

Chapter 4

NATAL DISPERSAL AND PERSONALITIES IN GREAT TITS (*PARUS MAJOR*)

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ABSTRACT

Dispersal is a major determinant of the dynamics and genetic structure of populations, and its consequences depend not only on average dispersal rates or distances, but also on the characteristics of dispersing and philopatric individuals. We investigated whether natal dispersal correlated with a pre-disposed behavioural trait: exploratory behaviour in novel environments. Wild great tits were caught in their natural habitat, tested the following morning in the laboratory using an open field test and released at the capture site. Natal dispersal correlated positively with parental and individual exploratory behaviour, using three independent data sets. First, fast exploring parents had offspring that dispersed furthest. Second, immigrants were faster explorers than locally born birds. Third, post-fledging movements, comprising a major proportion of the variation in natal dispersal distances, were larger for fast females than for slow females. These findings suggest that parental behaviour influenced offspring natal dispersal either via parental behaviour *per se* (e.g. via post-fledging care) or by affecting the phenotype of their offspring (e.g. via their genes). Because this personality trait has a genetic basis, our results imply that genotypes differ in their dispersal distances. Therefore, the described patterns have profound consequences for the genetic composition of populations.

INTRODUCTION

Natal dispersal – the movement between the place of birth and first breeding – is a major determinant of the dynamics and genetic structure of populations (Hamilton & May 1977; Johnson & Gaines 1990; Whitlock 2001). Dispersal rates and distances have been shown to correlate with properties of the individual – like body mass or wing shape – or properties of its parents (Swingland 1983; Lidicker & Stenseth 1992; Clobert et al. 2001), many of which have a substantial heritability (reviewed by Roff & Fairbairn 2001). To predict the consequences of dispersal for the genetic structure of populations, we need to know both the phenotypic correlates of dispersal and their heritability. Furthermore, most theoretical models are based on population mean values and ignore individual variation (Johnson & Gaines 1990; Clobert et al. 2001).

Most studies of dispersal involved attempts to relate dispersal rates and distances to traits that are known to be important in understanding life histories (see Clobert et al. 2001). Avian dispersal has, for instance, been related to parental clutch size (Pärt 1990), date of birth (Dhondt & Hublé 1968; Nilsson 1989; van de Castele 2002) and fledgling mass (Greenwood et al. 1979; Drent 1984; Nilsson 1989; Verhulst et al. 1997; Altwegg et al. 2000; van der Jeugd 2001; but see Dhondt 1979). Behavioural traits – like aggression, sociability, or boldness – may also explain variation in dispersal behaviour (Svendsen 1974; Brandt 1992; Fraser et al. 2001). For example, the Chitty–Krebs hypothesis (Chitty 1967; Krebs 1978) predicts that aggressive individuals force docile individuals to disperse when population densities are high. The relationship between dispersal and behavioural traits has received little attention so far (Wilson et al. 1994; Fraser et al. 2001).

The aim of this study was to examine whether natal dispersal correlates with individual exploratory behaviour. We used an experimental procedure to measure individual differences in behaviour towards novel environments ('exploratory behaviour') of great tits (Dingemanse et al. 2002, *chapter 2*). Our measure of exploratory behaviour has a substantial heritable component in both captive-bred and wild-caught great tits (h^2 estimates between 0.3–0.6), and is unrelated to condition during the nestling phase or at the time of measurement, age, sex or body size (Verbeek et al. 1994, 1996; Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003). Exploratory behaviour correlates with other types behaviours, including boldness towards novel objects, aggression in pair-wise confrontations, and foraging behaviour in social and non-social situations (Verbeek et al. 1994, 1996; Drent & Marchetti 1999; Marchetti & Drent 2000). These co-varying behaviours reflect general strategies that individuals use to cope with novel social and non-social situations (Benus et al. 1991; Verbeek et al. 1994; Koolhaas et al. 1999) and can be viewed as evidence for the concept of coping strategies (Koolhaas et al. 1999), personality (Buss 1991), or temperament (Boissy 1995; Segal & MacDonald 1998).

We have studied natal dispersal in a nest box population of great tits. We first showed that in our study population natal dispersal distance is not correlated with date of birth or individual morphology, i.e. traits previously shown to affect natal dispersal in great tits (Dhondt & Hublé 1968; Greenwood et al. 1979; Drent 1984; Verhulst et al. 1997; van de Castele 2002). We then used three independent data sets to examine the correlation between natal dispersal and exploratory behaviour. Because exploratory behaviour has a substantial heritability (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003) and we cannot measure exploratory behaviour in nestlings, we first examine the correlation between natal dispersal of juveniles and the exploratory

Table 1 The relation between natal dispersal distance and nestling traits for great tits hatched from first broods. The results are from a GLM with normal errors after backward elimination for females ($n=80$) and males ($n=84$). Dispersal distances were transformed as $\log_{10}(x+1)$ and year of birth was forced in the model irrespective of significance. F values are for the inclusion of the variable in the final model.

Variable	Females			Males		
	df	F	p	df	F	p
Fledgling mass	1,73	0.90	0.35	1,77	0.31	0.58
Tarsus	1,73	0.00	0.98	1,77	0.06	0.81
Hatching date	1,73	0.02	0.89	1,77	1.21	0.27
Year of birth	5,74	1.54	0.19	5,78	1.19	0.10

behaviour of their parents. Parents can influence natal dispersal of their offspring either via their behaviour *per se* or by affecting the phenotype of their offspring, and we discuss both possible causes. Second, we compared individual exploration scores of immigrants and locally born birds captured in their first year of life. Third, we show that great tits disperse at or shortly after independence and we examine the correlation between individual post-fledging movement and individual exploratory behaviour.

MATERIALS AND METHODS

Study area and field methodology

We used 7 years of data (1995-2001) from a nest box population of great tits in the southern Veluwe area (study areas ‘Westerheide’ and ‘Warnsborn-West’) near Arnhem, the Netherlands, to study phenotypic correlates of natal dispersal. The study area consists of a mixed pine-deciduous wood of 250 ha with about 600 nest boxes (for further details see Dingemanse et al. 2002, *chapter 2*). We checked the nest boxes weekly during the breeding season, and daily before the day of expected egg hatching to determine hatching date of the chicks (measured as the day the first egg in a brood hatched, in days from 1 April). We captured both parents when their chicks were 8–10 days old. Parents were ringed and released immediately afterwards. The chicks were ringed and measured (i.e. body weight to the nearest 0.1 g, tarsus to the nearest 0.1 mm) 14–16 days after hatching. We measured natal dispersal as the distance in metres between the nest box of birth and first breeding (Greenwood 1980). We located *ca.* 5% of all fledged chicks as breeding adults.

Outside the breeding season, we used two methods to capture immigrants and locally born birds. First, we captured individuals in mist nests at 6–8 feeding stations baited with sunflower seeds (about twice a week). Second, we captured birds roosting in the nest boxes at night (twice a year, in November and February/March). We used molecular markers to sex juvenile birds captured in July or August (see Griffiths et al. 1998), and used plumage characteristics to sex all other birds (Jenni & Winkler 1994).

Birds not ringed as nestlings were aged and sexed according to Jenni & Winkler (1994). We used the captures in July and August to calculate individual post-fledging movement, defined as the distance in metres between the nest box of birth and the feeding station of first capture in the summer of birth.

Birds captured between November 1998 and March 2001 were transported to the laboratory, where they were individually housed and provided with food and water. The following morning, we measured exploratory behaviour of each bird individually, before we released them near their individual place of capture within 14–24 hours of capture. Each bird was taken to the laboratory only once. For further details on housing and field methodology see Dingemanse et al. (2002, *chapter 2*).

Measuring exploratory behaviour

We measured exploratory behaviour using the ‘novel environment test’ (Verbeek et al. 1994), a variant of the classical open field test of animal psychologists (Walsh & Cummins 1976). We recognize that this single test may reflect the total effect of several behavioural traits (e.g. exploration, fear, curiosity; see Barnett & Cowan 1976). Results from previous studies, however, suggest that birds acquire information in a novel environment, and their behaviour thus reflects exploratory behaviour (Drent & Marchetti 1999; Dingemanse et al. 2002, *chapter 2*).

Each bird was tested individually between 0800 and 1400 hours in a sealed room (4.0×2.4×2.3 m) under artificial light, containing five artificial wooden trees. Trials began at least one h after sunrise, allowing the birds to eat before the first trials started. We introduced each bird into the room without handling. We observed their behaviour in the observation room for the first two minutes after arrival and used the total number of movements (hops between branches within the trees, and flights among trees or other perches) as an index of exploratory behaviour (‘exploration score’). For further details see Dingemanse et al. (2002, *chapter 2*). We corrected the scores for date of capture, based on within-individual changes in behaviour with capture date (Dingemanse et al. 2002, *chapter 2*).

Statistical analyses

We used General Linear Models (GLMs) with normal errors to evaluate the relationship between natal dispersal distance and sex (104 females, 123 males) and between natal dispersal distance and morphological traits at fledging (listed in table 1; 80 females, 84 males). We fitted all main effects in the model and removed non-significant terms in inverse order of significance. For a smaller data set, we tested the relation between natal dispersal distance and mid-parent exploration score (mean of paternal and maternal scores), using the mean dispersal distance of all offspring per nest as the unit of analysis to avoid pseudoreplication (16 nests for females, 20 nests for males). Unequal sample sizes in the number of offspring measured were taken into account by weighting by the square root of the number of offspring in the nest (Sokal & Rohlf 1995). To investigate whether natal dispersal distance was equally affected by the behaviour of both parents, we re-ran this model and included both maternal and paternal scores – instead of mid-parent score – as independent effects and tested each effect after simultaneously controlling for the other, using type III sums of squares. We did not, however, have sufficient data to also test the relation between natal dispersal distance and individual exploratory behaviour of nestlings that were later

scored for exploratory behaviour. Year of birth was fitted in each model irrespective of significance, to avoid misleading results due to variation between years in natal dispersal distances. We analysed data for females and males separately, because dispersal patterns in great tits have previously been shown to differ between the sexes (Greenwood 1980; Clarke et al. 1997). In the analyses, we included only birds that hatched from first broods, thus omitting 8 (2.6%) of 233 birds with known dispersal distance. Dispersal distances were transformed as $\log_{10}(x+1)$. Kolmogorov–Smirnov tests confirmed that the transformed distances were normally distributed.

Earlier studies on great tits have suggested that natal dispersal starts at or shortly after independence (Dhondt & Hublé 1968; Dhondt 1979; Drent 1984). To evaluate whether individual post-fledging movements comprised most of the variation in natal dispersal distances, we calculated Pearson's correlations between post-fledging care movement and natal dispersal distance. We used GLMs with normal errors to evaluate the relationship between post-fledging movement, transformed as $\log_{10}(x+1)$, and properties of the individual (individual exploration score, body mass during capture, fledging mass, tarsus length, hatching date) for individuals captured in July/August 2000 (25 females, 24 males).

We used randomization tests to check whether significant relationships between dispersal distance and explanatory variables were caused by a non-random distribution of phenotypes over natal nest boxes (van Noordwijk 1984, 1995). In each test we calculated the distance between the natal nest box and a random nest box. We then calculated F values by following simple or multiple regression procedures outlined in Sokal & Rohlf (1995; page 626-629) and took the proportion of 1000 tests on randomized data giving a F value larger than the observed value as an approximate p value. The approximate p value derived from the 1000 randomization tests was very similar to the observed p value in all analyses ($r^2=0.996$, results not shown, number of tests=8). Hence, the position of the natal nest box did not affect our results and therefore we present the parametric statistics. The data were analysed with SPSS v.10.1 software. Values of p are two-tailed throughout.

RESULTS

Correlates of natal dispersal distance

Females dispersed further than males (females: 643 ± 376 (mean \pm SD) m, males: 498 ± 310 m; ANCOVA: year: $F_{1,220}=1.71$, $p=0.13$; sex: $F_{1,220}=7.33$, $p=0.007$), and the effect of sex did not differ between years (interaction sex \times year: $F_{5,215}=0.54$, $p=0.74$). Females also dispersed further than males in a comparison of nest mates (ANCOVA controlling for nest and year: $F_{1,39}=5.42$, $p=0.025$, $n=31$ nests), implying that the observed sex-bias in dispersal was not caused by a non-random distribution of offspring sexes among natal nest boxes (van Noordwijk 1984, 1995). Natal dispersal distance was not related to hatching date, tarsus length or fledging mass in either females or males (table 1). Moreover, quadratic terms were all non-significant (all $p>0.43$), confirming that these results were not caused by a poor fit of linear terms.

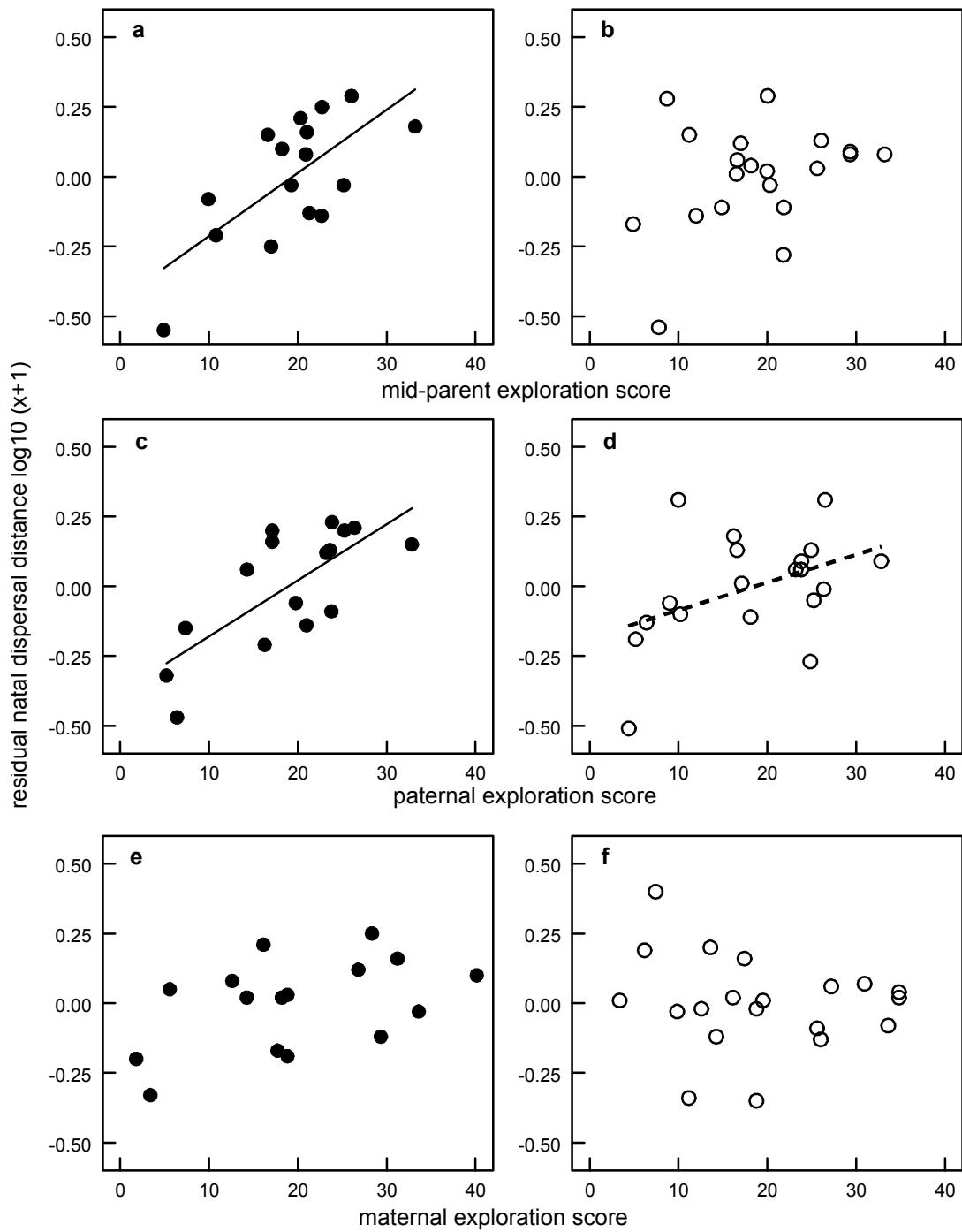


Figure 1 The relation between natal dispersal distance and mid–parent exploration score (a,b), paternal exploration score (c,d) and maternal exploration score (e,f) for female (filled circles) and male great tits (open circles). Dispersal distances were transformed as $\log_{10}(x+1)$ and corrected for the effect of year (a–f), maternal score (c,d) and/or paternal score (e,f). The lines are the fitted regression equations (solid lines: $p < 0.05$, broken line: $p < 0.1$) weighted for the square root of the number of offspring sampled per nest (females: $n = 16$ nests, males: $n = 20$ nests).

Female natal dispersal distance was related to mid-parent exploration score: females with fast parents (i.e. high mid-parent scores) moved over larger distances than females with slow parents ($F_{1,11}=7.48$, $p=0.019$; figure 1a). Female natal dispersal distance increased with paternal score ($F_{1,10}=8.58$, $p=0.015$; figure 1c) but not with maternal score ($F_{1,10}=2.15$, $p=0.17$; figure 1e). Although these results seem to suggest that female natal dispersal distance was not equally affected by the behaviour of both parents, we cannot show that the effect of paternal and maternal score differed (F test for difference between two regression coefficients, Sokal & Rohlf 1995: $F_{1,28}=0.17$, $p=0.68$). Male natal dispersal distance was not related to mid-parent exploratory behaviour ($F_{1,15}=1.81$, $p=0.20$; figure 1b). Male natal dispersal distance tended to increase with paternal score ($F_{1,14}=3.89$, $p=0.069$, figure 1d) but not with maternal score ($F_{1,14}=0.11$, $p=0.74$; figure 1f). However, our ability to detect phenotypic correlates of male natal dispersal distance may have been limited, because natal dispersal distances tended to be less variable in males compared to females (Levene's test for equal variances: $F_{1,34}=3.15$, $p=0.085$). Moreover, the effect of mid-parent exploration score did not differ between the sexes when both sexes were fitted in the same model (interaction, sex \times parental score: $F_{1,29}=2.45$, $p=0.13$), and only the main effect of mid-parent exploration score remained in the final model ($F_{1,30}=5.32$, $p=0.028$). There was also no effect of the interaction between sex and paternal ($F_{1,27}=0.83$, $p=0.37$) or maternal score ($F_{1,27}=2.11$, $p=0.16$), and the main effect of paternal ($F_{1,29}=8.34$, $p=0.007$) but not maternal score ($F_{1,29}=0.33$, $p=0.57$) affected natal dispersal distance when both terms were fitted in the same model. These results therefore suggest that the correlation between natal dispersal distance and mid-parent or paternal behaviour did not differ between the sexes.

Behaviour of immigrants versus locals

Immigrants had higher exploration scores (i.e. were faster explorers) than locally born birds among juvenile birds captured before first reproduction (year: $F_{1,514}=13.43$, $p<0.0001$; Immigration status (local/immigrant): $F_{1,514}=11.43$, $p=0.001$), and the effect of immigration status did not vary between either years (interaction, year \times immigration status: $F_{1,513}=0.21$, $p=0.65$) or the sexes (interaction, sex \times immigration status: $F_{1,512}=0.84$, $p=0.36$; figure 2).

Timing of dispersal

Post-fledging movement comprised a major proportion of the variation in natal dispersal distance in both females ($r=0.79$, $n=14$, $p<0.001$; average proportion of total distance = 0.86) and males ($r=0.80$, $n=10$, $p=0.005$; average proportion of total distance = 0.95). The distance covered after post-fledging movement (defined as distance between site of first capture in summer and site of first breeding) was relatively small and did not explain significant variation in natal dispersal distance in either females ($r=0.32$, $n=14$, $p=0.26$) or males ($r=0.07$, $n=10$, $p=0.85$). These results strongly suggest that dispersing juveniles move to their new neighbourhood at or shortly after independence. Female post-fledging movement was correlated with individual exploration score: fast females moved over larger distances than slow females ($F_{1,24}=6.01$, $p=0.022$; slope: $3.35 \cdot 10^{-2} \pm 0.014$ (SE) \log_{10} m/unit of score). Post-fledging movement of males was not correlated with individual exploration score ($F_{1,23}=0.49$, $p=0.49$, slope: $-1.24 \cdot 10^{-2} \pm 0.018$ (SE) \log_{10} m/unit of score), and

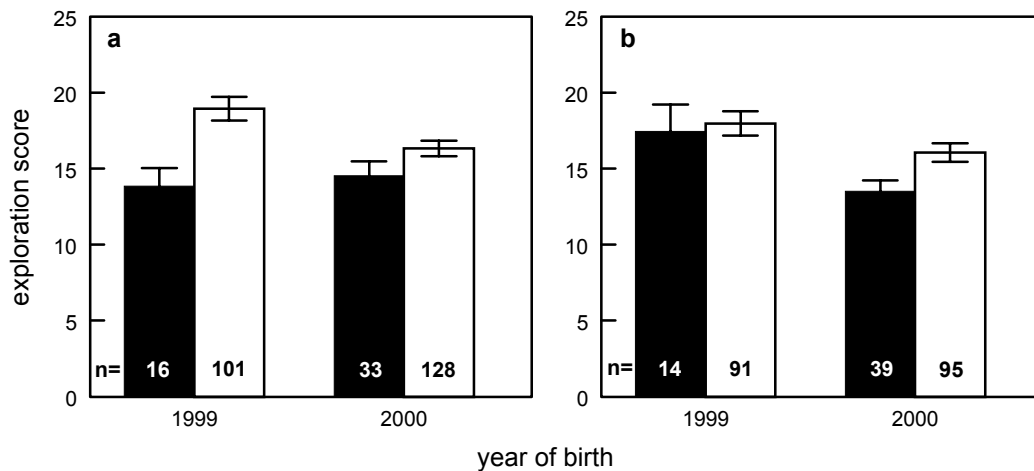


Figure 2 Exploration scores (+SE) and immigration status (filled bars: locals, open bars: immigrants) for (a) female and (b) male great tits that were scored during their first year of life.

the effect of individual exploration score differed between the sexes (interaction, sex \times individual score: $F_{1,47}=4.25$, $p=0.045$). Post-fledging movement neither related to fledgling traits (fledging mass, tarsus length, hatching date) nor to body mass at capture (all $p>0.36$), confirming our results presented in table 1.

DISCUSSION

We showed that natal dispersal distance correlated positively with a personality trait, phenotypic exploratory behaviour, using three largely independent data sets. First, natal dispersal distances were largest for individuals with fast parents. Second, immigrants were faster explorers than locally born birds. Third, post-fledging movements, comprising a major proportion of the variation in natal dispersal distances, were largest for fast females. Our results are qualitatively similar to findings of Fraser et al. (2001) who showed that fast or 'bold' (in their terminology) Trinidad killifish, *Rivulus hartii*, moved over larger distances than slow or 'shy' fish.

Individual differences in morphology, physiology, or behaviour may either be the cause or consequence of dispersal (Dufty & Belthoff 2001; Ims & Hjermann 2001). Most investigators who have reported correlations between dispersal and individual behaviour have only measured individual behaviour during or after dispersal (e.g. Myers & Krebs 1971; Svendsen 1974; Ims 1990), making it difficult to separate cause and effect (Brandt 1992; Ims & Hjermann 2001). Because individual differences in exploratory behaviour arise early in life (Verbeek et al. 1994; Drent et al. 2003), before the onset of dispersal, our data suggest that differences in exploratory behaviour are the cause and not the consequence of dispersal. This suggestion is further confirmed by the correlation between mid-parent exploration score and offspring natal dispersal distance.

Parents may have affected natal dispersal of their offspring via parental behaviour *per se* (e.g. via post-fledging care or aggression directed towards offspring) or by influencing the phenotype of their offspring (e.g. via their genes, egg steroids, or parental investment), which in turn affected offspring dispersal strategy. Effects of

parental behaviour *per se* are likely to occur during the period of post-fledging care, when the male great tit parent guides the brood to good foraging sites (Drent 1984; Verhulst & Hut 1996). Furthermore, fast-exploring fathers (and mothers) may not only be more aggressive to conspecific competitors (Verbeek et al. 1996; Drent & Marchetti 1999) but also towards their fledged offspring than slow exploring fathers, and as a consequence force their offspring to disperse further. We think, however, that the patterns described are not caused by parental behaviour *per se*, because we would have expected that paternal behaviour differed in its effects from maternal behaviour. Moreover, movements during post-fledging care do not predict natal dispersal distances in great tits (van de Castele 2002). We therefore think it is more likely that parents influenced the phenotype of their offspring which in turn affected natal dispersal.

Effects of parental behaviour on the phenotype of their offspring may be mediated via variation among females in egg steroids (Schwabl 1993), thus indirectly affecting offspring natal dispersal (Dufty & Belthoff 2001). If so, we would have expected a correlation between natal dispersal distance and maternal – not paternal – exploratory behaviour, unless male behaviour affected female breeding condition (Schwabl 1997; Gil et al. 1999). We therefore favour the idea that parents influenced natal dispersal by genes passed to their offspring and that the substantial heritability of exploratory behaviour (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003) explains the correlation between parental exploratory behaviour and offspring natal dispersal.

Our results may seem to suggest that natal dispersal is relatively inflexible and inherited (Howard 1960). However, field studies have failed to show a significant heritability of natal dispersal (Greenwood et al. 1979; van Noordwijk 1984; Waser & Jones 1989; van de Castele 2002). It is therefore usually assumed that dispersal behaviour is flexible and depending on prevailing environmental conditions (Howard 1960; Ims & Hjermann 2001). This notion of environmental dependence is not incompatible with our result of phenotype-dependent dispersal, because environmental effects may differentially affect these behavioural phenotypes. In our study system we have evidence that slow exploring individuals are better in coping with social defeat (Verbeek 1998; Verbeek et al. 1999), which may enable them to remain in highly competitive situations. The slower exploratory behaviour may thus be traded-off against the ability to cope with social stress, resulting in phenotypes differing in their optimal dispersal strategy. The sex difference in the relationship between post-fledging dispersal and individual exploratory behaviour further illustrates that patterns of phenotype-dependent dispersal may also differ between the sexes (Greenwood 1980; Clarke et al. 1997), although we could not detect sex differences in the relationship between natal dispersal and phenotypic exploratory behaviour. A next step would be to understand how phenotype-dependent dispersal depends on the environmental conditions (see also Drent et al. 2003). For instance, conflicting evidence for a relationship between dispersal and aggressiveness in rodents, or dispersal and nestling traits (e.g. fledging mass, tarsus length) in birds, is likely to result from variation in the amount and distribution of resources, levels of competition, and social structure of the population (Brandt 1992; Verhulst et al. 1997).

Because exploratory behaviour has a substantial heritable component (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003), differential dispersal with respect to exploratory behaviour may have profound consequences for the genetic composition of metapopulations (Bohonak 1999; Roff & Fairbairn 2001; Whitlock

2001). In rodents, for instance, genetically docile individuals may be more likely become founders of new populations (Chitty 1967; Krebs 1978), potentially affecting the composition of behavioural phenotypes in source and sink populations (Pulliam 1996). Moreover, dispersal may allow a certain genotype to persist that has a lower fitness in general, but is better adapted to new and changing circumstances.

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