

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

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

Keywords Personality · Natal dispersal · Lifetime fitness · Correlational selection · *Parus major*

Introduction

Natal dispersal (i.e. the movement from place of birth to the site of first reproduction; hereafter “dispersal”) is a key life-history trait that affects the social and genetic structure,

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and persistence of spatially structured populations (Clobert et al. 2012; Stenseth and Liddicker 1992). Dispersal implies movement away from the natal habitat and therefore can involve a multitude of different costs (reviewed in Bonte et al. 2012) but can also increase the dispersers' fitness by avoiding competition or inbreeding or locating habitat and mates (Clobert et al. 2012). Dispersal behaviour is often influenced by multiple social and environmental factors that vary in space and time (Matthysen 2012; Bowler and Benton 2005; Clobert et al. 2009). Dispersers therefore often constitute a heterogeneous group of individuals that may not only differ from each other in the underlying causation of dispersal (i.e. ecological and social factors driving the decision to disperse), but also in a range of phenotypic characteristics that make them respond differentially to these external factors. Indeed, dispersal tactics often depend on morphological and physiological characteristics that may help to reduce the various costs associated with dispersal and/or to facilitate settlement (Bonte et al. 2012; Bowler and Benton 2005). In recent years, however, it has become increasingly clear that dispersers may also differ from philopatric individuals in various aspects of their behaviour. In many vertebrates, for example, there is accumulating evidence that behaviours such as boldness, aggressiveness and exploration, are often closely integrated with an individual's propensity to disperse (reviewed in Cote et al. 2010). When such behaviours form consistent suites of traits they are also referred to as differences in "personality" (e.g. Gosling 2001; Wilson et al. 1994) or a "behavioural dispersal syndrome" in the specific case of consistent links with dispersal (Duckworth and Kruuk 2009; Cote et al. 2010; Clobert et al. 2009). Differences in personality have been described in widely different taxa (Reale et al. 2010), suggesting personality-dependent dispersal to be potentially widespread. To date, however, actual links between personality and dispersal have been reported for only a limited number of species (Cote et al. 2010). The proximate mechanisms and evolutionary causes underlying these associations are therefore still poorly understood.

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

Studies showing that the costs and benefits of dispersal may vary with personality are, however, very scarce. So far, one of the best examples is a study on western bluebirds (*Sialia mexicana*) (Duckworth 2012). In this species, aggressive males have a competitive

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

Here we investigate the fitness consequences of a previously established link between a well-known personality trait (exploratory behaviour, hereafter EB) and dispersal in a small passerine, the great tit (*Parus major*). Extensive work on this species has shown EB to be repeatable and heritable (Dingemans et al. 2002; Korsten et al. 2013), and to correlate with other behavioural traits both in the laboratory (reviewed in Groothuis and Carere 2005) and in the wild (Cole and Quinn 2012; Dingemans and de Goede 2004; Hollander et al. 2008), leading to the widespread use of this measure as a proxy to describe variation in personality. Associations between natal dispersal and EB have been documented in three different populations in Western Europe [Westerheide (The Netherlands): Dingemans et al. 2003; Wytham Woods (UK): Quinn et al. 2011], including the population of the current study [the ‘Boshoek’ (Belgium): van Overveld et al. 2014]. Studies in all three populations show that fast-exploring individuals have a higher tendency to disperse over large distances. Yet, the extent to which these behavioural differences may enhance the fitness of dispersers still remains unstudied, hampering our understanding of the evolutionary processes underlying these behavioural dispersal syndromes. We recently showed that in our study population both natal dispersal distance and EB have a considerable heritable component and are genetically correlated (Korsten et al. 2013), suggesting that the co-expression of both traits is the result of correlational selection (e.g. Cheverud 1996; Lande 1984). Correlational selection may occur during the process of dispersal itself, for instance, when slow-exploring dispersers have a lower post-fledging survival and/or reduced settlement success. An alternative explanation may be that certain combinations of EB and dispersal lead to a higher fitness after settlement, for instance, when fast-exploring dispersers and/or slow-exploring residents obtain the highest quality mates or territories.

Our main aim in this study is to investigate whether the co-expression of EB and dispersal is shaped by natural selection acting after the termination of the dispersal phase, i.e. after settlement. To measure the extent of selection acting on EB and dispersal we use data on lifetime reproductive success. Natal dispersal was defined in two ways: (1) as a categorical trait, based on movements within and between isolated woodlots in our highly fragmented study area: residents (breeding in the natal woodlot), local dispersers (dispersing between woodlots) and immigrants into the study area, and (2) as a continuous trait, by the distance travelled between place of birth and site of first reproduction (for locally born birds only).

We first examine whether lifetime reproductive success (measured by number of fledglings and recruits) differs between dispersal categories and/or varies with absolute dispersal distance. Because previous studies have documented large differences in the costs of dispersal between males and females (Gros et al. 2008; Greenwood 1980), we included interactions with sex in all analyses. We then examine whether the fitness consequences of

natal dispersal vary with regard to EB and test the hypothesis that correlational selection shapes the (genetic) co-expression of EB and dispersal. This was done by (1) comparing the relationship between EB and fitness components among the three dispersal categories, and (2) by examining how fitness components may vary with regard to absolute natal dispersal distance and EB. In both analyses, we expect a significant interaction between EB and natal dispersal as predictors of fitness. In particular, we expect the relationship between EB and fitness to change from negative in birds with short dispersal distances (the resident category) to positive for birds with longer dispersal distances (local dispersers and immigrants). In the next step, we examine whether any of the above detected relationships resulted from differences in annual survival and/or annual fecundity (i.e. fledglings and recruits). In addition, we test for consistency in patterns of selection by examining whether relationships between EB and fitness components vary among years (Dingemanse and de Goede 2004; Quinn et al. 2009). Finally, we tested whether selection on dispersal and EB occurs only during the first breeding attempt, or continues during the lifetime of the individual.

Materials and methods

Study population and field methodology

The study was conducted in a mosaic landscape with scattered woodland fragments called the ‘Boshoek’ in northern Belgium (518080N, 48320E). This area of approximately 10 km² contains 13 woodlots of mature forest ranging in size from 0.4 to 12 ha. Neighbouring woodlots are 100–600 m apart and separated by small residential areas and agricultural land. Since 1993 all forest woodlots have been equipped with standard nest-boxes (height 1.5 m, dimensions 23 × 9 × 12 cm, entrance 32 mm) at a high density of about six per hectare, containing virtually the entire breeding population inside the woodlots (for more details see Matthysen 2002; Nour et al. 1998). Each year during the breeding season (April–June) all nest boxes are checked weekly to determine the date of the first egg laid (laying date), total number of eggs produced (clutch size) and the total number of nestlings and fledglings. Parents are captured when their nestlings are 8–10 days old and ringed with metal and colour rings. Nestlings are ringed when they reach a development stage equivalent to an age of 15 days which is used as a proxy for fledging date (Matthysen et al. 2011). At this date, total body mass of the brood is measured.

Novel environment test

Since 2006, we have routinely screened great tits on their exploratory behaviour using a novel environment test. Tests were carried out from July until February to avoid any negative effects on territory settlement and breeding success. Birds captured in the field were transported to the lab within 1 h (if captured by mistnet) or 2 h (roosting birds captured in the evening) and housed in individual cages for one night. The exploratory behaviour of birds was measured on the following morning, following the exact procedure described in Dingemanse et al. (2002). Briefly, each bird was entered separately into a sealed room (4.0 × 2.4 × 2.3 m) containing five artificial trees and during the following 2 min, all movements among the different artificial trees (flights) and among the branches of individual trees (hops) were counted, including movements towards other structures such as lamps or sliding doors or to the floor, but not including movements on a single

branch. The total number of movements was used as a measure of exploratory behaviour. All birds were released near their site of capture within 24 h after capture. Our exploration scores increase from summer to the start of the breeding season, a pattern consistent with other studies on exploratory behaviour in great tits (Dingemanse et al. 2012). To correct for this seasonal trend we used the equation: ‘season corrected exploration score’ = ‘measured exploration score’ – (0.036 × ‘July date’) + 10, where ‘July date’ was the number of days from 1 July onwards (for details see Dingemanse et al. 2002). Our corrected exploration score is significantly repeatable ($r = 0.42, p < 0.001$, i.e., based on 154, 46, 24 individuals tested two to four times respectively, with scores adjusted for effects of time of season, test-sequence and interval (for details see Dingemanse et al. 2012). Our (corrected) individual exploration scores have a heritability estimate of $h^2 0.30 \pm 0.11$ SE (Korsten et al. 2013). Exploration scores are unrelated to sex ($F_{2,820} = 0.33, p = 0.56$), age ($F_{5,817} = 1.46, p = 0.20$), body size ($F_{2,802} = 0.68, p = 0.41$) or body mass (i.e., residuals over tarsus corrected for capture date and time of the day, $F_{2,711} = 0.13, p = 0.72$). Note that in our analyses we used the first exploration score in case birds were tested multiple times.

Dispersal and fitness data

Dispersal was quantified in two different ways: (1) as a categorical trait, and (2) by the straight line distance in m between place of birth and site of first breeding. To categorize dispersal, we distinguished between three dispersal strategies (‘dispersal status’ hereafter), based on the highly patchy distribution of breeding habitat (woodlots): (1) birds captured in their natal woodlot were defined as ‘residents’; (2) birds captured in a woodlot different from their natal woodlot were defined as ‘local dispersers’; and (3) birds that were not ringed as a nestling in the study area were defined as ‘immigrants’ (cf. Snoeijis et al. 2004). The six smallest woodlots (0.4–1.25 ha) were pooled with the nearest larger woodlots in the analysis because in these particular cases between-woodlot dispersal distances were less than the average within-woodlot dispersal distances (for details see Matthysen 2002). After pooling these small woodlots, dispersal distances of residents varied from 0 to 529 m (median distance 177 m, $n = 110$), those of local dispersers from 390 to 2,241 m (median distance 812 m, $n = 96$). Table 1 gives an overview of dispersal distances by sex. The origin of unringed birds was by definition unknown, but the distance to the nearest wooded area without nestboxes varied from 350 for some of the peripheral woodlots to 1,200 m for the most centrally located woodlot, and was generally more than 1,000 m. A fraction of unringed birds may have been born in nestboxes in gardens in the matrix between woodlots (estimated at 10–15 %). Thus, quantifying natal dispersal as a categorical trait allowed us to include immigrants as an additional dispersal category even though their actual dispersal distances are unknown.

Lifetime reproductive success (LRS) was quantified by: (1) lifetime fledgling production (LFP), i.e., the total number of fledglings produced over an individual’s lifetime, and (2) lifetime recruitment production (LRP), i.e., total number of fledglings that returned as local breeders over an individual’s lifetime. We analysed both measures because local recruitment patterns may be confounded by heritable variation in offspring dispersal (Doligez and Part 2008). To calculate LFP and LRP, we included all reproductive data available from first, second and replacement broods. We also looked at variation in annual fitness to examine whether differences in LFP and LRP were the result of differences in reproduction or survival, and to examine whether fitness components differed between first-year breeders and older birds. Annual fitness variation was quantified by (1) number of

Table 1 Overview of differences in dispersal distance, exploratory behaviour (EB), lifetime fledgling production (LFP) and lifetime recruitment production (LRP) for male and female great tits categorized as resident, local disperser and immigrant

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 ± 1.02	68	20.11 ± 1.65	29	21.96 ± 0.88	92
LFP	18.94 ± 1.33	68	22.14 ± 2.82	29	14.75 ± 1.02	92
LRP	0.98 ± 0.16	68	1.82 ± 0.42	29	0.88 ± 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 ± 1.32	42	21.28 ± 1.14	67	20.10 ± 0.82	111
LFP	16.62 ± 1.62	42	16.70 ± 1.36	67	19.15 ± 1.14	111
LRP	1.24 ± 0.23	42	0.85 ± 0.16	67	1.10 ± 0.13	111

The dataset consists of birds born in 2001–2010. Mean ± SE are provided for EB, LFP and LRP and the median for dispersal distance (m) and number of breeding events

fledglings produced, i.e. the total number of offspring that survived until 2 weeks of age, (2) number of recruits, i.e. the number of fledglings that survived and bred in the local study population and (3) adult survival, i.e. survival between subsequent breeding seasons.

Data selection

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

We had data available for 189 males (68 residents, 29 dispersers, 92 immigrants) and 220 females (42 residents, 67 residents, 111 immigrants) with known exploration scores. In both sexes, data were distributed over nine cohorts (2001–2009) and 10 breeding seasons (range 2002–2011) with a total of 410 breeding events for males and 522 breeding events for females. Because birds were tested on exploratory behaviour from January 2006 to February 2010, but many of these birds had been ringed in previous years, our dataset contained many breeding events of birds that at the time were not yet tested for exploratory behaviour. As a consequence, breeding events from the seasons 2002–2004 were biased in the sense that they only contained birds that survived at least one more year. For breeding events in the 2005 breeding season, this bias was somewhat smaller, but still >85 % survived at least 1 year. Since these birds may represent a subset of high quality individuals (or territories), we repeated all analyses on a restricted dataset (cf. Quinn et al. 2011), which only contained breeding seasons 2006–2010, by removing all birds born in 2001–2004 and all birds that were still alive in 2012. This substantially reduced sample sizes [females: 138 individuals, 247 breeding events (11–32 % of all females per breeding season); males: 119 individuals, 196 breeding events (8–27 % of all males per breeding season)]. Because the outcomes of analyses on both the unrestricted and restricted dataset were highly comparable, we only present results of analyses on the unrestricted dataset.

Note that in the unrestricted dataset: (1) the lifetime number of broods produced, and hence LFP and LRP, are higher than the population average, and (2) 11 males (6 %) and 6 females (3 %) were still alive by the end of the study and for these individuals lifetime fitness may have been underestimated.

Statistical analyses

Lifetime selection on dispersal

Lifetime selection on dispersal was analysed using general linear mixed models (LFP) or generalized linear mixed models (LRP, with a log link function for Poisson-distributed data). We ran different models with either dispersal status or dispersal distance included as fixed effects. We included sex and sex-specific interactions in all models to test whether selection on dispersal differed between males and females. Woodlot of first breeding was included as a random variable to account for the spatial structure of the population (Van Noordwijk 1984). We also included year of birth as random variable to account for cohort effects on LFP or LRP (either due to natural variation or to the study design, see higher). LFP was $\log(x + 0.5)$ transformed to ensure normality of residuals (Shapiro–Wilk test).

Correlational selection on EB and dispersal

To test for correlational selection on dispersal and EB, we used two different approaches. First, we compare the relationship between EB and lifetime fitness (LFP and LRP) among the three dispersal categories (residents, local dispersers, immigrants) by including EB and its interactions with dispersal status in the above mentioned models. We also include the quadratic effects of EB to test for non-linear selection which may be stabilizing (negative sign of quadratic coefficient) or disruptive (positive sign). Thus, full models included EB, EB^2 , sex, dispersal status, and all first-order interactions as fixed effects and year of birth and woodlot of first breeding as random variables. We then estimated selection on EB within each dispersal category by calculating standardized directional (S') and nonlinear (c') selection differentials. This was done by standardizing EB to zero mean and unit variance and by using relative fitness measures (scaled to a mean of 1, after Arnold and Wade 1984a, b).

Secondly, we estimated selection acting on the phenotypic covariance between EB and natal dispersal distance (i.e., for locally born birds only), by calculating standardized correlational selection gradients from regression models using LFP or LRP. Correlational coefficients between EB and dispersal distance were estimated from full models that included linear terms (EB and dispersal distance), quadratic terms (EB^2 , dispersal distance²) and cross-product terms ($EB \times$ dispersal distance) (Brodie et al. 1995). Quadratic selection gradients and their standard errors were doubled following Stinchcombe et al. (2008). Selection gradients are estimated separately for males and females using standardized measures of EB and relative fitness measures (see above). Dispersal distance was $\log(x + 10)$ transformed to reach normality of residuals (Shapiro–Wilk test).

Variation in survival and fecundity

To examine whether patterns of lifetime selection on dispersal and EB resulted from differences in yearly survival or fecundity we used general linear mixed models for the

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

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

Results

Lifetime selection on natal dispersal

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

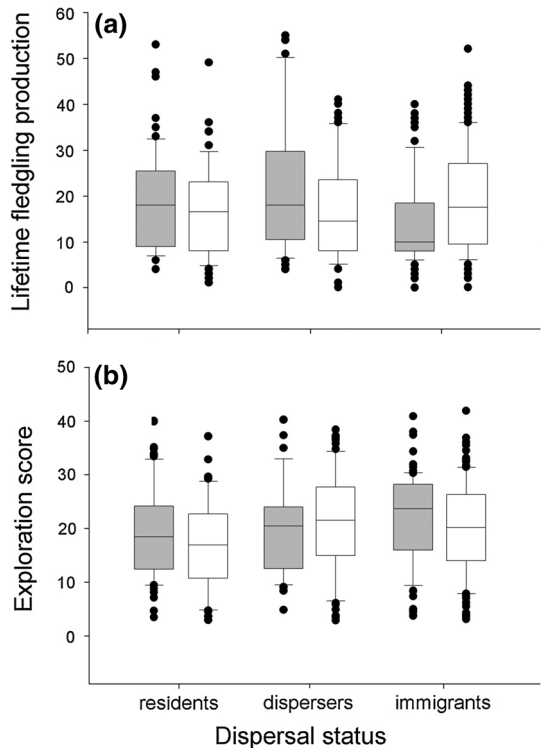
Lifetime production of fledglings and recruits differed between dispersal categories in a sex-specific manner (LFP: EB × sex × dispersal status; $F_{2,394} = 4.58$, $p = 0.011$; LRP: $F_{2,403} = 8.66$, $p = 0.0003$, Fig. 1). In males, immigrants produced fewer fledglings during their life ($F_{2,180}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

For locally born birds, there was no relationship between natal dispersal distance and 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 females (LFP: $F_{1,101} = 0.58$, $p = 0.45$; LRP: $F_{1,108} = 0.07$, $p = 0.80$).

Variation in survival and fecundity

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

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



($F_{1,187} = 4.33$, $p = 0.039$, Table 1) and immigrant females (sex \times dispersal category: $F_{1,390} = 4.93$, $p = 0.026$, Table 1), suggesting that the lower LFP of immigrant males resulted from a shorter lifespan.

Correlational selection on EB and dispersal

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

There was no evidence for directional or non-linear selection acting on EB based on either LFP or LRP (all dispersal categories pooled, $p > 0.2$ for both sexes). There was evidence for differences in directional selection on EB with respect to dispersal category and sex using LFP (EB \times sex \times dispersal status: $F_{5,389} = 4.12$, $p = 0.007$). In males

selection on EB was positively directional and of similar strength in both residents and local dispersers (Fig. 2; see Table 2 for SSD on EB for both categories). When male residents and local dispersers were pooled selection on EB remained positive and significant ($F_{1,92.9} = 9.83$, $p = 0.002$). By contrast, no selection on EB was detected in immigrants [$p > 0.2$, Table 2; Fig. 2, interaction EB \times dispersal status (locally born vs. immigrants); $F_{1,182} = 6.43$, $p = 0.012$]. There was no evidence for correlational selection on EB and dispersal category through LRP in either of the sexes ($p > 0.1$, Table 2) nor did we find evidence for non-linear selection using either LFP or LRP ($p > 0.1$, Table 2).

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

Variation in survival and fecundity

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

In females, there was evidence for heterogeneity in selection on EB through recruitment with respect to year (Table 4), showing selection on EB to be negative (2004, 2005), positive (2007) and stabilizing (2010), while no selection was found in other years (2006, 2008, 2009). In males, there was no evidence for selection on EB to fluctuate between years (EB \times year: $p = 0.87$; EB² \times year: $p = 0.84$). Yearly fluctuations in selection on EB did not differ between the sexes in all years (sex \times EB \times year: $F_{13,834} = 1.59$, $p = 0.082$; sex \times EB² \times year: $F_{13,833} = 1.62$, $p = 0.075$), but were significantly different in 2004 ($F_{1,49} = 6.46$, $p = 0.014$) and 2007 ($F_{1,179} = 6.50$, $p = 0.012$) only.

Discussion

Here, we investigated the post-settlement fitness consequences of a previously established link between a personality trait—exploratory behaviour (EB)—and dispersal in the great tit (Dingemanse et al. 2003; Quinn et al. 2011; van Overveld et al. 2014). Two main patterns emerged from our study. First, overall selection on dispersal appeared generally weak, with lower fitness for immigrant males (but not females) in terms of lifetime fledgling production, and no difference between residents and local dispersers. Second, we found strong evidence that EB is correlated with different components of fitness in males and females. However, in neither of the sexes did the fitness consequences of personality depend on its interaction with dispersal, thus providing no evidence for correlational selection on both

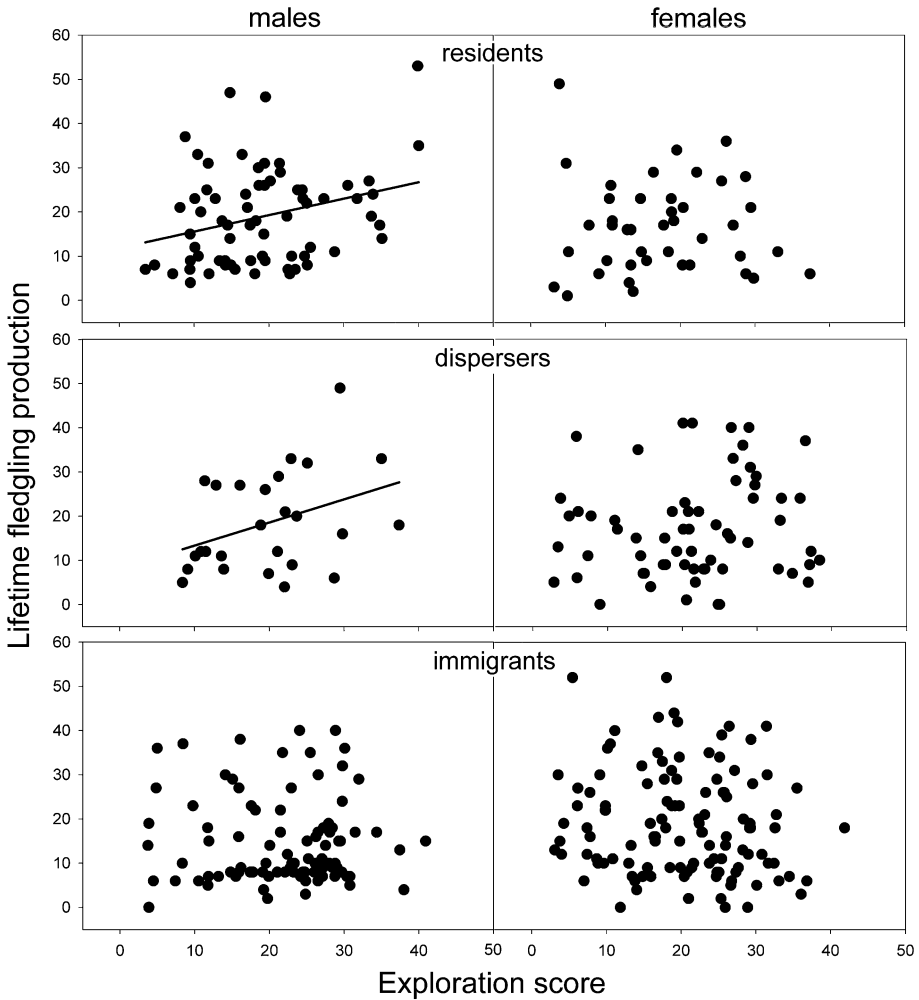


Fig. 2 Lifetime selection on exploratory behaviour (EB) using lifetime number of fledglings produced (LFP) for male and female great tits categorized as resident, local disperser and immigrant. For details on categories see Fig. 1. As a measure of exploratory behaviour we used the total number of movements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

traits. In addition, we found no evidence for lifetime selection acting on EB using recruits as a measure of fitness. Taken together, our results do not support the hypothesis that the co-expression of personality and dispersal is shaped by selection after settlement.

Selection on natal dispersal

Studies investigating the long-term fitness consequences of natal dispersal in birds are generally scarce, but those that did have generally found negative associations between dispersal and fitness, in particular for individuals dispersing over large distances (reviewed

Table 2 Standardized directional (S') and nonlinear (c') selection differentials on exploratory behaviour (EB) for male and female great tits categorized as resident, local disperser and immigrant

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

Selection differentials are estimated using two components of fitness: lifetime fledgling production (LFP) and lifetime recruit production (LRP). Note that the strength of selection on male EB (using LFP) was similar for residents and local dispersers, while absent in immigrants

* $p = 0.017$

Table 3 Matrices of standardized directional (β) and quadratic (γ) selection gradients for exploratory behaviour (EB) and natal dispersal distance for male and female great tits

Fitness component	Trait	β	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

Selection gradients are partial regression slopes \pm one standard error. Note that the quadratic gradients and their standard errors are doubled. Gradients are estimated separately for males ($n = 97$) and females ($n = 109$), using two components of fitness: lifetime fledgling production (LFP) and lifetime recruit production (LRP)

* $p = 0.0046$

in Doligez and Part 2008; see also Gienapp and Merilä 2011; Pärn et al. 2009; Serrano and Tella 2012 for later studies). Similar to our results, several of these studies reported negative fitness consequences of long-distance dispersal in males only (e.g. Bensch et al. 1998; Forero et al. 2002; Gienapp and Merilä 2011; Pärn et al. 2009). Two non-exclusive explanations may exist for this result. First, sex-specific patterns of selection may reflect asymmetries in the costs and benefits associated with dispersal between the sexes (Greenwood 1980; Gros et al. 2008). That is, for males, natal philopatry is generally considered more advantageous because of the importance of prior residency for the defence of reproductive resources and/or territory acquisition (e.g. Nilsson 1989; Pärt 1995; Sandell and Smith 1991), while for females it may be more advantageous to disperse, allowing them to choose among territory holding males (Clarke et al. 1997; Greenwood 1980). Hence, a possible explanation for the lower lifetime reproductive performance of immigrant males, as compared to females in the same situation, may be that they suffer more from prior residency effects and as a result occupy lower quality territories. However, it is unclear why this mechanism does not apply to local male dispersers, since they also dispersed over considerable distances moving between physically isolated woodlots (i.e., median 800 m). An additional explanation may therefore be that the weaker reproductive performance of immigrant males may not reflect true costs of dispersal, but rather be the result of differences in phenotypic quality (e.g. Hansson et al. 2004; Pärn et al. 2009). For example, in the philopatric sex in particular, large distance dispersers may be typically those birds that lack competitive abilities to settle in or close to their natal area and represent a group of poor quality individuals that are expelled from their local population. An experimental way of manipulating dispersal costs is needed to distinguish between the two hypotheses.

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

Table 4 The effect of exploratory behaviour (EB) and dispersal status (residents, local dispersers and immigrants) on annual fecundity (fledglings and recruits) and survival for male and female great tits

Variable	Fledglings			Recruits			Survival		
	<i>df</i>	F	<i>p</i>	<i>df</i>	F	<i>p</i>	<i>df</i>	F	<i>p</i>
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 × dispersal status	2,168	1.75	0.19	2,82.99	0.51	0.60	2,1	1.75	0.47
EB × age							1,1	11.0	0.001
EB × age × 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 × dispersal status	2,157	2.81	0.06	2,179.8	0.08	0.93	1,1	0.82	0.62
EB × year				6,469	4.04	0.001^b			
EB ² × year				6,469	4.28	<0.001^b			

The dataset consists of 10 breeding seasons (range 2002–2011) with a total of 410 breeding events for males and 522 breeding events for females

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

Significant effects are highlighted in bold

[§] Not applicable, higher order interaction is significant

^a Yearling or older

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

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

Selection on personality-dependent dispersal

Based on previous findings in our populations showing positive phenotypic and genetic correlations between EB and dispersal (Korsten et al. 2013; van Overveld et al. 2014), we

expected to find selection favouring a close functional integration of both traits. Nevertheless, we found no evidence that fast or slow explorers gain differential fitness benefits by remaining in or leaving their natal area. Moreover, in males, we found that immigrants had on average higher EB scores than residents and local dispersers, but also produced the lowest lifetime number of fledglings. Furthermore, while fast-exploring males survived better in both residents and local dispersers, this was not the case in immigrants. This suggests that either (1) personality-related advantage did not counterbalance the costs associated with being immigrant in our population and/or (2) that selection on EB was confounded by the poor quality of immigrants. Either way, this finding clearly shows that traits linked to dispersal do not necessarily confer any fitness benefits.

An obvious question arising from our results is why fast explorers are more inclined to disperse over large distances, while there may not be clear post-settlement fitness benefits associated with this decision. First, since dispersal typically consists of multiple movements before individuals eventually settle in a territory, it is possible that the association between dispersal distance and fast exploration scores resulted from selection during the process of dispersal itself, for instance, if slow-exploring dispersers have a lower post-fledging survival and/or reduced settlement success. In previous work, however, we did not find any evidence that recruitment probability of first-year birds depended on the combination of exploratory behaviour and dispersal distances (van Overveld et al. 2014), which seems to refute this hypothesis. Nevertheless, a more comprehensive study investigating effects of personality-dependent dispersal on post-fledging survival may be necessary to fully evaluate this hypothesis.

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

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

Sex-specific selection on personality

Our study revealed that fitness associations of EB differed markedly between the sexes, suggesting that different selective mechanisms may be responsible for the maintenance of personality variation in males and females. In males, there was evidence for positive directional survival selection on EB in four out of 5 years of study. However, survival selection on male EB was highly context-dependent, favouring fast explorers only among first-year residents and local dispersers, but not immigrants or older birds. The higher survival of fast-exploring resident and local dispersers resulted in a positive association

between EB and number of lifetime fledglings, but somewhat surprisingly, there was no evidence for lifetime selection on EB using recruits as a measure of fitness. As stated earlier, one possible explanation may be that offspring from fast-exploring males are more likely to recruit outside the study area (cf. Doligez and Part 2008). However, when we restricted the analyses to only those woodlots in the central part of the study area to reduce a potential bias in the detection of recruits, this did not change the results ($F_{1,55} = 0.19$, $p = 0.66$). An alternative hypothesis might be that slow explorers compensate for their lower productivity with higher parental investment. Indeed, a number of recent studies have shown that reactive personalities have a better reproductive performance than proactive individuals (Barnett et al. 2012; Both et al. 2005; Duckworth 2006; Schuett et al. 2012; Mutzel et al. 2013), possibly because the former group allocates more time into other parental activities such as nest defence (e.g. Hollander et al. 2008). Interestingly, additional analyses revealed a negative relationship between EB and brood mass in males ($F_{1, 401} = 4.03$, $\beta = -0.014 \pm 0.007$, $p = 0.04$), with this negative relationship being most pronounced in first-year local recruits ($F_{1, 94} = 11.06$, $\beta = -0.044 \pm 0.013$, $p = 0.001$). Since heavy offspring usually have high survival chances (Tinbergen and Boerlijst 1990; Vedder et al. 2014), the fitness gains of slow and fast explorers may be subject to a trade-off between offspring quality versus quantity. Clearly, experimental tests are needed to confirm this hypothesis. For example, brood size manipulations could be used to test whether an experimental increase or decrease in work load differentially affects the survival probabilities of fast- and slow-exploring parents and their offspring.

In females, there was evidence for selection on EB through offspring recruitment, which was independent of age or dispersal status. Instead, selection on EB varied strongly between years, including years with negative, positive and stabilizing selection. These strong yearly fluctuations in selection together with the absence of any lifetime selection on EB, indicates a potential role of balancing selection in this sex. Interestingly, similar temporal variability in selection on EB through recruitment in females, but not males, has been previously reported in great tits (Dingemanse et al. 2004; Quinn et al. 2009). Although both the direction and strength of these associations varied among the different studies (i.e., negative selection in one out of 4 years of study in Wytham Woods (UK, Quinn et al. 2009) and stabilizing selection in two out of 3 years of study in the Weste-rheide (The Netherlands, Dingemanse et al. 2004), this independent replication of results is remarkable. Moreover, heterogeneous selection on female personality through offspring survival has also been reported in other taxa than birds (i.e., squirrels, Boon et al. 2007), further indicating this to be a potentially widespread selective mechanism. Although it remains unknown how female personality may exactly be linked to offspring survival, heterogeneous selection on personality is most commonly attributed to temporal and spatial variation in environmental conditions, such as food availability (Dingemanse et al. 2004), social environment (Both et al. 2005) or predator abundance (Réale and Festa-Bianchet 2003).

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

Conclusion

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

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