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No evidence for correlational selection on exploratory behaviour and natal dispersal in the great tit

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1 **No evidence for correlational selection on exploratory**
2 **behaviour and natal dispersal in the great tit**

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32 **Abstract**

33 A growing number of studies have recently reported links between personality and dispersal,
34 yet the adaptive significance of personality-dependent dispersal strategies still remain poorly
35 understood. Here, we tested whether birds differing in exploratory behaviour (EB, quantified
36 by a novel environment test), gain differential fitness benefits when remaining in or leaving
37 their natal area in a natural population of great tits (*Parus major*). Using data on lifetime
38 fecundity, we found no evidence that particular combinations of EB and dispersal lead to a
39 higher fitness after settlement. In males, we found positive selection acting on EB through
40 first-year survival, resulting in a positive relationship between EB and number of lifetime
41 fledglings. However, contrary to expectation, these effects were only present in local recruits
42 and not in immigrants. Male immigrants produced fewer fledglings during their lifetime than
43 did local recruits, suggesting selection against dispersal at a scale exceeding the size of our
44 study area. In females, we found selection on EB through recruitment with respect to year
45 (i.e., negative, positive and stabilizing selection), but neither the strength nor the direction
46 differed among birds with different dispersal strategies. We found no evidence in either sex
47 for lifetime selection acting on EB using recruits as a measure of fitness. In conclusions, our
48 results do not support the hypothesis that the co-expression of personality and dispersal is
49 shaped by selection after settlement.

50

51

52 **Introduction**

53 Natal dispersal (i.e. the movement from place of birth to the site of first reproduction;
54 hereafter “dispersal”) is a key life-history trait that affects the social and genetic structure,
55 and persistence of spatially structured populations (Clobert et al. 2012; Stenseth and Lidicker
56 1992). Dispersal implies movement away from the natal habitat and therefore can involve a
57 multitude of different costs (reviewed in Bonte et al. 2012) but can also increase the
58 dispersers’ fitness by avoiding competition or inbreeding or locating habitat and mates
59 (Clobert et al. 2012). Dispersal behaviour is often influenced by multiple social and
60 environmental factors that vary in space and time (Matthysen 2012; Bowler and Benton 2005;
61 Clobert et al. 2009). Dispersers therefore often constitute a heterogeneous group of
62 individuals that may not only differ from each other in the underlying causation of dispersal
63 (i.e. ecological and social factors driving the decision to disperse), but also in a range of
64 phenotypic characteristics that make them respond differentially to these external factors.
65 Indeed, dispersal tactics often depend on morphological and physiological characteristics that
66 may help to reduce the various costs associated with dispersal and/or to facilitate settlement
67 (Bonte et al. 2012; Bowler and Benton 2005). In recent years, however, it has become
68 increasingly clear that dispersers may also differ from philopatric individuals in various
69 aspects of their behaviour. In many vertebrates, for example, there is accumulating evidence
70 that behaviours such as boldness, aggressiveness and exploration, are often closely integrated
71 with an individual’s propensity to disperse (reviewed in Cote et al. 2010). When such
72 behaviours form consistent suites of traits they are also referred to as differences in
73 “personality” (e.g. Gosling 2001; Wilson et al. 1994) or a “behavioural dispersal syndrome”
74 in the specific case of consistent links with dispersal (Duckworth and Kruuk 2009; Cote et al.
75 2010; Clobert et al. 2009). Differences in personality have been described in widely different
76 taxa (Reale et al. 2010), suggesting personality-dependent dispersal to be potentially

77 widespread. To date, however, actual links between personality and dispersal have been
78 reported for only a limited number of species (Cote et al. 2010). The proximate mechanisms
79 and evolutionary causes underlying these associations are therefore still poorly understood.

80 Personalities are generally conceived as alternative behavioural strategies to cope with
81 socially or ecological challenging situations that may reflect inter-individual differences in
82 foraging styles (e.g. van Overveld and Matthysen 2010; Herborn et al. 2010; Wilson and
83 McLaughlin 2007; Marchetti and Drent 2000; Verbeek et al. 1994), risk-taking tendencies
84 (e.g. Dammhahn and Almeling 2012; van Oers et al. 2004; Godin and Dugatkin 1996;
85 Coleman and Wilson 1998) and/or social tactic use (reviewed in Bergmueller and Taborsky
86 2010; Montiglio et al. 2013). Consequently, personalities have the potential to explain
87 individual responses to a wide range of social and ecological conditions that have previously
88 been shown to affect dispersal, such as population density (Matthysen 2005), social
89 environment (Michler et al. 2011; Nicolaus et al. 2012) or landscape structure (e.g. Long et
90 al. 2005; Serrano et al. 2001; Matthysen et al. 1995). How different personalities respond to
91 their external environment (i.e. dispersal decision) as well as the pay-off of their decision will
92 depend on the specific costs and benefits of dispersal associated with their personality. Thus,
93 dispersal (or lack thereof) may be a means by which some personality types increase their
94 fitness more than others. However, given that dispersal itself is often costly and under strong
95 selection (Bonte et al. 2012), it is hypothesized that links between personality and dispersal
96 have evolved as a consequence of selection for a close functional integration of both traits
97 (Duckworth and Kruuk 2009). Note that this can be achieved by either increasing the success
98 of dispersal itself (i.e. surviving the dispersal episode) or by benefiting dispersers after
99 settlement through effects of habitat and/or mate quality.

100 Studies showing that the costs and benefits of dispersal may vary with personality are,
101 however, very scarce. So far, one of the best examples is a study on western bluebirds (*Sialia*

102 *mexicana*) (Duckworth 2012). In this species, aggressive males have a competitive advantage
103 over less-aggressive males for nesting sites and territories, which increases their success in
104 colonizing new habitats, whereas nonaggressive males have greater success in obtaining a
105 territory through cooperation with relatives in their natal populations (Duckworth 2008). The
106 benefits of dispersal, however, are counterbalanced by the reproductive costs of being
107 aggressive (Duckworth 2006), leading to an increase in the frequency of less aggressive
108 individuals within newly colonized areas (Duckworth 2008). Another example comes from
109 work on the common lizard (*Lacerta vivipara*). In this species less social individuals are more
110 likely to disperse from high- to low-density populations, whereas the opposite is true for more
111 social individuals (Cote and Clobert 2007). Since less social individuals have a higher
112 survival when densities are low (Cote et al. 2008), this illustrates that benefits of dispersal
113 may depend on the interaction between personalities and their environment.

114 Here we investigate the fitness consequences of a previously established link between
115 a well-known personality trait (exploratory behaviour, hereafter EB) and dispersal in a small
116 passerine, the great tit (*Parus major*). Extensive work on this species has shown EB to be
117 repeatable and heritable (Dingemanse et al. 2002; Korsten et al. 2013), and to correlate with
118 other behavioural traits both in the laboratory (reviewed in Groothuis and Carere 2005) and in
119 the wild (Cole and Quinn 2012; Dingemanse and de Goede 2004; Hollander et al. 2008),
120 leading to the widespread use of this measure as a proxy to describe variation in personality.
121 Associations between natal dispersal and EB have been documented in three different
122 populations in Western Europe (Westerheide (The Netherlands): Dingemanse et al. 2003;
123 Wytham Woods (UK): Quinn et al. 2011), including the population of the current study (the
124 'Boshoek' (Belgium): van Overveld et al. 2014). Studies in all three populations show that
125 fast-exploring individuals have a higher tendency to disperse over large distances. Yet, the
126 extent to which these behavioural differences may enhance the fitness of dispersers still

127 remains unstudied, hampering our understanding of the evolutionary processes underlying
128 these behavioural dispersal syndromes. We recently showed that in our study population both
129 natal dispersal distance and EB have a considerable heritable component and are genetically
130 correlated (Korsten et al. 2013), suggesting that the co-expression of both traits is the result of
131 correlational selection (e.g. Cheverud 1996; Lande 1984). Correlational selection may occur
132 during the process of dispersal itself, for instance, when slow-exploring dispersers have a
133 lower post-fledging survival and/or reduced settlement success. An alternative explanation
134 may be that certain combinations of EB and dispersal lead to a higher fitness after settlement,
135 for instance, when fast-exploring dispersers and/or slow-exploring residents obtain the highest
136 quality mates or territories.

137 Our main aim in this study is to investigate whether the co-expression of EB and
138 dispersal is shaped by natural selection acting after the termination of the dispersal phase, i.e.
139 after settlement. To measure the extent of selection acting on EB and dispersal we use data on
140 lifetime reproductive success. Natal dispersal was defined in two ways: i) as a categorical
141 trait, based on movements within and between isolated woodlots in our highly fragmented
142 study area: residents (breeding in the natal woodlot), local dispersers (dispersing between
143 woodlots) and immigrants into the study area, and ii) as a continuous trait, by the distance
144 travelled between place of birth and site of first reproduction (for locally born birds only).

145 We first examine whether lifetime reproductive success (measured by number of
146 fledglings and recruits) differs between dispersal categories and/or varies with absolute
147 dispersal distance. Because previous studies have documented large differences in the costs of
148 dispersal between males and females (Gros et al. 2008; Greenwood 1980), we included
149 interactions with sex in all analyses. We then examine whether the fitness consequences of
150 natal dispersal vary with regard to EB and test the hypothesis that correlational selection
151 shapes the (genetic) co-expression of EB and dispersal. This was done by i) comparing the

152 relationship between EB and fitness components among the three dispersal categories, and ii)
153 by examining how fitness components may vary with regard to absolute natal dispersal
154 distance and EB. In both analyses, we expect a significant interaction between EB and natal
155 dispersal as predictors of fitness. In particular, we expect the relationship between EB and
156 fitness to change from negative in birds with short dispersal distances (the resident category)
157 to positive for birds with longer dispersal distances (local dispersers and immigrants). In the
158 next step, we examine whether any of the above detected relationships resulted from
159 differences in annual survival and/or annual fecundity (i.e. fledglings and recruits). In
160 addition, we test for consistency in patterns of selection by examining whether relationships
161 between EB and fitness components vary among years (Dingemanse and de Goede 2004;
162 Quinn et al. 2009). Finally, we tested whether selection on dispersal and EB occurs only
163 during the first breeding attempt, or continues during the lifetime of the individual.

164

165 **Material and Methods**

166 **Study population and field methodology**

167 The study was conducted in a mosaic landscape with scattered woodland fragments called the
168 'Boshoek' in northern Belgium (518080 N, 48320 E). This area of approximately 10 km²
169 contains 13 woodlots of mature forest ranging in size from 0.4 to 12 ha. Neighbouring
170 woodlots are 100 to 600 m apart and separated by small residential areas and agricultural
171 land. Since 1993 all forest woodlots have been equipped with standard nestboxes (height 1.5
172 m, dimensions 23 x 9 x 12 cm, entrance 32 mm) at a high density of about six per hectare,
173 containing virtually the entire breeding population inside the woodlots (for more details see
174 Matthysen 2002; Nour et al. 1998). Each year during the breeding season (April-June) all nest
175 boxes are checked weekly to determine the date of the first egg laid (laying date), total
176 number of eggs produced (clutch size) and the total number of nestlings and fledglings.

177 Parents are captured when their nestlings are 8-10 days old and ringed with metal and colour
178 rings. Nestlings are ringed when they reach a development stage equivalent to an age of 15
179 days which is used as a proxy for fledging date (Matthysen et al. 2011). At this date, total
180 body mass of the brood is measured.

181

182 **Novel Environment test**

183 Since 2006, we have routinely screened great tits on their exploratory behaviour using a novel
184 environment test. Tests were carried out from July until February to avoid any negative
185 effects on territory settlement and breeding success. Birds captured in the field were
186 transported to the lab within one hour (if captured by mistnet) or two hours (roosting birds
187 captured in the evening) and housed in individual cages for one night. The exploratory
188 behaviour of birds was measured on the following morning, following the exact procedure
189 described in Dingemanse et al. (2002). Briefly, each bird was entered separately into a sealed
190 room (4.0 x 2.4 x 2.3 m) containing five artificial trees and during the following 2 minutes, all
191 movements among the different artificial trees (flights) and among the branches of individual
192 trees (hops) were counted, including movements towards other structures such as lamps or
193 sliding doors or to the floor, but not including movements on a single branch. The total
194 number of movements was used as a measure of exploratory behaviour. All birds were
195 released near their site of capture within 24 h after capture. Our exploration scores increase
196 from summer to the start of the breeding season, a pattern consistent with other studies on
197 exploratory behaviour in great tits (Dingemanse et al. 2012). To correct for this seasonal trend
198 we used the equation: 'season corrected exploration score' = 'measured exploration score' –
199 $(0.036 \times \text{'July date'}) + 10$, where 'July date' was the number of days from 1 July onwards (for
200 details see Dingemanse et al. 2002). Our corrected exploration score is significantly
201 repeatable ($r = 0.42$, $p < .001$, i.e., based on 154, 46, 24 individuals tested two to four times

202 respectively, with scores adjusted for effects of time of season, test-sequence and interval (for
203 details see Dingemanse et al. 2012). Our (corrected) individual exploration scores have a
204 heritability estimate of h^2 0.30 ± 0.11 s.e. (Korsten et al. 2013). Exploration scores are
205 unrelated to sex ($F_{2, 820} = 0.33$, $p = 0.56$), age ($F_{5, 817} = 1.46$, $p = 0.20$), body size ($F_{2, 802} = 0.68$,
206 $p = 0.41$) or body mass (i.e., residuals over tarsus corrected for capture date and time of the
207 day, $F_{2, 711} = 0.13$, $p = 0.72$). Note that in our analyses we used the first exploration score in
208 case birds were tested multiple times.

209

210 **Dispersal and fitness data**

211 Dispersal was quantified in two different ways: i) as a categorical trait, and ii) by the straight
212 line distance in m between place of birth and site of first breeding. To categorize dispersal, we
213 distinguished between three dispersal strategies ('dispersal status' hereafter), based on the
214 highly patchy distribution of breeding habitat (woodlots): (i) birds captured in their natal
215 woodlot were defined as 'residents'; (ii) birds captured in a woodlot different from their natal
216 woodlot were defined as 'local dispersers'; and (iii) birds that were not ringed as a nestling in
217 the study area were defined as 'immigrants' (cf. Snoeijs et al. 2004). The six smallest
218 woodlots (0.4 – 1.25 ha) were pooled with the nearest larger woodlots in the analysis because
219 in these particular cases between-woodlot dispersal distances were less than the average
220 within-woodlot dispersal distances (for details see Matthysen 2002). After pooling these small
221 woodlots, dispersal distances of residents varied from 0 to 529 m (median distance 177 m, $n =$
222 110), those of local dispersers from 390 to 2241 m (median distance 812 m, $n = 96$). Table 1
223 gives an overview of dispersal distances by sex. The origin of unringed birds was by
224 definition unknown, but the distance to the nearest wooded area without nestboxes varied
225 from 350 for some of the peripheral woodlots to 1200 m for the most centrally located
226 woodlot, and was generally more than 1000 m. A fraction of unringed birds may have been
227 born in nestboxes in gardens in the matrix between woodlots (estimated at 10-15%). Thus,

228 quantifying natal dispersal as a categorical trait allowed us to include immigrants as an
229 additional dispersal category even though their actual dispersal distances are unknown.

230 Lifetime reproductive success (LRS) was quantified by: (i) lifetime fledgling
231 production (LFP), i.e., the total number of fledglings produced over an individual's lifetime,
232 and (ii) lifetime recruitment production (LRP), i.e., total number of fledglings that returned as
233 local breeders over an individual's lifetime. We analysed both measures because local
234 recruitment patterns may be confounded by heritable variation in offspring dispersal (Doligez
235 and Part 2008). To calculate LFP and LRP, we included all reproductive data available from
236 first, second and replacement broods. We also looked at variation in annual fitness to examine
237 whether differences in LFP and LRP were the result of differences in reproduction or survival,
238 and to examine whether fitness components differed between first-year breeders and older
239 birds. Annual fitness variation was quantified by (1) number of fledglings produced, i.e. the
240 total number of offspring that survived until 2 weeks of age, (2) number of recruits, i.e. the
241 number of fledglings that survived and bred in the local study population and (3) adult
242 survival, i.e. survival between subsequent breeding seasons.

243

244 **Data selection**

245 We only included birds in our analyses for which we had data on their complete reproductive
246 history, i.e., breeding for the first time as yearling and with a breeding record in every
247 subsequent year. We excluded five females that dispersed between woodlots after their first
248 breeding attempt. No breeding dispersal was observed in males.

249 We had data available for 189 males (68 residents, 29 dispersers, 92 immigrants) and
250 220 females (42 residents, 67 residents, 111 immigrants) with known exploration scores. In
251 both sexes, data were distributed over nine cohorts (2001-2009) and 10 breeding seasons
252 (range 2002 -2011) with a total of 410 breeding events for males and 522 breeding events for

253 females. Because birds were tested on exploratory behaviour from January 2006 to February
254 2010, but many of these birds had been ringed in previous years, our dataset contained many
255 breeding events of birds that at the time were not yet tested for exploratory behaviour. As a
256 consequence, breeding events from the seasons 2002-2004 were biased in the sense that they
257 only contained birds that survived at least one more year. For breeding events in the 2005
258 breeding season, this bias was somewhat smaller, but still > 85% survived at least one year.
259 Since these birds may represent a subset of high quality individuals (or territories), we
260 repeated all analyses on a restricted dataset (cf. Quinn et al. 2011), which only contained
261 breeding seasons 2006-2010, by removing all birds born in 2001-2004 and all birds that were
262 still alive in 2012. This substantially reduced sample sizes (females: 138 individuals, 247
263 breeding events (11% -32% of all females per breeding season); males: 119 individuals, 196
264 breeding events (8%-27% of all males per breeding season)). Because the outcomes of
265 analyses on both the unrestricted and restricted dataset were highly comparable, we only
266 present results of analyses on the unrestricted dataset. Note that in the unrestricted dataset: 1)
267 the lifetime number of broods produced, and hence LFP and LRP, are higher than the
268 population average, and 2) 11 males (6%) and 6 females (3%) were still alive by the end of
269 the study and for these individuals lifetime fitness may have been underestimated.

270

271 **Statistical analyses**

272 *Lifetime selection on dispersal*

273 Lifetime selection on dispersal was analysed using general linear mixed models (LFP) or
274 generalized linear mixed models (LRP, with a log link function for Poisson-distributed data).
275 We ran different models with either dispersal status or dispersal distance included as fixed
276 effects. We included sex and sex-specific interactions in all models to test whether selection
277 on dispersal differed between males and females. Woodlot of first breeding was included as a

278 random variable to account for the spatial structure of the population (Van Noordwijk 1984).
279 We also included year of birth as random variable to account for cohort effects on LFP or
280 LRP (either due to natural variation or to the study design, see higher). LFP was $\log(x + 0.5)$
281 transformed to ensure normality of residuals (Shapiro-Wilk test).

282

283 *Correlational selection on EB and dispersal*

284 To test for correlational selection on dispersal and EB, we used two different approaches.
285 First, we compare the relationship between EB and lifetime fitness (LFP and LRP) among the
286 three dispersal categories (residents, local dispersers, immigrants) by including EB and its
287 interactions with dispersal status in the above mentioned models. We also include the
288 quadratic effects of EB to test for non-linear selection which may be stabilizing (negative sign
289 of quadratic coefficient) or disruptive (positive sign). Thus, full models included EB, EB²,
290 sex, dispersal status, and all first-order interactions as fixed effects and year of birth and
291 woodlot of first breeding as random variables. We then estimated selection on EB within each
292 dispersal category by calculating standardized directional (S') and nonlinear (c') selection
293 differentials. This was done by standardizing EB to zero mean and unit variance and by using
294 relative fitness measures (scaled to a mean of 1, after Arnold and Wade 1984a, b).

295 Secondly, we estimated selection acting on the phenotypic covariance between EB and
296 natal dispersal distance (i.e., for locally born birds only), by calculating standardized
297 correlational selection gradients from regression models using LFP or LRP. Correlational
298 coefficients between EB and dispersal distance were estimated from full models that included
299 linear terms (EB and dispersal distance), quadratic terms (EB², dispersal distance²) and cross-
300 product terms (EB * dispersal distance) (Brodie et al. 1995). Quadratic selection gradients and
301 their standard errors were doubled following Stinchcombe et al. (2008). Selection gradients
302 are estimated separately for males and females using standardized measures of EB and

303 relative fitness measures (see above). Dispersal distance was $\log(x + 10)$ transformed to reach
304 normality of residuals (Shapiro-Wilk test).

305

306 *Variation in survival and fecundity*

307 To examine whether patterns of lifetime selection on dispersal and EB resulted from
308 differences in yearly survival or fecundity we used general linear mixed models for the
309 number of fledglings, generalized linear mixed models with a log link function for the number
310 of recruits, and a logit function for survival. Given sex-specific patterns of selection (see
311 results), we ran separate models for males and females. Fixed effects included EB, EB² and
312 dispersal status and the interaction thereof. Year was included as a fixed effect to test for
313 between-year variation in selection pressure using two-way interactions (year*EB, year* EB²
314 and year*dispersal status). We also included age (yearling or older) as a fixed effect to test
315 whether selection on EB was more pronounced during the first breeding attempt using three-
316 way interactions (EB * dispersal status * age). In case of significant effects, we repeated all
317 analyses on first-year breeders only. Random effects included in all models were individual,
318 year of birth and woodlot of first breeding. Because models on annual fluctuations in
319 recruitment and survival did not converge, either because of low sample sizes in particular
320 years (i.e., 2002-2003 and 2011) or because (nearly) all birds survived (i.e., breeding seasons
321 2002-2005), we excluded these years from these particular analyses.

322

323 All analyses were performed using SAS 9.2 software. In all models we used Satterthwaite
324 correction for the degrees of freedom (df) (Littell et al. 1996). Final models included all main
325 fixed effects and random effects irrespective of their significance. Testing of interaction terms
326 occurred by stepwise removal of the weakest non-significant interaction terms, except for the
327 interaction EB x dispersal status, which was kept in all models.

328 **Results**

329

330 **Lifetime selection on natal dispersal**

331 The number of individuals producing 1 to 6 broods was 152, 102, 83, 40, 23 and 9
332 respectively. Most individuals fledged at least one offspring during their life (median number
333 of fledglings = 15, range 0-55, n = 409), but only 50% of them recruited 1 or more offspring
334 (median number of recruits = 2, range 1-8, n = 204). Males and females did not differ in the
335 number of broods produced ($F_{1, 407} = 2.11$, $p = 0.15$), LFP ($F_{1, 395} = 0.14$, $p = 0.71$) or LRP ($F_{1, 407} = 0.22$, $p = 0.64$).

337 Lifetime production of fledglings and recruits differed between dispersal categories in
338 a sex-specific manner (LFP: EB * sex * dispersal status;: $F_{2, 394} = 4.58$, $p = 0.011$; LRP: $F_{2, 403} =$
339 8.66 , $p = 0.0003$, Figure 1). In males, immigrants produced fewer fledglings during their life
340 ($F_{2, 180} = 3.43$, $p = 0.035$, Table 1) and local male dispersers produced more recruits ($F_{2, 186} =$
341 8.82 , $p = 0.0002$, Table 1). In females, there were no differences in LFP and LRP between
342 dispersal categories (LFP: $F_{2, 209} = 2.20$, $p = 0.11$; LRP: $F_{2, 217} = 1.51$, $p = 0.22$), but female
343 immigrants produced more lifetime fledglings than immigrant males ($F_{1, 190} = 4.75$, $p =$
344 0.031).

345 For locally born birds, there was no relationship between natal dispersal distance and
346 LFP or LRP in neither males (LFP: $F_{1, 63.2} = 1.58$, $p = 0.21$; LRP: $F_{1, 95} = 1.84$, $p = 0.18$) nor
347 females (LFP: $F_{1, 101} = 0.58$, $p = 0.45$; LRP: $F_{1, 108} = 0.07$, $p = 0.80$).

348

349 *Variation in survival and fecundity*

350 There was no evidence that the lower LFP of immigrant males resulted from a poor annual
351 fledgling production ($p > 0.3$) or low annual survival rates ($p > 0.4$). Nevertheless, immigrants
352 produced fewer broods during their life as compared to locally born males ($F_{1, 187} = 4.33$, $p =$

353 0.039, Table 1) and immigrant females (sex * dispersal category: $F_{1, 390} = 4.93$, $p = 0.026$,
354 table 1), suggesting that the lower LFP of immigrant males resulted from a shorter lifespan.

355

356 **Correlational selection on EB and dispersal**

357 Correlational selection was tested by examining the interaction between effects of EB and
358 dispersal (category or distance) on fitness. Residents had on average lower exploration scores
359 as compared to local dispersers and immigrants in both sexes (dispersal status: $F_{2, 393} = 3.43$, p
360 $= 0.034$; sex: $F_{1, 399} = 1.54$, $p = 0.22$; dispersal status* sex: $p > 0.4$, Figure 1b). In males,
361 differences in EB were most pronounced between residents and immigrants ($F_{1, 156} = 5.33$, $p =$
362 0.022 , Table 1, Figure 1b), while in females this was between residents and local dispersers
363 ($F_{1, 88.9} = 4.68$, $p = 0.033$, Table 1, Figure 1b). In locally born males there was no relationship
364 between EB and natal dispersal distance ($\beta = -0.003 \pm 0.013$, $F_{1, 95} = 0.09$, $p = 0.76$). In locally
365 born females there was a marginally significant positive correlation between EB and natal
366 dispersal distance ($\beta = 0.018 \pm 0.009$, $F_{1, 108} = 3.82$, $p = 0.053$), but this relationship did not
367 differ significantly from males (EB * sex: $p > 0.3$).

368 There was no evidence for directional or non-linear selection acting on EB based on
369 either LFP or LRP (all dispersal categories pooled, $p > 0.2$ for both sexes). There was
370 evidence for differences in directional selection on EB with respect to dispersal category and
371 sex using LFP (EB * sex * dispersal status: $F_{5, 389} = 4.12$, $p = 0.007$). In males selection on EB
372 was positively directional and of similar strength in both residents and local dispersers (Figure
373 2, see Table 2 for SSD on EB for both categories). When male residents and local dispersers
374 were pooled selection on EB remained positive and significant ($F_{1, 92.9} = 9.83$, $p = 0.002$). By
375 contrast, no selection on EB was detected in immigrants ($p > 0.2$, Table 2 and Figure 2,
376 interaction EB*dispersal status (locally born vs. immigrants); $F_{1, 182} = 6.43$, $p = 0.012$). There
377 was no evidence for correlational selection on EB and dispersal category through LRP in

378 either of the sexes ($p > 0.1$, Table 2) nor did we find evidence for non-linear selection using
379 either LFP or LRP ($p > 0.1$, Table 2).

380 For locally born birds, there was no significant evidence for correlational selection on
381 EB and natal dispersal distance in either sex, using LFP (males: $F_{1, 91} = 0.17$, $p = 0.67$;
382 females: $F_{1, 104} = 0.61$, $p = 0.44$, for selection gradients see table 3) or LRP (males: $F_{1, 91} =$
383 0.04 , $p = 0.84$; females: $F_{1, 104} = 1.36$, $p = 0.25$, for selection gradients see table 3).

384

385 *Variation in survival and fecundity*

386 There was no evidence that patterns of lifetime selection on EB and dispersal observed in
387 males were the result of differences in annual fledgling production or survival (i.e., EB *
388 dispersal status: $p > 0.1$, Table 4). There was, however, positive directional selection on male
389 EB through survival, but only in first-year birds (EB* dispersal status * age: $p = 0.046$, table
390 4). Survival selection on male EB corresponded with patterns of lifetime selection on EB
391 (based on LFP), being the strongest in resident males ($F_{1, 66} = 7.80$, $p = 0.007$), marginally
392 significant in local dispersers ($F_{1, 27} = 3.78$, $p = 0.062$) and absent in immigrants ($F_{1, 90} = 0.80$,
393 $p = 0.37$). Again, when resident and local dispersers were pooled, survival selection on EB
394 remained significant ($F_{1, 95} = 10.82$, $p = 0.001$). In addition, survival selection on EB in locally
395 born males differed significantly from immigrants ($F_{1, 185} = 5.25$, $p = 0.023$) and between the
396 sexes (EB* dispersal status (resident and immigrants pooled)*sex: $F_{1, 402} = 2.85$, $p = 0.037$).

397 In females, there was evidence for heterogeneity in selection on EB through
398 recruitment with respect to year (Table 4), showing selection on EB to be negative (2004,
399 2005), positive (2007) and stabilizing (2010), while no selection was found in other years
400 (2006, 2008, 2009). In males, there was no evidence for selection on EB to fluctuate between
401 years (EB*year: $p = 0.87$; EB²*year: $p = 0.84$). Yearly fluctuations in selection on EB did not
402 differ between the sexes in all years (sex * EB * year: $F_{13, 834} = 1.59$, $p = 0.082$; sex * EB² *

403 year: $F_{13, 833} = 1.62$, $p = 0.075$), but were significantly different in 2004 ($F_{1, 49} = 6.46$, $p =$
404 0.014) and 2007 ($F_{1, 179} = 6.50$, $p = 0.012$) only.

405

406

407 **Discussion**

408 Here, we investigated the post-settlement fitness consequences of a previously established
409 link between a personality trait - exploratory behaviour (EB) - and dispersal in the great tit
410 (Dingemanse et al. 2003; Quinn et al. 2011; van Overveld et al. 2014). Two main patterns
411 emerged from our study. First, overall selection on dispersal appeared generally weak, with
412 lower fitness for immigrant males (but not females) in terms of lifetime fledgling production,
413 and no difference between residents and local dispersers. Second, we found strong evidence
414 that EB is correlated with different components of fitness in males and females. However, in
415 neither of the sexes did the fitness consequences of personality depend on its interaction with
416 dispersal, thus providing no evidence for correlational selection on both traits. In addition, we
417 found no evidence for lifetime selection acting on EB using recruits as a measure of fitness.
418 Taken together, our results do not support the hypothesis that the co-expression of personality
419 and dispersal is shaped by selection after settlement.

420

421 *Selection on natal dispersal*

422 Studies investigating the long-term fitness consequences of natal dispersal in birds are
423 generally scarce, but those that did have generally found negative associations between
424 dispersal and fitness, in particular for individuals dispersing over large distances (reviewed in
425 Doligez and Part 2008; see also Gienapp and Merilä 2011; Pärn et al. 2009; Serrano and Tella
426 2012 for later studies). Similar to our results, several of these studies reported negative fitness
427 consequences of long-distance dispersal in males only (e.g. Bensch et al. 1998; Forero et al.

428 2002; Gienapp and Merilä 2011; Pärn et al. 2009). Two non-exclusive explanations may exist
429 for this result. First, sex-specific patterns of selection may reflect asymmetries in the costs
430 and benefits associated with dispersal between the sexes (Greenwood 1980; Gros et al. 2008).
431 That is, for males, natal philopatry is generally considered more advantageous because of the
432 importance of prior residency for the defence of reproductive resources and/ or territory
433 acquisition (e.g. Nilsson 1989; Pärt T. 1995; Sandell and Smith 1991), while for females it
434 may be more advantageous to disperse, allowing them to choose among territory holding
435 males (Clarke et al. 1997; Greenwood 1980). Hence, a possible explanation for the lower
436 lifetime reproductive performance of immigrant males, as compared to females in the same
437 situation, may be that they suffer more from prior residency effects and as a result occupy
438 lower quality territories. However, it is unclear why this mechanism does not apply to local
439 male dispersers, since they also dispersed over considerable distances moving between
440 physically isolated woodlots (i.e., median 800 m). An additional explanation may therefore be
441 that the weaker reproductive performance of immigrant males may not reflect true costs of
442 dispersal, but rather be the result of differences in phenotypic quality (e.g. Hansson et al.
443 2004; Pärn et al. 2009). For example, in the philopatric sex in particular, large distance
444 dispersers may be typically those birds that lack competitive abilities to settle in or close to
445 their natal area and represent a group of poor quality individuals that are expelled from their
446 local population. An experimental way of manipulating dispersal costs is needed to
447 distinguish between the two hypotheses.

448 Two important caveats of our study should be noted. First, great tits have moderate
449 rates of extra-pair paternity (EPP), and since our reproductive measures are not based on
450 genetic information, we cannot rule out that LFP of immigrant males may have been higher
451 than based on social parentage only. Future studies are needed to clarify to what extent EPP
452 may affect measures of individual fitness in our population. Secondly, given that both natal

453 dispersal and EB have a considerable heritable component in our population (Korsten et al.
454 2013), our measurements of LRP may have been underestimated (Doligez and Part 2008). We
455 believe, however, that this potential bias in our fitness measurements did not affect the
456 outcomes of our study. First, since females disperse over larger distances than males
457 (Greenwood et al. 1979; Matthysen et al. 2001; Verhulst et al. 1997), the reduction of LRP
458 should be more pronounced in female immigrants, but this was not the case. Second, male
459 immigrants produced fewer lifetime fledglings but not recruits, contrary to what would be
460 expected in case of strong genetic effects on dispersal.

461

462 *Selection on personality –dependent dispersal*

463 Based on previous findings in our populations showing positive phenotypic and genetic
464 correlations between EB and dispersal (Korsten et al. 2013; van Overveld et al. 2014), we
465 expected to find selection favouring a close functional integration of both traits. Nevertheless,
466 we found no evidence that fast or slow explorers gain differential fitness benefits by
467 remaining in or leaving their natal area. Moreover, in males, we found that immigrants had on
468 average higher EB scores than residents and local dispersers, but also produced the lowest
469 lifetime number of fledglings. Furthermore, while fast-exploring males survived better in both
470 residents and local dispersers, this was not the case in immigrants. This suggests that either (i)
471 personality-related advantage did not counterbalance the costs associated with being
472 immigrant in our population and/or (ii) that selection on EB was confounded by the poor
473 quality of immigrants. Either way, this finding clearly shows that traits linked to dispersal do
474 not necessary confer any fitness benefits.

475 An obvious question arising from our results is why fast explorers are more inclined to
476 disperse over large distances, while there may not be clear post-settlement fitness benefits
477 associated with this decision. First, since dispersal typically consists of multiple movements

478 before individuals eventually settle in a territory, it is possible that the association between
479 dispersal distance and fast exploration scores resulted from selection during the process of
480 dispersal itself, for instance, if slow-exploring dispersers have a lower post-fledging survival
481 and/or reduced settlement success. In previous work, however, we did not find any evidence
482 that recruitment probability of first-year birds depended on the combination of exploratory
483 behaviour and dispersal distances (van Overveld et al. 2014), which seems to refute this
484 hypothesis. Nevertheless, a more comprehensive study investigating effects of personality-
485 dependent dispersal on post-fledging survival may be necessary to fully evaluate this
486 hypothesis.

487 Alternatively, associations between EB and dispersal may depend on the causal factors
488 driving variation in dispersal. For example, in previous work in our population we found that
489 links between EB and dispersal are particularly pronounced in the first months after fledgling
490 (van Overveld et al. 2014), indicating that larger dispersal distances by fast explorers do not
491 develop gradually, but are mainly driven by factors operating at the early stages of dispersal.
492 Thus, personality-dependent dispersal may be a response to conditions experienced early in
493 the first year, but without carry-over effects on fitness after settlement. In this case, larger
494 dispersal distances by fast explorers are merely a secondary consequence of these individuals
495 being disposed differently with regard to behavioural components of spatial behaviour rather
496 than dispersal propensity *per se*.

497 The lack of evidence for correlational selection in our results strongly contrasts with
498 previous work on western bluebirds (Duckworth 2008; Duckworth and Kruuk 2009), in which
499 correlational selection seems to be the main driving force behind the evolution of distinct
500 dispersal phenotypes (see also introduction). Since both species differ markedly in general
501 ecology this may not be surprising, but nevertheless, an important implication of our results is

502 that different selective scenarios may be responsible for the evolution of personality-
503 dependent dispersal.

504

505 *Sex-specific selection on personality*

506 Our study revealed that fitness associations of EB differed markedly between the sexes,
507 suggesting that different selective mechanisms may be responsible for the maintenance of
508 personality variation in males and females. In males, there was evidence for positive
509 directional survival selection on EB in four out of five years of study. However, survival
510 selection on male EB was highly context-dependent, favouring fast explorers only among
511 first-year residents and local dispersers, but not immigrants or older birds. The higher survival
512 of fast-exploring resident and local dispersers resulted in a positive association between EB
513 and number of lifetime fledglings, but somewhat surprisingly, there was no evidence for
514 lifetime selection on EB using recruits as a measure of fitness. As stated earlier, one possible
515 explanation may be that offspring from fast-exploring males are more likely to recruit outside
516 the study area (cf. Doligez and Part 2008). However, when we restricted the analyses to only
517 those woodlots in the central part of the study area to reduce a potential bias in the detection
518 of recruits, this did not change the results ($F_{1, 55} = 0.19$, $p = 0.66$). An alternative hypothesis
519 might be that slow explorers compensate for their lower productivity with higher parental
520 investment. Indeed, a number of recent studies have shown that reactive personalities have a
521 better reproductive performance than proactive individuals (Barnett et al. 2012; Both et al.
522 2005; Duckworth 2006; Schuett et al. 2012; Mutzel et al. 2013), possibly because the former
523 group allocates more time into other parental activities such as nest defence (e.g. Hollander et
524 al. 2008). Interestingly, additional analyses revealed a negative relationships between EB and
525 brood mass in males ($F_{1, 401} = 4.03$, $\beta = -0.014 \pm 0.007$, $P = 0.04$), with this negative relationship
526 being most pronounced in first-year local recruits ($F_{1, 94} = 11.06$, $\beta = -0.044 \pm 0.013$,

527 $P=0.001$). Since heavy offspring usually have high survival chances (Tinbergen and Boerlijst
528 1990; Vedder et al. 2014), the fitness gains of slow and fast explorers may be subject to a
529 trade-off between offspring quality vs. quantity. Clearly, experimental tests are needed to
530 confirm this hypothesis. For example, brood size manipulations could be used to test whether
531 an experimental increase or decrease in work load differentially affects the survival
532 probabilities of fast- and slow-exploring parents and their offspring.

533 In females, there was evidence for selection on EB through offspring recruitment,
534 which was independent of age or dispersal status. Instead, selection on EB varied strongly
535 between years, including years with negative, positive and stabilizing selection. These strong
536 yearly fluctuations in selection together with the absence of any lifetime selection on EB,
537 indicates a potential role of balancing selection in this sex. Interestingly, similar temporal
538 variability in selection on EB through recruitment in females, but not males, has been
539 previously reported in great tits (Dingemanse et al. 2004; Quinn et al. 2009). Although both
540 the direction and strength of these associations varied among the different studies (i.e.,
541 negative selection in one out of four years of study in Wytham Woods (UK, Quinn et al.
542 2009) and stabilizing selection in two out of three years of study in the Westerheide (The
543 Netherlands, Dingemanse et al. 2004), this independent replication of results is remarkable.
544 Moreover, heterogeneous selection on female personality through offspring survival has also
545 been reported in other taxa than birds (i.e., squirrels, Boon et al. 2007), further indicating this
546 to be a potentially widespread selective mechanism. Although it remains unknown how
547 female personality may exactly be linked to offspring survival, heterogeneous selection on
548 personality is most commonly attributed to temporal and spatial variation in environmental
549 conditions, such as food availability (Dingemanse et al. 2004), social environment (Both et al.
550 2005) or predator abundance (Réale and Festa-Bianchet 2003).

551 The links between EB and adult survival observed in our study differ greatly from
552 previous work on great tits by Dingemanse et al. (2004), who found complex patterns of
553 temporal selection acting through adult survival in both sexes, with selection pressures being
554 opposite between males and females and reversed between years. In the study by Quinn et al.
555 (2009) there was no evidence for selection through survival in either sex. We currently do not
556 have a clear explanation as to why links between EB and survival vary so greatly among the
557 different studies, or even among the sexes within the same population, and this clearly
558 deserves further investigation.

559

560 **Conclusion**

561 Two broad conclusions can be drawn from our study. First, given that selection did not favour
562 certain combinations of EB and natal dispersal, our results do not support the correlational
563 selection hypothesis as an explanation for the evolution of personality-dependent dispersal in
564 our population. The previous reported genetic correlation between EB and natal dispersal
565 (Korsten et al. 2013) may therefore be due to pleiotropic effects rather than linkage
566 disequilibrium, which may be further supported by the fact that the phenotypic co-expression
567 of both traits is most pronounced early in life (van Overveld et al. 2014). We acknowledge,
568 however, that information on survival selection during the process of dispersal itself is needed
569 to fully reject the correlational selection hypothesis. Second, our results contribute to a
570 growing number of studies showing personality traits to be subject to natural selection
571 (reviewed in Dingemanse and Reale 2013). We are currently not aware of other studies
572 showing both directional and fluctuating selection operating simultaneously on personality
573 traits within the same population, and differentially affecting males and females. Our results
574 therefore highlight the importance of using different components of fitness to fully evaluate
575 how natural selection may help to maintain variation in personality.

576

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583

584

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783 **Figure Captions**

784

785 Figure 1. Differences in (a) lifetime fledgling production and (b) exploratory behaviour for
786 male and female great tits categorized as residents (breeding in the natal woodlot), local
787 dispersers (dispersing between woodlots) and immigrants. As a measure of exploratory
788 behaviour we used the total number of movements during a novel environment test (i.e.,
789 ‘exploration score’, see text for further details). Note that immigrants had on average higher
790 EB scores than residents and local dispersers, but also produced the lowest lifetime number of
791 fledglings.

792

793 Figure 2. Lifetime selection on exploratory behaviour (EB) using lifetime number of
794 fledglings produced (LFP) for male and female great tits categorized as resident, local
795 disperser and immigrant. For details on categories see figure 1. As a measure of exploratory
796 behaviour we used the total number of movements during a novel environment test (i.e.,
797 ‘exploration score’, see text for further details). Data consists of individuals born in 2001-
798 2010.

799

800 Table 1. Overview of differences in dispersal distance, exploratory behaviour (EB), lifetime
801 fledgling production (LFP) and lifetime recruitment production (LRP) for male and female
802 great tits categorized as resident, local disperser and immigrant. The dataset consists of birds
803 born in 2001-2010. Mean \pm SE are provided for EB, LFP and LRP and the median for
804 dispersal distance (m) and number of breeding events.

Variable	resident	N	disperser	N	immigrant	N
Males						
Dispersal distance	178	68	828	29	N/A	
Breeding events	2.0	68	2.0	29	1.0	92
EB	18.43 \pm 1.02	68	20.11 \pm 1.65	29	21.96 \pm 0.88	92
LFP	18.94 \pm 1.33	68	22.14 \pm 2.82	29	14.75 \pm 1.02	92
LRP	0.98 \pm 0.16	68	1.82 \pm 0.42 ^b	29	0.88 \pm 0.13	92
Females						
Dispersal distance	190	42	799	67	N/A	111
Breeding events	2.0	42	2.0	67	2.0	111
EB	17.45 \pm 1.32	42	21.28 \pm 1.14	67	20.10 \pm 0.82	111
LFP	16.62 \pm 1.62	42	16.70 \pm 1.36	67	19.15 \pm 1.14	111
LRP	1.24 \pm 0.23	42	0.85 \pm 0.16	67	1.10 \pm 0.13	111

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807

808 Table 2. Standardized directional (S') and nonlinear (c') selection differentials on exploratory
809 behaviour (EB) for male and female great tits categorized as resident, local disperser and
810 immigrant. Selection differentials are estimated using two components of fitness: lifetime
811 fledgling production (LFP) and lifetime recruit production (LRP). Note that the strength of
812 selection on male EB (using LFP) was similar for residents and local dispersers, while absent
813 in immigrants.

	LFP			LRP		
	resident	disperser	immigrant	resident	disperser	immigrant
Males						
$S' \pm SE$	0.166 ± 0.068 *	0.187 ± 0.127	-0.030 ± 0.070	0.262 ± 0.156	0.152 ± 0.216	-0.061 ± 0.140
$c' \pm SE$	0.045 ± 0.056	0.170 ± 0.105	0.011 ± 0.095	0.079 ± 0.125	0.150 ± 0.171	-0.047 ± 0.126
Females						
$S' \pm SE (P)$	-0.025 ± 0.099	0.081 ± 0.082	-0.069 ± 0.060	-0.156 ± 0.199	0.111 ± 0.179	0.030 ± 0.120
$c' \pm SE (P)$	-0.056 ± 0.090	0.088 ± 0.096	-0.035 ± 0.053	-0.329 ± 0.229	-0.152 ± 0.173	0.079 ± 0.104

814 * $p = 0.017$

815 Table 3. Matrices of standardized directional (β) and quadratic (γ) selection gradients for
816 exploratory behaviour (EB) and natal dispersal distance for male and female great tits.
817 Selection gradients are partial regression slopes \pm one standard error. Note that the quadratic
818 gradients and their standard errors are doubled. Gradients are estimated separately for males
819 (n = 97) and females (n = 109), using two components of fitness: lifetime fledgling production
820 (LFP) and lifetime recruit production (LRP).

821

fitness component	trait	β	γ	
			EB	Dispersal distance
Males				
LFP	EB	0.178 \pm 0.061*	0.178 \pm 0.102	
	Dispersal distance	0.052 \pm 0.057	0.024 \pm 0.058	-0.022 \pm 0.068
LRP	EB	0.248 \pm 0.136	0.280 \pm 0.226	
	Dispersal distance	0.224 \pm 0.127	-0.026 \pm 0.128	0.234 \pm 0.152
Females				
LFP	EB	0.035 \pm 0.064	0.012 \pm 0.118	
	Dispersal distance	0.013 \pm 0.069	0.069 \pm 0.089	0.016 \pm 0.094
LRP	EB	-0.042 \pm 0.137	-0.358 \pm 0.246	
	Dispersal distance	-0.058 \pm 0.145	0.217 \pm 0.186	-0.174 \pm 0.196

* p = 0.0046

822

823 Table 4. The effect of exploratory behaviour (EB) and dispersal status (residents, local
824 dispersers and immigrants) on annual fecundity (fledglings and recruits) and survival for male
825 and female great tits. The dataset consists of 10 breeding seasons (range 2002 -2011) with a
826 total of 410 breeding events for males and 522 breeding events for females.

variable	Fledglings			Recruits			Survival		
	DF	F	P	DF	F	P	DF	F	P
males									
EB	1,145	0.05	0.82	1,90.51	0.00	0.96	NA§		
EB ²	1,133	0.00	0.97	1,83.07	0.00	0.95	1,1	2.07	0.15
dispersal status	2,166	0.14	0.71	2,106	2.84	0.06	NA§		
year	9,159	3.42	0.001	6,361	3.96	0.001	5,1	0.75	0.70
age ^a	1,176	0.17	0.68	1,361	2.97	0.08	NA§		
EB x dispersal status	2,168	1.75	0.19	2,82.99	0.51	0.60	2,1	1.75	0.47
EB X age							1,1	11.0	0.001
EB X age X dispersal status							3,1	3.11	0.046
Females									
EB	1,170	0.76	0.38	NA§			1,1	0.03	0.89
EB ²	1,175	1.00	0.32	NA§			1,1	0.03	0.88
dispersal status	2,165	0.47	0.63	2,160.6	0.69	0.50	2,1	1.47	0.54
year	9,126	2.50	0.011	NA§			5,1	0.25	0.82
age ^a	1,86.2	0.32	0.57	1,173.2	3.81	0.05	1,1	0.60	0.58
EB x dispersal status	2,157	2.81	0.06	2,179.8	0.08	0.93	1,1	0.82	0.62
EB x year				6,469	4.04	0.001 ^b			
EB ² x year				6,469	4.28	< 0.001 ^b			

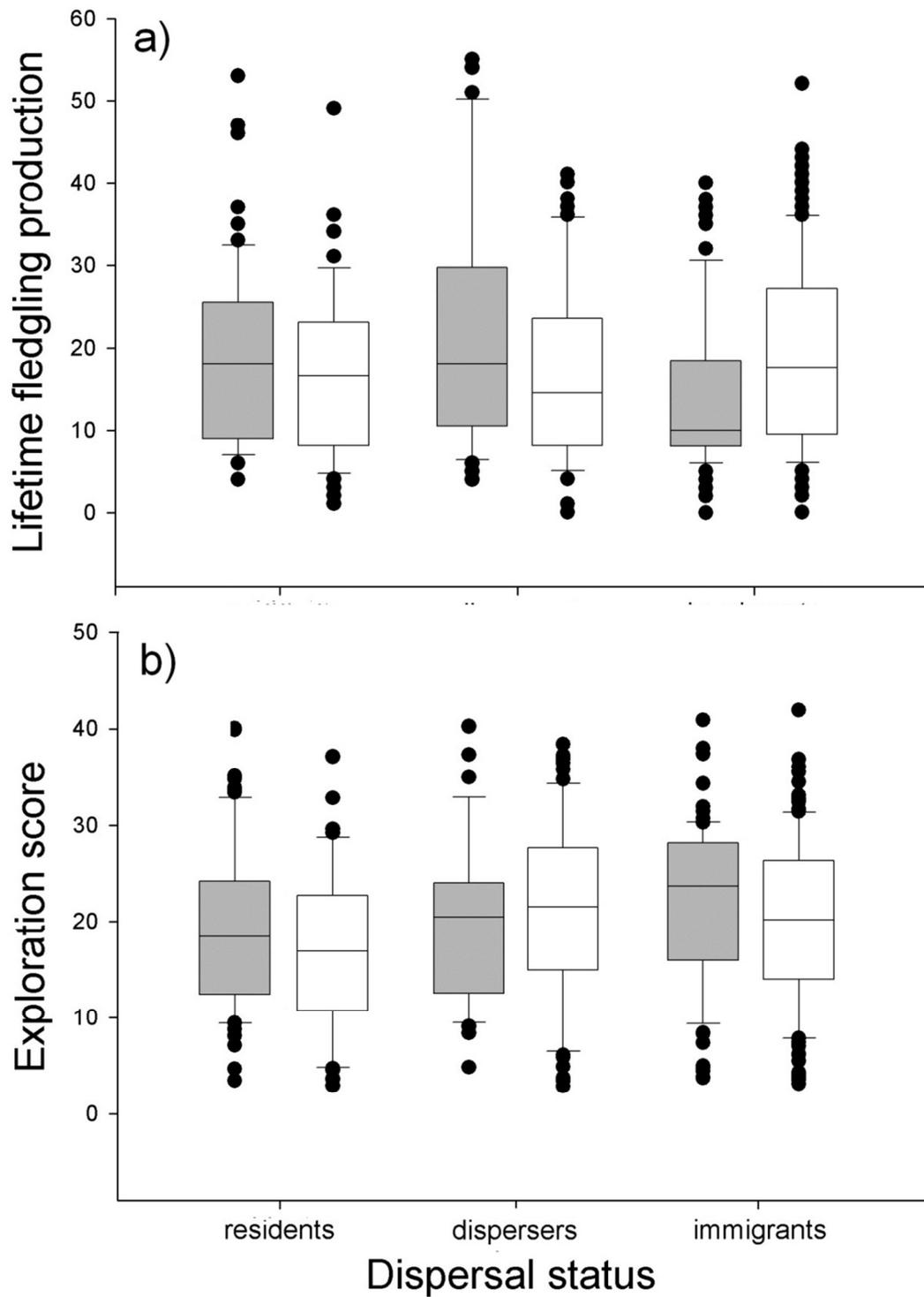
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828 Results are from generalized linear mixed models with individual, year of birth and woodlot
829 of first breeding included as random terms. Final models included all a priori chosen fixed
830 effects and significant interaction terms.

831 ^a Yearling or older

^b non-significant if both interaction terms are entered in the model

§Not applicable, higher order interaction is significant

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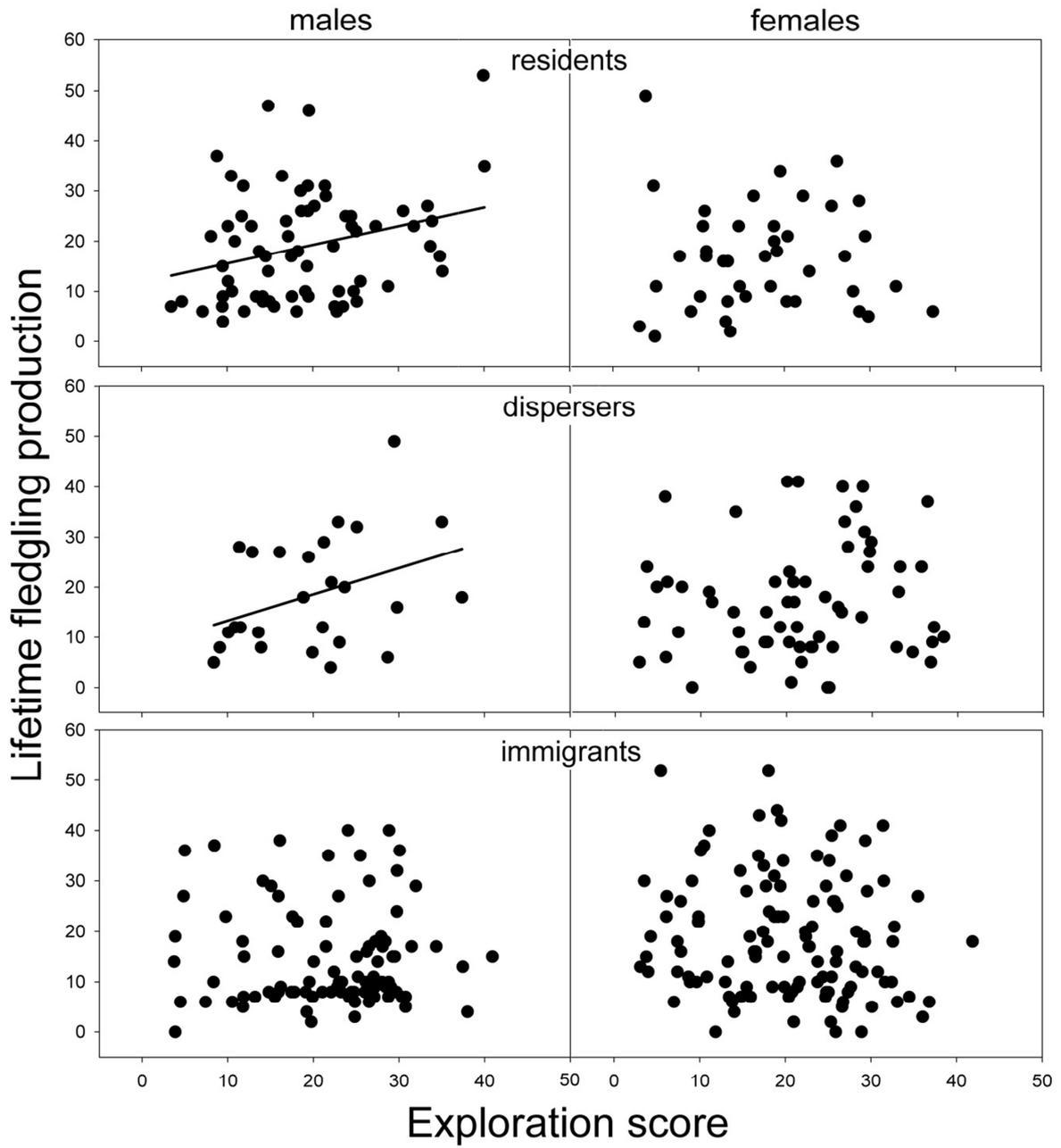
835 Fig. 1 van Overveld *et al.* Lifetime fitness consequences of personality and dispersal in the

836 great tit

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841 Fig. 2 van Overveld *et al.* Lifetime fitness consequences of personality and dispersal in the

842 great tit

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