (*T*) probabilities depending on sex (*s*), age (*a*), parental (*pd*) and individual (*id*) dispersal status. Parent–offspring resemblance in dispersal probability was estimated through the influence of parental dispersal status on the first between-state transition (age 0 to age 1), separating the dispersal status of same-sex (*spd*) and opposite-sex (*opd*) parents. We considered three age classes: yearlings [or age 0 to age 1 for survival *S* and transition *T* parameters; *a*(*1*)], 2-year-old individuals [or age 1 to age 2; *a*(*2*)] and 3-year-old or older individuals [or after age 2; *a*(*3*)]. Here, we ignored temporal variations in parameters in order to keep the number of parameters tractable and obtain parameter estimates. Furthermore, year effects when implemented in animal models were very weak (unpublished results).

Because family (random) effects cannot be included in current CMR models, we used an indirect approach to investigate the impact of the non-independence of sibling recruits on model selection. In a first step, we analyzed all recruits (thus with non-independent individuals for nests having recruited several siblings). In a second step, we analyzed 10 of the 100 data subsets created for parent–offspring regressions by randomly selecting one recruit for each nest having recruited several siblings (thus with independent individuals only). The 10 repetitions were chosen to explore the range of heritability values obtained using parent–offspring regressions. Model selection may indeed be expected to differ when estimated heritability values are high and low (i.e., for high and low expected parent–offspring resemblance, respectively). We therefore analyzed the restricted datasets for which estimated heritability was the lowest (three sets) and highest (three sets), closest to the mean value (two sets), and intermediate in the lowest (one set) and highest half of values (one set) (Appendix). We then compared the models selected for the restricted datasets (with one recruit per nest) and the full recruit dataset. We conducted this comparison only for the data with parental dispersal status in the year of offspring birth here, but it could be extended to the data with parental natal dispersal status. See Doligez et al. 2009 for further discussion about other sources of data non-independence (e.g., presence of the same parents in different years).

The validity of the starting models was checked in U-CARE using GOF tests for multi-state capture–recapture data (Choquet et al. 2005; Pradel et al. 2003, 2005). These tests examine (1) whether past encounter history affects the future of individuals when released in the same conditions (test 3G), and in particular transience (effect of past capture; test 3G.Sr) and memory (effect of past state; test WBWA) processes, and (2) whether being caught at occasion *t* affects the future of individuals (test M), and in particular short-term trap-dependence (effect on capture probability in the next occasion $t + 1$; test M.ITEC) (Pradel et al. 2005). Model notation was extended from Lebreton et al. 1992 and Nichols and Kendall 1995. Model selection was performed using E-SURGE (Choquet et al. 2009) and was based on quasi-Akaike Information Criteria corrected for small sample size (QAICc; Anderson and Burnham 1994). We started from model $S_{s\times a(2,3)\times id}$ $T_{s\times[a(1)\times sdp\times opd+a(2,3)\times id]}$ $P_{s\times a\times id}$ (53 parameters), which included full sex and age effects, dispersal status of both parents on the first transition parameter (age 0 to age 1) and individual dispersal status thereafter on all parameters, down to the simplest, constant model, testing intermediate models including additive effects. Juvenile survival (from age 0 to 1) was here fixed to 1 in all analyses, since only recruits, i.e., individuals surviving up to at least age 1, were considered. However, the total number of models to be tested in this case was above 10^5. Therefore, in order to reduce the number of models, we used a simplified "step-

down" procedure: first, we selected models on capture probabilities while keeping the original parametrization of survival and transition probabilities; second, we simplified survival probabilities using the parametrization of capture probabilities selected in the first step; and, finally, we simplified transition probabilities using the parametrization of survival probabilities selected in the second step (see Doherty et al., this volume, for a discussion about the validity of such a model selection procedure). Models with QAICc of less than five units difference with the best model were kept during the temporary steps of model selection in order to avoid excluding potentially good candidate models. Because we aimed here at comparing the level of parent–offspring resemblance in dispersal propensity obtained using CMR models and parent–offspring regressions, we did not present here the full model selection but focused on the best models selected.

Results

Parent–offspring regressions

Dispersal status of both parents significantly influenced offspring natal dispersal probability in the subsequent year(s). Offspring dispersal probability was higher for dispersing compared to philopatric parents (Fig. 1, white bars; Appendix), both when considering parental dispersal status in the year of offspring birth ($F_{1,404} = 20.47$, $P < 0.0001$ and $F_{1,404} = 14.10$, $P = 0.0002$ for maternal and paternal status, respectively) and parental natal dispersal status ($F_{1,171} = 17.03$, $P < 0.0001$ and $F_{1,171} = 6.61$, $P = 0.011$ for maternal and paternal status, respectively), accounting for offspring sex in each case. When considering parental dispersal status in the year of offspring birth, offspring subsequent dispersal probability was highest when both parents were dispersers, leading to a significant interaction between maternal and paternal dispersal status ($F_{1,404} = 9.30$, $P = 0.0024$).

When considering parental dispersal status in the year of offspring birth, the estimated heritability level of dispersal was 0.30 ± 0.07 (not different between father–offspring and mother–offspring regressions; Doligez et al. 2009). When considering parental natal dispersal status, estimated heritability level was higher: 0.47 ± 0.10 (again, not different between father–offspring and mother–offspring regressions) (Table 1; see Doligez et al. 2009 for further details).

Animal models

Animal models confirmed a significant heritability of dispersal when discriminating genetic from other effects (parental and environmental effects combined). When all dispersal events were considered (i.e., combining natal and breeding dispersal), the additive genetic and residual variances (95% CI) were 0.024 (0.020–0.029) and 0.186 (0.180–0.191), respectively, corresponding to a heritability value h^2 of 0.19 (0.16–0.21) (Table 1). When only natal dispersal events were considered, the additive genetic and residual variances were 0.053 (0.042–0.064) and 0.166 (0.155–0.176), respectively, corresponding to a heritability value h^2 of 0.39 (0.31–0.47) (Table 1). In both cases, males had a lower dispersal probability compared to females, and in the first case, dispersal probability decreased with age. Importantly, the global heritability levels were not fully identical in parent–offspring regressions and animal models. In parent–offspring regressions, this global level corresponded to regressions of offspring natal dispersal status on a mixture of parental natal and breeding dispersal status, while in animal models, it corresponded to a mixture of natal and breeding dispersal heritability. Natal dispersal heritability estimates were however directly comparable with both methods.

CMR models: GOF tests, selected models and parameter estimates

GOF tests

The global GOF tests were highly significant for all datasets (full recruit datasets with parental dispersal status in the year of offspring birth and parental natal dispersal status and 10 restricted subsets to test the effect of sibling non-independence): $845.2 < \chi^2 < 2{,}123.2$, $232 < df < 332$, all $P < 0.001$. This was due to strong apparent transience (test 3G.Sr: $479.4 < \chi^2 < 1{,}210.3$, $42 < df < 46$, all $P < 0.001$) and, to a lesser extent, immediate trap-dependence effects (test M.ITEC: $35.6 < \chi^2 < 63.0$, $26 < df < 40$, all $P < 0.02$ except for the data with parental natal dispersal status: $P = 0.10$). The WBWA ("memory") tests were not significant ($9.67 < \chi^2 < 32.71$, $27 < df < 38$, all $P > 0.71$). However, these apparent transience and trap-dependence effects were probably artificial, due to the way the datasets were built: taking into account recruits only eliminates transients by definition. The current multi-state GOF tests may therefore not be fully adapted to our data. When GOF tests were performed on the same datasets in which the first capture for each individual was deleted, all tests became non-significant for both the data with parental dispersal status in the year of offspring birth (general GOF test: $\chi^2 = 146.7$, $df = 184$, $P = 0.98$; test 3G.Sr: $\chi^2 = 38.3$, $df = 43$, $P = 0.68$; test M.ITEC: $\chi^2 = 15.8$, $df = 18$, $P = 0.60$) and data with parental natal dispersal rate (general GOF test: $\chi^2 = 89.3$, $df = 129$, $P = 0.99$; test

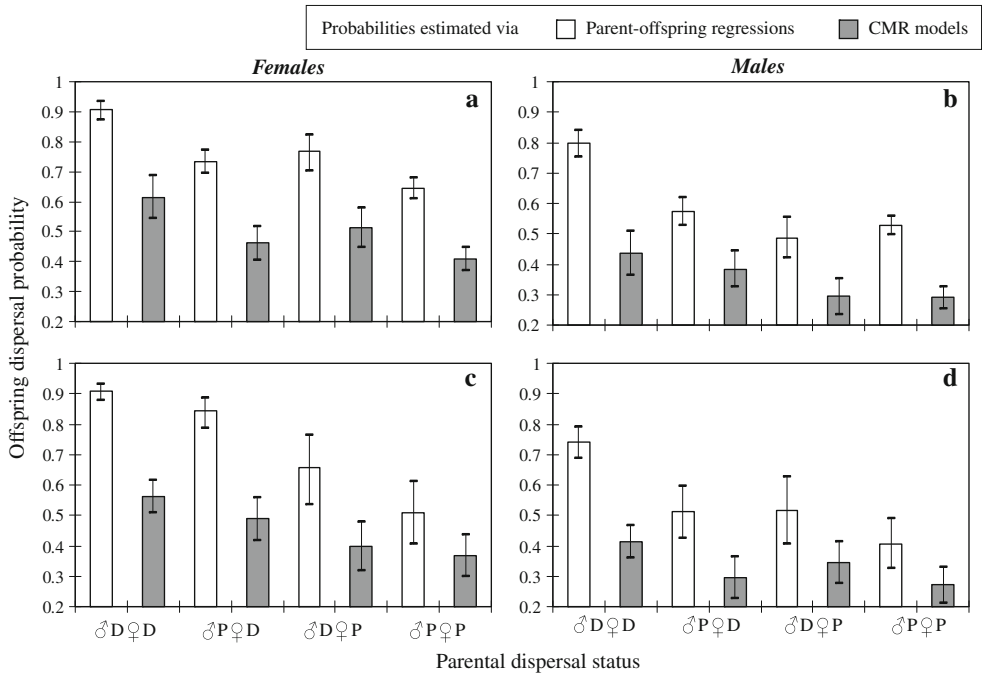

Fig. 1 Offspring dispersal probabilities (±1 SE) according to parental dispersal status obtained via parent–offspring regressions (*white bars*) and CMR models (*gray bars*), for females (**a**, **c**) and males (**b**, **d**). **a**, **b** Parental dispersal status in the year of offspring birth; **c**, **d** parental natal dispersal status. *D* Dispersing parent, *P* philopatric parent. Parameter estimates for CMR models come from the selected model $S_{a(2,3)\times id}\ T_{a(1)\times sdp\times opd\ +\ a(2,3)\times id+sdp/id\times s}\ P_{s+a\times id}$

Table 1 Comparison of dispersal heritability estimates obtained via parent–offspring regressions and animal models, using the threshold model (Falconer and Mackay 1996; see Roff 1997 and Doligez et al. 2009 for more details)

Model	$h^2_{0,1}$	CI($h^2_{0,1}$)	h^2	CI(h^2)
Global heritability level: p(disp) = 0.30				
Parent–offspring regression	0.19	0.10–0.27	0.30	0.16–0.44
Animal model	0.12	0.10–0.13	0.21	0.17–0.23
Natal dispersal alone: p(disp) = 0.60				
Parent–offspring regression	0.29	0.17–0.41	0.47	0.28–0.66
Animal model	0.24	0.19–0.29	0.39	0.31–0.47

$h^2_{0,1}$ (with respect to h^2) is the heritability measured on the 0,1 scale (with respect to the underlying continuous scale), CI are the associated 95% confidence intervals. p(disp) is the proportion of dispersing individuals in the population used to compute h^2

3G.Sr: $\chi^2 = 37.1$, $df = 40$, $P = 0.60$; test M.ITEC: $\chi^2 = 9.9$, $df = 14$, $P = 0.77$; full recruit data in both cases). For this reason, and because apparent transience is taken into account by including an age effect in our models, we proceeded with model selection by correcting QAICc values by the overdispersion parameter $\hat{c}$ = (general GOF test − 3G.Sr test)/remaining df (Pradel et al. 2005). Here, $\hat{c} = 3.19$ and 1.93 for the data with parental dispersal status in the year of offspring birth and parental natal dispersal rate, respectively.

Model selection and parameter estimates for full recruit datasets

Several best models were selected on the full recruit data with parental dispersal status in the year of offspring birth and parental natal dispersal status, but their structure was very close in all cases (Table 2). Transition probability between age 0 and 1 depended on the interaction between the dispersal status of both parents and subsequent transition probabilities depended on the dispersal status of the individual, with an addititional interaction between sex and dispersal status in both cases: $T_{a(1)\times sdp\times opd+a(2,3)\times id+sdp/id\times s}$ (note that *sdp* and *id* correspond to the dispersal status in the capture history at different ages: age 0 for *sdp* and subsequent ages for *id*). The model without dispersal status of the opposite-sex parent could, however, not be excluded for the data with parental natal dispersal status ($T_{a(1)\times sdp+a(2,3)\times id+sdp/id\times s}$; QAICc = 2,508.8 and 2,507.0 for the two models, respectively; Table 2). In all cases, as for parent–offspring regressions, offspring dispersal probability was higher for dispersing compared to philopatric parents (Fig. 1, gray bars; Appendix) and higher for female compared to male offspring. In the case of parental dispersal status in the year of offspring birth, the dispersal status of the opposite-sex parent seems to affect offspring dispersal probability more than the same-sex parent, which leads to the interaction between the dispersal status of the two parents.

Survival probability depended on the interaction between dispersal status and age (2 year-old versus older, juvenile survival *a(1)* being in this case fixed to 1): $S_{a(2,3)\times id}$ (Table 2). However, survival rate of philopatric individuals between age 1 and 2 was non-estimable (fixed to 1), while the other three values were similar. However, forcing survival to depend on age and dispersal status in an additive way, or deleting one or the other effect, strongly increased model QAICc. Therefore, we kept the selected parametrization for survival here. When the first observation for each individual was deleted, the selected model included a constant survival (although models with age or dispersal status alone could not be excluded). The reason for survival probability of philopatric individuals between age 1 and 2 being non-estimable in the general models is not clear and needs further exploration. It should, however, not affect the results since model selection and parameter estimates for transition and capture probabilities were little affected by survival parametrization (results not detailed here).

As expected, detection probability strongly depended on dispersal status in addition to sex and age: $P_{s+a\times id}$ for the data with parental dispersal status in the year of offspring birth and $P_{a\times(s+id)}$ for the data with parental natal dispersal status (Table 2). Detection probability was always higher for females compared to males and for philopatric compared to dispersing individuals (Fig. 2). In addition, detection probability increases with age for dispersing individuals, while it is constantly high for philopatric individuals (Fig. 2).

Restricted recruit datasets testing for the effect of sibling non-independence

For all 10 restricted data subsets including only one recruit randomly selected for nests having recruited several siblings, the same model as for the full recruit data, i.e., $S_{a(2,3)\times id}$ $T_{a(1)\times sdp\times opd+a(2,3)\times id+sdp/id\times s}$ $P_{s+a\times id}$ (with juvenile survival fixed to 1), was selected, although the model with no effect of the dispersal status of the opposite-sex parent on the first transition probability was also retained. This strongly suggested that the non-independence of sibling recruits in the full data did not influence model selection and therefore was not a major issue here.

Differences in estimates obtained via the different models

As expected, heritability levels were lower when estimated using animal models compared to parent–offspring regressions, with a reduction of 30% for global dispersal heritability and 17% for natal dispersal heritability. However, heritability always remained significant. Furthermore, in all cases, offspring dispersal probability was lower when estimated via CMR models compared to parent–offspring regressions, for both sexes and both parental dispersal status (Fig. 1). Offspring dispersal probability varied between 0.51 and 0.91 for females and 0.40 and 0.80 for males when estimated via parent–offspring regressions,

Table 2 CMR models selected for the full recruit data with parental dispersal status in the year of offspring birth and parental natal dispersal status

S	*T*	*P*	QAICc	Δ QAICc	NP	Deviance
Parental dispersal status in the year of offspring birth						
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*s + a × id*	3,575.67	0.00	22	11,265.17
a(2,3) × id	*a(1) × sdp × opd + a(2,3) × id + sdp/id × s*	*s + a × id*	3,576.44	0.77	22	11,267.64
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*a × [s + id]*	3,577.26	1.59	24	11,257.34
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*s + a × id*	3,577.47	1.80	23	11,264.47
[a(2,3) × id] + s	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*s + a × id*	3,577.59	1.92	23	11,284.83
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s*	*s + a × id*	3,577.81	2.14	20	11,284.89
Parental natal dispersal status						
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s*	*a × [s + id]*	2,507.01	0.00	25	4,740.42
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s*	*a × id*	2,507.29	0.28	22	4,752.90
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*a × [s + id]*	2,508.74	1.73	27	4,735.77
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s*	*id × [s + a]*	2,508.80	1.79	22	4,755.79
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s + sdp × opd*	*a × id*	2,508.81	1.80	24	4,747.87
a(2,3) × id	*a(1) × sdp + a(2,3) × id + sdp/id × s*	*s + a × id*	2,508.96	1.95	20	4,764.05
a(2,3) × id	*a(1) × sdp × opd + a(2,3) × id + sdp/id × s*	*a × [s + id]*	2,510.21	3.20	27	4,738.61

In both cases, the models presented are those with QAICc of less than two units difference with the best model, plus the next model. Survival (*S*), transition (*T*) and capture (*P*) probabilities depending on age (*a*, differentiating 1, 2 and 3 or more years old individuals), sex (*s*), individual dispersal status (*id*) and parental dispersal status (same-sex parent: *sdp*, opposite-sex parent: *odp*). *Δ QAICc* difference between the QAICc values of the model considered and the best model, *NP* number of parameters. Note that juvenile survival $S_{a(1)}$ is fixed to 1 here since we considered only recruits, i.e., individuals that survived at least up to age 1. See text for further details

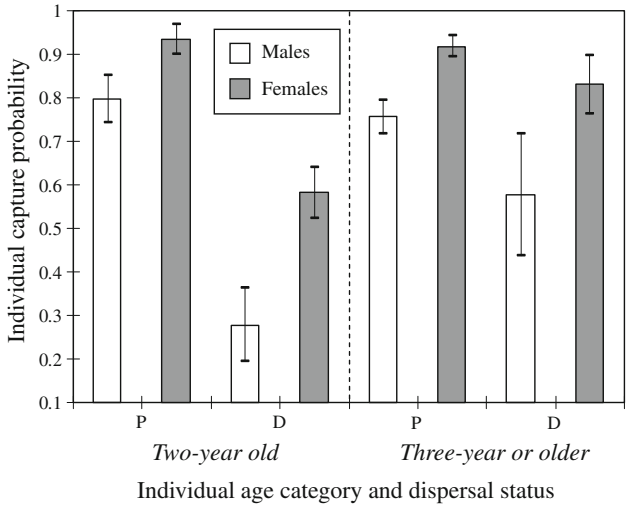

Fig. 2 Individual capture probability (±1 SE) according to sex, age and dispersal status, for individuals aged 2 years or more. *D* Dispersing individual, *P* philopatric individual. Parameter estimates come from model $P_{s+a\times id}$ for capture probability on data with parental dispersal status in the year of offspring birth, after the first capture was deleted for all individuals. This was done in order to ensure valid GOF tests and precise parameter estimates since the capture probability of some yearling categories appeared to be non-estimable in CMR models on full recruit data. No capture probability was therefore estimated here for yearlings

and between 0.37 and 0.62 for females and 0.27 and 0.44 for males when estimated via CMR models on full recruit data. Depending on sex and parental dispersal status (natal dispersal or dispersal in the year of offspring birth), offspring dispersal probability was reduced by 33–45% in CMR models (Fig. 1). However, and more importantly, the increase in offspring dispersal probability for a dispersing compared to a philopatric pair was similar for parent–offspring regressions (1.52 and 1.41 for males and females, respectively) and CMR models (1.51 and 1.50 for males and females, respectively), for the data with parental dispersal status in the year of offspring birth. It was slightly reduced for the data with parental natal dispersal (parent–offspring regressions: 1.83 and 1.79; CMR: 1.53 and 1.52, for males and females, respectively). In other words, accounting for imperfect detection probability did not change the observed pattern of parent–offspring resemblance in dispersal probability.

Discussion

Estimates of parent–offspring resemblance and heritability of dispersal probability

All three methods used here showed significant parent–offspring resemblance and/or heritability of between-patch dispersal propensity in our Collared Flycatcher population. Offspring of dispersing parents were more likely to disperse than offspring of philopatric parents. Comparisons of dispersal status of genetically unrelated individuals sharing similar small-scale environmental conditions (offspring and neighboring breeders) using simple regressions suggested that genetic (and/or parental) effects explain a significant part of the observed parent–offspring resemblance (Doligez et al. 2009). This was confirmed by animal models. Taking into account imperfect individual detection with capture–recapture models (Lebreton et al. 1992) did not change the main results obtained here from quantitative genetic models, even though individual detection probability appeared both sensibly lower than 1 and heterogeneous between individuals depending on dispersal status, sex and age. Dispersing individuals were indeed always less likely to be detected/captured compared to philopatric ones. Whether this lower detection probability is due to lower mating and/or breeding success (Pärt 1991, 1994) or temporary dispersal out of the study area (Doligez et al. 1999; Doligez and Pärt 2008; Pärt and Gustafsson 1989) needs to be investigated. Contrary to previous examples mainly addressing survival rates (Gimenez et al. 2008; Martin et al. 1995; Schmidt et al. 2002), we therefore did not observe a major change in parent–offspring resemblance levels or patterns when accounting for imperfect detection probability.

Nevertheless, we obtained different estimates using different approaches. The heritability estimates given by animal models were, as expected, lower than the estimates given by classical parent–offspring regressions. A decrease of 5–50% is usually observed in heritability values for animal models compared to parent–offspring regressions (review in Kruuk 2004; see, e.g., MacColl and Hatchwell 2003; Réale et al. 1999 for examples of comparisons of estimates between parent–offspring regressions and animal models). The decrease observed here (30 or 17%) lies within this interval. Estimates of dispersal heritability using both parent–offspring regressions and animal models in the same population (but over different time periods) have so far been obtained for only one population (Greenwood et al. 1979; McCleery et al. 2004). For this Great Tit *Parus major* population, estimates were very similar for females but differed strongly for males (females: 0.24 ± 0.10 and 0.25 ± 0.06; males: 0.50 ± 0.15 and 0.25 ± 0.06, with parent–offspring regressions and animal models, respectively). However, these studies were based on dispersal distance that may be subject to biases due to spatial constraints and spatial heterogeneity of observing long-distance dispersal movements (see Doligez and Pärt 2008; van Noordwijk 1984). For the sake of simplicity when comparing methods, maternal and environment effects have not been considered here. Because these effects have been shown to strongly affect individual dispersal decisions in

this and other populations (e.g., Doligez et al. 2004; Tschirren et al. 2007), further work is needed to separate additive genetic from other sources of phenotypic variation in dispersal using animal models (Kruuk and Hadfield 2007). The levels of parent–offspring resemblance in dispersal were similar when estimated using parent–offspring regressions and CMR models, but the estimated offspring dispersal probability was notably lower with CMR models. The reason for this lower offspring dispersal probability is unclear and needs further investigation.

Ignoring imperfect individual detection may be expected to lead to biased estimates of parent–offspring resemblance if detection probability depends not only on the dispersal status of the individual but also of its parents. In other words, only complex patterns of detection heterogeneity among individuals, involving memory effects, may bias estimates of parent–offspring resemblance. Such situations are likely to occur because dispersal often represents a single behavioral response to many potential selective pressures in a given population (Clobert et al. 2001, 2008; Dobson and Jones 1985). For instance, offspring dispersal may simultaneously be a response to local competition for offspring of dispersing parents if parental dispersal is triggered by lower competitiveness and a response to the risk of inbreeding for offspring of philopatric parents. This could lead to different dispersal modes, thus different detection probability for dispersing offspring depending on parental dispersal status. Ultimately, this could bias resemblance estimates since fewer dispersing offspring would be detected for either dispersing or philopatric parents. The absence of a clear bias in the present example does not preclude such an influence of imperfect individual detection on patterns of parent–offspring resemblance in dispersal since our CMR models did not test for the influence of parental dispersal status on offspring capture probability. In order to test for such effects, memory models in which capture probability depends on both current and previous state, i.e., here parental dispersal status at age 0, should be implemented (Brownie et al. 1993; see also Pradel et al. 2003).

Each method used here allowed us to account for a specificity of the data when estimating heritability of dispersal probability or parent–offspring resemblance but ignored other issues. First, parent–offspring regressions do not easily allow discriminating between genetic and environmental effects in natural populations (i.e., uncontrolled environments) (Kruuk 2004, 2008). Second, reliable estimates using animal models require knowledge of parentage relationships over a large number of generations (i.e., a good pedigree depth). Because animal models use the full parentage relationship information, they are, however, more powerful when they can be used than both parent–offspring regressions and our CMR approach, which use only the restricted direct links between parents and offspring. Third, neither parent–offspring regressions nor animal models can account for imperfect detection of individuals in the wild, which can lead to flawed biological inferences (Gimenez et al. 2008; Martin et al. 1995). Finally, classical CMR software do currently not account for random effects such as genetic and family effects (e.g., non-independence of siblings or same parents in different breeding events), although the incorporation of genetic random effects in CMR models has very recently been undertaken and is thus starting to become available (Papaïx et al. 2010). Computing heritability estimates of discrete traits using multi-state CMR models will be particularly relevant to compare with estimates obtained using quantitative genetic approaches (see also below).

State uncertainty: the particular case of dispersal

An additional difficulty arises when defining individual state requires comparing two successive observations of the individual. This is the case here with dispersal status, defined by comparing the successive breeding locations where the individual is captured. By construction, this leads to individual state uncertainty following non-detection (which also applies to parental dispersal status). When an individual is not caught, its subsequent dispersal status may be misassigned depending on whether the individual bred and stayed in the same patch or changed patch during the year when it was not detected, and stayed or changed patch again in the subsequent year (see Appendix). Recent CMR multi-event models take into account state uncertainty by incorporating probabilities of assigning a given state to a given observed event (Pradel 2005). However, these methods address one-step processes in which uncertainty is associated to the observation itself, i.e., without temporal delay. Here, uncertainty is linked to imperfect detection in the previous capture occasion rather than being intrinsically linked to direct observations, and thus has a somewhat different structural origin. In other words, individual dispersal state will be known with certainty when an individual is observed in two successive years, but the same state will be uncertain when the individual is not detected in the previous year(s). Therefore, applying multi-event models to address this type of uncertainty may require including memory effects, which may not be straightforward.

Including non-recruited young: data non-independence and unknown sex

Because dispersing individuals have a lower detection probability than philopatric individuals at all ages, including non-recruited fledglings in the data could be expected to increase the overall estimated offspring dispersal probabilities in CMR models, and thus reduce the

observed differences between parent–offspring regressions and CMR models. However, to what extent this change would affect the influence of parental dispersal status on offspring dispersal probability (i.e., the first transition probability), that is, the estimated level of parent–offspring resemblance in dispersal probability, needs to be investigated. Two main problems arise when considering non-recruited fledglings: (1) non-independence of siblings and (2) unknown sex of non-recruited individuals. The results obtained here on restricted recruit data suggest that sibling non-independence may not strongly affect model selection or parameter estimates. However, including non-recruited fledglings will considerably increase the level of data non-independence since nests fledged on average 3–4 young per nest (range 1–9; Doncaster et al. 1997). Because family effects cannot be included as random effects in current CMR models, an indirect approach by randomly selecting one fledged young per family may in that case also be needed to investigate the effect of data structure on GOF tests and model selection. Such an approach should, however, strongly decrease the power of analyses since juvenile survival is close to 15% (Doncaster et al. 1997).

The unknown sex of non-recruited fledglings poses problem because dispersal is sex-biased in this population as in many other bird populations (Greenwood and Harvey 1982; Paradis et al. 1998), and sex may also interact with dispersal status on detection and future dispersal probability. Because only sex-specific numbers of recruits are known, sex-specific juvenile survival and capture probabilities cannot be obtained by modeling uncertainty on fledgling sex using multi-event models due to parameter identifiability problems. Again, fledgling sex could be taken into account using indirect approaches, for instance by randomly attributing sex to each non-recruited fledgling according to observed fledging sex ratio in the population (which is known for a subset of nests; Ellegren et al. 1996; Sheldon and Ellegren 1996) and running model selection on repetitions of simulated data.

The need for non-biased heritability estimates with "capture–recapture animal models"

Based on the comparison of currently available quantitative genetic and capture–recapture methods, it is difficult and at best indirect to conclude that imperfect and heterogeneous individual detection probability does not affect the estimation of dispersal propensity heritability in our population. To predict evolutionary responses to environmental changes in terms of dispersal, it is, however, crucial to obtain unbiased heritability estimates of realised 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 under frequent imperfect individual detection (Doligez and Pärt 2008; Kokko and López-Sepulcre 2006; van Noordwijk 1984). A statistical framework combining quantitative genetic and multi-state capture–recapture approaches into "capture–recapture animal models" (O'Hara et al. 2008; Papaïx et al. 2010) is still needed to estimate heritability of discrete traits while accounting for imperfect detection in the wild. The incorporation of random effects into capture–recapture models has recently been initiated using state-space model formulation (Royle 2008), especially in the context of estimating survival heritability (Papaïx et al. 2010). We expect this integration of random effects to be one of the main developments of multi-state CMR models in the near future, allowing in particular the unbiased estimation of heritability of many life-history and behavioral traits.

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Appendix 1: Map of the study area and choice of between-patch dispersal probability as the variable of interest

Figure 3 shows the spatial configuration of the study site, which comprises 14 spatially discrete forest patches of varying size, in which nest boxes have been provided for breeding flycatchers. The patches are separated by >100 m of habitat unsuitable for breeding. Dispersal was defined here as a change of patch between successive years. We preferred this binary definition of dispersal (dispersal versus philopatry) over dispersal distance because distance was likely to be strongly constrained by the spatial configuration of our study area. In particular, when dispersal distance is used to compute heritability estimates (e.g., McCleery et al. 2004; Pasinelli et al. 2004), constraints linked to the spatial configuration of the study area may lead to biased estimates as soon as true (rather than observed) dispersal distance in the population is large compared to the size of the study area (see Doligez and Pärt 2008). Estimates of dispersal distance heritability 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

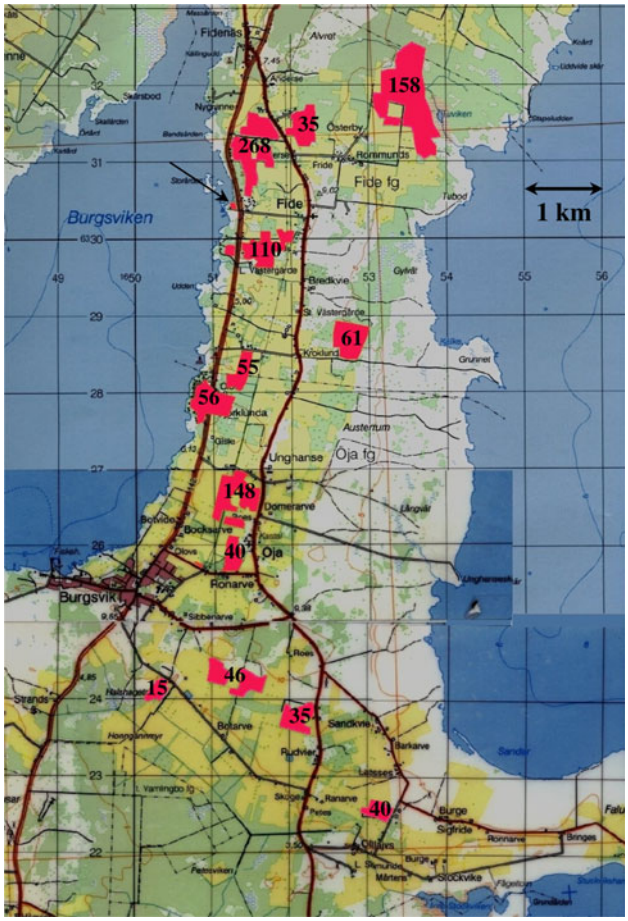


Fig. 3 The study area. The 14 breeding patches are shown in *red*, with the average number of boxes per patch (the smallest patch, comprising only a few nest boxes, is indicated by an *arrow*)

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). Conversely, in our unsaturated population, individual emigration and immigration decisions at the patch scale should be relatively unconstrained. See Doligez et al. 2009 for more discussion.

Over the 26 years of the study, we obtained data from 999 nests where the dispersal status of both parents in the year of offspring birth was known compared with 403 for which the natal dispersal status of both parents was known, corresponding to 1,404 and 576, repectively, local recruits.

See Fig. 3.

Appendix 2: Causes of individual non-capture in the study population and the issue of misclassifying individuals

In our Collared Flycatcher study population, adult capture was tightly linked to sex, breeding status and success. Adults could be missed for at least three different reasons.

1. A fraction of adults breeding in nest boxes was missed each year because of early breeding failure (on average 7.1 and 27.4% of breeding females and males are missed, respectively; Doligez et al. 2004). The fraction of missed individuals was lower for females than males because females were caught early during the breeding cycle (during incubation) while males were caught later (when feeding young).
2. An unknown, but potentially high (up to 15–20%; Gustafsson and Pärt 1990), fraction of adults did not breed each year. In this facultatively polygynous species, approximately 10% of males were estimated to attract a secondary female (Gustafsson 1989), thus leaving some males with no mate. The fraction of non-breeding individuals seemed, however, also high in females, and this may in part be due to higher success obtained when delaying breeding is compared to when starting breeding at age 1 (Gustafsson and Pärt 1990; Sendecka 2007).
3. Some individuals may have temporarily emigrated out of the study area or bred in natural holes (whose availability was highly variable among years and patches) or boxes in gardens, which were less accessible.

As a result, non-capture events were frequent in the population (see text). Because individual dispersal status was defined by comparing current to previous location, there was a risk of misclassifying individuals when they were not caught in the year before, depending on the reason for missing them. If individuals were missed because they did not breed, we considered that their dispersal status was not defined in the year when they were missed and therefore their subsequent location defined their dispersal status without ambiguity (Table 3). However, when individuals bred in the year when they were missed, their dispersal status may have been misassigned depending on their breeding location in the year preceding and following the non-capture. There were two cases of misclassification (Table 3). First, apparently non-dispersing individuals (i.e., breeding in patch A in years t and $t + 2$) may in fact have been dispersing individuals if they bred in another patch (B) in year $t + 1$. Second, apparently dispersing individuals (i.e., breeding in patch A in year t and in patch B in year $t + 2$) may in fact have been non-dispersing individuals if they had already dispersed to patch B in year $t + 1$ where they were missed. In all other cases, missed individuals were correctly classified (Table 3).

It is difficult to assess the relative importance and impact of such misclassification. In particular, the percentage of non-capture due to non-breeding was unknown, although it could have reached up to 15–20% (Gustafsson and Pärt 1990). Nevertheless, in this population as in many

Table 3 Potential cases of misassignment of individual dispersal status in the study population when comparing individual's breeding patch in years t and $t + 2$, i.e., following a non-capture event in year $t + 1$

Year t	Year $t + 1$ (non-capture event)	Year $t + 2$	Assigned status	Misclassification?
A	–	A	Non-dispersing	No
A	*A*	A	Non-dispersing	No
A	*B*	A	Non-dispersing	Yes
A	–	B	Dispersing	No
A	*A*	B	Dispersing	No
A	*B*	B	Dispersing	Yes
A	*C*	B	Dispersing	No

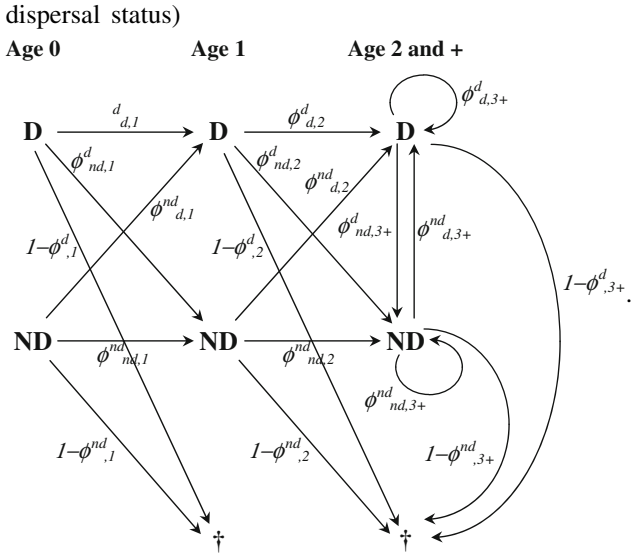
A and *B* are breeding patches of the study area, – represents individuals that did not breed. These examples are presented in the case when individuals were missed during one year, but the same reasoning applies when individuals were missed during several years in a row

others (Switzer 1993), reproductive success was one of the main determinants of individual dispersal decisions (Doligez et al. 1999; Pärt and Gustafsson 1989), while simultaneously affecting capture probability. Failed individuals were both more likely to disperse following failure and less likely to be caught during the year of failure. If we assume that most breeding individuals were missed because of reproductive failure (i.e., if we neglect temporary emigrants and individuals breeding in natural holes and garden boxes within the study area), misclassification should therefore mostly relate to the case when individuals returned to their previous breeding patch after a breeding failure in another patch (third case in Table 3). Individuals should indeed have a relatively low probability to stay in their new patch after a failure (sixth case in Table 3).

Unfortunately, there is, however, no way to discriminate between these situations or reliably assess their relative importance with the current data. In order to explore the potential impact of such individual dispersal status misassignment, detailed movement data should be obtained on non-breeding and failed individuals. This may require the use of radio-tracking devices in the field. Alternatively, simulation approaches could be used to explore different scenarios and assess the impact of different rates of misclassification on parameter estimates.

Appendix 3: Diagram of the capture–recapture models used to estimate parent–offspring resemblance in dispersal behavior

The three states in the multi-event capture–recapture models (Pradel 2005) used here were: disperser (D), non-disperser (ND) and dead (†). The first state of the capture history (initial state, age 0) corresponded to parental dispersal status since dispersal status could not be defined for juveniles (only recruits with parents of known dispersal status were included in the analysis; see text). The graph shows the transition parameters ϕ combining survival and transitions between dispersing states D and ND for the three age classes considered (survival and transitions between dispersing states were modelled separately in E-SURGE; Choquet et al. 2009). Note that $\phi_a^X = \phi_{D,a}^X + \phi_{ND,a}^X$, where X is the initial dispersal status, D and ND are the arrival dispersal status, and a is the age class. The parameters testing the existence of parent–offspring resemblance in dispersal were therefore included in parameters $\phi_{D,1}^X$ and $\phi_{ND,1}^X$ (age 0 to 1): if resemblance occurred, we predicted that $\phi_{D,1}^D > \phi_{D,1}^{ND}$ and $\phi_{ND,1}^D < \phi_{ND,1}^{ND}$ (if survival did not differ depending on dispersal status)



Appendix 4: Choice of the 10 restricted recruit datasets used to test for the effect of sibling non-independence on CMR model selection

See Fig. 4.

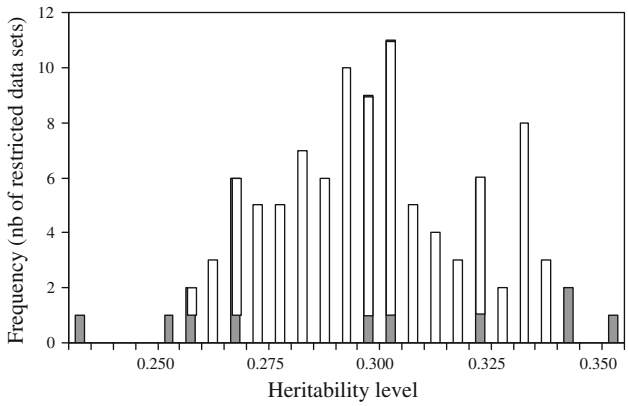


Fig. 4 Distribution of the 100 values of heritability obtained with parent–offspring regressions using restricted recruit datasets (with one randomly chosen recruit per nest) and (in *gray*) the 10 datasets chosen to test for the effect of non-independence of sibling recruits on CMR model selection and parameters estimates

Appendix 5: Estimates of parent–offspring resemblance in dispersal behavior: increase in offspring dispersal probability between philopatric and dispersing parents

See Table 4.

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Table 4 Percentages of increase in offspring between-patch dispersal probability from a philopatric to dispersing parent, depending on (1) offspring sex, (2) sex of the parent, (3) parental dispersal status considered (in the year of offspring birth or parental natal dispersal) and (4) dispersal status of the other parent (*D* dispersing, *P* philopatric)

Offspring sex	Parent	Method	Parental dispersal in the year of offspring birth		Parental natal dispersal	
			Other parent D	Other parent P	Other parent D	Other parent P
♂	Mother	P–O regr	43.5	26.2	64.2	8.8
		CR	20.2	9.3	48.8	32.7
	Father	P–O regr	45.3	27.7	39.6	−7.5
		CR	39.9	27.3	13.8	1.5
♀	Mother	P–O regr	38.1	66.1	18.4	14.1
		CR	40.8	32.1	19.6	12.8
	Father	P–O regr	7.9	29.7	23.6	19.1
		CR	15.1	8.0	33.4	25.8

Percentages of increase are computed as $(d_D - d_P)/d_P \times 100$, where d_X is the offspring dispersal probability for the considered parent of dispersing status X (X = D or P), estimated using parent–offspring regressions (P–O regr) and capture–recapture models (CR). The negative value indicates a decrease in offspring dispersal probability

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