Natal dispersal and personalities in great tits (*Parus major*)

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Dispersal is a major determinant of the dynamics and genetic structure of populations, and its consequences depend not only on average dispersal rates and distances, but also on the characteristics of dispersing and philopatric individuals. We investigated whether natal dispersal correlated with a predisposed 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 datasets. 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 greater 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.

Keywords: natal dispersal; immigration; *Parus major*; exploration; boldness; personality

1. 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 have 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 Casteele 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 relation 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 (see Dingemanse *et al.* 2002). Our measure of exploratory behaviour has a substantial heritable component in both captive-bred and wild-caught great tits (h^2 estimates of 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; Drent *et al.* 2003). Exploratory behaviour correlates with other types of behaviour, 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 types of behaviour 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

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shown to affect natal dispersal in great tits (Dhondt & Hublé 1968; Greenwood *et al.* 1979; Drent 1984; Verhulst *et al.* 1997; Van de Casteele 2002). We then used three independent datasets to examine the correlation between natal dispersal and exploratory behaviour. Because exploratory behaviour has a substantial heritability (Dingemanse *et al.* 2002; 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 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 exploratory behaviour 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.

2. MATERIAL AND METHODS

(a) *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 (10 000 m^2) with about 600 nest-boxes (for further details see Dingemanse *et al.* 2002). 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 nest-box of 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 h of capture. Each bird was taken to the laboratory only once. For further details on housing and field methodology see Dingemanse *et al.* (2002).

Table 1. Relation between natal dispersal distance and nestling traits for great tits hatched from first broods.
(The results are from a general linear model 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 inclusion of the variable in the final model.)

variable	females		males	
	F_{df}	p	F_{df}	p
fledgling mass	$0.90_{1,73}$	0.35	$0.31_{1,77}$	0.58
tarsus	$0.00_{1,73}$	0.98	$0.06_{1,77}$	0.81
hatching date	$0.02_{1,73}$	0.89	$1.21_{1,77}$	0.27
year of birth	$1.54_{5,74}$	0.19	$1.19_{5,78}$	0.10

(b) *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).

Each bird was tested individually between 0800 and 1400 hours in a sealed room (4.0 m × 2.4 m × 2.3 m) under artificial light, containing five artificial wooden trees. Trials began at least 1 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 2 min 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). We corrected the scores for date of capture, based on within-individual changes in behaviour with capture date (Dingemanse *et al.* 2002).

(c) *Statistical analyses*

We used general linear models (GLMs) with normal errors to evaluate the relation 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 dataset, 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 the 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 distances. 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 composed most of the variation in natal dispersal distances, we calculated Pearson's correlations between post-fledging movement and natal dispersal distance. We used GLMs with normal errors to evaluate the relation between post-fledging movement, transformed as $\log_{10}(x + 1)$, and properties of the individual (individual exploration score, body mass at capture, fledgling mass, tarsus length, hatching date) for individuals captured in July/August 2000 (25 females, 24 males).

We used randomization tests to check whether significant relations between dispersal distance and explanatory variables were caused by non-random distribution of phenotypes among natal nest-boxes (Van Noordwijk 1984, 1995). In each test we measured the distance between the natal nest-box and a random nest-box. We then calculated F values by following simple or multiple regression procedures, as outlined in Sokal & Rohlf (1995; pp. 626–629), and took the proportion of 1000 tests on randomized data giving an 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 by using SPSS v. 10.1 software. Values of p are two-tailed throughout.

3. RESULTS

(a) Correlates of natal dispersal distance

Females dispersed further than males (females: 643 ± 376 m (mean ± s.d.), 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 × 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 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 fledgling 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.

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 1*a*). Female natal dispersal distance increased with paternal score ($F_{1,10} = 8.58$, $p = 0.015$; figure 1*c*) but not with maternal score ($F_{1,10} = 2.15$, $p = 0.17$; figure 1*e*). 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 effects of paternal and maternal scores 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 exploration score ($F_{1,15} = 1.81$, $p = 0.20$; figure 1*b*). Male natal dispersal distance tended to increase with paternal score ($F_{1,14} = 3.89$, $p = 0.069$, figure 1*d*) but not with maternal score ($F_{1,14} = 0.11$, $p = 0.74$; figure 1*f*). 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 than in 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 × 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 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.

(b) 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 years (interaction, year × immigration status: $F_{1,513} = 0.21$, $p = 0.65$) or the sexes (interaction, sex × immigration status: $F_{1,512} = 0.84$, $p = 0.36$; figure 2).

(c) Timing of dispersal

Post-fledging movement comprised a major proportion of the variation in natal dispersal distance in 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: $3.35 \times 10^{-2} \pm 0.014$
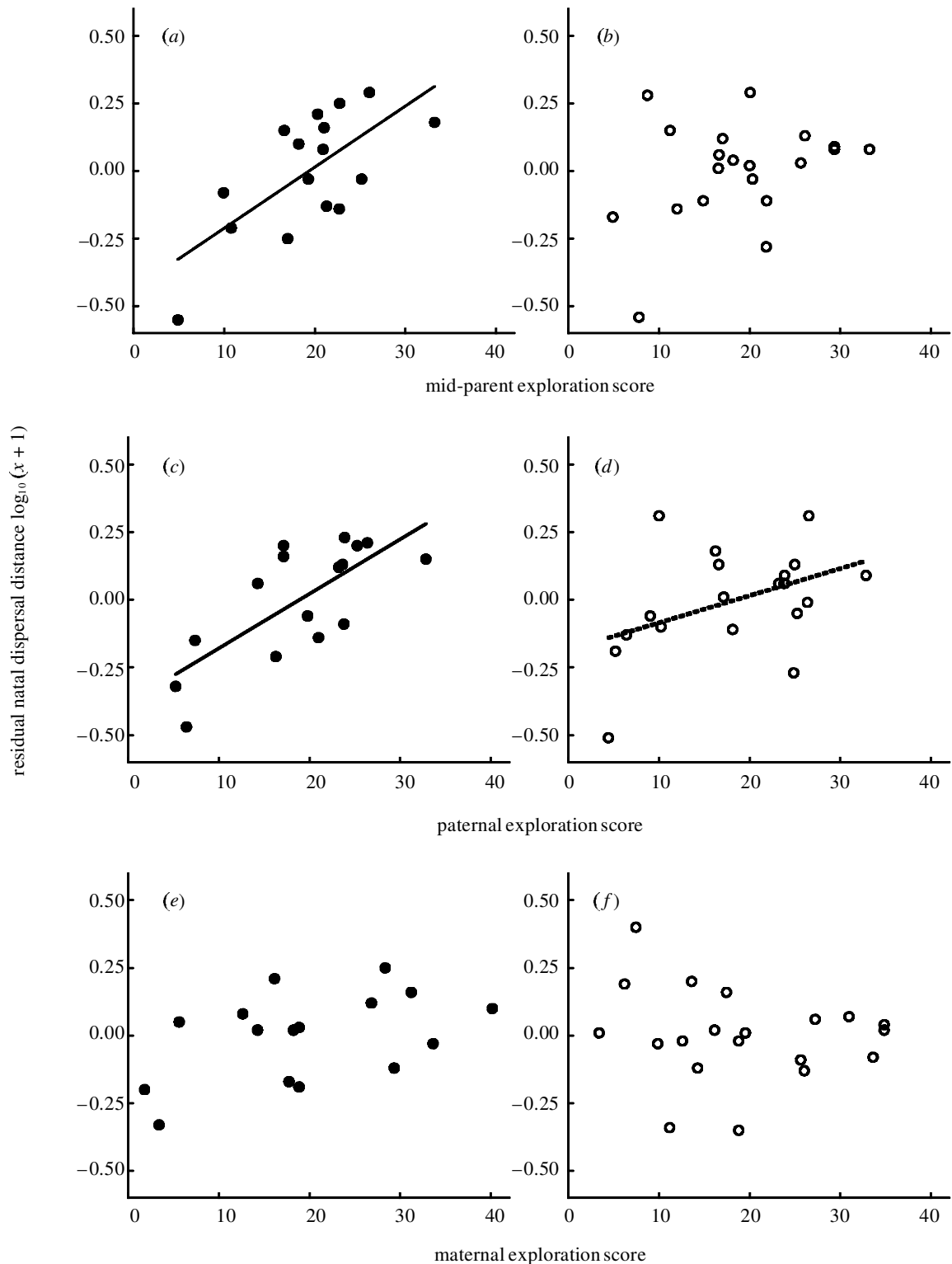
Figure 1. The relation between natal dispersal distance and mid-parent exploration score (*a*,*b*), paternal exploration score (*c*,*d*) and maternal exploration score (*e*,*f*) for female (filled circles) and male great tits (open circles). Dispersal distances (in metres) were transformed as $\log_{10}(x + 1)$ and corrected for the effects of year (*a–f*), maternal score (*c*,*d*) and/or paternal score (*e*,*f*). The lines are fitted regression lines (solid lines: $p < 0.05$, broken line: $p < 0.1$) weighted by the square root of the number of offspring sampled per nest (females: 16 nests, males: 20 nests).

(s.e.m.) $\log_{10}$ metres per unit of score). Post-fledging movement of males was not correlated with individual exploration score ($F_{1,23} = 0.49$, $p = 0.49$, slope: $-1.24 \times 10^{-2} \pm 0.018$ (s.e.m.) $\log_{10}$ metres per unit of score), and the effect of individual exploration score dif-

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

4. DISCUSSION

We showed that natal dispersal distance correlated positively with a personality trait, phenotypic exploratory behaviour, using three largely independent datasets. First, natal dispersal distances were largest for individuals with fast parents. Second, immigrants were faster than locally born birds. Third, post-fledging movements, representing a major proportion of the variation in natal dispersal distances, were greatest for fast females. Our results are qualitatively similar to the 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 more aggressive 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 Casteele 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 influence natal dispersal by genes passed to their offspring and that the substantial
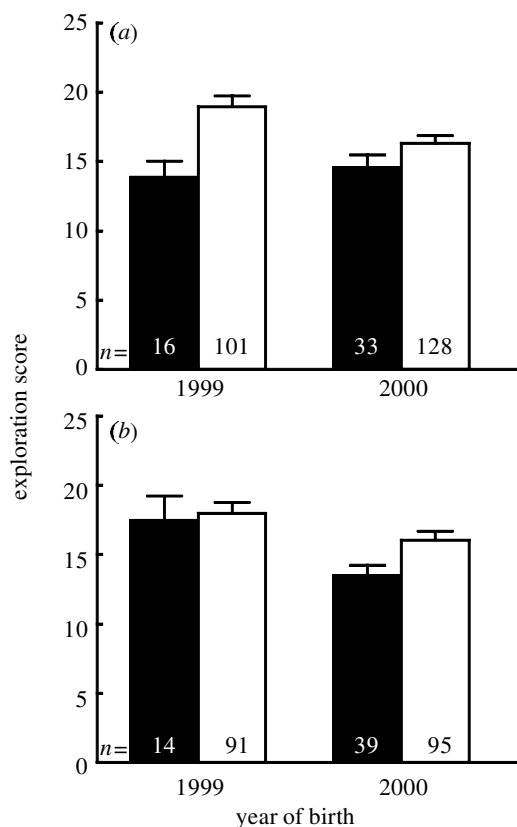

Figure 2. Individual exploration scores (+ s.e.m.) and immigration status (filled bars: locals, open bars: immigrants) for (*a*) female and (*b*) male great tits that were scored during their first year of life.

heritability of exploratory behaviour (Dingemanse *et al.* 2002; 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 significant heritability of natal dispersal (Greenwood *et al.* 1979; Van Noordwijk 1984; Waser & Jones 1989; Van de Casteele 2002). It is therefore usually assumed that dispersal behaviour is flexible and dependent 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 at 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 relation between post-fledging dispersal and individual exploratory behaviour further illustrates the fact 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 relation 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 relation between dispersal and aggression in rodents, or dispersal and nestling traits (e.g. fledgling 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; Drent *et al.* 2003), differential dispersal for 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 to 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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