**Testing the matching habitat choice hypothesis in nature: phenotype-environment
correlation and fitness in a songbird population**

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Abstract

The matching habitat choice hypothesis holds that individuals with different phenotypes actively select the habitats to which they are best adapted, hence maximizing fitness. Despite the potential implications of matching habitat choice for many ecological and evolutionary processes, very few studies have tested its predictions. Here, we use a 26-year dataset on a spatially structured population of pied flycatchers (*Ficedula hypoleuca*) to test whether phenotype-dependent dispersal and habitat selection translate into increased fitness, as measured by recruitment success. In our study system, males at the extremes of the body size range segregate into deciduous and coniferous forests through nonrandom dispersal. According to the matching habitat choice hypothesis, fitness of large-sized males is expected to be higher in the deciduous habitat, where they preferentially settle to breed, while the reverse would be true for small-sized males, which are more frequent in the coniferous forest. Our results showed that recruitment success in the coniferous forest increased non-linearly with body size, with males at the middle of the size range having higher fitness than both large and small-sized males. However, no clear trend was observed in the deciduous forest where males of either size had similar fitness. After empirically discarding other important processes potentially confounding matching habitat choice, as genotype- and body condition-dependent dispersal, competitive exclusion remains the most likely force shaping the nonrandom distribution of male pied flycatchers. A conclusive demonstration of the operation and occurrence of matching habitat choice in nature remains therefore to be done.

Introduction

Habitat selection and preceding dispersal decisions can strongly influence individuals' survival and reproductive success, and therefore have important consequences for many ecological and evolutionary processes (Fretwell and Lucas 1970; Cody 1984; Morris 2003). Evidence is accumulating that individuals disperse non-randomly with respect to genotype and morphological, physiological or behavioural traits (Edelaar and Bolnick 2012). Specifically, dispersal can be affected by attributes such as age, sex, dominance rank, body size and condition, physiological/biomechanical dispersal capacities, or personality, thereby leading to phenotype-dependent dispersal and settlement (reviewed in Clobert et al. 2009). Many empirical studies have revealed an adaptive relationship between the phenotype of individuals and the location of settlement, and shown that organisms may move non-randomly across environments to settle in those habitats that may enhance individual performance (e.g., Blondel et al. 1999; Garant et al. 2005; Dreiss et al. 2012). Along this line, the matching habitat choice hypothesis, unlike other forms of phenotype-dependent dispersal (e.g. size-dependent dispersal driven by competitive exclusion of less competitive phenotypes towards less appreciated habitats, or increased dispersal propensity or distance in bold, explorative animals), states that individuals –assumed to be able to assess fitness prospects in each habitat prior to settlement– modify habitat selection according to their phenotype so that they settle in the habitats with the highest fitness prospects (Holt and Barfield 2008; Edelaar et al. 2008).

Under the hypothesis' predictions, similar phenotypes are expected to have similar habitat preferences and segregate together in the environments they are best suited to, and further increase the fitness benefits of habitat selection (Edelaar et al. 2008). Thus, matching habitat choice may contribute to the spatial sorting of

phenotypes through phenotype-dependent dispersal, thereby leading to local differentiation of fitness-related traits and even potentially driving sympatric speciation (Edelaar et al. 2008; Holt and Barfield 2008).

Despite its likely ecological and evolutionary implications (see Edelaar et al. 2008), to the best of our knowledge only three studies have examined the matching habitat choice hypothesis or evaluated its evolutionary consequences (but see Bolnick and Otto 2013 for a theoretical outline). The evidence from two experimental studies has so far provided positive support for the hypothesis' predictions by showing that manipulation of colour phenotype in the pygmy grasshopper (*Tetrix subulata*) influences microhabitat choice and affects subsequent fitness (Wennersten et al. 2012; Karpestam et al. 2012). In addition, a field study has shown that female barn owls (*Tyto alba*) showing reddish and whitish phenotypes settle in alternative habitats, and that such colour-dependent habitat choice apparently increases fitness and reinforces local adaptation (Dreiss et al. 2012). Yet, to our knowledge, the hypothesis' predictions remain to be comprehensively tested under field conditions.

A possible explanation for the scarcity of studies is that testing for matching habitat choice may be challenging, particularly in the wild, because: (1) an extensive effort is usually required, as individuals' traits need to be measured and then linked to departure and settlement decisions; (2) its effects are typically subtle and may not be readily detectable in natural environments; (3) convincing tests to demonstrate that it actually occurs, such as phenotype or environment manipulation or habitat translocations, are not easy to perform due to logistic constraints; and (4) it may be hard to distinguish from several additional processes that also may result in the assortment of phenotypes to different habitats (e.g., selective mortality and phenotypic plasticity; Garant et al. 2005; Edelaar et al. 2008). In addition, providing evidence that differential

habitat choice translates into enhanced fitness would be required. Consequently, matching habitat choice remains to be unequivocally demonstrated in the field, and accumulating evidence from empirical studies is needed to determine its relative occurrence in nature.

The pied flycatcher is a long-distance migrant passerine using cavities in temperate forests as breeding sites. Although the species is able to reproduce in a wide array of forest habitats, the first males arriving from wintering quarters settle preferentially in deciduous forests (Alatalo et al. 1985; Lundberg and Alatalo 1992) possibly because they may find it easier to find suitable nesting sites or food. In Central Spain, however, males (and, to a lesser degree, females) move from coniferous to deciduous forests and *vice versa* according to their body size (Camacho et al. 2013). By following locally-born birds from fledging to their first breeding attempt, as well as the recruiting individuals from cross-fostering experiments, we have shown that natal habitat preference induction strongly influences dispersal decisions of pied flycatchers (Camacho et al. submitted). Natal habitat preference may act concurrently with phenotype-dependent dispersal, since large-sized individuals commonly settled to breed in the deciduous forest, the reverse being true for small-sized males, which are more often found in the coniferous site (see Supplementary Material 1).

Other studies, from the community to the individual level, have reported similar observations that large and small birds are generally found in deciduous and coniferous forests, respectively (Gaston 1974; Price 1991; Forstmeier et al. 2001; Korner-Nievergelt and Leisler 2004). In an attempt to link individual morphology to function and, ultimately, performance, some authors have suggested that larger individuals may prefer larger prey items and, therefore, use the habitats holding a higher proportion of large arthropods (i.e. deciduous forests; Price 1991; Forstmeier et al. 2001). In contrast,

small individuals may preferentially use coniferous habitats because their small body size could enable them to forage most efficiently in the outermost twigs of coniferous trees (Gaston 1974; Korner-Nievergelt and Leisler 2004). In the pied flycatcher, the average prey size is smaller in coniferous than in deciduous forests (Lundberg et al. 1981) and, although adaptive size-related dietary or microhabitat shifts have not been reported, individuals of different size might specialize on different habitats or prey species and perform differently in coniferous and deciduous forests, as occurs in other songbirds (Forstmeier et al. 2001).

In this study, we examined the fitness consequences of breeding habitat choice of male pied flycatchers to test whether small and large-sized individuals are suited to different habitats and, therefore, as predicted by the matching habitat choice hypothesis, settle accordingly to maximize fitness. The coniferous/deciduous study plots occupied by pied flycatchers for more than two decades provides us with a good opportunity to address matching habitat choice, as (1) it represents a pseudoexperimental setting in which, since artificial nest boxes for pied flycatchers were provided in the coniferous forest, all individuals are assumed to be able to assess the same set of environments (Camacho et al. submitted); (2) an association between male size, a highly heritable trait (Lundberg and Alatalo 1986; Potti and Merino 1994), and breeding habitat exists, (3) it results from size-dependent dispersal and settlement (Camacho et al. 2013), and (4) annual data on individual reproductive success are available.

Under matching habitat choice, we would expect that the fitness of large-sized males would be higher in the deciduous forest, where they preferentially settle to breed, regardless of their origin. On the other hand, fitness of small-sized males is expected to be higher in the coniferous habitat, where they are more frequently found. It should be noted that matching habitat choice may operate at both the departure and the settlement

stage of dispersal, since individuals may decide to stay in their natal habitat following a positive assessment of their fitness prospects, or to move to another habitat due to e.g. a perceived mismatch between their phenotype and the natal habitat. To evaluate the above mentioned expectations, we followed locally-born individuals until recruitment to investigate whether body size-dependent habitat choice of males had an effect on the recruitment success of their offspring. In addition, we assessed the influence of alternative processes potentially confounding matching habitat choice, such as genotype- and body condition-dependent dispersal (Edelaar and Bolnick 2012).

Materials and methods

Study system and data collection

We used data obtained in a long term study (1988–2013) of a pied flycatcher population in central Spain inhabiting deciduous and coniferous forest plots located 1.1 km apart (see Camacho et al. 2013). The deciduous forest (DF) is a highly heterogeneous and structurally complex habitat of 9.3 ha dominated by old oaks (*Quercus pyrenaica*) at a mean density of 460 trees ha⁻¹. Resource exploitation ceased over 50 years ago, and a dense ground cover and understory re-evolved, mostly oak saplings, *Erica arborea*, *Cistus laurifolius* and *Crataegus monogyna* (0.5–3 m high; mean cover 80%). The coniferous forest (CF) represents a more homogeneous habitat of 4.8 ha characterized by a monoculture of Scots pine (*Pinus sylvestris*) at a mean density of 200 trees ha⁻¹ and scattered *Cupressus arizonica*, *Pinus pinaster* trees. Sparse shrub cover of *Cistus laurifolius* and *Crataegus monogyna* is restricted to open areas (0.5–2 m high; mean cover 5%). At the beginning of the study, pied flycatchers were confined to natural tree holes in DF (Potti and Montalvo 1990) and no cases of breeding had been observed in CF due to the absence of natural cavities. In 1984 (DF) and 1988 (CF), wooden nest

boxes (172 and 81, respectively) at a mean distance of 20 m (SD 9.2) were provided and pied flycatcher densities gradually increased in both habitats (Camacho et al. 2013).

After the first males arrived from spring migration, nest boxes were regularly checked to determine exact laying dates, clutch sizes, hatching dates and numbers of fledged young. Nestlings surviving from hatching to day 13 were then marked with numbered metal rings and their ectoparasite loads were recorded (Merino and Potti 1995). Adults were captured while incubating (females) or feeding nestlings (both sexes) by means of a nest box trap. All adults were marked with a unique combination of metal and colour-coded rings and measured for body mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.05 mm) as a proxy for body size (Senar and Pascual 1997). Each male was ascribed to the habitat in which it settled to breed, regardless of his origin. Breeding densities were determined by quantifying nest box occupancies by pied flycatchers (Blondel et al. 1999; Garant et al. 2005).

Fitness measurement

To characterize fitness, as measured as the annual number of recruits relative to that of non-recruiting fledglings (i.e. recruitment success), we used a longitudinal dataset containing all the information on each individual (annual data on reproductive success are shown in Supplementary Material 2). In contrast to males, the settlement patterns of female pied flycatchers are determined by where they can find males that have already found a suitable cavity for nesting (Lundberg and Alatalo 1992). Hence, female assortment across habitats would be more a reflection of male distribution than of female size-based settlement decisions. As expected, female dispersal and habitat selection is unaffected by body size in our study system (Camacho et al. 2013) and, because this is the main prerequisite of the matching habitat choice hypothesis, females

were hence not further considered. Because habitat familiarity, previous breeding experience and age-related improvements in individual performance may influence reproductive output and subsequent fitness (e.g., Doligez et al. 1999; Brown et al. 2008; Limmer and Becker 2010) and thus potentially confound matching habitat choice (e.g., potentially masking a fitness mismatch between phenotype and environment), only first-time breeders of known origin were considered, whether they move from their natal habitat to a new one (dispersers) or remain in their natal habitat to breed (philopatric). All nests that were known replacement clutches (i.e. laid after failure (1.7%) or predation (10.1%) of the first one) were omitted from analyses. Breeding date is likely the most important determinant of breeding success and recruitment in *Ficedula* flycatchers (Lundberg and Alatalo 1992; Potti et al. 2002) and thus variation in success of replacement clutches may likely reflect the effects of extremely delayed timing, rather than a possible mismatch between phenotype and habitat type. All nests subjected to experimental manipulations (e.g., cross-fostering) were also omitted. Because of discontinuities in the intensity of fieldwork, the years 2002 and 2003 were omitted from the dataset. As recruits may postpone their first reproduction until the second or, more rarely, third year of life (Potti and Montalvo 1991), all nests of males breeding between 1999 and 2003 were excluded from analyses to avoid underestimating their true recruitment success (Potti et al. 2013). For the same reason, all nests of males breeding beyond 2010 were also excluded. Dispersal outside the study plots is an extremely rare event (pers. obs. from non-systematic explorations of surrounding areas); therefore, we are confident that the spatial scale of the study area is not a source of bias in recruitment rates. Overall, for fitness analyses we used data from the first reproductive attempts by 304 individuals (202 and 102 males in DF and CF, including 27 and 29 dispersers, and 175 and 73 philopatric birds) belonging to 23 cohorts (see also Table 1).

Familial resemblance in dispersal patterns and effect of body condition

Genetic-based variation in dispersal or the body condition of the first-time breeders could lead to individual variation in the propensity to exchange habitats, thus potentially confounding matching habitat choice (Edelaar and Bolnick 2012). Therefore, we examined if there is detectable familial resemblance and influence of body condition in the propensity to 'stay' (i.e. returning to the natal forest at the first breeding attempt) or exchange habitats (oak vs. pine or *vice versa*), and also examined the similarity in dispersal movements of full sibs. We are aware that these tests may be considered as crude approximations to familial resemblance in dispersal propensity due to the local scale of our sampling. To assess differences in body condition between dispersers and philopatric individuals, we also used data from first-time breeders, as pied flycatchers rarely (<1%) exchange habitats after natal dispersal (Camacho et al. 2013).

Data analyses

To investigate matching habitat choice, we fitted a Generalized Linear Mixed Model (GLMM; binomial errors, logit link function) jointly including the number of recruits and the number of non-recruiting fledglings as the response variable. Tarsus length and its quadratic term (to test for linear and non-linear relationships respectively; Fig. 1), breeding habitat and their interactions were included as predictor variables. The interaction between phenotype and habitat is considered to be an important test of the hypothesis (Karpestam et al. 2012; Fig. 1), as it would indicate whether males of a particular size perform differently in a particular habitat than do others. Furthermore, its shape will reveal whether males preferentially settle in the habitat type in which their particular phenotype performs best, thereby supporting matching habitat choice.

Breeding date was included as a covariate in the model, as it is one of the most important determinants of breeding success and recruitment in *Ficedula* flycatchers (Potti and Montalvo 1991; Lundberg and Alatalo 1992; Potti et al. 2002). Nest box and female identity were included in the model to account for territory quality and mate quality variation, respectively, and we also included year as a random effect to account for annual heterogeneity in breeding performance. The GLMM was fitted in R 2.14.0 ([http://wwwR-project.org](http://www.R-project.org)) using the function *lmer* of the package 'lme4' (Bates et al. 2011). Selection of the minimum adequate models was carried out by sequentially dropping non-significant terms from fully saturated models (containing all main effects and interactions), in a hierarchical way, starting with the least significant order terms.

Initial exploratory analyses showed no significant influence of factors potentially affecting fitness, as mating status (i.e. primary or secondary broods of bigamous males; Lundberg and Alatalo 1992), ectoparasite loads in nests (i.e. numbers of blowfly larvae and prevalence of blood-sucking mites; Merino and Potti 1995), breeding density, or male age at first breeding (results from the GLMMs are shown in Supplementary Material 3); these terms were hence not further considered in the models. Other potentially important factors, such as natal habitat, dispersal behaviour (i.e. disperser *vs.* philopatric) and their interaction also dropped from exploratory models. On the other hand, dispersers are often more likely to produce dispersing young than philopatric individuals (Bélichon et al. 1996), which may lead to underestimation of dispersers' fitness (Doligez and Pärt 2008). However, initial analyses on recruitment success showed no differences in local recruitment between disperser and philopatric males breeding in both study environments (authors' unpubl. data).

To test whether body condition affects the propensity of males to exchange habitats irrespective of their origin we fitted a linear model (normal distribution, identity

link function) including body mass of locally born males at their first breeding as the response variable. Tarsus length was included as a covariate and dispersal behaviour (disperser vs. philopatric) as a fixed effect. To test for familial resemblance in the propensity to stay or exchange habitats we fitted a GLMM (binomial errors, logit link function) as explained above with son dispersal behaviour coded as a binary response variable (0 = stay in natal habitat, 1 = disperse from natal habitat) and father dispersal behaviour (0, 1) as the explanatory variable. As male movement between forests is nonrandom with respect to body size and directionality (Camacho et al. 2013), we included in the model son tarsus length and natal habitat as a covariate and a fixed effect, respectively. Family identity and son cohort were also included as random effects. Similarity in dispersal movements of full sibs were examined by means of a chi-square test with Yates continuity correction. Sample sizes differ among analyses because not all data were known for all individuals.

Results

Male size, habitat choice and fitness

Local males breeding in CF were significantly smaller than those from DF (mean $\pm$ SE: 19.24 ± 0.04 vs. 19.37 ± 0.03 ; GLM: $t_{1,303} = 2.09$, $P = 0.038$). Linear and non-linear interactions between male size and forest type (Fig. 2) had a significant influence on recruitment success, after controlling for the significant effect of breeding date (Table 1). Even though the interaction terms indicate that male fitness varied spatially according to body size, fitness variation was not in line with matching habitat choice' predictions. Recruitment success in CF increased non-linearly with body size, with males at the very middle of the size range having higher fitness than both large and small-sized males. However, no clear trend was observed in DF, where males of either

size had similar fitness (Fig. 2). A test of the relationship between recruitment success and body size including only the recruits remaining in the natal plot showed similar results to those obtained by including also the dispersers from the nearby plot (details not shown). Fitness effects of habitat matching might be mediated via laying date (e.g., advantage of larger males in DF if they would breed earlier therein than in CF, and *vice versa* for smaller males). However, results remained unaltered after excluding the laying date from the GLMM.

Familial resemblance in dispersal patterns and effect of body condition

Results of the GLMM (number of males: 238; number of families: 164; number of cohorts: 21; see Table 2) showed no influence of father dispersal behaviour on the staying/dispersing propensities of their sons (estimate $\pm$ SE: 0.12 ± 0.38 , $P = 0.75$), after controlling for the significant effect of son origin (0.88 ± 0.34 , $P = 0.009$) and removing the non-significant effect of son tarsus length (0.48 ± 0.31 , $P = 0.12$) from the final model. There was also no association between full sibs in their dispersal behaviour (29 sibling pairs stayed in their natal forest vs. 15 dyads differing in their direction of movement: $\chi^2_1 = 1.83$, $P = 0.18$). The propensity of males to exchange habitats was not dependent on body condition, as dispersers ($n = 92$) and philopatric birds ($n = 342$) had similar body masses ($t_{1,463} = -0.16$, $P = 0.88$) after controlling for the significant effect of tarsus length ($t_{1,463} = 6.66$, $P < 0.0001$).

Discussion

Male pied flycatchers move between coniferous and deciduous forests according to body size (Camacho et al. 2013) and, as shown here, their size influenced recruitment success differently in each forest type. Males are therefore assumed to have the

307 opportunity to improve their fitness by moving between habitats. Nevertheless,
308 recruitment success following habitat choice was not in line with the observed
309 movement propensities of males in relation to size, suggesting that habitat matching is
310 little or not influential for the spatial sorting of pied flycatcher phenotypes. We have
311 also shown that the dispersal propensity of males do not seem to be affected by
312 individual quality (i.e. body condition) or influenced by their genetic background.
313 Therefore, potentially confounding effects of matching habitat choice in relation to
314 individual variation in dispersal propensities have been discarded.

315 Male pied flycatchers of similar body size segregate together (Camacho et al.
316 2013) so that the central prerequisite of the matching habitat choice hypothesis is
317 fulfilled (Edelaar et al. 2008). Nonetheless, it should be noted that associations between
318 phenotype and environment are not unique to matching habitat choice, but may also
319 result from some alternative mechanisms (e.g., selective mortality, phenotypic
320 plasticity; Edelaar et al. 2008). However, those processes do not appear to be
321 responsible for the nonrandom distribution of pied flycatchers since, as we have shown
322 previously, the spatial sorting of phenotypes actually results from differential dispersal
323 and habitat use (Camacho et al. 2013).

324 Under matching habitat choice, similar-sized individuals should segregate
325 together in the forest type accruing higher fitness (Edelaar et al. 2008); nevertheless, as
326 shown here, habitat preferences and subsequent fitness in the pied flycatcher are
327 apparently decoupled. Large males are more often found in the deciduous forest, but
328 their fitness is not greater than that of smaller males breeding there. Neither the fitness
329 of small-sized males breeding in the coniferous forest, where they commonly settle to
330 breed, is greater than that of small-sized males breeding in the deciduous site. Several
331 hypotheses can be proposed to explain the observed mismatch between habitat

preferences and fitness. Size compatibility of mates has been implied in increased reproductive success in other species (Selander 1966; Gosler 1987; but see Wiggins and Pärt 1995) and could influence male fitness differently in the coniferous and the deciduous forest. Although pied flycatchers show slight reversed size dimorphism (females > males; Potti et al. 2002), it does not influence recruitment success in either habitat (authors' unpubl. data). Another possibility is that underestimation of dispersers' recruitment relative to that of philopatric individuals might have masked or attenuated differences in recruitment success (Doligez and Pärt 2008). However, we found no effect of natal habitat or dispersal behaviour on recruitment success, suggesting that our estimates of recruitment success were apparently not confounded by male origin or movement. Aside from body size or condition, the fitness of pied flycatchers could be influenced by other ecologically important traits not considered here (e.g., temperament; Duckworth 2006).

Regarding the particular fitness trends we observed, one could easily notice that matching habitat choice fails to explain, for example, why the recruitment success of large-sized (presumably high-quality) males in the forest type they preferentially settle (i.e. oak forest) is comparable to that of smaller males. On one hand, habitat preferences of high quality phenotypes may not match the actual quality of selected sites due to e.g., density-dependent effects (Garant et al. 2005). Breeding density of hole-nesting songbirds is increasingly higher in the oakwood (Camacho et al. 2013) and thus, any form of habitat matching might be obscured by potential density-dependent effects on fitness. On the other hand, in contrast to the pine monoculture, the highly heterogeneous and structurally complex oak forest could provide pied flycatchers with multiple microhabitat and foraging opportunities (Lundberg et al. 1981), so that the breeding success of all males might be similar regardless of their morphology. Matching habitat

choice also fails to explain the trend for small males to reproduce in the coniferous habitat. As reported in other songbirds, small body size allows more efficient use of foraging techniques in coniferous forests (Gaston 1974; Forstmeier et al. 2001), where the average size of pied flycatcher prey is smaller than in broadleaved forests (Lundberg et al. 1981). Accordingly, the fitness of large-sized males is reduced in the coniferous forest but, strikingly, that of the smallest males there was also very low despite reproducing in an apparently promising habitat. A plausible explanation is that, due to habitat simplicity, the coniferous forest might be most suitable for a particular phenotype (e.g., males ranking at the very middle of the size range). In addition, in the scarcely productive pine monoculture food resources may be often limited, so that the smallest males might be unable to compete for nest holes (i.e. territories) and/or rich food patches with medium-sized, potentially dominant individuals (Lundberg et al. 1981).

A review of the scant literature attempting to test the matching habitat choice hypothesis reveals that we are still far from a conclusive demonstration of its operation in nature. In the experiments with grasshoppers, phenotype manipulations did not completely recapitulate the natural tendencies of non-manipulated individuals (Karpestam et al. 2012; Wennersten et al. 2012). As proposed by the authors, their phenotype manipulation might result in a mismatch between the individuals' highly integrated and complex natural phenotype and their novel appearance that might have hindered experimental grasshoppers from making colour-matched habitat choices. A second possibility is that grasshoppers' behaviour reflects additional influential processes (e.g., competitive exclusion; Edelaar et al. 2008) that are seldom reproduced, or hard to control for, in experimentally manipulated environments. Another potential source of bias is that grasshoppers involved in the experiments aiming to provide

evidence for matching habitat choice were actually unable to choose, but they were instead subjected to particular environments with no appropriate habitat to choose. Finally, although findings from free-ranging barn owls (Dreiss et al. 2012) are consistent with matching habitat choice, the authors recognized that other concurrent ecological processes could be operating (see also Bolnick et al. 2009). In this case, it was proposed that individual movements to new breeding sites might not result from active habitat choice, but instead reflect differences in competitiveness, for example, if some colour morphs are more aggressive and able to settle in the preferred habitats. Along this line, it seems likely that the nonrandom dispersal and subsequent distribution of pied flycatchers mainly results from competitive exclusion during settlement in the deciduous forest, although underlying –but hard to detect– matching habitat choice cannot be ruled out. Pied flycatchers first explore the preferred deciduous habitats before searching for alternative breeding sites (Alatalo et al. 1985; Lundberg and Alatalo 1992). Nonetheless, their ability to succeed in settling in the preferred territories is generally determined by their body size-based fighting potential (Alatalo et al. 1985; Sirkia and Laaksonen 2009). It may be due to this reason that most of the smallest males are likely 'relegated' to the underappreciated coniferous site by large, potentially dominant males that, regardless of their origin, may have the ability to actively choose where to settle (Camacho et al. 2013). Note that a small fraction of small-sized males also occurs in the deciduous forest, possibly as a result of natal habitat preferences (Camacho et al. submitted), or perhaps they benefited from an early arrival from spring migration or an extremely aggressive behaviour that compensated for their presumably reduced competitive abilities.

To summarize, matching habitat choice alone fails to explain the fitness accrued by pied flycatchers exerting differential dispersal and habitat use according to body size.

Several potentially confounding processes commonly present in nature (e.g., natal habitat preference and male-male competition) might act additively to matching habitat choice, swamp its presumably subtle effects, and thus make it difficult to detect and demonstrate.

We will conclude by suggesting some ways in which the matching habitat choice hypothesis can be tested in natural settings. Comparisons of the settlement patterns and fitness of naturally different phenotypes across spatially heterogeneous environments may be a valuable means to determine the actual occurrence of matching habitat choice in nature. For example, as a general rule, small individuals cool faster than large ones (Schmidt-Nielsen 1984), and thus differently sized individuals are expected to use thermal environments differentially. Dispersal responses of individuals to thermal gradients in some taxa (e.g., grasshoppers, Ahnesjö and Forsman 2006; nightjars, Camacho 2013) provide ample opportunities for testing whether naturally distinct phenotypes move between 'thermal patches' differently and whether those movements translate into direct fitness benefits. Experimental alteration of the phenotype (e.g., by altering food supply to young individuals through brood manipulations; Gustafsson and Sutherland 1988; or by hormonal 'phenotypic engineering'; Ketterson et al. 1996) or of the future fitness expectations of individuals (e.g. by modifying parental brood size or competitive regimes via manipulations of fledgling sex ratio; Nicolaus et al. 2012), as well as translocation experiments between contrasting environments (see Burger and Both 2011) may help researchers to determine whether manipulated or naturally different phenotypes 'match' the habitats where they would predictably disperse and whether those dispersal decisions influence their fitness prospects. Because additional processes leading to phenotype-dependent dispersal may operate concurrently with matching habitat choice, disentangling its

effects from those of other processes is a major challenge for testing the hypothesis under field conditions. For example, as shown here and in Garant et al.'s (2005) work, dominance rank appears as a major determinant of the directionality of dispersal in spatially heterogeneous environments. In such cases, perhaps researchers should rather focus on functionally relevant phenotypic traits that are not involved in competitive interactions but, at the same time, likely related to their dispersal decisions. For example, background-matching colour pattern (Merilaita and Lind 2005) or anatomical adaptations to resource exploitation *vs.* predator avoidance (Moore et al. 2015), which might determine the dispersal decisions of phenotypically different individuals experiencing spatial variability in resource availability or predation pressure.

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Figure legends

Figure 1. Three examples of expected phenotype x environment interaction scenarios in fitness, showing how individuals' decisions on where to settle may be contingent on the habitat features that best match their particular phenotype to maximize fitness. (A) Fitness increases linearly with trait size in habitats A and B. However, individuals ranking in the lower extreme of the trait size range will only maximize fitness after settling in habitat A, while fitness of large phenotypes will be high in either habitat. (B) Fitness increases linearly with trait size in habitat A, but so decreases in habitat B. As a result, large phenotypes will maximize fitness in habitat A, while the reverse is true in habitat B. (C) Fitness increases non-linearly with trait size in habitat A and B, which are both suboptimal for the phenotypes ranking in the upper and lower extremes of the trait size range. However, the optimal phenotype differs between habitats, as medium-small and medium-large phenotypes best match habitats A and B, respectively.

Figure 2. Relationship between body size and male fitness in the deciduous and the coniferous forest. Shown are the values predicted by the model.

609 Table 1. Effect of tarsus length, breeding habitat type and their interaction on the
610 recruitment success of male pied flycatchers. Number of males = 304; number of nest
611 boxes = 220; number of mates = 273; number of years = 18.

	Estimate	SE	Z	P
Intercept	-784.37	290.52	-2.70	0.0069
Tarsus length	83.98	30.33	2.70	0.0069
Breeding habitat	807.89	305.41	2.64	0.0082
Breeding date	-0.05	0.01	-3.76	0.0002
Tarsus length x Breeding habitat	-84.49	31.86	-2.65	0.0080
Tarsus length ²	-2.14	0.79	-2.71	0.0068
Tarsus length ² x Breeding habitat	2.21	0.83	2.66	0.0079

612

613 Table 2. Father-son comparison of the propensity to change habitats as part of natal
614 dispersal from the hatching habitat to that of first breeding. Note that if fathers disperse
615 from A to B, their prospective dispersing sons ‘only may’ move from B to A. Therefore,
616 for more meaningful father-son comparisons, we grouped together ‘resident’ vs.
617 ‘dispersing’ individuals in both the parents and sons classes in a 2-way table. Figures
618 are numbers of families.

Father dispersal	Son dispersal			Total
	stay in natal plot	oak to pine	pine to oak	
stay in natal plot	104	12	12	128
oak to pine	13	-	4	17
pine to oak	16	3	-	19
Total	133	15	16	164