

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

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10

11 **Abstract**

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

32 **Introduction**

33 Habitat selection and preceding dispersal decisions can strongly influence individuals'
34 survival and reproductive success, and therefore have important consequences for many
35 ecological and evolutionary processes (Fretwell and Lucas 1970; Cody 1984; Morris
36 2003). Evidence is accumulating that individuals disperse non-randomly with respect to
37 genotype and morphological, physiological or behavioural traits (Edelaar and Bolnick
38 2012). Specifically, dispersal can be affected by attributes such as age, sex, dominance
39 rank, body size and condition, physiological/biomechanical dispersal capacities, or
40 personality, thereby leading to phenotype-dependent dispersal and settlement (reviewed
41 in Clobert et al. 2009). Many empirical studies have revealed an adaptive relationship
42 between the phenotype of individuals and the location of settlement, and shown that
43 organisms may move non-randomly across environments to settle in those habitats that
44 may enhance individual performance (e.g., Blondel et al. 1999; Garant et al. 2005;
45 Dreiss et al. 2012). Along this line, the matching habitat choice hypothesis, unlike other
46 forms of phenotype-dependent dispersal (e.g. size-dependent dispersal driven by
47 competitive exclusion of less competitive phenotypes towards less appreciated habitats,
48 or increased dispersal propensity or distance in bold, explorative animals), states that
49 individuals –assumed to be able to assess fitness prospects in each habitat prior to
50 settlement– modify habitat selection according to their phenotype so that they settle in
51 the habitats with the highest fitness prospects (Holt and Barfield 2008; Edelaar et al.
52 2008).

53 Under the hypothesis' predictions, similar phenotypes are expected to have
54 similar habitat preferences and segregate together in the environments they are best
55 suited to, and further increase the fitness benefits of habitat selection (Edelaar et al.
56 2008). Thus, matching habitat choice may contribute to the spatial sorting of

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

60 Despite its likely ecological and evolutionary implications (see Edelaar et al.
61 2008), to the best of our knowledge only three studies have examined the matching
62 habitat choice hypothesis or evaluated its evolutionary consequences (but see Bolnick
63 and Otto 2013 for a theoretical outline). The evidence from two experimental studies
64 has so far provided positive support for the hypothesis' predictions by showing that
65 manipulation of colour phenotype in the pygmy grasshopper (*Tetrix subulata*)
66 influences microhabitat choice and affects subsequent fitness (Wennersten et al. 2012;
67 Karpestam et al. 2012). In addition, a field study has shown that female barn owls (*Tyto*
68 *alba*) showing reddish and whitish phenotypes settle in alternative habitats, and that
69 such colour-dependent habitat choice apparently increases fitness and reinforces local
70 adaptation (Dreiss et al. 2012). Yet, to our knowledge, the hypothesis' predictions
71 remain to be comprehensively tested under field conditions.

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

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

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

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

107 small individuals may preferentially use coniferous habitats because their small body
108 size could enable them to forage most efficiently in the outermost twigs of coniferous
109 trees (Gaston 1974; Korner-Nievergelt and Leisler 2004). In the pied flycatcher, the
110 average prey size is smaller in coniferous than in deciduous forests (Lundberg et al.
111 1981) and, although adaptive size-related dietary or microhabitat shifts have not been
112 reported, individuals of different size might specialize on different habitats or prey
113 species and perform differently in coniferous and deciduous forests, as occurs in other
114 songbirds (Forstmeier et al. 2001).

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

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

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

140

141 **Materials and methods**

142 Study system and data collection

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

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

159 After the first males arrived from spring migration, nest boxes were regularly
160 checked to determine exact laying dates, clutch sizes, hatching dates and numbers of
161 fledged young. Nestlings surviving from hatching to day 13 were then marked with
162 numbered metal rings and their ectoparasite loads were recorded (Merino and Potti
163 1995). Adults were captured while incubating (females) or feeding nestlings (both
164 sexes) by means of a nest box trap. All adults were marked with a unique combination
165 of metal and colour-coded rings and measured for body mass (to the nearest 0.1 g) and
166 tarsus length (to the nearest 0.05 mm) as a proxy for body size (Senar and Pascual
167 1997). Each male was ascribed to the habitat in which it settled to breed, regardless of
168 his origin. Breeding densities were determined by quantifying nest box occupancies by
169 pied flycatchers (Blondel et al. 1999; Garant et al. 2005).

170

171 Fitness measurement

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

182 were hence not further considered. Because habitat familiarity, previous breeding
183 experience and age-related improvements in individual performance may influence
184 reproductive output and subsequent fitness (e.g., Doligez et al. 1999; Brown et al. 2008;
185 Limmer and Becker 2010) and thus potentially confound matching habitat choice (e.g.,
186 potentially masking a fitness mismatch between phenotype and environment), only first-
187 time breeders of known origin were considered, whether they move from their natal
188 habitat to a new one (dispersers) or remain in their natal habitat to breed (philopatric).
189 All nests that were known replacement clutches (i.e. laid after failure (1.7%) or
190 predation (10.1%) of the first one) were omitted from analyses. Breeding date is likely
191 the most important determinant of breeding success and recruitment in *Ficedula*
192 flycatchers (Lundberg and Alatalo 1992; Potti et al. 2002) and thus variation in success
193 of replacement clutches may likely reflect the effects of extremely delayed timing,
194 rather than a possible mismatch between phenotype and habitat type. All nests subjected
195 to experimental manipulations (e.g., cross-fostering) were also omitted. Because of
196 discontinuities in the intensity of fieldwork, the years 2002 and 2003 were omitted from
197 the dataset. As recruits may postpone their first reproduction until the second or, more
198 rarely, third year of life (Potti and Montalvo 1991), all nests of males breeding between
199 1999 and 2003 were excluded from analyses to avoid underestimating their true
200 recruitment success (Potti et al. 2013). For the same reason, all nests of males breeding
201 beyond 2010 were also excluded. Dispersal outside the study plots is an extremely rare
202 event (pers. obs. from non-systematic explorations of surrounding areas); therefore, we
203 are confident that the spatial scale of the study area is not a source of bias in recruitment
204 rates. Overall, for fitness analyses we used data from the first reproductive attempts by
205 304 individuals (202 and 102 males in DF and CF, including 27 and 29 dispersers, and
206 175 and 73 philopatric birds) belonging to 23 cohorts (see also Table 1).

207

208 Familial resemblance in dispersal patterns and effect of body condition

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

220

221 Data analyses

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

232 Breeding date was included as a covariate in the model, as it is one of the most
233 important determinants of breeding success and recruitment in *Ficedula* flycatchers
234 (Potti and Montalvo 1991; Lundberg and Alatalo 1992; Potti et al. 2002). Nest box and
235 female identity were included in the model to account for territory quality and mate
236 quality variation, respectively, and we also included year as a random effect to account
237 for annual heterogeneity in breeding performance. The GLMM was fitted in R 2.14.0
238 ([http://wwwR-project.org](http://www.R-project.org)) using the function *lmer* of the package 'lme4' (Bates et al.
239 2011). Selection of the minimum adequate models was carried out by sequentially
240 dropping non-significant terms from fully saturated models (containing all main effects
241 and interactions), in a hierarchical way, starting with the least significant order terms.

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

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

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

270

271 **Results**

272 Male size, habitat choice and fitness

273 Local males breeding in CF were significantly smaller than those from DF (mean \pm SE:
274 19.24 ± 0.04 vs. 19.37 ± 0.03 ; GLM: $t_{1,303} = 2.09$, $P = 0.038$). Linear and non-linear
275 interactions between male size and forest type (Fig. 2) had a significant influence on
276 recruitment success, after controlling for the significant effect of breeding date (Table
277 1). Even though the interaction terms indicate that male fitness varied spatially
278 according to body size, fitness variation was not in line with matching habitat choice'
279 predictions. Recruitment success in CF increased non-linearly with body size, with
280 males at the very middle of the size range having higher fitness than both large and
281 small-sized males. However, no clear trend was observed in DF, where males of either

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

289

290 Familial resemblance in dispersal patterns and effect of body condition

291 Results of the GLMM (number of males: 238; number of families: 164; number of
292 cohorts: 21; see Table 2) showed no influence of father dispersal behaviour on the
293 staying/dispersing propensities of their sons (estimate \pm SE: 0.12 ± 0.38 , $P = 0.75$),
294 after controlling for the significant effect of son origin (0.88 ± 0.34 , $P = 0.009$) and
295 removing the non-significant effect of son tarsus length (0.48 ± 0.31 , $P = 0.12$) from the
296 final model. There was also no association between full sibs in their dispersal behaviour
297 (29 sibling pairs stayed in their natal forest vs. 15 dyads differing in their direction of
298 movement: $\chi^2_1 = 1.83$, $P = 0.18$). The propensity of males to exchange habitats was not
299 dependent on body condition, as dispersers ($n = 92$) and philopatric birds ($n = 342$) had
300 similar body masses ($t_{1,463} = -0.16$, $P = 0.88$) after controlling for the significant effect
301 of tarsus length ($t_{1,463} = 6.66$, $P < 0.0001$).

302

303 **Discussion**

304 Male pied flycatchers move between coniferous and deciduous forests according to
305 body size (Camacho et al. 2013) and, as shown here, their size influenced recruitment
306 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

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

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

357 choice also fails to explain the trend for small males to reproduce in the coniferous
358 habitat. As reported in other songbirds, small body size allows more efficient use of
359 foraging techniques in coniferous forests (Gaston 1974; Forstmeier et al. 2001), where
360 the average size of pied flycatcher prey is smaller than in broadleaved forests (Lundberg
361 et al. 1981). Accordingly, the fitness of large-sized males is reduced in the coniferous
362 forest but, strikingly, that of the smallest males there was also very low despite
363 reproducing in an apparently promising habitat. A plausible explanation is that, due to
364 habitat simplicity, the coniferous forest might be most suitable for a particular
365 phenotype (e.g., males ranking at the very middle of the size range). In addition, in the
366 scarcely productive pine monoculture food resources may be often limited, so that the
367 smallest males might be unable to compete for nest holes (i.e. territories) and/or rich
368 food patches with medium-sized, potentially dominant individuals (Lundberg et al.
369 1981).

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

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

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

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

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

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

442

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592

593 Figure legends

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

606

607 **Figure 2.** Relationship between body size and male fitness in the deciduous and the
608 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



