Original Article

Natal dispersal correlates with behavioral traits that are not consistent across early life stages

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Behavioral differences between dispersers and residents have long been recognized in animal species, but it remains unclear whether these dispersal syndromes represent consistent differences over time and in different contexts (i.e., personalities) or short-term changes in behavior during dispersal. We analyzed interindividual differences in sociability (attraction to unfamiliar adult males or females), exploration, and locomotor activity in disperser and resident root voles, *Microtus oeconomus*. We recorded these behavioral traits in 50 animals before weaning, around weaning age but before dispersal, and after a dispersal test in the field. Dispersing root voles displayed marked social behavior at the youngest age, being more attracted to unfamiliar adult males than residents. Dispersers were also, on average, faster explorers and were more active than residents. However, the observed variation between individuals in terms of social, exploration, and activity behaviors was not consistent over early life stages. These data indicate that behavioral differences between dispersers and residents may be only temporary in some species. *Key words:* dispersal syndrome, exploration, mammal, natal dispersal, personality trait, sociability. *[Behav Ecol 22:176–183 (2011)]*

O ne of the major decisions that an animal must take is whether to stay in the area in which it was born (natal philopatry) or to find a new area in which to settle and breed (natal dispersal). If the success of dispersal depends on individual phenotype, then dispersers should differ from nondispersers, referred to hereafter as residents (Swingland 1983; Bowler and Benton 2005; Clobert et al. 2009). Such phenotypic differences have been found in animals of all types, from unicellular organisms to mammals, and involve a syndrome of morphological, behavioral, or life-history traits reducing the costs of dispersal and facilitating settlement (see Clobert et al. 2009). The importance of behavioral traits in accounting for dispersal strategies has long been recognized in mammals (Myers and Krebs 1971; Svendsen 1974; Bekoff 1977) and has more recently been demonstrated for birds (Dingemanse et al. 2003; Duckworth and Badyaev 2007) and other animals (Clobert et al. 2009).

Behavioral differences between dispersers and residents may reflect alternative "personalities," when behavioral traits are consistent across contexts and/or times (Sih et al. 2004; Cote, Clobert, et al. 2010). Behavioral traits, such as aggression, exploration, and boldness, often differ consistently between individuals over time and/or contexts (reviewed in Réale et al. 2007). There is also evidence of personality traits for social behavior (Cote and Clobert 2007). In the species investigated to date, it has been demonstrated that the tendency

to disperse is correlated with various personality traits (reviewed in Cote, Clobert, et al. 2010). These traits include boldness in the killifish *Rivulus hartii* (Fraser et al. 2001) and the great tit *Parus major* (Dingemanse et al. 2003), sociability in the common lizard (*Lacerta vivipara*) and the mosquitofish (*Gambusia affinis*) (Cote and Clobert 2007; Cote, Fogarty, et al. 2010), and aggressiveness in western bluebird *Sialia mexicana* (Duckworth and Badyaev 2007). However, an alternative to dispersal syndromes based on personality traits is that behavioral differences between dispersers and residents reflect short-term effects observed only when the decision to disperse is made (Clobert et al. 2009; Cote, Clobert, et al. 2010). Indeed, the consistency of behavioral traits over different stages of life and contexts may vary strongly between species and for different behavioral traits within the same species (Bell and Stamps 2004).

A description of the behavioral traits associated with dispersal and their consistency is important for our understanding of spatial population dynamics and dispersal (Duckworth 2008; Clobert et al. 2009; Cote, Clobert, et al. 2010). First, analyses of behavioral traits can provide insight into the proximate mechanisms of dispersal (Cote, Clobert, et al. 2010). In vertebrates, including mammals in particular, dispersal often occurs over a short intensive period around puberty, and the internal state (e.g., hormonal balance) of an individual may determine both its dispersal propensity and its behavioral profile (Holekamp 1986; Belthoff and Dufty 1998). Thus, dispersal syndromes may be a consequence of short-term changes in hormonal balance. However, genes controlling neural circuits and endocrine pathways may also have a permanent influence on behavioral traits and dispersal decisions. In prairie voles (*Microtus ochrogaster*), for example, molecular variation of a neuroendocrine gene encoding the vasopressin

1a receptor is involved in mating, territorial, and parental care behaviors and controls space use and dispersal in the field (e.g., Ophir et al. 2008; Solomon et al. 2009). Second, consistent behavioral differences between dispersers and residents may influence spatial population dynamics and genetics. For example, personality-dependent dispersal can facilitate colonization (Clobert et al. 2009; Cote, Clobert, et al. 2010), range expansion (Duckworth 2008), and the maintenance of genetic diversity (Duckworth 2008). Such carryover effects of dispersal are unlikely to occur if behavioral differences between dispersers and residents are only temporary.

In microtine rodents (voles and lemmings), natal dispersal has been linked with aggression and sociability on the one hand (Myers and Krebs 1971; Ims 1990; Brandt 1992) and exploratory behavior and activity on the other (Myers and Krebs 1971). The exploration of new environments and locomotor activity may be of particular importance in dispersing voles, making them more likely to cover larger distances and to settle away from their natal site. Consistent with this prediction, faster exploration behavior has been observed in dispersing individuals than in residents in 2 vole species (Myers and Krebs 1971). Social behavior may also be an important determinant of the likelihood of dispersal in voles with kin structures and neighbor–stranger discrimination (Bekoff 1977; Ims 1990; Rosell et al. 2008; Blumstein et al. 2009). In particular, young animals socializing with others would be expected to be less likely to disperse (Bekoff 1977). Consistent with this prediction, Ims (1990) reported a positive correlation between dispersal distance and avoidance behavior in female gray-sided voles, *Myodes rufocanus*. Unfortunately, published studies of dispersal syndromes in microtine rodents did not investigate personality traits (Cote, Clobert, et al. 2010). The same behavioral trait must be measured at several life stages and/or in several different contexts to determine whether behavioral differences between dispersers and residents involve personalities.

We analyzed a dispersal syndrome involving social behaviors, locomotor activity, and exploration in 3 age classes of male and female root voles (*Mi. oeconomus*, Pallas 1776). The offspring of this species may reach maturity at 1 month of age, and natal dispersal is synchronized with the onset of sexual maturation (Andreassen and Ims 2001; Le Galliard et al. 2007), which may occur when the animal is only 18 days old (Gundersen G, personal communication). Thus, relationships between behavioral traits and natal dispersal were examined by repeatedly testing the same animals before weaning (~10 days of age), immediately after weaning but before natal dispersal (~21 days), and after a natal dispersal test conducted in the field (~33 days). The age classes studied correspond to particular stages from the time at which voles start to explore their surroundings until they decide whether to stay or to leave their place of birth. Using neutral arena tests, as in previous studies of voles (Myers and Krebs 1971; Ims 1990), we measured locomotor and exploration behaviors and assessed social behavior by comparing the preferences of root voles for an empty area, an area occupied by a sexually mature female or an area occupied by a sexually mature male. We investigated attraction to unfamiliar adult males or females because such behavior has been shown to be relevant for natal dispersal in root voles (Brandt 1992; Wolff 1994). Root voles begin exploring the area around their nest while still very young as live trapping of individuals weighing as little as 5–7 g is not uncommon, and both males and females visit nests occupied by young animals (Hoset KS, personal observation). Juveniles compete for space with adults, and adults may aggress juveniles; consequently, natal dispersal provides a means of avoiding competition (Andreassen and Gundersen 2006; Le Galliard et al. 2006, 2007). We also thought it likely that social behavior would vary with age and sex. A juvenile's susceptibility to antagonistic adult behavior decreases with increasing age (e.g., Koskela et al. 2000): individuals may therefore become less solitary as they age. Competition for food and space would be expected to be stronger between individuals of the same sex, and root voles may also disperse to seek sexual partners (Le Galliard et al. 2006). In this case, dispersers may become less repulsed by adult strangers of the opposite sex as they age.

MATERIALS AND METHODS

Source animals and field study

The test root voles studied were obtained by crossing wild parents originating from the Valdres population with wild parents originating from the Finse population from southern Norway (Le Galliard et al. 2006). The day of birth was determined by checking nest-boxes on a daily basis, and each animal was individually tagged, at the age of 10 days, with a passive integrated transponder (Trovan ID-100) implanted under the skin. We counted the number of test animals per litter at the age of 15 days (weaning age) and separated test litters from their parents at the same time. One day before release in the field, test animals were sexed and weighed. The adult voles used in the trials were maintained in individual plastic boxes throughout the study in the same standardized conditions as the test voles.

The experimental area consisted of 6 plots (50 by 17 m) enclosed by vole-proof barriers. Each plot contained 2 separate habitat patches (8 by 8 m) of tall dense meadow vegetation, each mimicking the size of the home range core area of a breeding root vole female (Le Galliard et al. 2006). The distance between the habitat patches was 26 m, sufficient to prevent movement between the patches during the course of the daily activities of the individual (Le Galliard et al. 2006). We conducted 3 consecutive trials in the late breeding season (on 5th, 16th, and 27th of September 2004). Each trial was started by releasing 4 test animals, aged 22.2 days (±0.33 standard error [SE]), into one habitat patch in each of the 6 plots. We released a fixed number of animals per patch to avoid the confounding effects of population density on dispersal (Andreassen and Ims 2001; Gundersen et al. 2002). Furthermore, the chosen density (2 animals per habitat patch) simulated realistic levels of competition for space. We placed animals in the center of the release habitat patch on the evening before release, and the cages were opened early the next morning. Voles were left undisturbed during a dispersal and settlement period of 10 days. They were then recaptured in Ugglan live traps. Live traps were active for 1 day and were checked every 6 h, beginning at midnight. During trapping, we recorded the identity of the individual, its location, body mass, and sexual maturation status. Males were considered sexually mature if they had scrotal testes, and females were considered sexually mature if they had an open vagina or obvious signs of pregnancy. Natal dispersal status was defined on the basis of the location of the individuals when they were recovered (for a justification, see Le Galliard et al. 2006). Individuals recovered from in and around the release patches were defined as residents (i.e., they had settled in the release patch), whereas individuals recovered from in and around the immigration patches were defined as dispersers (i.e., they had settled in the immigration patch).

Behavioral tests

Behavioral tests were conducted on the same individuals, with a preweaning test at 10 days of age ($n = 90$), a postweaning test 1 day before release in the field (mean age: 21.2 days, $n = 81$, 9 animals died before the postweaning test), and

Table 1

Estimates and Kendall's *W* coefficient test of concordance for sociability (proportion of time spent in each type of compartment), exploratory behavior (number of compartments visited per unit time), and locomotor behavior (time spent walking) based on 3 measurements for all individuals and for residents and dispersers separately

	All individuals	Residents	Dispersers
Sociability			
Start vs. choice compartments	$W = 0.40$, $\chi^2_{46} = 54.9$, $P = 0.17$	$W = 0.38$, $\chi^2_{25} = 28.7$, $P = 0.28$	$W = 0.42$, $\chi^2_{20} = 25.1$, $P = 0.20$
Empty vs. occupied compartments	$W = 0.51$, $\chi^2_{45} = 68.8$, $P = 0.01$	$W = 0.48$, $\chi^2_{24} = 34.7$, $P = 0.07$	$W = 0.73$, $\chi^2_{20} = 44.0$, $P < 0.01$
Male vs. female compartments	$W = 0.34$, $\chi^2_{45} = 46.3$, $P = 0.42$	$W = 0.33$, $\chi^2_{24} = 23.9$, $P = 0.47$	$W = 0.32$, $\chi^2_{20} = 19.4$, $P = 0.50$
Exploration	$W = 0.40$, $\chi^2_{48} = 57.0$, $P = 0.18$	$W = 0.35$, $\chi^2_{26} = 27.6$, $P = 0.38$	$W = 0.26$, $\chi^2_{21} = 16.2$, $P = 0.76$
Locomotion			
Empty compartment	$W = 0.37$, $\chi^2_{45} = 50.7$, $P = 0.27$	$W = 0.33$, $\chi^2_{24} = 23.6$, $P = 0.49$	$W = 0.42$, $\chi^2_{20} = 25.5$, $P = 0.18$
Male compartment	$W = 0.37$, $\chi^2_{46} = 51.7$, $P = 0.26$	$W = 0.30$, $\chi^2_{24} = 21.6$, $P = 0.61$	$W = 0.40$, $\chi^2_{20} = 27.4$, $P = 0.16$
Female compartment	$W = 0.34$, $\chi^2_{45} = 46.2$, $P = 0.42$	$W = 0.34$, $\chi^2_{24} = 24.4$, $P = 0.44$	$W = 0.34$, $\chi^2_{21} = 20.5$, $P = 0.43$

a postdispersal test 1 day after recapture from the field (mean age: 33.2 days, $n = 50$, 31 animals died during the field test). Behavioral tests were carried out in neutral arenas consisting of galvanized steel sheet covered with clean blotting paper. Each arena included 3 choice compartments ($15 \times 30 \times 20$ cm) freely accessible by test voles from a start compartment in the center of the area. The back of each choice compartment was separated from a box ($15 \times 10 \times 20$ cm) by wire netting. During each test, this box was 1) empty, 2) occupied by an adult male, or 3) occupied by an adult female. All the adult males ($n = 9$, mean weight $= 48.4$ g ± 4.46 SE) had scrotal testes, and the adult females ($n = 8$, 34.1 g ± 2.69 SE) were all postparturient. No adult was ever used twice in 2 successive trials on the same day or with the same test vole. The wire netting allowed olfactory, visual, and acoustic interactions to occur between adults and test voles. No physical contact between adults and test voles was allowed to prevent infanticide and other aggressive interactions.

Each trial was started by the addition of the adults to their boxes. The treatment (empty, adult male, or adult female) and the identity of the individual introduced were chosen at random. One minute after the start of the test, a test vole was placed in the closed central start compartment for a period of 3 min. The sliding doors connecting this compartment to the choice compartments were then removed, and the behavior of the test vole was recorded for 15 min with a mini-DV camcorder. After the trial, the voles were removed from the arena, the arena was cleaned, and the blotting paper was replaced. The recordings were scored by a person who was blind to the treatment and could not see whether the boxes were empty or occupied. We excluded the first and last 30 s from the analysis to avoid disturbance effects. In 4 trials, the recording period lasted less than normal (mean $= 624$ s, range $= 515–704$ s). We noted active behavior (walking on the ground, climbing on the grid mesh, or scratching the walls), inactive behavior (resting on the ground and resting on the grid mesh of a -treatment box), and grooming behavior. We also noted whether the test animal was inside the start compartment, inside a choice compartment, or in direct contact with the wire netting within a choice compartment. Behavioral measurements and location were recorded continually with Etho-Log v.2.2.5 software (Ottoni 2000). For each trial, we calculated the time spent at each location, the number of compartments visited, and the time spent walking on the ground at each location. We calculated the time spent walking on the ground in the front of empty, male-occupied, and female-occupied boxes to compare the locomotor activities of test voles across treatments. We interpreted differences in the time spent in each test compartment as differences in the sociability of the test voles (Ims 1990; Cote and Clobert 2007; Cote, Fogarty, et al. 2010). We interpreted differences in the number of compartments visited per unit time as differences in the exploration behavior of test voles (Myers and Krebs 1971; Réale et al. 2007). Finally, we interpreted differences in time spent walking on the ground as differences in locomotor activity (Myers and Krebs 1971; Réale et al. 2007).

Statistical analyses

All analyses were performed with data from individuals measured on 3 separate occasions. We first calculated the proportion of time spent in the start compartment, then the proportion of time spent in the empty choice compartment from the total time spent in the choice compartments, and finally, the proportion of time spent in the male choice compartment from the total time spent in occupied compartments (see Supplementary Material, Supplementary Table for raw data). We also calculated the proportion of time spent walking on the ground (locomotor activity) and the number of compartments visited per second (exploration behavior). We analyzed proportions because these are independent of the total length of the recording and conform well to the assumptions of our statistical model (see below). We assessed the consistency of these behavioral traits by calculating Kendall's *W* coefficient of concordance. This coefficient is a non-parametric statistic measuring consistency in rank scores of behavioral traits among individuals from different age classes.

We investigated the relationship between social behavior and dispersal status by first analyzing separately the relative times spent in start versus choice compartments, in empty versus occupied compartments, and in male versus female compartments using generalized linear mixed models (GLMM). GLMM were fitted by Laplace approximation assuming a quasi-binomial distribution. We tested for effects of age class, dispersal status, sex, and their 2-way interactions. We also added individual identity as a random factor and selected the best model by a process of backward elimination of nonsignificant terms with Wald z tests (Bolker et al. 2009). We tested for 2-way interactions because we wanted to check for age- and sex-related differences in the relationship between sociability and dispersal. We also analyzed differences in the number of compartments visited per second (exploration). Exploration was treated as the dependent variable in a linear mixed effects model (LMM), including age class, sex, dispersal category, and 2-way interactions as fixed effects, with individual identity as a random effect. We also analyzed the proportion of time spent walking on the ground in each type of compartment (locomotor activity). Normal distributions were generated by log-transforming data before analysis and
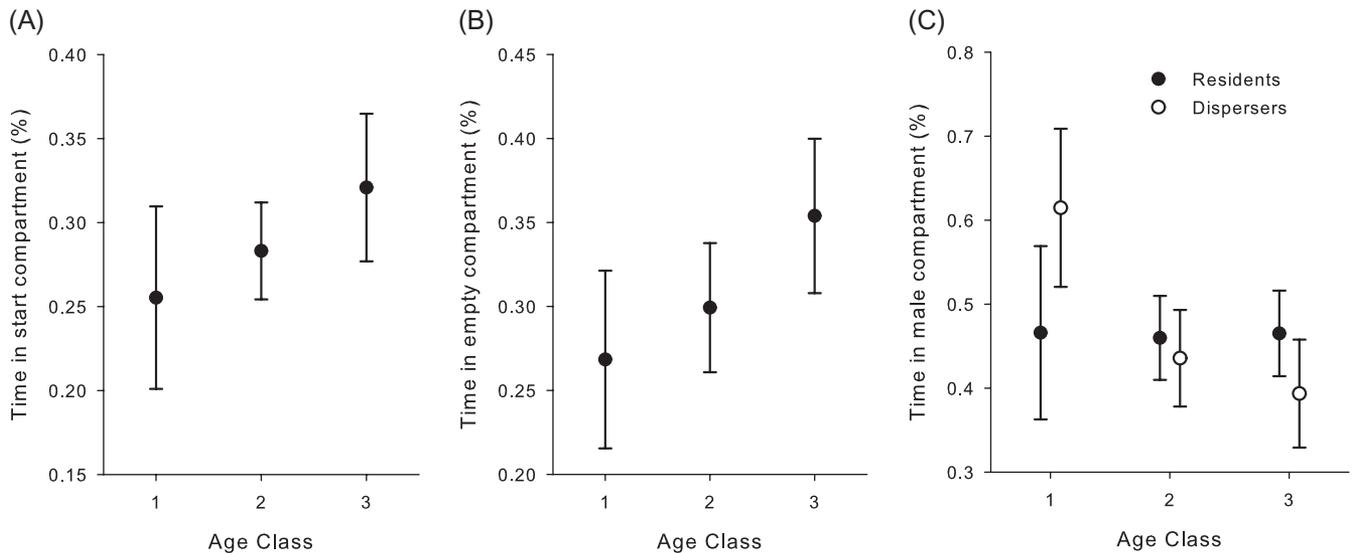
Figure 1

Behaviors of young root voles of 3 age classes before and after a dispersal test in the field ($n = 50$). The data shown are means (±confidence intervals) for the proportions of time spent in the start versus choice compartments (A), the proportions time spent in the empty versus occupied compartments (B), and the proportions of time spent in male versus female compartments (C). For this last item, data were calculated separately for residents and dispersers. Age class: 1 = before weaning, 2 = after weaning and before dispersal, and 3 = after the dispersal test. Raw data are reported in Table 2.

testing them with an LMM, including individual identity as a random effect and age class, dispersal status, sex, treatment (empty, male, or female compartment), and their 2-way interactions. We used log transformation because this transformation better fitted the assumptions underlying our data than an arcsine square root transformation.

We also carried out a principal component analysis (PCA) because our behavioral traits were obtained from the same trials and might be correlated. Our PCA included 7 behavioral traits (see Table 2) and was implemented with the *princomp* procedure, using a correlation matrix implicitly rescaling all the variables (Venables and Ripley 2002). Based on the broken-stick method, we retained 2 principal components (PCs) accounting for 63.9% of the variance for further analyses (Legendre and Legendre 1998). We identified statistically significant contributions of behavioral traits to these 2 PCs by the bootstrapped eigenvector method with 1000 samples. For each individual and each trial, we calculated a score for each PC. These scores were normally distributed and were analyzed with an LMM, including age class, sex, dispersal category, and 2-way interactions as fixed effects, and with individual identity as a random effect. For all LMMs, an autocorrelation term was included to account for the repeated structure. The inclusion of the autocorrelation term was based on an assessment of the fit of the model with and without this structure. In all statistical analyses, the best models were chosen by a stepwise backward selection procedure. From each best model, we calculated a repeatability coefficient (RC) as the ratio of between-individual variance to total (between-individual and residual) variance and assessed the significance of random effects with likelihood ratio tests.

RESULTS

Outcome of the field study

We recaptured 50 of the 81 animals tested in the field at the end of the trials. The other 31 animals died. Mortality among released animals and sex ratio (24 males), dispersal probabilities (28 resident voles and 22 dispersers), and maturation probabil-ities (24 sexually mature animals) among survivors were typical of findings for the late breeding season (Andreassen and Ims 2001). Mean body mass was 9.18 g (±0.16 SE) before weaning, 13.06 g (±0.21) after weaning, and 22.42 g (±0.50) after the dispersal test. Body mass did not differ between the sexes before ($F_{1,36} = 0.05$, $P = 0.82$) or just after weaning ($F_{1,36} = 1.32$, $P = 0.26$), but males were larger than females after the dispersal test ($F_{1,35} = 6.02$, $P = 0.02$; contrast = 1.99 g ± 0.81 SE). In addition, sexually mature animals were larger than immature animals ($F_{1,35} = 8.66$, $P = 0.006$; difference = 2.46 g ± 0.83 SE). Dispersers did not differ from residents in terms of body mass, sex ratio, or sexual maturation probability (all $P > 0.05$).

Rank consistency of behavioral traits

For the 50 surviving voles, we were able to score the recordings of 49 voles at 3 times points in their lives. Voles ranked equally across age class for the proportion time spent in the empty compartment versus occupied compartments ($W = 0.51$, $\chi^2 = 68.8$, degrees of freedom [df] = 45, $P = 0.013$), but not for time spent in the start versus choice compartments, time spent in male versus female compartment, exploration, and locomotor behavior (all $P > 0.18$, Table 1). As the dispersal history of individuals may reduce consistency, we checked whether behaviors were consistent for residents and dispersers separately. We found that dispersers ranked equally across age class for the proportion time spent in the empty compartment versus occupied compartments ($W = 0.73$, $\chi^2 = 44.0$, df = 20, $P < 0.002$) and also marginally for residents ($W = 0.48$, $\chi^2 = 34.7$, df = 25, $P = 0.073$). Neither dispersers nor residents showed rank consistency in any of the other behavioral measurements (all $P > 0.16$, Table 1).

Social behavior and natal dispersal

Age class had a strong effect on the proportions of time spent in the start versus choice compartments ($\chi^2 = 430.72$, df = 2, $P < 0.001$). Individuals spent a greater proportion of the time in the start compartment as they got older (Figure 1A).
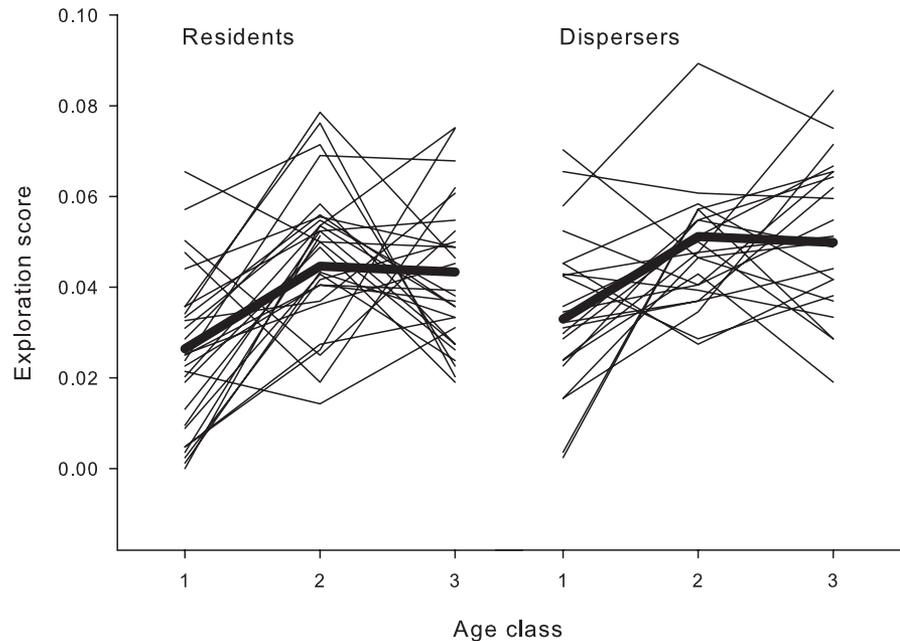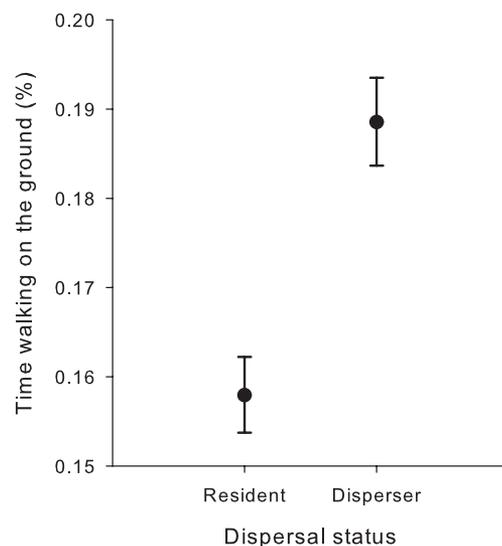
Figure 2
Individual response curves for exploration score (number of compartments visited per second) for resident ($n = 28$) and dispersing ($n = 22$) root voles as a function of age class. The thick lines represent the mean response curves predicted by the model (see main text). Age class labels as in Figure 1.

Differences between age classes were not offset by an influence of dispersal status ($\chi^2 = 0.33$, df = 1, $P = 0.57$) or sex ($\chi^2 = 0.46$, df = 1, $P = 0.5$). Age class also affected the proportions of time spent in the empty choice versus occupied compartments ($\chi^2 = 638.14$, df = 2, $P < 0.001$). The proportion of time spent in the empty compartment relative to that spent in the occupied compartments increased as the individuals aged (Figure 1B) with no effects of dispersal status ($\chi^2 = 0.33$, df = 1, $P = 0.57$) or sex ($\chi^2 = 0.005$, df = 1, $P = 0.94$). However, the proportions of time spent in the male versus female compartments depended on an interaction between age class and dispersal status ($\chi^2 = 541.99$, df = 2, $P < 0.001$) with no difference between the sexes ($\chi^2 = 0.16$, df = 1, $P = 0.69$). Post hoc tests showed that dispersers spent more time than residents in the male than in the female compartment at age class 1 ($\beta = 0.64$, $z = 4.439$, $P < 0.001$, Figure 1C) but not at age class 2 ($\beta = -0.17$, $z = -1.17$, $P = 0.241$) and age class 3 ($\beta = -0.25$, $z = -1.74$, $P = 0.08$). RC for behavioral traits describing sociability was very low (RC < 0.001).

Exploration, locomotion, and natal dispersal

Exploratory behavior depended on age class ($F_{2,95} = 19.67$, $P < 0.001$) and dispersal status ($F_{1,46} = 5.35$, $P = 0.025$). On average, individuals visited more compartments per unit time at age classes 2 and 3 than at age class 1, and dispersers visited more compartments than residents (difference = 0.0065 ± 0.0028 SE). Individual differences in exploratory behavior were not consistent (RC < 0.001, see Figure 2). Differences between dispersers and residents were independent of age class (age by dispersal interaction: $F_{2,95} = 1.37$, $P = 0.26$) and sex (sex by dispersal interaction: $F_{1,46} = 1.85$, $P = 0.18$). Similarly, locomotor activity was influenced by dispersal status ($F_{1,45} = 4.08$, $P = 0.05$), a significant interaction between treatment (empty, male-, and female-occupied compartment) and age class ($F_{4,371} = 3.63$, $P = 0.006$) and a sex effect ($F_{1,45} = 7.58$, $P = 0.008$). On average, dispersing root voles spent more time walking than residents (Figure 3), and males spent more time walking than females ($\beta = 0.11 \pm 0.05$). The interaction between age and treatment factors resulted from an increase in the proportion of time spent walking in the

male compartment with age but not in the proportion of time spent walking in the female and empty compartments (results not shown). Individual differences in locomotor activity were small but significant (RC = 0.124; $\chi^2 = 7.22$, df = 1, $P = 0.007$). This consistency was due to significant correlations between the locomotor activity measured for the same individual in different compartments during the same trial (Spearman's rank correlation coefficient >0.37, all $P < 0.05$) rather than to consistency between trials (see Table 1). A positive correlation was found between the locomotion and exploration behaviors measured during the same trial (Spearman's rank correlation coefficients >0.39, all $P < 0.01$).

Figure 3
Mean locomotor activity of young root voles of 3 age classes for resident and dispersing root voles. Data shown are mean (±confidence intervals) proportions of time spent walking on the ground.

Principal component analysis

The PCA revealed 2 major behavioral dimensions (Table 2). PC1 had significant positive loadings for locomotor activity, exploration, and percentage time spent in the start arena and thus measured an exploration–activity syndrome. By contrast, PC2 had significant positive loadings for percentage time spent in male versus female compartments and time spent walking in empty compartments and negative loadings for percentage time spent in empty versus occupied compartments and time spent walking in male compartments. PC2 therefore measured some aspects of sociability. Positive values on this axis identified animals that spent a larger proportion of time in nonwalking activities in the male compartment.

An analysis of PC1 resulted in the identification of a best model including significant effects of age ($F_{2,92} = 4.57$, $P = 0.01$) and marginal effects of sex ($F_{1,47} = 3.34$, $P = 0.07$) and dispersal status ($F_{1,47} = 1.848$, $P = 0.07$). In accordance with our previous analyses, exploration–activity behaviors were markedly more pronounced in older animals and marginally so in males and dispersers. Individual differences in exploration–activity syndrome were small and nonsignificant (RC = 0.07; $\chi^2 = 0.61$, df = 1, $P = 0.43$). For individual scores on the PC2 axis, we found a significant interaction between age and dispersal status (age: $F_{1,90} = 1.52$, $P = 0.22$; dispersal: $F_{1,48} = 3.32$, $P = 0.07$; and age × dispersal: $F_{2,90} = 3.28$, $P = 0.04$). Post hoc tests showed that dispersers had higher scores on PC2 than residents before weaning ($t_{48} = 1.82$, $P = 0.07$) but not after weaning ($t_{48} = 1.03$, $P = 0.31$) or in postdispersal tests ($t_{48} = -1.47$, $P = 0.14$). Again, individual differences in this exploration–activity syndrome were small and nonsignificant (RC = 0.02; $\chi^2 = 2.95$, df = 1, $P = 0.09$).

DISCUSSION

Our investigation highlights one major dimension of behavioral variation associated with activity and exploration and another independent dimension of behavioral variation associated with sociability. In accordance with our initial hypothesis, the activity–exploration syndrome differed between dispersers and residents. Dispersing root voles explored more

rapidly than residents as shown by the number of compartments visited per unit time. Exploratory behavior has also been associated with dispersal in other species (Holekamp 1986; Belthoff and Dufty 1998; Dingemanse et al. 2003), and it has been suggested that such behavior develops before the dispersal event (Holekamp 1986; Drent et al. 2003). In addition, dispersing root voles were more active than residents at all age classes tested as shown by their walking behavior on the ground. The independent association of dispersal with both exploration and activity is not entirely surprising because exploration and activity were positively correlated in root voles. Positive correlations between exploration and locomotor activity have been detected in other species (Sih et al. 2004; Réale et al. 2007; Cote, Fogarty, et al. 2010). In general, locomotor activity is associated with exploration and dispersal because individuals may prepare for exploration and dispersal by increasing their mobility. In ground squirrels (*Spermophilus beldingi*), locomotor activity increases just before dispersal events and decreases thereafter (Holekamp 1986). Mobility depends on hormone levels in screech owls (*Otus* spp.), and hormones, in particular corticosterone, are thought to influence locomotor activity and dispersal in birds (Belthoff and Dufty 1998) and ground squirrels (Holekamp 1986). The differences in activity levels and exploration behavior between dispersers and residents in root voles may be controlled by similar hormonal balances.

We also demonstrated differences in sociability between dispersers and residents but only for the preweaning tests. Dispersing root voles spent a greater proportion of time close to unfamiliar adult males than unfamiliar adult females during the preweaning tests. Thus, dispersers did not differ from residents in their social behavior after the dispersal event by contrast to what has been reported for gray-sided voles (Ims 1990). Few other studies have examined the potential correlation between social behavior and dispersal. This relationship has been found to be significant in common lizards in which residents are more strongly attracted to odors from conspecifics or relatives (Léna et al. 2000; Cote and Clobert 2007). Cote, Fogarty, et al. (2010) also demonstrated that an individual tendency to disperse in the invasive mosquitofish (*G. affinis*) is associated with asocial behavior as measured by the tendency to form shoals with conspecifics. This dispersal syndrome is also thought to reflect a widespread correlation in mammals in which social bonding is important for individual and group fitness (Bekoff 1977; Blumstein et al. 2009). The differences observed in this study contrast with our predictions that dispersers would be more asocial, particularly when young. Instead, they indicate that disperser root voles bonded less with adult females and were more "risk prone" than residents during the preweaning tests because they showed a preference for compartments located closed to an unfamiliar adult male, presenting a greater potential threat of infanticide. In small mammals, males often display aggressive behavior against young subordinate individuals, and the probability of adult males committing infanticide may be high (Boonstra 1978; Ebensperger 1998; Andreassen and Gundersen 2006).

In addition to the differences between dispersers and residents described, behaviors also differed considerably between age classes but only slightly between the sexes. Root voles spent an increasingly large proportion of time in the empty than in the occupied compartments as they aged. This ontogenic change indicates that the youngest animals are not repulsed by adult strangers and therefore lack one potential defensive response against the threat of infanticide (Ebensperger 1998). The increase in asocial behavior with age may reflect the need of individuals to establish home ranges as they approach maturity. Root vole females aggregate with their mother in kin clusters, but juvenile females compete for space with adults (Hoset et al.

Table 2

PCA of behavioral data based on a correlation matrix

	PC 1 Exploration–activity	PC 2 Sociability
Loadings		
Time spent start vs. treatment compartments	**0.387**	0.074
Time spent empty vs. occupied compartments	0.148	**−0.579**
Time spent male vs. female compartments	−0.025	**0.531**
Exploration score	**0.468**	0.005
Time spent walking in empty compartment	**0.319**	**0.515**
Time spent walking in male compartment	**0.490**	**−0.315**
Time spent walking in female compartment	**0.516**	0.113
Eigenvalue	2.736	1.733
Variance explained (%)	39.1	24.8
Broken-stick percentage (%)	37.0	22.75

Bold typeface indicates the statistically significant loadings for each variable.

2008) and tend to avoid adult females when they choose a breeding patch (Le Galliard et al. 2006). Juvenile males may also remain immature, with no fixed territorial boundaries, but young males usually move longer distances and more frequently than females, to avoid other adult males when settling in a breeding patch (Andreassen and Ims 2001). Root voles also moved around more as they grew older as shown by the analysis of exploratory behavior traits. This change was expected based on the increases in locomotor capacity with age and the need to explore and become familiar with the immediate surroundings. In addition, males spent more time walking on the ground than females. There may be several reasons for this difference in mobility, such as males having different hormone levels or a greater need for mobility as their home ranges are larger.

We evaluated the consistency of behavioral traits over time by 2 complementary approaches—a rank consistency score (Kendall's W rank consistency) and a repeatability measurement obtained from a random effect model. Despite the correlation of exploration, locomotor activity, and social behavior with dispersal status, the consistency of behavioral traits over time was generally nonsignificant, except for the proportion of time spent in the empty compartment versus the occupied compartments, which was not correlated with dispersal. RCs across life stages early in life varied between less than 1–12% in our study, these values being lower than the mean repeatability reported in a recent meta-analysis (Bell et al. 2009). The observed behavioral differences between dispersers and residents were therefore caused by inconsistent behavioral traits. These results contrast with those of similar studies in which dispersal was correlated with differences in consistent behavioral traits, such as exploratory behavior (Dingemanse et al. 2003), social behavior (Cote and Clobert 2007; Cote, Fogarty, et al. 2010), and aggressiveness (Duckworth and Badyaev 2007).

Differences between residents and dispersers in the proportions of time spent near adult males and females were only evident at the preweaning stage. It is difficult to explain why dispersing root voles behaved differently before weaning and at later age stages. In our study, individuals in the youngest age class may have behaved differently due to innate differences or maternal effects. Behavior may be also adjusted differently between dispersers and residents on the basis of prior experience as observed in strains of fast and slow explorers in the great tit, P. major (Carere et al. 2005) and between bold and shy rainbow trout, Onchorhyncus mykiss (Frost et al. 2007). Behavioral differences between dispersers and residents may also be larger at the preweaning stage because dispersal decisions are affected by mother–offspring interactions (Le Galliard et al. 2003). In addition, exploration and locomotor activity were inconsistent, but their mean values differed between dispersers and residents. This result might suggest that ontogenic increases in activity and exploration associated with dispersal occur asynchronously among individuals. For example, individuals may differ in the timing of dispersal events and, therefore, in the timing of the concomitant increase in activity. Overall, these data indicate that behavioral differences between dispersers and residents may be only temporary in some species.

SUPPLEMENTARY MATERIAL

Supplementary table can be found at http://www.beheco.oxfordjournals.org

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