

Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent

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Summary

1. Individuals should benefit from settling in high-quality habitats, but dispersers born under favourable conditions have a better physical condition and should therefore be more successful at settling in high-quality habitats.
2. We tested these predictions with root voles (*Microtus oeconomus*) by a manipulation of individual condition through litter-size enlargement and reduction during lactation combined with a manipulation of habitat quality through degradation of the vegetation cover. We accurately monitored movements of 149 juveniles during a settlement and breeding period of 3 months.
3. The litter size treatment had long-lasting effects on body size, life-history traits and home range size, but did not influence dispersal behaviour.
4. Different stages of dispersal were influenced by habitat quality. In low-quality patches, females dispersed earlier, spent more time prospecting their environment before settling, and settlers had a smaller adult body size than in high-quality patches. Preference and competition for high-quality patches is likely adaptive as it increased fitness both in terms of survival and reproduction.
5. We found no interactive effect of individual condition and habitat quality on natal dispersal and habitat selection.
6. These findings suggest that immediate conditions are more important determinants of dispersal decisions than conditions experienced early in life.

Key-words: delayed effects, dispersal movements, heterogeneous habitat, life-history trade-off, *Microtus oeconomus*

Introduction

Natal dispersal includes movements of individuals from a natal site to a future breeding site and is an important demographic trait (Clobert *et al.* 2001). The costs and benefits of natal dispersal are influenced by the internal state of individuals and by environmental conditions experienced both in the natal and future breeding sites (Benard & McCauley 2008; Clobert *et al.* 2009). Thus, models and data indicate that natal dispersal behaviour is often a plastic, phenotype- and condition-dependent strategy (reviewed in Ims & Hjermann 2001; Bowler & Benton 2005; Clobert *et al.* 2009). Relevant phenotypic traits associated with dispersal include body condition (O'Riain, Jarvis & Faulkes 1996; van der

Jeugd 2001; del Mar Delgado *et al.* 2010) and social behaviour (Ims 1990; Cote & Clobert 2007; Hoset *et al.* 2011). Relevant environmental conditions include patch size (Andreassen & Ims 2001), habitat quality (Haughland & Larsen 2004) and population density (see Lambin, Aars & Piertney 2001 for review).

The internal state of individuals at dispersal may be greatly influenced by the conditions experienced during their development. Prenatal and early postnatal conditions can cause long-lasting effects on morphological and life-history traits (Lindström 1999; Monaghan 2008). A spectacular form of delayed effects caused by the natal environment arises when individuals born in favourable conditions have a higher condition and enjoy fitness benefits throughout their life, i.e. silver spoon effects (Grafen 1988). For example, conditions in the natal territory influence fledging and adult survival,

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and reproductive success in red-billed choughs (*Pyrrhocorax pyrrhocorax*; Reid *et al.* 2006). By affecting the internal state, natal conditions can therefore change the propensity of individuals to disperse later in life, though contrasted patterns have been reported. For example, postnatal malnutrition increases emigration in female meadow voles (*Microtus pennsylvanicus*; Bondrup-Nielsen 1993), but prenatal and postnatal stress had no effect on dispersal in grey-sided voles (*Clethrionomys rufocanus*; Ims 1990). In addition, individuals born in suboptimal habitats can improve their fitness by dispersing and settling into a better habitat (e.g. McPeck & Holt 1992). This process leads to habitat selection and a non-random spatial distribution of individuals (Fretwell & Lucas 1970; Stamps 2001). However, if individuals differ consistently from each other, models of habitat selection predict that high-quality habitats should be held by more competitive residents or immigrants, leading to an ideal despotic distribution (Fretwell 1972). In particular, silver spoon effects should influence habitat selection because individuals born in favourable environments are superior at searching for and settling into high-quality habitats (Stamps 2006).

Previous studies have found significant silver spoon effects on natal dispersal and habitat selection in birds by showing a positive association between the condition of dispersers and the quality of their settlement habitat (Verhulst, Perrins & Riddington 1997; Garant *et al.* 2005; van Oort & Otter 2005; van de Pol *et al.* 2006). For example, van de Pol *et al.* (2006) discovered that oystercatchers (*Haematopus ostralegus*) born in high-quality habitats were heavier at fledging, more likely to survive early and late in life, and more likely to settle and breed in a high-quality habitat. Unfortunately, evidence obtained in these wild populations cannot distinguish silver spoon effects from other behavioural mechanisms leading to differential habitat selection according to the natal habitat, such as natal imprinting (reviewed in Stamps 2001). This study experimentally tests for interactive effects between individual condition and habitat quality on the different stages of dispersal, i.e. departure, transience and settlement (Clobert *et al.* 2009), in a small rodent, the root vole *Microtus oeconomus* (Pallas, 1776). We investigated the three dispersal stages separately because they involve different cues for decision making (Ims & Hjernmann 2001) and different behaviours (e.g. prospection, aggressiveness; for review, see Stamps 2001).

Small rodents are sensitive to environmental conditions experienced early in life during lactation (Andreassen & Ims 1990; Bondrup-Nielsen 1993; Mappes, Koskela & Ylönen 1995; Koskela 1998) and to habitat quality (Andreassen, Ims & Steinset 1996; Aars & Ims 1999; Andreassen & Ims 2001). We manipulated individual condition by changing litter size during lactation (enlarged and reduced litters). We also altered habitat quality in six experimental fields by destroying the vegetation to create, within each field, three patches of decreasing cover (0%, 25% and 75% degraded). Weanlings from manipulated litters were released with their foster mother into each habitat patch, and populations were monitored during a settlement and breeding period of 3 months.

We predict that individuals of lower body condition from enlarged litters would be forced to leave earlier their release patches and to settle in suboptimal habitats relative to individuals in better condition from reduced litters (Garant *et al.* 2005; Stamps 2006).

Materials and methods

STUDY SPECIES AND HABITAT CONFIGURATION

The root vole (*M. oeconomus*) is a small microtine rodent from patchy landscapes, which requires humid grasslands for cover and food (Tast 1966). In our field site located in Evenstad Research Station, Southeast Norway (250 m above sea level, 61°25'N, 11°04'E), reproduction occurs mainly from early spring to late autumn. Litter size ranges from one to 11 pups in the laboratory, lactation lasts up to the age of 15 days, and weaning occurs a few days after lactation ends (Andreassen & Ims 2001). During the summer, natal dispersal occurs around sexual maturity, *c.* at the age of 1 month (Le Galliard, Gundersen & Steen 2007).

Our experiment took place between June and October 2005. The experimental area consisted of six plots fenced with vole-proof barriers and measuring each 50 × 50 m². To prevent mammalian predation, a fence 1.5 m high topped with an electric wire surrounded the area. Prior to our study, in May 2005, former habitat patches were burned and ploughed, and three habitat patches were seeded in each plot (see Fig. 1). Each habitat patch measured 15 × 15 m (225 m²), which matches the home range size of adult female root voles (Andreassen, Hertzberg & Ims 1998). Each patch can host from one to three adult females and presumably one reproductive male (Andreassen, Hertzberg & Ims 1998). The patches were separated from each other by a linear distance of 15 m. Previous radiotelemetry studies have found that inter-patch distances larger than 8 m severely limit the use of multiple patches within a home range (Andreassen, Hertzberg & Ims 1998; Hovland, Andreassen & Ims 1999). The inter-patch distance used here was therefore sufficient to impede movements within an individual's daily activities range.

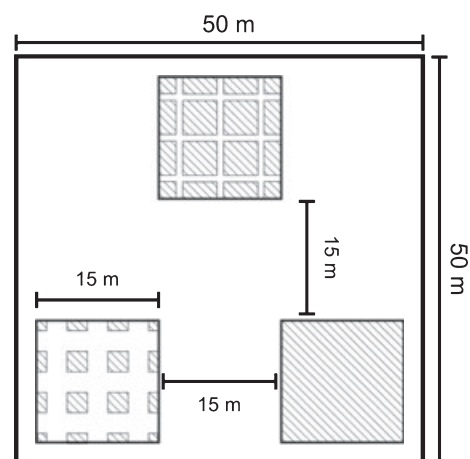


Fig. 1. Habitat configuration. Habitat patches consisted of dense meadow vegetation (shaded areas) surrounded by a non-habitat matrix (white area). One patch had intact vegetation ('high-quality patch'; lower right corner), one patch had 25% of its area removed by mowing and applying herbicides ('intermediate quality'; upper middle) and one patch had 75% of its area removed ('lower quality'; lower left corner).

MANIPULATION OF HABITAT QUALITY

The field experiment was performed in an area with highly fertile soil. Because natural plant productivity is high and the forage biomass of wild plants does not respond to over-grazing (J.-F. Le Galliard & T. Ergon, pers. obs.), we expected the potential demographic effects of food supplementation during the summer to be weak. Thus, we chose to manipulate habitat quality by reducing the vegetation cover in habitat patches, which decreases the availability of high-quality forage and increases the risk of avian predation (Lin & Batzli 2001). Within each study plot, we set up one 'high-quality' patch (HQ treatment), one 'intermediate-quality' patch (IQ treatment) and one 'low-quality' patch (LQ treatment; see Fig. 1). This manipulation was conducted one month before the release of animals by mowing and applying herbicides along stripes. According to the concentrations of herbicide and time delay until the start of the experiment, effects of herbicides on study animals must be weak (Williams, Kroes & Munro 2000). Thereafter, habitat degradation was maintained throughout the experiment by regularly mowing non-habitat areas to keep them hostile for root voles.

MANIPULATION OF INDIVIDUAL CONDITION

Studies in the closely related bank vole (*Myodes glareolus*) have shown that a mother cannot fully compensate for the increased energetic requirement induced by an enlarged litter (Mappes, Koskela & Ylönen 1995; Koskela 1998). Therefore, weanlings from enlarged litters are smaller and less competitive than those born from reduced litters (e.g. Koskela 1998). We used litter-size manipulation to change offspring condition at weaning. This manipulation worked with root voles as it induced differences in structural growth, juvenile survival, space use and sexual maturation (see Results section for details).

We used parents originating from a southern Norwegian strain of root voles at the Animal Division, Biology Department of the University of Oslo (Ims 1997). Animals were kept in cages (dimensions: 50 × 30 × 30 cm³) and fed with carrots, apples, oat and sunflower seeds every 2 days and provided with water *ad libitum*. To obtain animals at the right age for release, 72 breeding pairs were initiated 41 days before the start of the field study. For each gravid female ($n = 40$), the exact day of parturition was determined, the number of newborns was counted ($n = 171$) and pups were weighed to the nearest 0.1 g. A few hours after birth, we manipulated litter sizes, forcing mothers to raise either small foster litters of 2–3 pups (mean = 2.6 ± 0.70 SD) to produce 'high-condition' offspring (hereafter named HC treatment), or large foster litters of 5–7 pups (mean = 5.8 ± 0.50 SD) to produce 'low-condition' offspring at weaning (LC treatment). Each newborn was randomly allocated to a foster litter either of HC or LC treatment ($n = 20$ litters per treatment). Within each foster litter, pups came from different litters and were individually marked by clipping one toe. Treatments were randomly allocated to each mother, but mothers never received one of their pups. This procedure allowed us to disentangle the effects of litter size *per se* from genetic and pre-lactation maternal effects. Then animals were left undisturbed until weaning age (*c.* 20 days). Before release, all animals were individually marked by toe clipping and implanted with a small Passive Integrated Transponder (PIT) tag under the skin (Trovan ID-100; Trovan Ltd, Hessele, United Kingdom). Weaned offspring ($n = 149$) were sexed, weighed to the nearest 0.1 g and measured for head width to the nearest 0.01 mm.

RELEASE AND MONITORING PROCEDURE

All rodents were removed from the field prior to the start of the field experiment. On July 23rd, one reduced litter and one enlarged litter together with foster mothers were released into each habitat patch. Litters and mothers were allocated randomly to standardize the initial sex and age structure, population density, body mass and head width between treatments and plots. On average, ten individuals (mothers and offspring) were introduced in each patch (range = 8–12) to induce strong competition for territories.

Animals were released in the centre of each patch from wire mesh cages (dimensions: 32 × 23 × 20 cm³) containing a mother and her litter, and cages were left undisturbed for a week to avoid release stress. Populations were monitored by live trapping during two nights every 10 days. We used a grid of Ugglan special live traps (Grahnb, Marieholm, Sweden) in a 4 × 4 array in each patch as well as six pitfall traps. Traps, baited with carrots and wholegrain oats, were activated at 20:00, checked every 4 h, and inactivated at 8:00. Baits were removed after each trapping night to avoid supplementation of food. We reached a mean trappability of 82% per traps' check and of *c.* 100% per trapping session. At every capture, we recorded trap location and sex, body mass, head width and reproductive status. Females were considered sexually mature after being recorded pregnant or lactating for the first time. Males were considered sexually mature if their testes were scrotal. To record movement patterns, each habitat patch was equipped with two antennas sensitive to the PIT tag inserted in each animal and located along two opposite edges of each habitat patch. Antennas were connected to Trovan[®] LID665 OEM PIT-tag decoders (LID665; EID Aalten B.V., Aalten, Netherlands) recording PIT tag ID, date and time, and were made of a plastic tube (20 × 4 cm) placed on the ground along runways.

DATA ANALYSES

We investigated effects of the manipulation of individual condition and habitat quality on the cohort of laboratory-born animals with statistical procedures available in R 2.8.0 (<http://cran.r-project.org/>). Our general models included fixed effect of condition treatment, habitat quality in the release or settlement patch (details elsewhere), sex and their interactions. Mass at birth was also incorporated to take into account variation between individuals before lactation. This variable also seems to have an influence on life-history traits in small mammals (Mappes & Koskela 2004). Mass at birth and mass at weaning were not significantly correlated ($r = 0.04$, $t = 0.5$, d.f. = 147, $P = 0.617$). Differences between plots were controlled for by including a fixed or a random effect of plot identity. Main effects and interactions were tested with an ANOVA procedure, and the best model was selected by backward elimination of non-significant terms. Results are given as mean ± SE unless otherwise stated.

We first checked that the litter-size manipulation had significant effects on the body mass at weaning and head size of juveniles during the summer (juveniles have not achieved their growth at weaning age). Mass at weaning was analysed with a linear mixed-effects model (LMM), where true and foster mothers' identities were entered as random effects. Growth for head width was measured from release to trapping session 9 when head width reached a plateau. Head width was analysed instead of body mass because the two variables were positively correlated at weaning age ($r = 0.85$, $t = 19.5$, $P < 0.001$), but head width is not influenced by the reproductive cycle. Growth was modelled using a von Bertalanffy model with three parameters (initial head width, growth rate and asymptotic head width) fitted on repeated measurements with a nonlinear

mixed-effects model (NLMM). The best random structure had a non-diagonal variance–covariance matrix with random inter-individual variation in all parameters (Pinheiro & Bates 2000). This model included effects of habitat quality in the recapture patch.

Next, we defined for each individual the three stages of natal dispersal, i.e. departure, transience and settlement, based on live trapping data and PIT tag recordings. Departure stage ended when the individual was detected for the first time in another patch than the release one. Transience ended and settlement began when the individual significantly reduced its inter-patch movements to none or few (< 5% of the spatial locations recorded outside of the settlement patch). For the latter stage, the settlement patch was defined as the patch where the individual spent most of its time. Using this procedure, we could examine differences in survival, spacing and movement behaviour, and reproductive success between treatments across the three dispersal stages (see Table S1 for a detailed list of study variables and sample sizes, in Supporting Information). Mortality rates were studied with a Cox proportional hazards model including a co-factor ‘dispersal stage’ to control for potential difference in mortality between the three stages of natal dispersal. For spacing behaviour, we calculated the home range sizes of juveniles before departure, i.e. during the first 15 days after release or before the date of departure from the release patch. Home range sizes were also estimated during a period of 2 weeks, 45 days after release, when almost all the individuals had settled in a breeding patch. We used the 95% Minimum Convex Polygon method to calculate home range size (Mohr 1947) and a linear model for statistical analysis. Home range sizes at settlement were log-transformed to achieve normality.

For movement behaviour, we first tested the decision to leave by looking at the timing of the first inter-patch movement with a Cox proportional hazards model. During transience, we investigated prospecting behaviour by recording the number of days when animals were moving between patches (duration of transience), as well as the number of consecutive visits of patches. Both variables were analysed with a negative binomial generalized linear model (GLM) controlling for time to death for the former and duration of transience for the latter. For settlers, we considered natal dispersal and habitat selection behaviour. Natal dispersal was analysed with a logistic regression, and habitat selection was modelled with a quasi-Poisson regression for multinomial data. For natal dispersal, we included a co-factor to test any effect of the presence or absence of the mother in the release patch. Finally, we analysed the reproductive success of settlers. As we could not measure directly reproductive success in the field, we used two other fitness proxies: age at sexual maturation for both sexes and number of litters per female. The number of litters is related to the rate of litter production and female survivorship, and provides a good proxy of lifetime reproductive success. Age at maturation was examined with a Cox regression and number of litters with a log-linear Poisson regression. We controlled for natal dispersal status in these analyses.

Results

MORPHOLOGICAL TRAITS

Individuals raised in small litters were significantly heavier at weaning (LC: 9.5 g ± 0.2, HC: 13.0 g ± 0.1; LMM: $t = 6.02$, $P < 0.001$), but sex and the interaction between sex and condition treatment did not influence weaning mass (sex: $\chi^2 = 0.072$, d.f. = 1, $P = 0.788$; sex * condition: $\chi^2 = 0.94$, d.f. = 1, $P = 0.333$). The analysis of post-weaning struc-

tural growth showed that males grew faster than females (NLMM: for the log of the negative exponential growth rate, contrast males = 0.28 ± 0.05, $t = 6.01$, $P < 0.001$) and that the initial and asymptotic head width of individuals from small litters were larger (NLMM: weaning head width: LC: 11.87 mm ± 0.04, HC: 12.60 mm ± 0.03, $t = 10.10$, $P < 0.001$; asymptotic head width: LC: 16.07 mm ± 0.05, HC: 16.21 mm ± 0.04, $t = 3.70$, $P < 0.001$; Fig. 2a,b). We found no effect of habitat quality on growth [Likelihood Ratio (LR) tests: models with interactive vs. additive habitat effect: LR = 2.73, $P = 0.604$; models with additive vs. no habitat effect: LR = 5.50, $P = 0.702$] and no effect of condition treatment on growth rate (NLMM: contrast HC = 0.12 ± 0.09, $t = 1.49$, $P = 0.138$).

DEPARTURE

Individuals originating from enlarged litters suffered higher mortality before transience than did individuals from reduced litters (LC: 25 deaths of 103, HC: 5 deaths of 46; Cox regression: contrast HC = -2.97 ± 0.62, $Z = -4.82$, $P < 0.0001$). Mass at birth also influenced mortality before

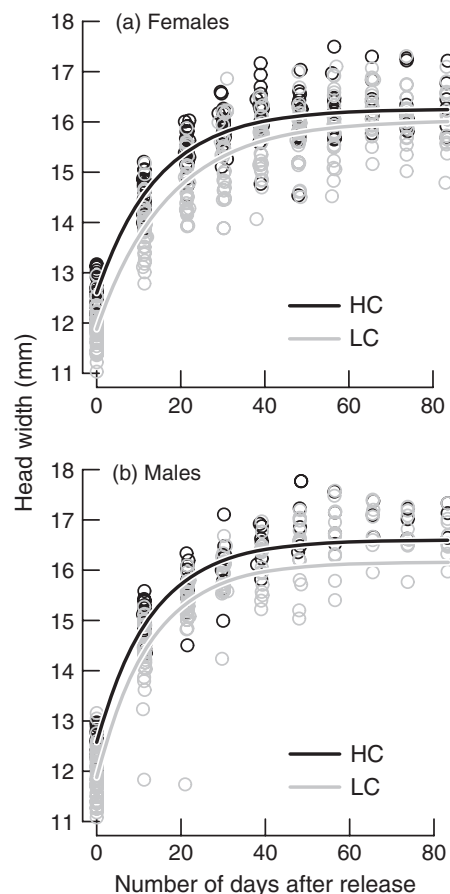


Fig. 2. Growth trajectories of female (a) and male (b) root voles released in the field ($N = 149$). Mean ‘von Bertalanffy’ growth curves and raw data for head width (a, b) are represented separately for juveniles raised in small litters (high-condition treatment, in black) and in large litters (low-condition treatment, in grey). Average head size at birth ranges between 9 and 10 mm in root voles (unpublished data).

transience (slope = -1.17 ± 0.48 , $Z = -2.41$, $P = 0.016$), with smaller individuals at birth displaying higher mortality. In addition, mortality from release to the end of the experiment was slightly but not significantly higher for males (Cox regression: contrast males = 0.39 ± 0.19 , $Z = 1.84$, $P = 0.065$), and lower for individuals living in HQ than in LQ patches (contrast IQ = 0.44 ± 0.24 , $Z = 1.85$, $P = 0.064$; contrast LQ = 0.57 ± 0.25 , $Z = 2.30$, $P = 0.022$). However, these latter mortality rates were not influenced by dispersal stages (LR tests: all $P > 0.15$). Finally, interaction between body condition treatment and habitat quality had no effects on survival at any stages of dispersal ($P = 0.98$).

Home range sizes before transience were affected by an interaction between sex and condition treatment ($F_{1,114} = 4.02$, $P = 0.048$). Juvenile males from the HC treatment had smaller ranges ($40 \pm 11 \text{ m}^2$) than LC males ($71 \pm 6 \text{ m}^2$), whereas no difference was found for females (mean range size = $63 \pm 8 \text{ m}^2$). Mass at birth, habitat quality and second-term interactions did not influence home range sizes before transience (ANOVA: all $P > 0.25$).

Sex and habitat quality of the release patch had an interactive effect on age at first inter-patch movement. Females dispersed earlier from LQ patches than from other patches (Cox regression: contrast HQ = -0.59 ± 0.33 , $Z = -1.78$, $P = 0.076$; contrast IQ = -0.72 ± 0.33 , $Z = -2.20$, $P = 0.028$; Fig. 3a), but males were insensitive to habitat quality (LR = 1.66, d.f. = 2, $P = 0.436$; Fig. 3b). After 11 days, 85% of females released in LQ patches have started exploring other patches, whereas only 57% and 46% of females moved out from HQ and IQ patches respectively (Fig. 3a). Age at first inter-patch movement was not influenced by the condition treatment (LR = 0.62, d.f. = 1, $P = 0.430$), the mass at birth (LR = 1.79, d.f. = 1, $P = 0.181$) and the interaction terms (sex * condition: LR < 0.01, d.f. = 1, $P = 0.989$; condition * habitat quality: LR = 3.57, d.f. = 2, $P = 0.168$).

TRANSCIENCE

Individuals spent an average 16 ± 2 days exploring their environment before settling. Females that settled in LQ or IQ patches spent more time prospecting than females settling in HQ patches (negative binomial GLM: HQ = 7 ± 3 days; IQ = 18 ± 4 days, $Z = 2.54$, $P = 0.011$; LQ = 27 ± 5 days, $Z = 2.98$, $P = 0.003$). Transience duration for males was not influenced by habitat quality of the settlement patch (LR = 2.77, d.f. = 2, $P = 0.251$). Moreover, transience duration was not affected by habitat quality of the release patch (LR = 0.31, d.f. = 2, $P = 0.857$), condition treatment (LR = 0.35, d.f. = 1, $P = 0.553$), mass at birth (LR = 0.78, d.f. = 1, $P = 0.377$), sex (LR = 2.43, d.f. = 1, $P = 0.119$) or any second-order interactions between these variables (LR tests: all $P > 0.30$). We tested a posteriori for differences in transience duration between philopatric and dispersing individuals (in regard to natal dispersal), but individuals that eventually dispersed from their natal patch did not spend more time prospecting than

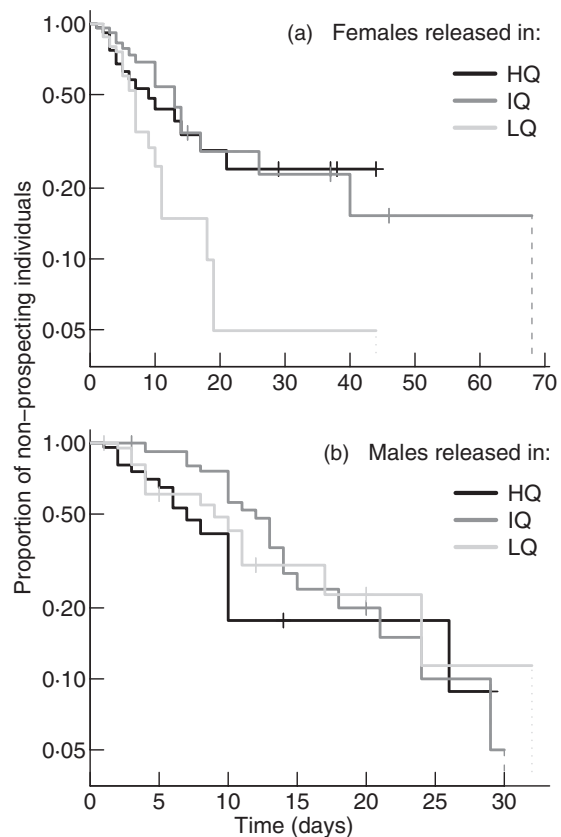


Fig. 3. Proportion of juveniles present in their release patch as a function of time. Kaplan-Meier estimates are represented separately for high-quality (black), intermediate-quality (grey) and low-quality (light grey) treatments, and, for females (a) and males (b).

philopatric individuals (sex * dispersal status: LR = 0.06, d.f. = 1, $P = 0.803$; dispersal status: LR = 1.02, d.f. = 1, $P = 0.312$).

The number of visited patches during transience was on average 14 ± 2 . When controlling for a significant positive effect of transience duration (GLM: $Z = 12.14$, $P < 0.0001$), the number of visited patches was not influenced by habitat quality in release patch (LR = 0.63, d.f. = 2, $P = 0.730$), condition treatment (LR = 0.44, d.f. = 1, $P = 0.506$), habitat quality in settlement patch (LR = 1.89, d.f. = 2, $P = 0.389$) or any other factor (LR tests: all $P > 0.25$). Survival during transience was not affected by the condition treatment (contrast HC = -0.70 ± 0.46 , $Z = -1.55$, $P = 0.121$) or by mass at birth (estimate = -0.73 ± 0.58 , $Z = -1.25$, $P = 0.210$).

SETTLEMENT

Males dispersed more from their release patch than females (GLM: contrast = 2.21 ± 0.54 , $Z = 4.10$, $P < 0.0001$; Table 1). Moreover, the propensity to disperse was negatively related to the mass at birth, and quality of the patch at release had also an influence on natal dispersal, as individuals from LQ habitats were less philopatric than individuals from

Table 1. Natal dispersal (probability of moving from the release patch to another settlement patch) in relation to sex, condition treatment, habitat quality in the release patch and their interactions, in addition to mass at birth and presence/absence of the mother in the patch ($N = 81$)

Factors	Parameter estimate \pm SE	Statistics	P
Intercept	4.04 \pm 2.27	$Z = 1.78$	0.076
Sex	Males: 2.53 \pm 0.61	$Z = 4.12$	<0.0001
Mass at birth	-1.53 \pm 0.74	$Z = -2.08$	0.037
Habitat quality	HQ: -0.32 \pm 0.68	$Z = -0.47$	0.639
	IQ: -1.46 \pm 0.71	$Z = -2.06$	0.040
Mother absence	Absent: 0.60 \pm 0.57	LR = 1.13	0.288
Condition treatment	HC: -0.25 \pm 0.59	LR = 0.18	0.674
Condition treatment	HC:HQ: 0.15 \pm 1.44	LR = 2.91	0.233
\times HabQuality	HC:IQ: -2.37 \pm 1.77		
Condition treatment	HC:Males: 1.16 \pm 1.44	LR = 0.71	0.401
\times sex			

The interaction between habitat quality and sex was not considered for the analysis because standard errors were very large, even when this interaction was added into the final model. When males and females were analysed separately, standard errors were very large for males, and natal dispersal of females was weakly influenced by habitat quality (LR = 4.08, d.f. = 2, $P = 0.130$). HC, 'high-condition' treatment (juveniles raised in small litters); HQ, 'high-quality' patch; IQ, 'intermediate-quality' patch; LR, likelihood ratio.

IQ habitats. However, neither condition treatment nor any of the interaction terms had an effect on natal dispersal (Table 1).

The analysis of habitat selection for males did not show any significant interaction between habitat quality of settlement patch and condition treatment (LR = 2.94, d.f. = 2, $P = 0.230$) or between habitat quality at settlement and habitat quality at release (LR = 5.67, d.f. = 4, $P = 0.225$; see Table S2 in Supporting Information). When considering females, condition treatment did not influence habitat quality of the settlement patch (LR = 0.65, d.f. = 2, $P = 0.721$), but quality of the release patch had a significant effect (LR = 27.58, d.f. = 4, $P < 0.0001$). The latter effect comes from the strong philopatry of females, especially in HQ and IQ patches (see Table S2 in Supporting Information). We tested for differences in head width at recapture between individuals that settled in the different patches and found significant differences (Kruskal-Wallis test: $\chi^2 = 15.27$, d.f. = 2, $P = 0.0005$). On average, individuals settled in LQ and IQ patches were smaller than individuals from HQ patches (Wilcoxon rank sum tests: $P < 0.002$; LQ = 16.1 \pm 0.10 mm, IQ = 16.0 \pm 0.10 mm, HQ = 16.56 \pm 0.09 mm).

Habitat quality and condition treatment additively affected home range sizes after settlement. Home range sizes increased with decreasing quality of the patch [HQ: 61.3 \pm 20.9 m², IQ: 96.3 \pm 30.1 m², LQ: 194.4 \pm 61.7 m²; linear model: contrast HQ = -0.97 \pm 0.32 log (m²), $t = -3.01$, $P = 0.004$; contrast IQ = -0.65 \pm 0.31, $t = -2.05$, $P = 0.045$]. Moreover, LC individuals had larger home ranges than HC individuals [LC: 164.6 \pm 46.8 m²,

HC: 70.1 \pm 29.7 m²; contrast HC = -0.59 \pm 0.27 log(m²), $t = -2.20$, $P = 0.032$] irrespective of the habitat quality ($F_{2,67} = 0.46$, $P = 0.636$). Home range sizes after settlement were not affected by mass at birth ($F_{1,64} = 0.03$, $P = 0.863$), sex ($F_{1,64} = 2.64$, $P = 0.110$) or interactions (all $P > 0.10$).

Age at maturation depended on sex, with males maturing earlier than females (Cox regression: $Z = 5.12$, $P < 0.001$). Moreover, HC individuals tended to mature faster (contrast HC = 0.50 \pm 0.27, $Z = 1.89$, $P = 0.058$). Age at maturation was not affected by other factors (ANOVA: all $P > 0.25$). With regard to the number of delivered litters per female, the only significant factor was habitat quality in the settlement patch (LR = 6.69, d.f. = 2, $P = 0.035$). Females settled in LQ patches delivered a smaller number of litters than females settled in HQ patches (Poisson GLM: contrast HQ = 1.12 \pm 0.49, $Z = 2.27$, $P = 0.023$; contrast IQ = 0.65 \pm 0.50, $Z = 1.30$, $P = 0.194$). No other factors influenced the number of delivered litters (LR tests: all $P > 0.10$). Finally, survival after settlement was not affected by the condition treatment (contrast HC = 0.20 \pm 0.30, $Z = 0.66$, $P = 0.509$) or by mass at birth (estimate = -0.57 \pm 0.37, $Z = -1.54$, $P = 0.124$).

POWER ANALYSES

We used prospective power analyses (see Appendix S1 in Supporting Information) to calculate the effect size that was likely to be detected given our sample size under three alternative hypothesis: habitat quality influences natal dispersal (hypothesis H1), condition treatment influences natal dispersal (H2) and an interaction between habitat and condition treatments influences natal dispersal (H3). The statistical power to detect the interaction (H3) reached the critical threshold of 80% for a deviation (on the logit-scale) of 1.01 from the mean dispersal probability (Fig. 4). For females, this would correspond on a probability scale to a dispersal rate of 0.106 for HC females from HQ patches and LC females from LQ patches, of 0.255 for females from IQ habitats, and of 0.497 for HC females from LQ habitats and LC females from HQ patches. For males, dispersal rates would correspond to 0.490, 0.735 and 0.889 respectively. Similar critical effect sizes were found for hypothesis H1 (Fig. 4), but an even smaller effect size would be sufficient to detect an effect of the condition treatment on dispersal (H2). This effect size corresponds to a change of probabilities from 0.138 for HC females to 0.423 for LC females, and from 0.565 for HC males to 0.856 for LC males.

Discussion

Our results suggest additive, not interactive, effects on dispersal behaviours and life-history traits of changes in individual condition induced by the litter-size manipulation and of changes in habitat quality induced by vegetation degradation. Root voles from small litters were characterized by larger structural size and body mass, but did not preferentially move to and settle in high-quality habitats. Yet, dispersal was

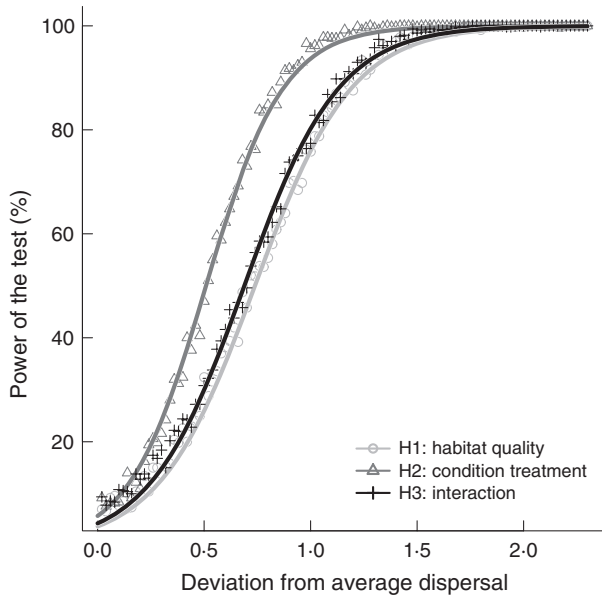


Fig. 4. Power (probability of rejecting a false null hypothesis) of the statistical analysis of natal dispersal for effects of habitat quality (hypothesis H1), condition treatment (H2) and their interaction (H3). Statistical power is plotted against a measure of effect size, which is the deviation on a logit scale from the average sex-specific dispersal probability (see Appendix S1 in Supporting Information for details).

not completely random because habitat quality, sex and adult body size differentially influenced departure, transience and settlement behaviours.

A recurrent result of our study is a female strategy of philopatry sensitive to environmental conditions, while dispersal in males was stronger and less plastic. A strong 'philopatry-dispersal' dichotomy between males and females is commonly observed in root voles (Gundersen & Andreassen 1998; Andreassen & Ims 2001) and in other polygynous microtine rodents (Boonstra *et al.* 1987; Sandell *et al.* 1990). Female root voles from low-quality habitats moved earlier than females from habitats of better quality, prospected more before settlement, and settled preferentially in habitats of higher quality. Similar effects of habitat quality on movement behaviour have been shown with prairie voles, *Microtus ochrogaster* (Lin & Batzli 2001; Lin *et al.* 2006), suggesting that vegetation cover is an important cue for small rodents to assess habitat quality. The LQ habitats had a lower carrying capacity with regard to the number of settled reproductive females (unpublished data). Differential rate of dispersal according to carrying capacities may actually evolve in a spatially, heterogeneous landscape (McPeck & Holt 1992). Moreover, the reduction of the vegetation cover in LQ habitats increased densities and competitive interactions within the suitable areas, which can also increase the propensity to leave a patch (see Bowler & Benton 2005 for review). Irrespective of the exact behavioural mechanisms, this sex-specific sensitivity is likely adaptive because females are more dependent upon habitat quality for their reproductive success than males in species with mono-parental and polygynous

mating systems such as root voles (Boonstra *et al.* 1987; Andreassen & Ims 1998; Lin & Batzli 2001). Negative fitness effects associated with settlement in LQ patches were observed for females in this study, including an overall increase in mortality rate and a decrease in the number of delivered litters.

Considering that females spent more time prospecting before settling in poor habitats and that individuals of both sexes had larger home range sizes after settlement in these habitats, voles seemed reluctant to settle and reside in a non-optimal habitat, but were unsuccessful in establishing in a better quality habitat. Considering further that voles settled in the lower-quality habitats were smaller at adulthood for their head width, these results support a 'despotic distribution' model of habitat selection (Fretwell 1972). Competitive advantage during territorial contests given by a larger body size has been observed in other rodent species (Schuler & Renne 1988; Luque-Larena, Lopez & Gosálbez 2003), even if our previous behavioural observations failed to find an influence of body mass on social dominance in root voles (Rosell, Gundersen & Le Galliard 2008). However, settlement was not influenced by the condition treatment *per se*. In other words, adult size influenced settlement success regardless of the conditions experienced by individuals during lactation. But mass at birth had an effect on natal dispersal and early survival. A pronounced effect of this variable on fitness traits has also been observed in bank voles (Mappes & Koskela 2004). This raises the interesting possibility that silver spoon effects on natal dispersal and habitat selection in root voles might be determined before lactation, i.e. during pregnancy.

An interesting finding of our detailed monitoring of individual movements is that most individuals explored their environment before settling. We found no evidence of extramortality during the transience stage, and natal dispersal status (philopatry or dispersal) was not linked with prospecting behaviour. In addition, there were no direct reproductive costs of dispersal independently from the effects of habitat quality in the settlement patch. These observations raise the possibility that philopatry resulted from frustrated and unsuccessful dispersal attempts in our study system. Whenever this is the case, we expect that the costs of natal dispersal are disconnected from the costs of transience.

Individual condition resulting from environmental conditions experienced during lactation had no effect on natal dispersal and habitat selection, even though our experimental design could detect reasonable differences in dispersal probabilities between condition treatments. Moreover, we had a good statistical power to detect the interaction between condition and habitat quality treatments, as critical effect sizes were similar to changes in dispersal behaviour observed in previous studies (Andreassen, Hertzberg & Ims 1998). This result is in sharp contrast with dispersal patterns in other small rodents, where malnourished individuals during infancy are more active (Watson, Smart & Dobbing 1976; Wong & Bondrup-Nielsen 1992) and more likely to emigrate later in life (Bondrup-Nielsen 1993). Perhaps conditions experienced before lactation are more important than those

experienced after lactation in root voles (see above). Also, the distance between patches in this study might be smaller than the spatial scale at which individual condition influences movements (but see Andreassen & Ims 2001).

Any weak effect of individual condition on dispersal behaviours might also be because of a failure of the litter manipulation to generate long-lasting differences between individuals (Metcalf & Monaghan 2001, 2003). However, several evidences run against this argument. First, we found clear long-lasting effects on head width throughout the summer reproductive season, which is in agreement with a study conducted during the non-reproductive season in bank voles (Koskela 1998). Thus, our results and those of Koskela (1998) indicate that structural size is importantly determined by environmental conditions experienced during lactation. Second, mortality immediately after release was much higher for low condition individuals – a result that could be explained by a significant correlation between post-release survival and weaning head width (Cox regression: slope = -0.49 ± 0.20 , $Z = -2.45$, $P = 0.014$). Smaller individuals were weaker competitors and might have died from starvation, aggression by congeners or higher exposure to predators (Hovland, Andreassen & Ims 1999). After this initial increase of mortality, survival was similar between treatments, which could be due to purging effects of natural selection at the beginning of the experiment. Third, data on space use showed that low-condition individuals had larger home ranges. A possible explanation for this is that low-condition weanlings were released with two times more foster siblings than high condition weanlings, which strengthens sibling competition and could increase activity and movement distances (Lambin, Aars & Piertney 2001). However, dispersal movements are not correlated with litter size and sibling competition in root voles (Gundersen & Andreassen 1998; Le Galliard *et al.* 2006; Le Galliard, Gundersen & Steen 2007). Finally, the litter size enlargement had marginal, negative effects on maturation age, similar to the effects of malnutrition and weaning mass on age at maturation in female grey-sided voles (Andreassen & Ims 1990). Unfortunately, we were not able to quantify accurately the reproductive success of females, as litter size was not available and offspring could not be assigned with certainty to a mother.

In conclusion, this study addresses issues of phenotype- and condition-dependent dispersal and habitat selection during the three successive stages of dispersal, and is to our knowledge the first experimental test of the silver spoon effect on habitat selection. In their reviews, Ims & Hjernmann (2001), Stamps (2006) and Clobert *et al.* (2009) predicted interactive effects of intrinsic (internal state) and extrinsic (environment) factors on dispersal. Recent studies also raised the issue of genetic-dependent dispersal in rodents (Selonen & Hanski 2010). The absence of silver spoon effects on natal dispersal and habitat selection in root voles suggest that immediate effects of habitat quality override any long-lasting effects of postnatal conditions. Similarly, Ergon, Lambin & Stenseth (2001) found that immediate environmental conditions were more important than intrinsic conditions in

shaping life-history traits in field voles (*Microtus agrestis*). Dispersal and other life-history strategies of these microtine rodents might have evolved to respond immediately to spatial and temporal changes in their environment, because of the relative long time-lag imposed by maternal effects and the short life span of these species (Ims & Hjernmann 2001).

Acknowledgements

We thank R. Guerreiro, E. Nivois, A.-L. Ferchaut and B. Deceni re for assistance in the field, and the personnel at the Animal Division at the University of Oslo for help in the laboratory. We also thank two anonymous referees for their constructive comments on the manuscript. This project was funded by a Marie Curie Intra-European Fellowship FP6-501658 to J.-F. L. G., a grant from the Norwegian Research Council (NFR project 182612) to H. P. A., and a start-up grant from the Biology Department, University of Oslo to H. S. The housing at the Animal Division and experimentations at Evenstad Research Station were carried out in accordance with the Norwegian 'Animal Welfare Act' of 20.12.74, the Norwegian 'Regulation on Animal Experimentation' of 15.01.96 and the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes of 18.03.86.

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Received 25 May 2010; accepted 28 March 2011

Handling Editor: Tim Benton

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Detailed list of study variables and sample sizes for the different analyses performed to detect an interactive effect of individual condition and habitat quality on dispersal and life-history traits.

Table S2. Numbers of juvenile voles released into each habitat type and numbers of voles that survived and settled into each habitat type at adulthood according to their origin (patch at release). Data from the six study plots are pooled together.

Appendix S1. Prospective power analyses.

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