

Mother–offspring interactions do not affect natal dispersal in a small rodent

J.-F. Le Galliard,^a G. Gundersen,^{a,b} and H. Steen^c

^aCentre for Ecological and Evolutionary Synthesis, Biology Department, University of Oslo, P.O. Box 1050, Blindern, Oslo NO-0316, Norway, ^bFaculty of Forestry and Wildlife Management, Hedmark University College, NO-2480 Koppang, Norway, and ^cProgram for Experimental Behavioral and population Ecological research, Biology Department, University of Oslo, P.O. Box 1050, Blindern, Oslo NO-0316, Norway

According to kin selection and inbreeding avoidance hypotheses, natal dispersal should be facultatively adjusted to balancing the costs and benefits of mother–offspring interactions. In polygynous mammals, it is hypothesized that female offspring should seek to avoid local resource competition with their mother, whereas male dispersal should be determined by inbreeding avoidance. We tested these hypotheses with a field experiment investigating the relationship between territory acquisition and mother's presence in the root vole *Microtus oeconomus*. This species has a flexible social system in which sisters' and mother's home ranges overlap substantially, whereas sons disperse to a greater extent. Immature sibling voles aged 20 days were released for 20 days together with an unrelated adult male in a 2-patch system either in the presence of their mother or in the presence of an unrelated adult female. Offspring movements were not influenced by mother's presence, but offspring, especially females, avoided the patch occupied by the adult female irrespective of kinship. Offspring remaining in contact with their mother were reproductively suppressed at the middle, but not by the end, of the experimental period. These results indicate that juvenile root voles adopted an opportunistic settlement strategy where they avoided the adult female irrespective of kinship and inbreeding risks. *Key words*: breeding dispersal, inbreeding avoidance, kin competition, natal dispersal, passive integrated transponders, sociality. [*Behav Ecol* 18:665–673 (2007)]

Sociality plays an important role in the genetic and demographic makeup of animal populations (Trivers 1985; Frank 1998). Behaviors like dispersal tactics and social investment in competitive or cooperative interactions are 2 crucial components of animal societies (Le Galliard et al. 2005). There is widespread variation in the social organization of natural populations (e.g., Crespi 1996), and it has been hypothesized that this variation results from concurrent adaptive changes in the spatial distribution and social investment of individuals (Emlen 1997; Le Galliard et al. 2005). Kin selection offers a comprehensive framework to understand this diversity and points out that variation in social organization should be explained by differences in the kinship structure of natural populations (Hamilton 1964; Frank 1998). Kinship structures are indeed involved both in the evolution of dispersal (e.g., Hamilton and May 1977) and in the evolution of social investment traits like competition or cooperation (reviewed by West et al. 2002).

When kinship structures vary in space and time or according to predictable demographic traits (e.g., age), evolutionary models predict that social partners should invest facultatively in social traits (competition, cooperation, or dispersal) according to cues indicative of kinship (Ronce et al. 1998; Kisdi 2004). Kinship-dependent dispersal strategies are likely to be superior to unconditional dispersal tactics because individuals may choose to pay the costs of dispersal only when the benefits derived from social interactions with relatives are small enough (e.g., Perrin and Lehmann 2001; Devillard et al.

2004; Le Galliard et al. 2005). Studies conducted in a wide range of taxa have found that social partners vary in their degree of cooperative or competitive investment according to kinship (e.g., nepotism), but the idea that individuals could also rely on kinship to disperse or aggregate is controversial (Lambin et al. 2001; Clobert et al. 2004). There are few examples where animals decide to settle according to direct genetic cues (Petrie et al. 1999; Baglione et al. 2003; Sinervo and Clobert 2003). However, indirect cues of kinship, like phenotypic signals learned early in life, are more often involved in kin recognition (Hepper 1991) and therefore may influence dispersal decisions in a larger diversity of taxa (e.g., Léna et al. 2000; Le Galliard et al. 2003).

Mother–offspring associations are widespread kinship structures in bird, mammal, and also in some reptile species and therefore should have strong effects on natal dispersal, that is, the dispersal of offspring out of their birth place (Wolff 1994; Lambin et al. 2001; Le Galliard et al. 2003). Social interactions between mother and their offspring are more likely than father–offspring interactions because females usually invest more in reproduction and parental cares than males. In species like mammals with a characteristic lactation period, bonding between mother and offspring may also promote the evolution of maternal and postnatal effects on natal dispersal according to the presence or characteristics of the mother (e.g., Bekoff 1977; Holekamp 1986; Ims 1989; Wolff 1994). In female-defense polygynous mammals, local resource competition between daughters and their mother is considered as a prime incentive for female natal dispersal, whereas male dispersal should be influenced by inbreeding avoidance with their mother (reviewed by Perrin and Mazalov 2000). However, female–female interactions can be cooperative, and kin cooperation among female mammals may also select for female philopatry (Perrin and Goudet 2001). Whether mothers may tolerate to share space with their daughters will depend

Address correspondence to J.-F. Le Galliard, who is now at CNRS—UMR 7625, Université Pierre et Marie Curie, 7 Quai St Bernard, 75005 Paris, France. E-mail: galliard@biologie.ens.fr.

Received 16 November 2006; revised 3 March 2007; accepted 7 March 2007.

on the balance between benefits and costs of kin aggregation (reviewed by Solomon 2003). The effects of kin interactions on sex allocation (primary or secondary sex ratio) are well supported in mammals (Lambin 1994; Lambin et al. 2001), including our study species (Aars et al. 1995), but how mother–offspring interactions influence sex-specific dispersal decisions is poorly known.

Here, we used a field experiment to study the influence of mother–offspring interactions on sex-specific natal dispersal and sexual maturation, hence territory acquisition, in the root vole *Microtus oeconomus*. The social structure of root vole populations is characterized by female philopatry, substantial spatial overlap between female home ranges, and matrilineal structures within local patches of habitat (Ims et al. 1993). Males disperse more and longer distance than females (Steen 1994). Like for many other microtine rodents, root voles are able to recognize relatives based on familiarity and preweaning associations (Batzli et al. 1977; Le Galliard et al. 2006). Inbreeding depression due to sib–sib mating has been detected and gives a reduction in litter size and pregnancy rates under laboratory conditions in the southern strain used for our experiments (dos Santos et al. 1995). Because the social organization of root voles is typical of female-defense polygyny (Boonstra et al. 1987), we first predict that daughters should disperse and/or delay maturation to avoid local resource competition when they remain in the range occupied by their mother. We also predict that sons should disperse and/or delay maturation to avoid inbreeding when they remain in the range of their mother. However, if sociality within female kin groups is as important for daughters' reproductive success as in other microtine species (e.g., McGuire et al. 1993; Mappes et al. 1995; Lambin and Yoccoz 1998), mothers could tolerate their daughters to a greater degree than unrelated female. In order to test these predictions, weaned sibling root voles were released together with an unrelated adult male in a 2-patch system either in the presence of their mother or in the presence of an unrelated adult female. We then assessed sexual maturation and movements of sibling using live trapping and passive integrated transponders technology during the critical stage for territory acquisition in this species.

MATERIALS AND METHODS

Model species

Root voles (*Microtus oeconomus*) are small and sexually dimorphic rodents that inhabit highly fragmented habitats in subarctic and arctic environments (Tast 1966). The basic social structure in this species involves territorial males and kin clusters of females (usually mothers and daughters) that share space (Andreassen et al. 1998). In our field site at Evenstad Research Station, Hedmark County, Southeast Norway (250 m above sea level, 61°25'N, 11°04'E), root voles breed from spring to late autumn. Litter sizes range from 1 to 11 pups (mean = 6.26 ± 1.43 standard deviation [SD]), weaning age ranges from 15 to 20 days, and mean age at natal dispersal and sexual maturation has been found to be approximately 25–26 days old in early summer cohorts (Ims 1997; Andreassen and Ims 2001).

Experimental system

Our field experiment took place between 11 June and 24 October 2005. The experimental area consisted of 6 plots fenced with vole-proof barriers and measuring each 50 × 17 m. In early May 2005, we created 2 habitat patches of tall and dense meadow vegetation in each of the 6 plots by mowing and applying herbicide along the edges and a 10-m strip

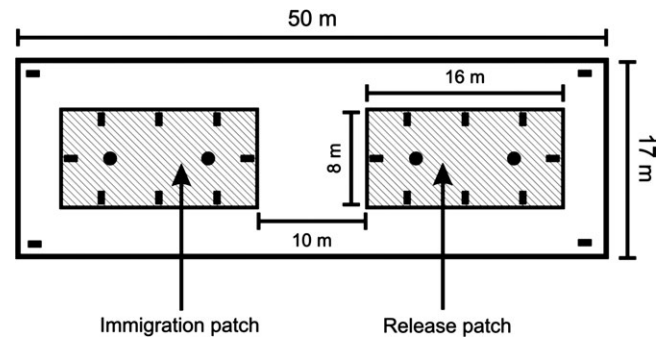


Figure 1

Habitat configuration, location of traps (filled rectangle), and location of PIT tag recording antenna (filled circle) in one of the 6 study plots. Hatched areas are habitat patches, and white areas are nonhabitat areas.

dividing the 2 patches (see Figure 1). We applied herbicide to the nonhabitat areas every other week throughout our study to maintain a barren matrix that prevented settlement of voles. Each habitat patch measured 16 × 8 m, which matches the typical area occupied by one matrilineal cluster of breeding and nonbreeding females at Evenstad (Andreassen et al. 1998; Andreassen and Ims 2001). Small patches like the one used in this study can also host kin clusters of female root voles in natural populations (Lambin et al. 1992; Viitala 1994). The 2 habitat patches of the same plot were located at a linear distance of 10 m. Previous studies at Evenstad have found that this interpatch distance impedes movements significantly in female root voles (Andreassen and Ims 2001). To prevent predation, the study area was covered by a net extending approximately 2 m above ground and surrounded by a chicken wire fence 1.5 m high topped with an electric wire.

Experimental procedures

The root voles originated from a southern Norwegian strain outbred for 2–3 generations at the Animal Division, Department of Biology, University of Oslo. To obtain juveniles for release at the right age, a group of 13–21 (mean = 18.7) breeding pairs was initiated on average 41 days before the start of each experimental trial. Adults usually mated right after initiation of the breeding pairs, and females delivered a litter on average 23.4 days later (± 2.21 SD). To obtain nongravid adult females for release in the field, the adult males were removed from the breeding cages and kept in isolated cages approximately 5 days prior to parturition. Pups were left with their mother and had no contact with their father in the laboratory. We hypothesized that contacts with fathers were also rare in natural populations because male root voles occupy much larger territories and invest less than females in parental cares (Gundersen G, personal observation, based on radiotelemetry). The day prior to release, the number of weaned offspring was again counted (mean = 4.5 ± 1.06 SD). We then individually marked all animals by toe clipping and implanted them with a small passive integrated transponder (PIT) tag (Trovan ID-100) under the skin. Offspring ($n = 161$) were sexed, and all animals were weighed (to the nearest 0.1 g) and measured for head width (to the nearest 0.01 mm) by the same person.

Each experimental trial started with the release of a litter, an adult female, and an adult male in one habitat patch of each of 6 study plots (see Figure 1). We released an adult male that had never been in contact with the adult female in the laboratory and that was not the father of the litter. The introduction of this adult male provided all females with

immediate mating opportunities and simulated natural levels of competition for mates between males (Andreassen and Ims 2001). Each study plot was assigned to one of 2 treatments: in control plots, the adult female was the mother of the litter, while in treatment plots, the adult female was unrelated to the litter. The introduction of an unfamiliar adult male did not confound this treatment, and we released adults of similar age, body mass, and head width in the 2 treatments. Treatment groups were also matched for offspring age, body mass, and head width, as well as for litter size and sex ratio (mixed-effects model, treatment comparisons, all $P > 0.26$). To ensure independence between treatments and plots, we interspersed the location of treatments during each trial and changed the location of treatments between trials.

In the evening before the release day, we introduced siblings and the adult female of the same release plot in 2 separate cages and placed the cages in the center of the release patch (Figure 1). The adult male was introduced in the release patch at the same time. Cages were opened in the early morning of the following day (ca. 6:00 PM) and kept at the release point during the whole trial. We used this procedure to familiarize siblings and the adult female with the release habitat and avoid movements due to release stress. Voles were then left undisturbed for a period of 20 days where we monitored their daily activity. For this aim, each habitat patch was equipped with 2 tube-shaped single coil antennas each placed at the center of each half of the habitat patches (Figure 1). The custom-made antenna consisted of a plastic tube (20×4 cm) and were placed on the ground along runways to maximize recording rates (Korslund and Steen 2006). Antennas were attached to Trovan LID665 OEM PIT tag decoders (LID665, EID Aalten BV, Aalten, Netherlands) that recorded PIT tag ID, date, and hour each time a tagged vole passed through the antenna.

We also trapped voles with Ugglan live traps on days 9 and 10 (middle of the experimental period) and on days 20 and 21 (end of the experimental period). Eight live traps were located in the vegetation on the edge of each patch and 2 by the fences (fence traps; see Figure 1). Traps, baited with carrots and wholegrain oats, were first activated at 20:00 h with trap checks every fourth hour until 12:00 noon on the next day. The same person recorded individual identity, trap station, body mass, head width, and sexual maturity for each trap event. At the end of the experimental period, all trapped animals were removed from the system. After removal, animals were killed by cervical dislocation and dissected to record the number of visible embryos in females (i.e., fecundity) and the size of testis in males. We measured length (L) and maximal breadth (B) of testis to calculate testis size using the ellipsoid formula

$$\text{Volume} = \frac{\pi}{6} \times L \times B^2.$$

Study variables and statistical analyses

We captured all surviving individuals at the end of each trial (100% capturability) and hence could determine individual fate (alive versus dead) without statistical uncertainty. Survival was analyzed with a mixed-effects logistic regression (McCullagh and Nelder 1989). The full model included the fixed effects of treatment groups, sex, season, and their 2-way interactions. We modeled seasonal changes with a linear effect of study trial after checking for nonlinearity. We used enclosure within treatment as a nested random factor and added the random effects of breeding pair identity.

Space use was analyzed using PIT tag records. Natal dispersal status and spatial overlap with the adult female were defined according to the location of individuals (Gundersen and Andreassen 1998; Le Galliard et al. 2006). Individuals

found in the release patch were defined as “residents,” individuals found in the immigration patch were called “immigrants,” and juveniles found in the same patch as the adult were classified as “overlapping with the adult.” The full data set involved 15 338 recordings (2520 for adult females, 5178 for adult males, and 7640 for juveniles). We calculated individual time series of PIT tag recordings over daily intervals (starting midnight) and calculated 3 different variables to characterize the daily space use of voles. We measured location (daily proportion of PIT tag recordings in the immigration patch), interpatch shifts (daily number of recorded movements between the 2 patches) and, for juveniles, overlap with the adult (daily proportion of time spent in the same patch as the adult). In the space use overlap analysis, we converted the PIT tag observations into individual continuous time series containing daily information on location. We then compared time series of location data of juveniles with those of adults to calculate the proportion p of time that juveniles spend in the same patch as the adult. These data had an asymmetric distribution, with most observations concentrated toward values of either 0 or 1. We therefore calculated a surrogate “preference index” that was given the value 0 when $p < 0.5$ and 1 otherwise. The location, interpatch shifts, and spatial overlap data were analyzed with mixed-effects generalized linear models. In addition to the main effects listed in the previous section, these statistical models included fixed effects of day to control for temporal variation in space use during the trial and random effects of individual identity to control for nonindependence among recordings made on the same animal. We used binomial error terms and logit links for location and spatial overlap data, and Poisson error terms and a log link for interpatch movements data (McCullagh and Nelder 1989). These models fit the data well, and their goodness-of-fit tests (Pearson chi-square tests) were all satisfactory.

We further investigated whether treatment and overlap with the adult female affected body growth and sexual maturation in juveniles. We did not analyze potential effects of overlap with the adult male because adult males used larger areas than adult females and therefore roamed over the entire areas of the experimental plot (see below). For these analyses, we excluded 6 replicates where the adult female died during the course of the study. To describe overlap with the adult female, we used data from the PIT tag recordings of the last 5 days before growth and sexual maturation were assessed. Overlap was calculated as the proportion of time that juveniles spend in the same patch as the adult female. We analyzed body growth using head width data. Head width relates to structural size in voles, and the repeatability of head width measurements was strong (analysis of repeated measurements, 160 individuals, 353 observations, $F_{1,19,233} = 65.54$, $P < 0.0001$, $r = 0.98$). We also studied sexual maturation in juveniles based on field observations (middle of the experiment) and dissection data from the laboratory (end of the experiment). In the field, voles were recorded as having reached sexual maturity if males had scrotal testes and if females had perforated vagina, indicating estrus. In the laboratory, females were considered sexually mature based on the presence of visible embryos, whereas males were recorded as sexually mature based on the presence of visible tubuli in the cauda epididymis. We also studied female fecundity and male testis size to get a better view of the reproductive success and onset of sexual maturation in juveniles. Testis size has been found to correlate positively with sexual maturation and sexual activity in mammals (e.g., Kerbeshian and Bronson 1996). All analyses were performed with SAS v.8.2 software (Littell et al. 1996), and for each response, a final model was selected after backward elimination of nonsignificant terms ($P > 0.05$). Results are shown as mean \pm standard error unless otherwise stated.

RESULTS

Effects of the manipulation on adults

We recaptured 28 of 36 males and 30 of 36 females after the field period, but 10 of the 14 adults' death took place during the 2 first trials where magpies (*Pica pica*) were seen to attack our traps. To avoid further predation by magpies, we covered all traps with a plastic box, which reduced mortality significantly ($F_{1,64} = 9.24$, $P = 0.003$). When excluding mortality due to magpies, survival was not affected by treatment (Fisher's exact test, $P = 0.25$). Potential effects of treatments on adults' space use were tested using daily PIT tag recordings of interpatch movements and spatial location. The treatments did not affect the number of interpatch shifts ($F_{1,69} = 1.23$, $P = 0.27$) and the spatial location of adults ($F_{1,65} = 0.68$, $P = 0.41$). The number of interpatch movements was strongly male biased ($F_{1,1051} = 57.62$, $P < 0.0001$, log contrast = 1.65 ± 0.22) and increased seasonally ($F_{1,1051} = 33.54$, $P < 0.0001$, log slope = 0.36 ± 0.06). The proportion of PIT tag recordings in the immigration patch was also strongly male biased ($F_{1,1055} = 44.78$, $P < 0.0001$, logit contrast = 2.03 ± 0.30) and increased seasonally ($F_{1,1055} = 44.78$, $P = 0.0005$, logit slope = 0.31 ± 0.09). These results imply that adult males made regular interpatch movements (3.17 per day [1.69, 5.95] 95% confidence interval) and used the 2 habitat patches extensively (proportion immigrants = 0.55 [0.44, 0.66]), whereas adult females showed pronounced philopatry (mean movement number per day = 0.07 [0.03, 0.15], proportion immigrants = 0.14 [0.09, 0.21]). Looking more closely at the individual recordings for adult females, we found 29 typical "residents" and 7 typical "immigrants." In residents, however, some females ($n = 11$) made occasional sallies out of the release patch, but these sallies were rare (0.12 ± 0.01 per day) and short term (percentage of time spent in immigration patch = 0.9 ± 0.02).

The head width of adults increased slightly during the course of the field study (average increase = 0.61 mm \pm 0.07 ; $t = 9.05$, degrees of freedom [df] = 57, $P < 0.0001$). Head width growth decreased linearly with season ($F_{1,50} = 8.16$, $P = 0.006$, slope = -0.094 mm per trial \pm 0.52) and also with initial head width ($F_{1,50} = 22.31$, $P < 0.001$, slope = -0.30 mm/mm \pm 0.06), but treatment had no effect on growth ($F_{1,47} = 0.02$, $P = 0.88$). After the field period, all recaptured adult males had scrotal testis, all adult females had visible embryos, and the number of visible embryos in females was not different between control and treatment groups ($F_{1,28} = 0.01$, $P = 0.91$; control: 4.86 ± 0.52 , treatment: 4.94 ± 0.48).

Juvenile survival

The survival of released offspring varied among trials but was not affected by treatment ($F_{1,27} = 0.64$, $P = 0.43$). The best model describing seasonal variation in juvenile survival indicated low survival during the 2 first trials (0.44 ± 0.11), high survival from trial 3 to trial 5 (0.89 ± 0.04), and a lower survival later in the season (0.70 ± 0.12 ; $F_{2,123} = 15.63$, $P = 0.006$). Females survived slightly better than males ($F_{1,123} = 4.26$, $P = 0.04$, logit contrast = 0.81 ± 0.39), and survival tended to increase with initial body mass ($F_{1,123} = 3.52$, $P = 0.06$, logit slope = 0.26 ± 0.14).

Space use by juveniles

Thanks to the PIT tag recordings, each of the 161 juveniles was observed on average 3.9 times per day (± 4.75 SD) during the experimental period. Males were seen more often than

females, but treatment had no effects on the number of observations (results not shown). The space use (spatial location, spatial overlap with the adult, and number of interpatch shifts) of juveniles could therefore be described accurately on a daily basis. Juveniles did not avoid the patch occupied by the adult male (overlap = 0.55 ± 0.02), and the spatial overlap between juveniles and the adult male was not affected by treatment, juvenile sex, and season (all $P > 0.18$). This result was expected because adult males made regular movements between the 2 habitat patches and therefore used the 2 habitat patches as part of the same home range. The other space use descriptors were not affected by the presence of the mother (treatment effect for spatial location: $F_{1,34} = 0.35$, $P = 0.55$; spatial overlap with the adult female: $F_{1,33} = 0.06$, $P = 0.81$; and number of interpatch shifts: $F_{1,34} = 0.58$, $P = 0.45$), irrespective of the sex of the offspring (treatment \times sex effects for spatial location: $F_{1,1804} = 0.03$, $P = 0.85$; spatial overlap with the adult female: $F_{1,2238} = 0.89$, $P = 0.35$; and number of interpatch shifts: $F_{1,1790} = 0.13$, $P = 0.72$; see Figure 2). The space use patterns showed significant temporal and seasonal variation, however (Table 1). The proportion of animals located in the immigration patch increased steadily during the first 4 days of the experiment, whereas the spatial overlap with the adult female decreased and the number of interpatch shifts plateaued (Figure 2). Furthermore, the onset of dispersal got advanced and the dispersal probability became lower from early to late summer (Table 1). Regarding sexual differences in space use, female juveniles avoided the adult female, irrespective of kinship, more often than males, and males made more interpatch shifts than females (Table 1 and Figure 2). Similar results were obtained when we described the spatial location of voles using live trapping data (results not shown).

Juvenile body growth

Head width growth was not influenced by treatment, spatial overlap with the female, or the interaction between both factors, although the interaction term between treatment and spatial overlap with the adult female was marginally significant (Table 2). Head width growth decreased with spatial overlap with the adult female in control plots but not in treatment plots. In addition, head width growth decreased seasonally as well as with initial head width, and females grew faster than males (Table 2).

Juvenile sexual maturation

In the middle of the experiment, sexual maturation probability was marginally affected by an interaction between treatment and spatial overlap with the adult female ($\chi^2 = 3.23$, df = 1, $P = 0.07$) and decreased logistically with season ($\chi^2 = 50.23$, df = 1, $P < 0.0001$, logit slope = -0.68 ± 0.11). In treatment plots, sexual maturation was not affected by overlap with the adult female (logit slope = -0.53 ± 0.62 ; $\chi^2 = 0.74$, df = 1, $P = 0.39$), whereas overlap with the mother suppressed maturation in the control group (logit slope = -2.24 ± 0.71 ; $\chi^2 = 10.07$, df = 1, $P = 0.001$). The same result was found when we used live trapping data to assess overlap with the adult female (Figure 3). At the end of the field trials, most juveniles (77 of 99) were sexually mature, and treatment or overlap with the adult female had no significant effects on sexual maturation (all P values > 0.19), as well as on testis size (all P values > 0.18). Males delayed maturation relative to females ($F_{1,68} = 5.34$, $P = 0.02$, logit contrast = -2.06 ± 0.89), and sexual maturation probability again decreased logistically with season ($F_{1,68} = 6.00$, $P = 0.02$, logit slope = -0.79 ± 0.32). Similarly, the fecundity of juvenile females was not

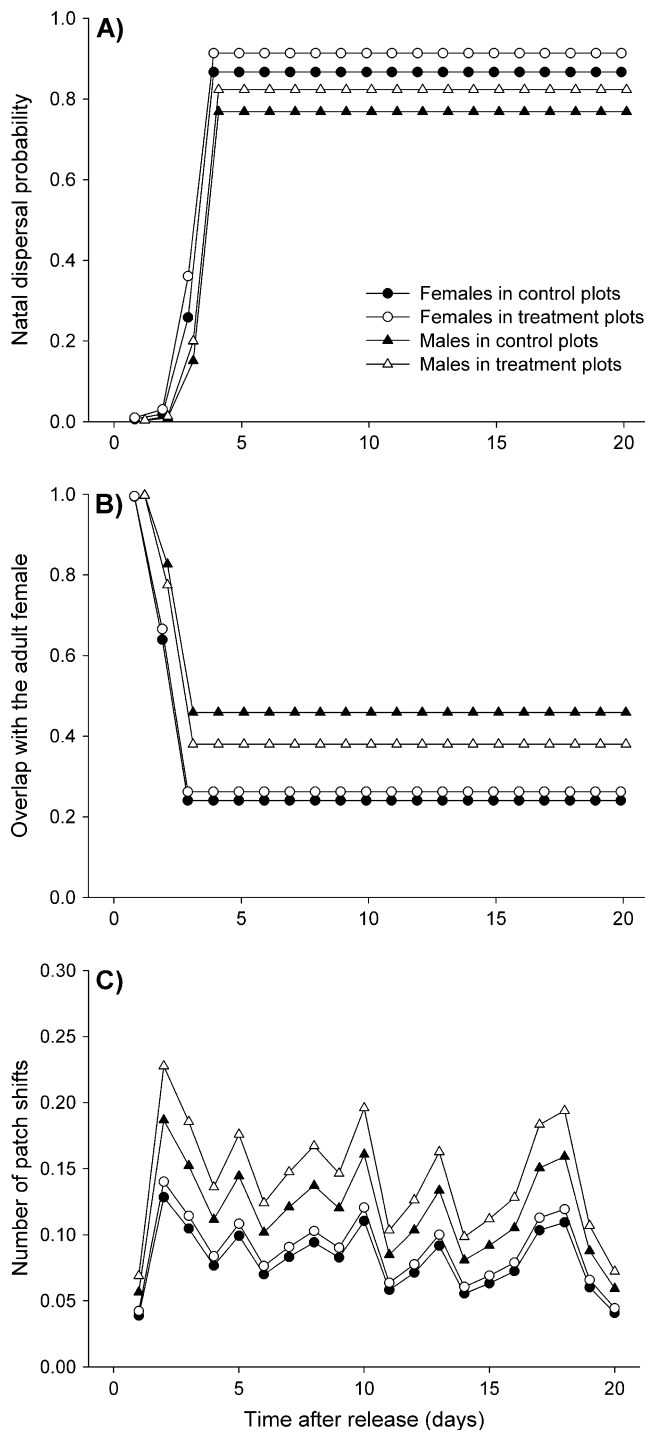


Figure 2
Daily patterns of space use by male and female juvenile root voles in the presence (control plots) and in the absence of the mother (treatment plots). Space use was monitored continuously throughout the experimental period using passive integrated transponders technology. (A) Proportion of observations in the immigration patch (natal dispersal probability) per day, sex, and treatment class. (B) Proportion of time spent in the same patch as the adult female (overlap with the adult female) per day, sex, and treatment class. (C) Number of interpatch shifts per day, sex, and treatment. Results are shown per day and treatment group to illustrate temporal variation in space use. Data are least square means of generalized mixed-effects linear models including sex and treatment effects and back transformed to the natural scale. The SEs have not been reported for ease of visualization (see Table 1 for statistical details).

influenced by the manipulation and by overlap with the adult female (treatment: $F_{1,20} = 0.19$, $P = 0.66$; overlap: $F_{1,21} = 0.29$, $P = 0.59$; treatment \times overlap: $F_{1,20} = 0.02$, $P = 0.88$).

DISCUSSION

Experimental design

Our field experiment quantified potential effects of mother–offspring interactions on sexual maturation and dispersal tactics by offspring. The field experiment mimicked colonization of a patchy landscape where offspring could settle in an initially empty patch or reside within the range occupied by their mother or by an unrelated adult female. The field experiment closely simulated root vole spatial population dynamics when adult females and their offspring colonize initially empty habitats (Tast 1966; Lambin et al. 1992). The population density (i.e., one family unit per habitat patch) was chosen to produce significant levels of competition for space and food resources in the release patch relative to the initially empty patch. Indeed, Gundersen et al. (2002) showed that competition between offspring and one adult female in the habitat patch would significantly depress offspring survival and body growth. Therefore, there should have been strong incentives to reduce kin competition, and more generally competition, through dispersal. The experiment covered a period from early summer to fall when offspring start to postpone their maturation to the next year (Andreassen and Ims 2001). Seasonal changes in food availability and life history decisions could confound our results; however, because the experiment was replicated throughout the study period, the seasonal variation was controlled for statistically, and we found a significant proportion of sexually mature offspring even at the end of the experimental period.

Juvenile and adult movements were assessed with PIT tag technology, enabling a detailed investigation of temporal dynamics in space use. However, because each patch was equipped with only 2 antennas, animal location could not be reported with perfect knowledge, and the PIT tag data involved some statistical uncertainty due to capturability. For example, some voles could move between habitat patches undetected, and there was an unknown lag time until detection when a vole entered a new patch. Our estimates of space use descriptors were therefore biased (in the statistical sense) due to nonexhaustive, and potentially unequal, capturability among individuals. However, we believe that this bias is unlikely to alter our main findings. First, the PIT tag data gave similar results as the live trapping data, which involved 100% capturability and were therefore not affected by statistical biases. Second, the behavioral activity of juveniles (measured by the number and time of the day of PIT tag records) was not influenced by spatial location and treatments (results not shown), suggesting that activity and therefore capturability of voles were homogeneous between habitat patches and treatments. The issue of controlling for unequal capturability in time-continuous observations of animal movements such as ours deserves further statistical work.

Mother–offspring competition

When mothers and daughters compete locally for critical resources, a significant proportion of the daughters should disperse to avoid the risks of kin competition even if dispersal is costly (Hamilton and May 1977; Perrin and Mazalov 2000). Local resource competition among females was first described by Clark (1978) and is considered of prime importance to explain the evolution of sex-biased dispersal strategies (Perrin and Mazalov 2000). In *Anthechinus* marsupials,

Table 1

Selected generalized mixed-effects models describing spatial location (release vs. immigration patch), spatial overlap with the adult female (overlapping vs. not overlapping), and number of interpatch shifts in juvenile root voles from the 2 treatment groups

	Estimates \pm SE	<i>t</i> Values	<i>F</i> statistics
Spatial location			
Fixed effects			
Intercept	1.61 \pm 0.81	1.98, $P = 0.05$	
Daily variation			
Day 1	-7.72 \pm 1.19	-6.49, $P < 0.0001$	$F_{3,1805} = 37.00^{***}$
Day 2	-7.86 \pm 1.10	-7.12, $P < 0.0001$	
Day 3	-4.42 \pm 0.74	-5.95, $P < 0.0001$	
Day >3	0		
Trial	-0.13 \pm 0.20	-0.65, $P = 0.51$	$F_{1,1805} = 19.39^{***}$
Trial \times daily variation			
Day 1	0.88 \pm 0.26	3.37, $P = 0.0008$	$F_{3,1805} = 39.81^{***}$
Day 2	2.06 \pm 0.26	7.99, $P < 0.0001$	
Day 3	1.49 \pm 0.18	8.07, $P < 0.0001$	
Day >3	0		
Random effects			
Enclosure	$\sigma^2 = 0$	—	
Family	$\sigma^2 = 3.03 \pm 1.01$	$Z = 3.00^{**}$	
Individual	$\sigma^2 = 3.16 \pm 0.55$	$Z = 5.79^{***}$	
Spatial overlap with the adult female			
Fixed effects			
Intercept	-0.33 \pm 0.23	-1.42, $P = 0.16$	
Sex			
Female	-0.75 \pm 0.23	-3.24, $P = 0.012$	$F_{1,2238} = 10.51^{**}$
Male	0		
Daily variation			
Day 1	6.33 \pm 1.01	6.27, $P < 0.0001$	$F_{2,2238} = 49.55^{***}$
Day 2	1.72 \pm 0.22	7.90, $P < 0.0001$	
Day >3	0		
Random effects			
Enclosure	$\sigma^2 = 0$	—	
Family	$\sigma^2 = 1.18 \pm 0.40$	$Z = 2.98^{**}$	
Individual	$\sigma^2 = 0.98 \pm 0.20$	$Z = 4.84^{***}$	
Number of interpatch shifts			
Fixed effects			
Intercept	-2.84 \pm 0.32	-8.85, $P < 0.0001$	
Sex			
Female	-0.44 \pm 0.14	-3.13, $P = 0.002$	$F_{1,1791} = 9.77^*$
Male	0		
Daily variation			
Trial	Not shown	Not shown	$F_{19,1791} = 3.07^{***}$
Trial	0.26 \pm 0.057	4.52, $P < 0.0001$	$F_{1,1791} = 20.44^{***}$
Random effects			
Enclosure	$\sigma^2 = 0$	—	
Family	$\sigma^2 = 0.14 \pm 0.07$	$Z = 1.94^*$	
Individual	$\sigma^2 = 0.27 \pm 0.07$	$Z = 3.74^{***}$	

Analyses are based on daily observations of PIT tag recordings collected from day 1 to day 20 of the experiment (see Materials and Methods for more explanations on the statistical models).

*** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$.

mothers may control daughter dispersal by behavioral dominance (Cockburn et al. 1985; Fisher 2005), but natal dispersal under parental consent appears to be the norm for most mammals (Wolff 1994). In microtine rodents, mothers often exhibit behavioral tolerance toward their daughters, sharing substantial space and food resources with female relatives (McGuire et al. 1993; Mappes et al. 1995; Lambin and Yoccoz 1998; Ims and Andreassen 1999; Solomon 2003). When the benefits of space sharing and cooperation are strong, local resource cooperation may thwart local resource competition and thus select for mother–daughter associations (Perrin and Goudet 2001; Perrin and Lehmann 2001; Devillard et al. 2004). Here, however, mother's presence did not cause natal

dispersal in daughters, and potential mother–daughter associations were disrupted due to frequent daughters' movements out of the release patch. Juvenile females avoided the patch occupied by the adult female, irrespective of kinship.

Resident male offspring may also compete for resources with their mother, and males may risk inbred mating with their mother or other female relatives if they remain within the natal home range. The synergetic effects of kin competition and inbreeding avoidance select for strongly male-biased dispersal in polygynous species (Perrin and Mazalov 2000). We therefore predicted that natal dispersal by sons should be strongly associated with the presence of the mother, as pointed out by reviews of juvenile male dispersal in mammals

Table 2
Mixed-effects model describing head width growth in juveniles from the 2 treatment groups

Factors	Estimates ± SE	<i>t</i> Values	<i>F</i> statistics
Fixed effects			
Intercept	10.70 ± 1.82	5.88, <i>P</i> = 0.002	
Treatment			
Control	−0.0006 ± 0.19	0.001, <i>P</i> = 0.99	<i>F</i> _{1,22} = 0.0001
Treatment	0		
Sex			
Females	0.25 ± 0.09	2.87, <i>P</i> = 0.005	<i>F</i> _{1,67} = 8.26**
Males	0		
Overlap with adult female			
Control	−0.09 ± 0.13	−0.72, <i>P</i> = 0.47	<i>F</i> _{1,65} = 0.05
Treatment × sex			
Control females	−0.24 ± 0.18	−1.32, <i>P</i> = 0.19	<i>F</i> _{1,66} = 1.74
Others	0		
Treatment × overlap			
Control	−0.47 ± 0.26	−1.84, <i>P</i> = 0.07	<i>F</i> _{1,64} = 3.40†
Treatment	0		
Trial	−0.55 ± 0.14	−4.04, <i>P</i> = 0.0001	<i>F</i> _{1,67} = 42.93***
Random effects			
Enclosure	σ ² = 0	—	
Family in enclosure	σ ² = 0.20 ± 0.07	<i>Z</i> = 3.00**	

Growth was measured from release to the end of the experimental period. Effects of treatment, spatial overlap with the adult female, juvenile sex, and study trial on head width growth (millimeter) were tested by backward elimination. Random effects were tested with a Wald *Z* test for variance components. Control: presence of the mother. Treatment: absence of the mother.

****P* < 0.001, ***P* < 0.01, †0.05 < *P* < 0.10.

(Pusey 1987; Clutton-Brock 1989; Wolff 1994). This prediction was not supported because natal dispersal by juvenile males was unrelated to the presence of the mother. As for females, juvenile males avoided the patch occupied by the adult female, irrespective of kinship.

Altogether, these results indicate that juvenile root voles adopted an opportunistic dispersal strategy where they

avoided the adult female irrespective of kinship. Thus, occupation of the range by an adult female rather than kinship was the social cue used by juveniles to emigrate and immigrate. Very few studies have tested experimentally for effects of parents on sex-specific offspring settlement in small mammals (Lambin et al. 2001; Wolff 1994) and their results are equivocal (Ims 1990; Wolff 1992; Jacquot and Vessey 1995). We can therefore only speculate on the reasons why natal dispersal was not strongly responsive to mother’s presence here. Root voles are inhabitant of temporary flooded habitats with strong population turnover (Andreassen and Ims 2001). These ecological conditions might have selected for density-dependent rather than kinship-dependent dispersal in this species (Cadet et al. 2003). An alternative explanation is that the presence of an adult female is used as a cue of mother’s presence by juveniles. However, this explanation runs against the fact that root voles are able to discriminate their mother from unrelated, unfamiliar females (Batzli et al. 1977; Le Galliard et al. 2006). Furthermore, in unstable habitats with high adult turnover, this cue would not be an efficient mean to avoid kin competition because mothers may die or disperse after breeding (Tast 1966).

Inbreeding avoidance

Although natal dispersal was not affected by mother’s presence, juveniles could be reproductively suppressed when they remained in contact with their mother. Reproductive suppression should be stronger for sons that risked inbred mating with their mother (Pusey 1987; Clutton-Brock 1989; Wolff 1994). Gundersen and Andreassen (1998) reported on reproductive suppression due to overlap with the mother in a short-term nonmanipulative study of space use in root voles. However, our longer term manipulative study of body size growth,

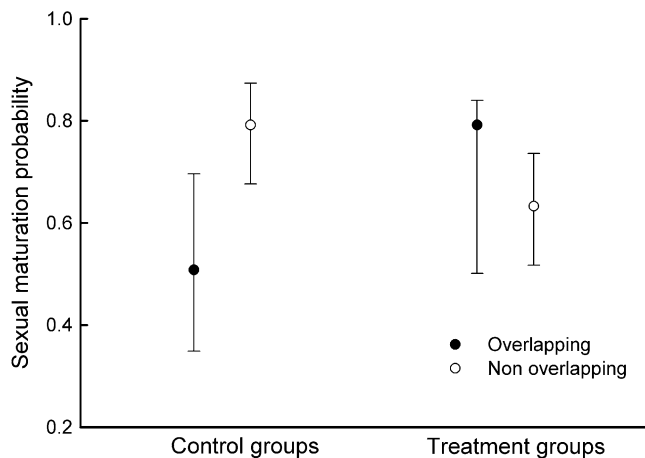


Figure 3
Sexual maturation of juvenile root voles at the middle of the experimental period (mean age = 30 days) in the presence (control plots) and in the absence of the mother (treatment plots) as a function of spatial overlap with the adult female. Spatial overlap was calculated based on live trapping data for ease of visualization. Sexual maturation probability was influenced by an interaction between treatment and spatial overlap with the adult female ($\chi^2 = 5.74$, *df* = 1, *P* = 0.02).

sexual maturation, testis size, and fecundity showed that reproductive suppression in juveniles due to mother's presence was weak and transitory. Body size growth was negatively influenced by overlap with the mother, but this effect was only marginally significant. Furthermore, sexual maturation in males and females was apparently decreased by overlap with the mother at the age of 30 days, but most male and female juveniles were reproductively active at the age of 40 days irrespective of the presence of or overlap with the mother. Because the fitness costs of inbred mating reported in the literature for root voles may be small relative to the strong fitness advantages of early maturation during the breeding season for small mammals living in Northern Europe (dos Santos et al. 1995), disproportionate costs of delayed maturation might have negated any potential benefits of reproductive suppression from inbreeding avoidance in this species. The absence of strong reproductive suppression between relatives is consistent with conclusions of a laboratory study on prairie and meadow voles by Wolff et al. (2001).

Conclusion

Current theory indicates that sociality and dispersal should be influenced by a web of multiple interacting selective pressures (Perrin and Goudet 2001; Le Galliard et al. 2005). Understanding family dynamics therefore requires combined field and experimental studies that address the multiple causes and consequences of social and dispersal strategies (Emlen 1997). Matrilineal female groups are an important feature of the social structure of root vole populations where breeding dispersal by adult females is rare while both juvenile and adult males disperse extensively (Ims and Andreassen 1999). At low population density, our results indicate that matrilineal groups should be disrupted by extensive natal dispersal toward empty patches of habitat. Mother–daughter associations might therefore build up from demographic constraints on natal dispersal at high population density. Our study did not find any fitness consequences of mother's presence or overlap with the mother's range for daughter's survival and reproduction, and therefore, the function of matrilineal remains unclear (see also Ims and Andreassen 1999). Females might simply do the best of a bad job by sharing space and food resources when social fences prohibit dispersal, but there might be inclusive fitness benefits of increased female tolerance, such as protection against infanticide (Andreassen and Gundersen 2006). To test this scenario for the emergence of female kin groups, joint manipulations of population density and mother's presence should be conducted.

We thank one anonymous reviewer and X. Lambin for comments that helped improve a previous version of the manuscript. We also acknowledge K. Hoset for providing us with some of the adult voles used in our experiment, and A.-L. Ferchaud, E. Nivois, R. Guerreiro, and J. Andrivot for assistance in the field. The personnel at the Animal Division provided some help in the laboratory. This project was funded by a grant from the Sixth Framework Programme of the European Commission (Marie Curie Intra-European Fellowship FP6-501658) to J.-F.L. and a startup grant from the Biology Department, University of Oslo, to H.S. The housing at the Animal Division and experimentations at Evenstad Research Station were done in accordance with the Norwegian "Animal Welfare Act" (#73) 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.

REFERENCES

Aars J, Andreassen HP, Ims RA. 1995. Root voles litter sex-ratio variation in fragmented habitat. *J Anim Ecol*. 64:459–472.

- Andreassen HP, Gundersen G. 2006. Male turnover generates population decline: an enclosure experiment on voles. *Ecology*. 87: 88–94.
- Andreassen HP, Hertzberg K, Ims RA. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology*. 79:1223–1235.
- Andreassen HP, Ims RA. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology*. 82:2911–2926.
- Baglione V, Canestrari D, Marcos JM, Ekman J. 2003. Kin selection in cooperative alliances of carrion crows. *Science*. 300:1947–1949.
- Batzli GO, Getz LL, Hurlley SS. 1977. Suppression of growth and reproduction of microtine rodents by social factors. *J Mammal*. 58: 583–591.
- Bekoff M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am Nat*. 111:715–732.
- Boonstra R, Krebs CJ, Gaines MS, Johnson ML, Craine ITM. 1987. Natal philopatry and breeding systems in voles (*Microtus spp.*). *J Anim Ecol*. 56:655–673.
- Cadet C, Ferrière R, Metz JAJ, van Baalen M. 2003. The evolution of dispersal under demographic stochasticity. *Am Nat*. 162:427–441.
- Clark AB. 1978. Sex ratio and local resource competition in a promiscuous primate. *Science*. 201:163–165.
- Clobert J, Ims RA, Rousset F. 2004. Causes, mechanisms and consequences of dispersal. In: Hanski I, Gaggiotti, editors. *Ecology, genetics and evolution of metapopulations*. London: Elsevier, Academic Press. p. 307–335.
- Clutton-Brock TH. 1989. Female transfer and inbreeding avoidance in social mammals. *Nature*. 337:70–72.
- Cockburn A, Scott MP, Scotts DJ. 1985. Inbreeding avoidance and male-biased dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Anim Behav*. 33:908–915.
- Crespi BJ. 1996. Comparative analysis of the origins and losses of eusociality: causal mosaics and historical uniqueness. In: Martins E, editor. *Phylogenies and the comparative method in animal behavior*. New York: Oxford University Press. p. 253–287.
- Devillard S, Allainé D, Gaillard J-M, Pontier D. 2004. Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids. *Behav Ecol*. 115:83–87.
- dos Santos EM, Andreassen HP, Ims RA. 1995. Differential inbreeding tolerance in two geographically distinct strains of root voles *Microtus oeconomus*. *Ecography*. 18:238–247.
- Emlen ST. 1997. Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB, editors. *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell Science. p. 228–253.
- Fisher DO. 2005. Population density and presence of the mother are related to natal dispersal in male and female *Antechinus stuartii*. *Aust J Zool*. 53:103–110.
- Frank SA. 1998. *Foundations of social evolution*. Princeton (NJ): Princeton University Press.
- Gundersen G, Andreassen HP. 1998. Causes and consequences of natal dispersal in root voles, *Microtus oeconomus*. *Anim Behav*. 56: 1355–1366.
- Gundersen G, Andreassen HP, Ims RA. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecol Lett*. 5:294–301.
- Hamilton WD. 1964. The genetical evolution of social behaviour, I. *J Theor Biol*. 7:1–16.
- Hamilton WD, May RM. 1977. Dispersal in stable habitats. *Nature*. 269:578–581.
- Hepper PG. 1991. *Kin recognition*. Cambridge: Cambridge University Press.
- Holekamp KE. 1986. Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). *Ecol Monogr*. 56: 365–391.
- Ims RA. 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. *Ecology*. 70:607–616.
- Ims RA. 1990. Determinants of natal dispersal and space use in grey-sided voles, *Clethrionomys rufocanus*: a combined field and laboratory experiment. *Oikos*. 57:106–113.
- Ims RA. 1997. Determinants of geographic variation in growth and reproductive traits in the root vole. *Ecology*. 78:461–470.
- Ims RA, Andreassen HP. 1999. Effects of experimental habitat fragmentation and connectivity on root vole demography. *J Anim Ecol*. 68:839–852.

- Ims RA, Rolstad J, Wegge P. 1993. Predicting space use responses to habitat fragmentation—can voles *Microtus oeconomus* serve as an experimental-model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest. *Biol Cons.* 63:261–268.
- Jacquot JJ, Vessey SH. 1995. Influence of the natal environment on dispersal of white-footed mice. *Behav Ecol Sociobiol.* 37:407–412.
- Kerbesian MC, Bronson FH. 1996. Running-induced testicular recrudescence in the meadow vole: role of the circadian system. *Physiol Behav.* 60:165–170.
- Kisdi E. 2004. Conditional dispersal under kin competition: extension of the Hamilton-May model to brood size-dependent dispersal. *Theor Popul Biol.* 66:369–380.
- Korslund L, Steen H. 2006. Small rodent winter survival: snow conditions limit access to food resources. *J Anim Ecol.* 75:156–166.
- Lambin X. 1994. Sex ratio variation in relation to female philopatry in Townsend's voles. *J Anim Ecol.* 63:945–953.
- Lambin X, Aars J, Pieltney SB. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert J, Danchin E, Dhondt A, Nichols JD, editors. *Dispersal.* Oxford: Oxford University Press. p. 110–122.
- Lambin X, Krebs CJ, Scott B. 1992. Spacing system of the tundra vole (*Microtus oeconomus*) during the breeding season in Canada's Western Arctic. *Can J Zool.* 70:2068–2072.
- Lambin X, Yoccoz NG. 1998. The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. *J Anim Ecol.* 67:1–16.
- Le Galliard J-F, Ferrière R, Clobert J. 2003. Mother-offspring interactions affect natal dispersal in a lizard. *Proc R Soc Lond B.* 270:1163–1169.
- Le Galliard J-F, Ferrière R, Dieckmann U. 2005. Adaptive evolution of social traits: origin, history, and correlation patterns of altruism and mobility. *Am Nat.* 165:206–224.
- Le Galliard J-F, Gundersen G, Andreassen HP, Stenseth NC. 2006. Interactions among siblings, intrasexual competition and natal dispersal. *Behav Ecol.* 17:733–740.
- Léna JP, de Fraipont M, Clobert J. 2000. Affinity towards maternal odour and offspring dispersal in the common lizard. *Ecol Lett.* 3:300–308.
- Littell RC, Millinken GA, Stroup WW, Wolfinger RD. 1996. SAS systems for mixed models. Cary (NC): SAS Institute.
- Mappes T, Ylönen H, Viitala J. 1995. Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). *Ecology.* 76:1276–1282.
- McCullagh P, Nelder JA. 1989. *Generalized linear models*, 2nd ed. London: Chapman & Hall.
- McGuire B, Getz LL, Hofmann JE, Pizzuto T, Frase B. 1993. Natal dispersal and philopatry in prairie voles (*Microtus ochrogaster*) in relation to population density, season, and natal social environment. *Behav Ecol Sociobiol.* 32:293–302.
- Perrin N, Goudet J. 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Nichols JD, Danchin E, Dhondt AA, editors. *Dispersal.* Oxford: Oxford University Press. p. 123–142.
- Perrin N, Lehmann L. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. *Am Nat.* 158:471–483.
- Perrin N, Mazalov V. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am Nat.* 155:116–127.
- Petrie M, Krupa A, Burke T. 1999. Peacock leks with relatives even in the absence of social and environmental cues. *Nature.* 401:155–157.
- Pusey AE. 1987. Sex-biased dispersal and inbreeding in birds and mammals. *Trends Ecol Evol.* 10:295–299.
- Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. *Proc Natl Acad Sci USA.* 95:600–605.
- Sinervo B, Clobert J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science.* 300:1949–1951.
- Solomon NG. 2003. A reexamination of factors influencing philopatry in rodents. *J Mammal.* 84:1182–1197.
- Steen H. 1994. Low survival of long-distance dispersers of the root vole (*Microtus oeconomus*). *Ann Zool Fenn.* 31:271–274.
- Tast J. 1966. The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. *Ann Zool Fenn.* 3:127–171.
- Trivers R. 1985. *Social evolution.* Menlo Park (CA): Benjamin/Cummings.
- Viitala J. 1994. Monogamy in free living *Microtus oeconomus*. *Ann Zool Fenn.* 31:343–345.
- West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. *Science.* 296:72–75.
- Wolff JO. 1992. Parents suppress reproduction and stimulated dispersal in opposite-sex juveniles white-footed mice. *Nature.* 359:409–410.
- Wolff JO. 1994. What is the role of adults in mammalian juvenile dispersal? *Oikos.* 68:173–176.
- Wolff JO, Dunlap AS, Ritchhart E. 2001. Adult female prairie voles and meadow voles do not suppress reproduction in their daughters. *Behav Processes.* 55:157–162.