INVITED REVIEW

Patterns and processes of dispersal behaviour in arvicoline rodents

JEAN-FRANÇOIS LE GALLIARD,*† ALICE RÉMY,‡§ ROLF A. IMS¶ and XAVIER LAMBIN**

*CNRS – UMR 7625, Laboratoire Ecologie-Evolution, Université Pierre et Marie Curie, Case 237, 7 Quai St Bernard, 75005 Paris, France, †CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France, ‡Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College, Campus Evenstad, Anne Evenstadsvei 80, NO-2480 Koppang, Norway, §Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PO Box 1066, Blindern, Oslo NO-0316, Norway, ¶Institutt for Arctic and Marine Biologi, Universitetty of Tromsø, 9073 Tromsø, Norway,**School of Biological Sciences, University of Aberdeen, AB24 2TZ Aberdeen, UK

Abstract

A good understanding of mammalian societies requires measuring patterns and comprehending processes of dispersal in each sex. We investigated dispersal behaviour in arvicoline rodents, a subfamily of mammals widespread in northern temperate environments and characterized by a multivoltine life cycle. In arvicoline rodents, variation in life history strategies occurs along a continuum from precocial to delayed maturation that reflects seasonal and ecological fluctuations. We compared dispersal across and within species focusing on the effects of external (condition-dependent) and internal (phenotype-dependent) factors. Our data revealed substantial, unexplained variation between species for dispersal distances and a strong variation within species for both dispersal distance and fraction. Some methodological aspects explained variation across studies, which cautions against comparisons that do not control for them. Overall, the species under consideration display frequent short-distance dispersal events and extremely flexible dispersal strategies, but they also have hitherto unexpected capacity to disperse long distances. Female arvicolines are predominantly philopatric relative to males, but we found no clear association between the mating system and the degree of sex bias in dispersal across species. Dispersal is a response to both various proximate and ultimate factors, including competition, inbreeding avoidance, mate searching and habitat quality. In particular, our review suggests that costs and benefits experienced during transience and settlement are prime determinants of condition dependence. Patterns of phenotype-dependent dispersal are idiosyncratic, except for a widespread association between an exploration/activity syndrome and natal dispersal. Consequences for population dynamics and genetic structures are discussed.

Keywords: condition-dependent dispersal, mammals, mating systems, natal and breeding dispersal, sex-biased dispersal

Received 30 August 2011; revision received 17 November 2011; accepted 17 November 2011

Introduction

The diverse social systems of mammals result from differences in behavioural and demographic processes such as dispersal behaviour (Wolff & Sherman 2007).

Correspondence: Jean-François Le Galliard,
Fax: +33-(0)1-44273516; E-mail: galliard@biologie.ens.fr

For instance, the spatial overlap of males and females, and the temporal dynamics and genetic structure of family groups are all importantly influenced by the dispersal behaviour of each sex (Arnaud *et al.* 2011; Holekamp *et al.* 2011; Schradin *et al.* 2011). Dispersal, in turn, depends on social organization, and previous analyses of mammalian dispersal suggested that territorial and mating systems in mammals are key factors that

determine the sexual biases in dispersal (reviewed in Lawson Handley & Perrin 2007; Clutton-Brock & Lukas 2011). Hence, a good understanding of mammalian societies requires measuring patterns and comprehending processes of dispersal in each sex.

Here, we used a comparative approach to investigate dispersal behaviour in male and female arvicoline rodents. These rodents are small mammals from the subfamily *Arvicolinae* that includes approximately 150 species of voles, lemmings and muskrats (Wilson & Reeder 2005). This subfamily is especially widespread in northern temperate and boreal environments, where it has been the focus of dispersal studies for almost four decades (Lidicker 1985; Anderson 1989; Stenseth & Lidicker 1992; Andreassen *et al.* 2002). In general, arvicolines are relatively small-bodied (<100 g), live above ground where they feed on green vegetation, seeds and roots and have a short (less than annual) life cycle. Population dynamics patterns range from rather stable populations, through violent but regular cycles, to various forms of irregular dynamics (Ims *et al.* 2008). Some species such as muskrats and water voles adapted to aquatic life may have a larger body and a slower life cycle (longer than annual). Our comparative analysis differs from most of the previous studies of mammalian dispersal (reviewed in Lawson Handley & Perrin 2007; Clutton-Brock & Lukas 2011), in that we focus on a smaller taxonomic group of closely related mammals, with relatively similar morphologies, lifestyles and life cycles. Our analysis is also the first attempt, to our knowledge, to quantify patterns and processes of intraspecific variation in a group of closely related species. Intraspecific variation in dispersal has until now been neglected because most approaches of social systems tend to assume that dispersal is a fixed trait. Yet, several studies have pointed out that intraspecific variation can be important in vertebrates (reviewed in Clobert *et al.* 2004; Bowler & Benton 2005), and evidence of social and dispersal plasticity is widespread in small mammals (e.g. Madison 1990; Andreassen *et al.* 2002; Schradin *et al.* 2011).

Dispersal behaviour depends upon external factors (condition dependence) and internal factors (phenotype dependence, see Ims & Hjermann 2001; Bowler & Benton 2005; Clobert *et al.* 2009). Within this framework, Ims & Hjermann (2001) highlighted the importance of the life cycle and developmental mechanisms as determinants of dispersal. In arvicolines, natal dispersal (movement out of the natal area) can occur early in life just after weaning. But natal dispersal can also be delayed for members of seasonal cohorts that do not mature in their year of birth, and breeding dispersal (movement out of the breeding area) can also happen at any time during adult life. Two basic pathways of

condition-dependent and phenotype-dependent dispersal have been recognized (see Fig. 1). First, condition dependence could act primarily in a direct and immediate manner because animals respond flexibly to changes in environmental conditions prior to and during dispersal. Individuals with different phenotypes or belonging to different age, sex classes or cohorts could respond differently to changes in environmental conditions because they may not value the costs and benefits of dispersal in the same way (Clobert *et al.* 2009). Second, environmental conditions may have lagged developmental effects on dispersal behaviour. In arvicolines, we expect in particular that environmental conditions experienced by lactating or gravid mothers translate into specific dispersal behaviours in offspring who make dispersal decision ahead of precocious reproduction (maternal effects, see Ims & Hjermann 2001). In particular, environmental conditions experienced early in life could induce delayed and sustained changes in some phenotypic and life history traits (e.g. body size or behavioural traits) that are strongly correlated with dispersal behaviour. Such dispersal syndromes, i.e. consistent suites of morphological, behavioural and life history traits associated with dispersal, have been found in some birds, fishes and reptiles (reviewed in Clobert *et al.* 2009; Cote *et al.* 2010), but their prevalence in small mammals has not been reviewed before now.

We recorded all published data on natal and breeding dispersal in arvicolines including studies of social dispersal (dispersal out of a natal or breeding group), population dispersal (dispersal out of a natal or breeding patch of habitat) and genetic dispersal (effective dispersal leading to genetic exchanges between two demes). These three types of dispersal all involved the three fundamental stages of departure, transience and settlement (Ims & Yoccoz 1997; Clobert *et al.* 2004, 2009). We gathered information on the methods and context of each study, quantitative information on dispersal fraction (emigration and immigration fractions) and distance (distance travelled between departure and settlement), as well as qualitative data on condition-dependent and phenotype-dependent dispersal. Based on this data set, we critically evaluated current knowledge of patterns and processes of dispersal behaviour during its three different stages, and we identified methodological and conceptual gaps. Our analysis is structured around three major issues. First, we summarize basic information about the ontogeny and behavioural mechanisms of dispersal, and we quantify variation in dispersal within and between species, including information for each sex and age class whenever available and potential correlations with the social system and body mass of the species. Second, we report on all external conditions that trigger dispersal to
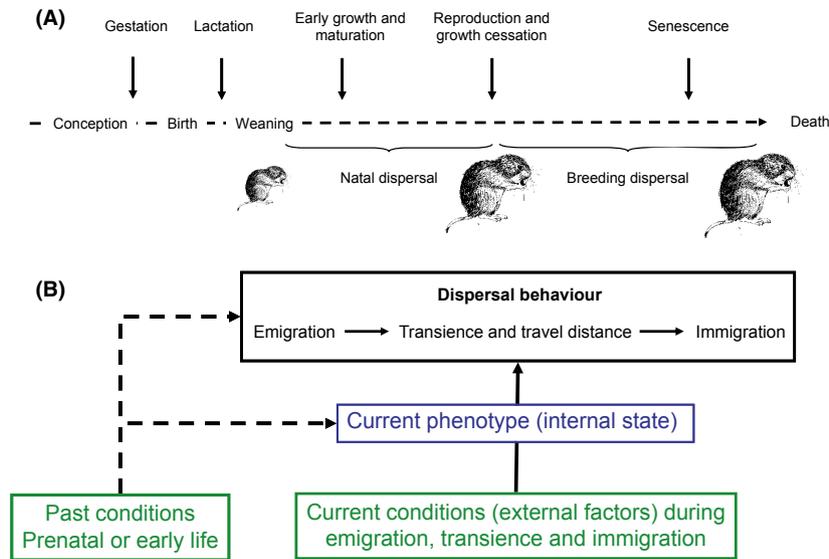
Fig. 1 (A) The life cycle of an arvicoline rodent involves first a gestation and lactation period, followed by a fast growth and sexual maturation period and then by reproduction and growth cessation. In seasonal environments, maturation can occur as early as few days old for most species but can also be delayed until the next breeding season upon condition that individuals survive the harsh winter conditions (see also Box 1). (B) This life cycle implies that the natal and breeding dispersal behaviour can be influenced by both direct (plain arrows) and indirect (dashed arrows) effects of external conditions (condition dependence) and by dependence upon the phenotype (phenotype dependence). Current external conditions during emigration, transience and immigration can have direct effects on natal dispersal behaviour, which usually happens around sexual maturation (age 30–50 days old) and on breeding dispersal (adult life averages a few weeks in most voles and lemmings but can reach several years in muskrats). It is also possible that conditions experienced before conception, during gestation or during lactation have indirect, delayed effects on natal and breeding dispersal. For example, exposure of females to male androgens *in utero* may explain the relationship between natal dispersal and litter sex ratio in two vole species (Lambin 1994a). A relationship between the phenotype (e.g. morphology or life history dispersal syndromes) could also be induced early in life when external conditions have joint effects on dispersal and other phenotypic traits.

identify most relevant proximate factors at each dispersal stage and attempt to separate indirect effects (e.g. maternal effects) from direct effects of each factor (see Fig. 1 for definitions of both effects). We also search for common patterns in phenotype-dependent dispersal to identify the most relevant morphological, behavioural and life history traits associated with dispersal, as well as interactive effects of condition and phenotype on dispersal behaviour. Third, we discuss the potential consequences of reported patterns of dispersal for the population dynamics and genetic structure of arvicoline rodents.

Literature survey

We searched for the literature on dispersal in arvicolines using Web of Knowledge. We separated studies by paper, species and populations as some articles provided information on multiple species and/or study sites ($n = 223$). For each item, we recorded the species name, the study setting (laboratory, semi-natural or natural), the study design (observational or experimental), the method used to quantify dispersal, the spatial scale (maximum distance from edge to edge within the study

area), landscape geometry (continuous, fragmented or mixed landscapes) and the geographic location (continent and country identity, see Appendix S1, Supporting Information for more details). Unavoidably, these studies encompass different definitions and estimates of dispersal (e.g. social or population dispersal). Clutton-Brock & Lukas (2011) discuss some of the difficulties associated with these differences. Here, we did not attempt to separate studies of social and population dispersal because the distinction is not necessarily clear cut in studies of arvicoline rodents.

In addition, quantitative data were extracted from each paper to estimate the emigration fraction (percentage of individuals from a given cohort leaving a patch or a natal environment within a given time duration, calculated as number of emigrants over the total number of individuals conditional on survival, $n = 231$) and immigration fraction (percentage of individuals entering a patch within a given time duration, calculated as number of immigrants over the total number of individuals conditional on survival, $n = 24$). In addition, we extracted data about the mean dispersal distance ($n = 100$), the shape of the dispersal kernels ($n = 20$, probability density function of the dispersal distance)

and the daily movement capacity (estimated in metres per day, $n = 47$). Real-time population genetic approaches can measure instantaneous dispersal by means of parentage or immigration assignment techniques (Paetkau *et al.* 2004). Only five of our direct, quantitative estimates of dispersal were obtained from real-time population genetic approaches (Telfer *et al.* 2003b; Aars *et al.* 2006; Schweizer *et al.* 2007; Gauffre *et al.* 2009; Guivier *et al.* 2011).

We further gathered quantitative data on the standardized genetic differentiation ($n = 63$) and the isolation-by-distance (IBD) patterns ($n = 13$). We noted which molecular marker was used, and we extracted or calculated the standardized genetic differentiation G'_{ST}, from the main text, tables or raw data of each study (Hedrick 2005). We calculated for each population G'_{ST} according to the method and formula in the study of Heller & Siegismund (2009, see Table S1, Supporting information). We also noted whether a significant IBD was found. Genetic dissimilarity and IBD patterns depend importantly on the effective dispersal (i.e. movement of individuals to another group in which they successfully breed) but also on the mutation rate, the effective population size (Rousset 1997; Whitlock 2011) and the demographic and social structure (e.g. for arvicoline rodents, see Aars *et al.* 2006). Hence, these statistics measure only indirectly dispersal; in particular, the high and fluctuating population sizes and the extinction-colonization dynamics of arvicoline rodents greatly influence genetic drift and consequently genetic differentiation, irrespective of dispersal (Aars *et al.* 2006; Berthier *et al.* 2006; Gauffre *et al.* 2008). We therefore did not attempt to estimate dispersal from these indirect genetic approaches; rather, we used them to compare the genetic structure of arvicoline rodents and discuss how dispersal could shape observed patterns. For each quantitative estimate of dispersal and genetic structure, we recorded the mean, the age (adult or juvenile) and sex class, the spatial scale over which the estimate was calculated (in metres), the sample size, the number of demes and, when relevant, the time duration during which the estimate was computed (in days).

These quantitative data were supplemented with qualitative data ($n = 467$), summarizing effects of all external and internal factors of dispersal tested in each study, as well as information on all interactions between factors tested in each study (see the framework in Fig. 1). In most instances, effect sizes were not available, and we therefore decided to note only the sign of the relationship (nonsignificant, negative or positive) between a change in the factor and a change in the 'dispersal metric' (emigration, immigration, dispersal distance, movement capacity or genetic dissimilarity). For each main effect of an external factor, we noted whether

direct and indirect pathways were involved. Effects on emigration and immigration may inform us on factors that affect departure and settlement behaviours, respectively. Effects on the dispersal distances may inform us on factors that affect the transience behaviour. However, most estimates of dispersal were conditional on survival during the transience and settlement stage, except for a small number of direct measurements based on telemetry techniques.

We also gathered information on the mean body mass and dominant social mating system of each species. Body masses were obtained from a database of the late quaternary mammals by Smith *et al.* (2003), except for eight species for which we checked the primary literature. Adult body mass was averaged across males and females and across locations. We further described the dominant social mating systems from spacing patterns in natural populations (Boonstra *et al.* 1987; Heske & Ostfeld 1990) and complemented this with information on the genetic mating system whenever available ($n = 9$ species). We identified three social mating systems: (i) polygyny, (ii) promiscuity and (iii) monogamy or facultative monogamy. Difficulties with such species typology are discussed in Appendix S1 (Supporting Information) and at the end of this review.

We compared patterns of dispersal behaviour across studies and species after having classified species by their mating system and body mass, and studies by their method, temporal and spatial scales and sample size. Analyses were conducted in two different ways. First, we present tallies of qualitative data to compare the strength of evidence for some qualitative patterns (e.g. male-biased dispersal). Second, we analysed quantitative estimates of dispersal with standard linear models. We first used the complete data set to compare emigration fraction and dispersal distance across all species controlling for species-specific and study-specific covariates. These models included a random species effect to control for the fact that multiple data were available for some species and to calculate variation within as well as between species. We implemented these models with the *lme* package in R 2.10.0 following guidelines in Pinheiro & Bates (2000) and tested fixed effects with the ANOVA procedure. We then tested for intraspecific variation in emigration fraction and dispersal distance according to age and sex, using the same statistical procedures as above. For this purpose, we included only data where dispersal was quantified within a given age and/or sex class. Fixed effects of age and sex were tested with the ANOVA procedure. We also compared measures of standardized genetic differentiation (G'_{ST}) across species and studies. We lastly tested for the effects of study-specific factors (type of molecular markers, landscape geometry, number of demes and

spatial scale) and of species-specific factor (body mass and social mating system) using the same statistical approach as outlined above.

General patterns of dispersal in arvicolines

Dispersal behaviour: ontogeny, transience and settlement

Quite surprisingly, we still know little about how dispersal behaviour changes throughout an individual's life. In arvicoline rodents, a relationship between the timing of natal departure and the onset of reproduction has been found, suggesting that natal dispersal is part of a life history decision associated with sexual maturation (see Box 1 for an overview). In studies that investigated cohorts of offspring born early in the breeding season, it was found that the age of natal dispersal matches the age of sexual maturation for meadow voles and root voles (as young as approximately 25–45 days old, see Bollinger *et al.* 1993; Andreassen & Ims 2001; Le Galliard *et al.* 2007), that natal dispersal is concomitant with mating and first reproduction in female *Microtus arvalis* (Boyce & Boyce 1988) and that individuals engage in longer movements typical of dispersal around sexual maturity in grey-sided voles (Saitoh 1995). A tentative proximate explanation could be that neuroendocrine mechanisms controlling the development of sexual behaviours, such as maturation and pair bonding, also mediate variation in natal dispersal behaviour (e.g. Solomon *et al.* 2009). Unfortunately, the neuroendocrine basis of natal dispersal has not been investigated, and field studies have yet to identify developmental mechanisms controlling dispersal behaviour.

Events of breeding dispersal by females and by males may also be associated with reproductive activities (Stoddart 1970; Kawata 1989; Lambin 1997; Rajska-Jurgiel 2000), but the mechanisms and timing of breeding movements have been generally very poorly investigated. Using our qualitative data, we found that studies most often reported that dispersal is less frequent in adults than in juveniles or subadults [age effect, stronger dispersal in adults: six studies, stronger dispersal in juveniles or subadults: 30, balanced dispersal (no detectable age difference): 10] and suggested that adults may disperse longer distances than juveniles. Our quantitative estimates of emigration fractions and dispersal distances found no detectable differences between age classes (emigration fraction: $F_{1,130} = 2.72$, $P = 0.10$, $n = 148$; dispersal distance: $F_{1,52} = 0.0002$, $P = 0.99$, $n = 69$). Thus, age differences in dispersal are ambiguous.

In actively dispersing animals, the transience and settlement stages involve a variety of behavioural strategies leading to habitat selection by dispersers. These stages are the least studied processes of dispersal in arvicolines, and the required continuous monitoring of individuals in their landscape has been carried out satisfactorily so far in only two vole species. In root voles, the transient behaviour of natal dispersers involves 1–3 weeks of active exploration where individuals move between patches on a daily basis (Le Galliard & Rémy, personal observation), and settlement in one patch is often the end result of multiple unsuccessful moves into other, more attractive patches (Le Galliard *et al.* 2007; Rémy *et al.* 2011). In the same species, adult males use a very different exploration strategy that involves brief but long-distance movements followed directly by settlement (Steen 1994). Tracking water voles

---

**Box 1 Life history plasticity and natal dispersal strategies in arvicoline rodents**

Arvicoline rodents display a very well-documented life history continuum from precocial sexual maturation (as early as 15–25 days old) and fast body growth to delayed maturation until the next breeding season and slower body growth (Lambin & Yoccoz 2001). In addition, arvicolines have a multivoltine life cycle and can produce up to 8 litters per year (Ergon *et al.* 2001). Variation along the precocial-delayed axis of sexual maturation is observed among muskrats and aquatic water voles characterized by maturation at the age of several months, and among most precocial species of voles and lemmings. The same life history variation occurs between early cohorts of offspring born at the beginning of the breeding season that mature during their birth year and late cohorts of offspring that postpone reproduction until the next breeding season (Lambin & Yoccoz 2001). This life history variation may contribute to variation in dispersal behaviour between and within species. In precocial species, the season of birth determines the benefits of early maturation and therefore of natal dispersal. Thus, natal dispersal decreases seasonally (Table 1), and conditions experienced during the breeding season are likely to be important for the natal dispersal decisions of early cohorts, while late cohorts postpone their dispersal until the next year (e.g. Lambin 1994b). In addition, natal dispersal is more constrained by time and competition with adults in fast- than in slow-maturing cohorts and species (Ims & Hjermann 2001). Fast-maturing dispersers may cue preferentially on conditions experienced by their mother or early in life because these conditions predict well conditions experienced as adults. Slow-maturing individuals have more time to sample their environment and could disperse longer distances but also experience substantial mortality costs. Hence, age at sexual maturation may contribute to explain both intraspecific and interspecific patterns of natal dispersal in microtine rodents and other mammals.

---

over much larger spatial scales in their natural environment, Fisher *et al.* (2009) observed that the transient dispersal behaviour of dispersers lasted for several days and involved long-distance movements of several hundreds of metres. Several animals used a 'stepping-stone' trajectory where voles successively stopped for several days in one patch and then moved to another patch until they settled down (Fisher *et al.* 2009).

Dispersal distances

One of the most consistent patterns was a nonuniform dispersal kernel with more short-distance than long-distance dispersal events (34 significant tests of 42 studies of distance-limited dispersal). A total of 13 (of 13) demographic studies reported a decreasing fraction of emigrants with distance to the settlement patch, and eight (of 8) demographic studies found support for a decreasing fraction of immigrants with dispersal distance from the source patch. Despite this observation, only 16 of 24 genetic studies found significant genetic IBD patterns. Yet, genetic IBD patterns may not necessarily be observed even if dispersal is actually restricted in space (Rousset 1997; Leblois *et al.* 2004; Guillot *et al.* 2009). In microtine rodents, the cause of no observation of a genetic IBD is not always clear but is attributed to migration–drift disequilibrium in two instances (Ehrich & Stenseth 2001; Francl *et al.* 2008), to dispersal barriers in one instance (Ratkiewicz & Borkowska 2006), to large effective population size in one case (Guivier *et al.* 2011) and to substantial, long-distance dispersal in three other studies (Ehrich *et al.* 2001; Redeker *et al.* 2006; Schweizer *et al.* 2007). In general, this demonstrates the difficulty of inferring directly distance-limited dispersal from spatial patterns of genetic variation.

Direct estimates of dispersal distances provided strong evidence for a fat-tailed, right-skewed dispersal kernel (17 of 19 studies of the shape of the kernel). However, a clear limitation of current studies is that only two corrected for lower capture rates of dispersers with distance (Watts 1970; Telfer *et al.* 2003b) and only two reported formal statistical tests of the shape of the dispersal kernel. Lambin (1994b) found that dispersal distances were skewed to the right in juvenile Townsend voles but did not follow a geometric distribution. Telfer *et al.* (2003a) found that dispersal distances of juvenile water voles could be approximated by a negative exponential distribution (Fig. 2A). Thus, more studies are needed if empirical kernels are to be compared or used in simulation studies. Long-distance movements are understudied, while determinants of short-distance dispersal have been thoroughly investigated (see next section).
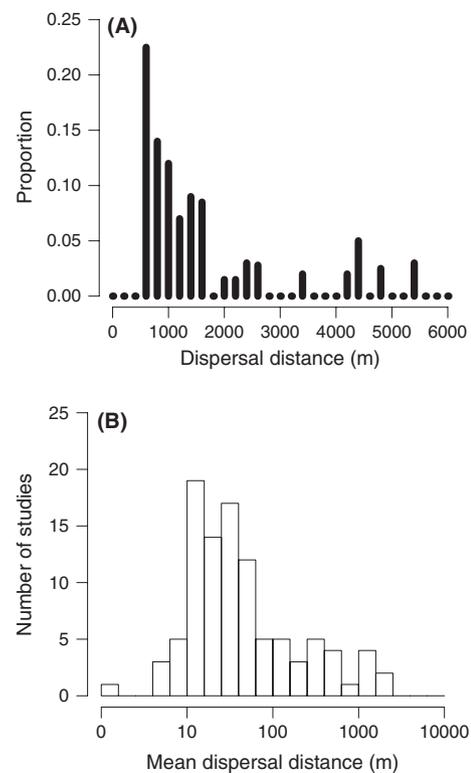
Fig. 2 General patterns of dispersal in arvicoline rodents. (A) Dispersal kernel in the water vole *Arvicola terrestris* from Scotland metapopulations. One of the best available estimate of a dispersal kernel was obtained by Telfer *et al.* (2003b). Dispersal distances were obtained by a combination of mark–recapture and genetic assignment methods accounting for unequal capture rates at the edges of the populations. The observed kernel fitted well to a negative exponential distribution with a mean of 1.8 km. (B) Average dispersal distances reported in the whole literature for arvicoline rodents (*n* = 100). Most estimates suggest relatively short-distance dispersal in these species of the order of a few 10 m although a tail of long-distance dispersal events was observed across species. Panel A was modified from Telfer *et al.* 2003b ©Molecular Ecology.

Estimates of the average dispersal distance ranged from a few metres in an enclosure study to more than 2 km in a metapopulation study (mean = 163 m, median = 31 m, see Fig. 2B). Dispersal distances were of the same order of magnitude as daily movement capacities calculated for the same species (mean = 68.2 m/day, median = 21 m/day). Thus, arvicolines are generally reported to be dispersing short distances well below what they are capable of. For instance, Steen (1995) recorded movements averaging 700–800 m per night in male root voles equipped with radio-transmitters in a natural population, while the mean dispersal distance for this species is only 167 m (note however that many of the distance estimates were from small-scale enclosure studies where the maximum possible dispersal distance was below 100 m). We compared estimates of

dispersal distances across studies and species, which demonstrated significant fixed effects of the method and spatial scale of the study and a significant random effect of the species identity (mixed-effect model after log transformation to ensure normality, method: $F_{3,79} = 3.01$, $P = 0.03$; spatial scale: $F_{1,79} = 34.6$, $P < 0.0001$; species identity(random): $\chi^2 = 46.4$, d.f. = 1, $P < 0.0001$). Not surprisingly, the mean dispersal distance in a study increases with the spatial scale of the study, and, after correcting for this effect, distance estimates were higher when dispersal was assessed by telemetry than by mark–recapture, removal grid or real-time genetic methods, which were undistinguishable. Interspecific differences in dispersal distances could not be explained by body mass ($F_{1,12} = 0.31$, $P = 0.59$) or by the social mating system ($F_{2,11} = 1.15$, $P = 0.35$).

Sex differences in dispersal

Previous reviews of mammalian dispersal have emphasized the strong link between sex-biased dispersal and mating systems (Greenwood 1980; Boonstra *et al.* 1987; Lawson Handley & Perrin 2007; Clutton-Brock & Lukas 2011). A high male bias in dispersal is expected to evolve in female-defence polygynous mating systems, which stems from the combined effects of inbreeding avoidance and of sexual differences in local mate and resource competition (Lawson Handley & Perrin 2007). Preferential cooperation among female kin and female mate choice for immigrants could strengthen the male bias in dispersal in social mammals. In monogamous species, which is observed less frequently in mammals, sexual asymmetries are weaker and dispersal is predicted to be more balanced (Greenwood 1980). To test this scenario, Boonstra *et al.* (1987) examined sex-biased natal philopatry and natal dispersal distances in five species of voles ranging from monogamous to polygynous mating systems and all studied through the same mark–recapture protocol (including grid size). They found female-biased philopatry in all species but male-biased dispersal distances only in polygynous species, supporting the contention that the mating system is a determinant of sex-biased dispersal in voles.

Our overview of sexual differences in dispersal in a larger sample of studies confirmed the male-biased pattern identified by Boonstra *et al.* (1987) but failed to support their relationship with the mating system. Dispersal was male-biased in most species, especially for emigration and immigration fractions, although as many as 45% of the statistical comparisons between sexes were not significant (sex effect on emigration, significant male bias: 44 tests, balanced: 32 tests; immigration, male-biased: five tests, balanced: seven tests; dispersal distance, male-biased: five tests, balanced: 12 tests, female-biased: one test; movement capacity, male-biased: nine tests, balanced: one test). A significant female-biased dispersal was found only for natal dispersal distances in the water vole in two different habitat types (Telfer *et al.* 2003b; Aars *et al.* 2006). In addition, and contrary to standard predictions, male-biased dispersal was not more often detected in polygynous or promiscuous than in monogamous mating systems (Fisher's exact test of independence, $P = 0.41$). The absence of a relationship between male-biased dispersal and the mating system must, however, be interpreted with caution because of the small number of species included in the comparison and the difficulties with classifying mating systems (see Appendix S1, Supporting Information).

Our quantitative estimates of sex-biased dispersal yielded a rather similar picture. Dispersal distances corrected for differences between studies and species (see section on 'Dispersal distances' above) were significantly longer in males ($F_{1,57} = 7.42$, $P = 0.008$, $n = 75$; females: mean = 114.3 m, males: mean = 149.5 m). Emigration fractions (median = 0.21, $n = 231$) was influenced by the study method (more emigration was recorded with the removal grid method, see Appendix S1, Supporting Information) and by a negative effect of the time duration during which emigration was calculated, but not by the spatial scale of the study (mixed-effect model after square root transformation to ensure normality; method: $F_{4,184} = 2.38$, $P = 0.05$; duration: $F_{1,184} = 14.4$, $P < 0.001$). After controlling for these methodological effects, emigration fraction varied more within than between species [species identity (random): $\chi^2 = 1.95$, d.f. = 1, $P = 0.16$], and when comparing sexes, emigration fraction was significantly higher for males ($F_{1,111} = 11.75$, $P < 0.001$, $n = 128$). However, we could not find effects of mating system on these sexual differences in dispersal distances and emigration fractions (interaction sex × social mating system, dispersal distance: $F_{2,55} = 0.62$, $P = 0.54$; emigration fraction: $F_{2,109} = 1.67$, $P = 0.19$).

On the other hand, several studies suggested that sex-biased dispersal could depend on other factors, such as age class or spatial scale. For example, a stronger male bias was found for adult dispersal compared to dispersal of juveniles (13 of 15 studies). This means that breeding dispersal appears to be more strongly male-biased than natal dispersal in several arvicolines. Gauffre *et al.* (2009) further reported male-biased dispersal at short spatial scales between neighbouring colonies (around 15–600 m) but no sex bias in dispersal between patches of habitat (around 2–23 km). Other field studies have, on the contrary, emphasized that long-distance dispersal is typical of males in polygynous species (Steen 1994).

Processes of dispersal in arvicolines

Condition-dependent dispersal

Strong evidence of condition dependence in dispersal behaviour is apparent in arvicolines (see Table 1). Clear effects of landscape features are seen, including substantial increases in dispersal fractions with landscape connectivity (presence of habitat connection between patches) and matrix quality. Movement capacities are also influenced by small-scale features of the environment, such as habitat gaps and boundaries (e.g. Andreassen *et al.* 1998a and references therein). Effects of habitat fragmentation, defined as the process during which a large expanse of habitat is transformed into a

Table 1 Patterns of condition-dependent dispersal in arvicoline rodents

Factor category	External factor	Sign of the relationship with movement capacity and dispersal fraction (emigration or immigration) or distance
Landscape features	Connectivity	Positive effect on movement capacity ($n = 2$), emigration fraction ($n = 9$) and dispersal distance ($n = 1$)
	Fragmentation	No effect on movement capacity ($n = 1$)
		Positive effect ($n = 2$) and negative effect ($n = 6$) on emigration fraction
		Positive effect on dispersal distance ($n = 1$)
	Corridor width	Intermediate corridor width increases movement capacity ($n = 2$)
	Landscape matrix	Low matrix quality and presence of dispersal barriers decrease emigration fraction ($n = 4$)
	Patch area	Negative effect on emigration fraction ($n = 1$)
	Patch shape	No effect of the edge-to-surface ratio on movement capacity ($n = 1$) and emigration fraction ($n = 3$)
Habitat quality features	Vegetation quality	Decreases ($n = 13$), increases ($n = 2$) or has no effect ($n = 2$) on emigration fraction
		Increases ($n = 7$) or has no effect ($n = 2$) on immigration fraction
	Habitat destruction	Increases emigration fraction ($n = 1$)
	Predation risk	No effect of simulated predation risk on movement capacity ($n = 1$) and emigration fraction ($n = 1$)
	Food availability	Decreases emigration fraction ($n = 4$), increases immigration fraction ($n = 1$), no effect on emigration ($n = 2$)
		Prolonged infant malnutrition increases emigration fraction later in life ($n = 1$)
	Site familiarity	Decreases movement capacity ($n = 1$) and increases immigration fraction ($n = 1$)
Social features	Population density	Positive density dependence ($n = 5$), negative density dependence ($n = 23$), no effect ($n = 16$) on emigration
		Negative density dependence ($n = 5$), no effect ($n = 7$) on immigration
	Population sex ratio	No effect on emigration fraction ($n = 4$)
	Population growth	Emigration fraction stronger in growing populations ($n = 2$)
	Population stress	More immigration into populations of testosterone implanted females ($n = 1$)
	Conspecifics and relatives	Presence of adult female increases natal emigration and decreases natal immigration by females ($n = 2$), no effect ($n = 1$)
		Presence of opposite sex increases immigration ($n = 3$), presence of same sex decreases immigration ($n = 3$)
		Presence of relatives increases emigration ($n = 6$), decreases emigration ($n = 4$), no effect ($n = 6$)
Maternal effects	Maternal factors	Significant family effects on emigration fraction ($n = 2$) and movement capacity ($n = 4$)
		No significant family effects on movement capacity ($n = 2$)
		No effect of maternal body mass and size on emigration fraction ($n = 2$)
	Food availability	No effect of maternal malnutrition during lactation on emigration fraction ($n = 2$)
	Maternal stress	No effect of maternal stress on emigration fraction ($n = 1$) and dispersal distance ($n = 1$)
	Litter characteristics	Litter sex ratio (percentage males) increases emigration fraction ($n = 3$)
		Litter sex ratio has no effect on emigration fraction ($n = 3$) and dispersal distance ($n = 2$)
		Litter size reduces emigration fraction ($n = 1$) or has no effect on emigration ($n = 4$) and dispersal distance ($n = 1$)

Sample size refers to the number of studies.

number of smaller patches, were not consistent (Table 1). Fine-grained habitat fragmentation (i.e. around the scale of individual home ranges) typically increases interpatch movements within home ranges. Indeed, fragmentation of a large habitat patch into several small patches may lead to an expansion of space use because of breeding and foraging requirements, and thus fragmentation can increase interpatch movements at short spatial scales (approximately 10–20 m), although this is not dispersal *sensu stricto* (Ims *et al.* 1993; Andreassen *et al.* 1998b). In landscapes including larger patches and longer interpatch distances (>50– 100 m) where interpatch movements could elicit dispersal, the departure stage of dispersal is generally negatively affected in more fragmented habitats (e.g. Diffendorfer *et al.* 1995). Interpatch distances and landscape geometry are also important determinants of a successful transience because dispersers are at risks of avian and mammalian predation (Ims & Andreassen 2000; Andreassen & Ims 2001; Lambin *et al.* 2004; Smith & Batzli 2006).

Habitat quality and familiarity with the home site are strong determinants of dispersal (Table 1). Features associated with high habitat quality include high vegetation cover and vegetation height, high plant forage quality or the availability of seeds. In most instances, individuals emigrate less from and immigrate more into high-quality habitat patches, which leads to an unequal spatial distribution along habitat quality gradients that can approach an ideal free distribution (Morris & MacEachern 2010). However, in two separate studies, individuals dispersed preferentially from high-quality to low-quality patches (Mazurkiewicz & Rajska 1975; Peles & Barrett 1996), which may be due to competitive exclusion of dispersers by dominant residents. The interaction between habitat quality and competitive exclusion was investigated in detail by Lin and Batzli in field experiments with prairie and meadow voles (Lin & Batzli 2001a,b, 2002). Meadow and prairie voles both preferred high-quality patches but meadow voles were more sensitive to habitat quality and dispersed more frequently than prairie voles. In the presence of meadow voles, the subdominant prairie voles dispersed into lower quality habitats, which resulted in some degree of habitat segregation between the two species. These experiments exemplify how differences in dispersal behaviour can lead to differential habitat choice and competitive exclusion between two sympatric rodents.

A wide range of social factors also influence dispersal fractions (Table 1). Competition with conspecifics should result in enhanced emigration, but most studies indicate that emigration is negatively density-dependent (23 out of 44 tests) or density-independent (16 tests). Negative density-dependent emigration was found in numerous comparisons between low and high densities within or across seasons. Such analyses confound density variation with temporal variation in food or climate conditions and prospects for reproduction early in life (Box 1, but see Andreassen & Ims 2001). A higher dispersal is often observed during the onset of breeding season and the early summer (e.g. Beacham 1979; Rajska-Jurgiel 1992; McGuire *et al.* 1993), and some controlled experiments suggest that this is partly related to seasonal cohort effects, independent from density fluctuations (Le Galliard *et al.* 2007; Hoset *et al.* 2008). Yet, negative density-dependent emigration was also detected using well-designed experiments (e.g. Fortier & Tamarin 1998; Lucia *et al.* 2008), and five studies of 12 have reached the conclusion that immigration is severely reduced at high population densities (e.g. Gundersen *et al.* 2002; Jacquot & Solomon 2004). On the other hand, some convincing evidence of positive density-dependent dispersal does exist (Saitoh 1995; Aars & Ims 2000; Gundersen *et al.* 2001). One way to reconcile these contradictory observations is to assume that selection promotes dispersal from locally high-density to low-density patches, but that the costs of transience and settlement are often higher at high regional population densities, leading to a strong reduction in dispersal movements in dense populations (Solomon 2003). This idea was first proposed under the framework of the 'social fence hypothesis' (Hestbeck 1982). Experimental studies with root voles found that density-dependent dispersal proceeds in this manner at small spatial scales (Aars & Ims 2000; Andreassen & Ims 2001; Gundersen *et al.* 2001).

In addition to the avoidance of competition with conspecifics, dispersal may be involved in mate searching, inbreeding avoidance and the avoidance of kin competition. Studies that have examined social factors in more detail support this multideterminism of natal dispersal, especially for emigration at small spatial scales (Table 1). Young female root voles and Townsend's voles are likely to emigrate through competition with adult females and are attracted by unrelated males (Lambin 1994b; Gundersen & Andreassen 1998; Gundersen *et al.* 1999; Le Galliard *et al.* 2003), while mate searching is a component of breeding dispersal in prairie voles and water voles (McShea 1990; Lambin *et al.* in press). Avoidance of same-sex individuals is also observed, mainly because of resource competition among females and mate competition among males (Table 1). The effects of kin selection on emigration vary between species. In the monogamous and communal breeding prairie voles, good evidence exists for joint effects of inbreeding avoidance and kin cooperation. Emigration from a natal group is more common when mates within a communal group

are related and opposite sex siblings tend to avoid each other (McGuire *et al.* 1993; Getz *et al.* 1994). On the other hand, natal philopatry is reduced when parents disappear or when groups are composed of unrelated individuals, and same-sex siblings tend to affiliate with each other (Getz *et al.* 1994; McGuire & Lowell 1995). In Townsend's voles, inbreeding avoidance is also involved because males are more likely to emigrate and disperse longer distances when a mother or a littermate is present in the natal range (Lambin 1994b), which is not the case in grey-sided voles (Ims & Andreassen 1991; Ishibashi & Saitoh 2008) and root voles (Le Galliard *et al.* 2006, 2007). We generally lack evidence that local competition among relatives is an important determinant of natal dispersal (Table 1).

Local kin associations are seen regularly among philopatric individuals, especially matrilineal clusters of females, and kin facilitation is considered as a potential benefit of philopatry because related females breeding in close proximity may benefit in terms of territory acquisition and juvenile survival (see Lambin 1994c; Lambin & Yoccoz 1998; Lambin *et al.* 2001). However, apart for communally breeding prairie voles, there is no firm evidence that siblings choose preferentially to associate with relatives rather than to emigrate from the natal group when opportunities for independent reproduction are available (Kawata 1987; Lambin 1994c; Le Galliard *et al.* 2006, 2007). One explanation for the occurrence of female kin clusters in noncommunal species is instead that young related females associate preferentially when strong constraints on dispersal make kin clusters of females a 'best of a bad job' solution (facultative philopatry sensu Solomon 2003). This hypothesis remains to be tested.

Condition dependence can occur through a direct behavioural response to current conditions or may involve delayed responses via the life history (see Fig. 1). Most studies conducted so far have tended to support the hypothesis of a direct pathway (277 of 297 tests). An indirect, delayed pathway was assumed only in two different contexts. First, maternal effects on emigration and movement capacities were hypothesized but found in less than one-third of the tests (10 of 29 tests, see Table 1). Maternal effects are still poorly understood, and some manipulative studies did not find effects of conditions experienced *in utero* or during gestation or lactation (Bondrup-Nielsen 1992; Lambin 1994a; Rémy *et al.* 2011). Second, it has been demonstrated once that a prolonged malnutrition early in life can increase natal dispersal later in life (Bondrup-Nielsen 1993). This indirect pathway involving scope for delayed life history effects of early-life conditions should be investigated in more detail.

Phenotype-dependent dispersal and dispersal syndromes

The relationship between phenotypic traits and dispersal abilities was examined in a few vole species. Many studies suggest that dispersers are often not a random subset of the population, yet the relationship between phenotypic traits and dispersal varies between studies (see Table 2). Regarding behavioural traits, dispersers are often more active and more thorough explorers than residents in arvicolines reviewed here (nine positive tests of 11). In addition, some inconsistent life history differences between dispersers and residents were detected (Table 2). Ebenhard (1990) predicted from life history theory and observed in an island population that a colonization strategy is associated with a faster growth and larger reproductive effort, but this prediction has not been held up by more recent studies. The support for a genetic basis of observed differences between dispersers and residents is also generally weak (Table 2). Earlier studies have found differences in allozyme diversity between dispersers and residents that could reflect functional differences. These results are difficult to interpret (Pugh & Tamarin 1991) but could fruitfully be revised in the light of recent work showing association between dispersal and enzyme variants in butterflies (Hanski *et al.* 2004). We therefore urge for the use of modern genetic tools to investigate in more detail the genetic architecture of dispersal and dispersal-related traits in arvicolines. These studies should identify whether genetic differences are associated with behavioural differences in dispersal behaviour rather than ability to survive dispersal (Selonen & Hanski 2010).

Interaction between phenotype- and condition-dependent dispersal

Of 157 studies that examined the joint effects of external and internal factors, 118 tested for interactive effects and 63 reported a significant interaction between external and internal factors. Most of these involved sexual differences in condition dependence (45 cases). For instance, females are more sensitive to habitat fragmentation and population density than males (Fortier & Tamarin 1998; Aars *et al.* 1999; Aars & Ims 2000), and sexes often differ in their sensitivity to other social factors (Table 1). A further five studies showed differences in condition dependence between age classes, in particular stronger effects of social factors and habitat quality on natal dispersal by juveniles (Lofgren *et al.* 1996; Andreassen & Ims 2001). These results are quite expected because sexes and age classes differ in their competitive ability and limiting resources. Other cases involved

Table 2 Patterns of phenotype-dependent dispersal in arvicoline rodents. For each category of phenotypic trait, we list the identity of the trait and describe the difference observed between dispersing and nondispersing (resident) individuals

Trait category	Trait identity	Differences between dispersers and residents
Morphology	Body condition	No differences in body condition ($n = 2$)
	Body size	Larger body size in dispersers ($n = 6$)
		Smaller body size in dispersers ($n = 4$)
		No differences ($n = 18$)
Behaviour	Activity	Dispersers more active than residents ($n = 4$)
		No differences in activity ($n = 2$)
	Exploration	Dispersers more explorer than residents ($n = 5$)
		No differences in exploration ($n = 1$)
	Social interactions	Dispersers more aggressive/dominant than residents ($n = 4$)
		Dispersers less dominant than residents ($n = 1$)
		Dispersers less social than residents ($n = 1$)
		Dispersers more social than residents ($n = 1$)
Life history	Size at birth	No differences ($n = 1$)
	Body growth	Dispersers have faster juvenile growth ($n = 1$)
		Dispersers have slower adult growth ($n = 1$)
	Age and size at maturation	Dispersers mature earlier ($n = 2$)
		Dispersers mature later ($n = 1$)
		Dispersers mature at a smaller body size ($n = 1$)
	Reproductive effort	Dispersers make a stronger reproductive effort ($n = 1$)
		No differences ($n = 1$)
Genetic	Allozyme	Dispersers differ from residents for allozymes ($n = 7$)
	Coloration	Dispersers exhibit different forehead blaze patterns ($n = 1$)
	Genetic strain	A strain disperses longer distances than another ($n = 1$)
		No differences ($n = 4$)

Sample size refers to the number of studies by species combination reporting a given relationship.

individual differences in behaviour ($n = 4$ of 4 tests), body size or condition ($n = 4$ of 8 tests) and genotypes ($n = 5$ of 7 tests) but could not provide clear explanations. Interactions involving body mass and condition are important to consider because size is relevant to social dominance and territorial defence in small rodents. Rémy *et al.* (2011) manipulated jointly habitat quality and the body size of juveniles to test the idea that dispersers in better physical condition are more successful at settling in high-quality habitats but found no interactive effects on natal dispersal.

Consequences for population dynamics and genetic structure

Dispersal and population dynamics in arvicolines

Arvicolines have violent and often distinctly cyclic population dynamics. Some early hypotheses regarded dispersal as potential cycle driving mechanism (reviewed in Stenseth & Lidicker 1992). Lessons from analytical models have shown that cycle arises in the presence of both direct and delayed density dependence (Stenseth 1999). The lack of strong evidence for delayed pathways for condition-dependent dispersal in the literature indicates that dispersal as such is not likely to be responsible for multiannual cycles. It remains that dispersal is a key demographic process because it is involved in the metapopulation dynamics.

A first major issue is distance-limited dispersal and colonization. Many studies indicate that interpatch distances and habitat quality between patches can severely constrain dispersal and colonization within distances of hundreds of metres and several kilometres (Crone *et al.* 2001; Witt & Huntly 2001; Pita *et al.* 2007; do Rosario & Mathias 2007). For example, colonization of patches separated by <15 km depends on relative isolation and the presence of forest in muskrats (Schooley & Branch 2009). An exception to this rule is the existence of extensive natal dispersal over several hundreds of metres in

tightly connected fragmented populations of water voles (reviewed in Lambin *et al.* 2004). Despite good evidence for distance-limited dispersal in all species at spatial scales ranging from 100 to 1000 m (see Fig. 2), demographic effects of habitat fragmentation were modest in five independent experimental studies (La Polla & Barrett 1993; Diffendorfer *et al.* 1995; Wolff *et al.* 1997; Davis-Born & Wolff 2000; Andreassen & Ims 2001). This result must however be interpreted with caution because most experiments were conducted at short spatial scales (approximately 50–100 m) relative to the dispersal capacity of microtine rodents and lasted only for one breeding season, while some demographic effects are only seen after several years of fragmentation (Robinson *et al.* 1992). Distance-limited dispersal has also consequences for spatial population synchrony and range expansion. Getz *et al.* (1978) and Lambin *et al.* (1998) reported demographic expansions moving at a mean speed of several kilometres per year in two vole populations. Interestingly, this fast spread at the demographic level is compatible with a relatively poor dispersal capacity at the individual level because demographic processes arise by contagion from nearest neighbour movements and several generations disperse each year (Sherratt *et al.* 2000).

A second major issue in arvicolines is density dependence given that population densities vary importantly between years and seasons in voles and lemmings and that density-dependent dispersal can contribute to these variations. Experimental studies conducted at short spatial scales with root voles indicate that negative density-dependent dispersal can quickly smooth out spatial differences in population densities (Aars & Ims 2000) and precludes the synchronizing effects of dispersal (Ims & Andreassen 2005). Density-dependent dispersal is also likely to interact with other demographic parameters, and such interactive effects are usually not included in population models. Specifically, dispersal may enhance mortality rates owing to increased exposure to avian predators (Aars *et al.* 1999). Ims & Andreassen (2000) showed that negative density- and population growth-dependent dispersal acted to enhance summer declines in fragmented root vole populations. Thus, although dispersal does not drive population cycles, it may affect the trajectory of the cycles by deepening the crash phase and binding low-phase populations into more connected networks (Lambin *et al.* 2004).

The last issue is whether some aspects of condition- and phenotype-dependent dispersal can influence population dynamics. Only a handful of empirical studies have addressed this issue. A first interesting possibility is that condition-dependent dispersal can increase demographic resilience to habitat fragmentation. For example, Lambin *et al.* (2004) observed that juvenile water voles

disperse over long distances to target mates and pointed out that this form of dispersal is efficient at buffering sex ratio variation among patches. On the other hand, non-random dispersal could destabilize population dynamics. In small fragmented patches of habitats, Andreassen & Ims (2001) observed that emigration contributed disproportionately more to extinction risk than birth and death. Similarly, Crone *et al.* (2001) detected increased dispersal in response to habitat degradation, which can precipitate local extinction. Immigration by the territorial sex can also have destabilizing effects on the social organization of residents. Frequent turnover of adult male root voles was associated with higher female mortality, especially when these females were overlapping, but also with higher rates of infanticide and therefore a lower population growth (Andreassen & Gundersen 2006).

Dispersal and genetic structure in arvicolines

The spatial genetic structure and relationship with dispersal are summarized in Table 3 for the best studied arvicoline species. Common patterns observed across these species include a significant genetic differentiation even at small spatial scales, cases of genetic isolation by distance even at spatial scales of a few hundred metres or kilometres, genetic clusters that extend typically over a few kilometres and the existence of local kin structures among females in two species. There are, however, also some intraspecific variation in genetic structure (Table 3). In particular, the fluctuating population dynamics of some arvicoline rodents may influence genetic differentiation. In fossorial water voles, Berthier *et al.* (2006) documented a change from a high genetic differentiation and low isolation by distance during the low year to a low genetic differentiation but stronger isolation by distance during the peak year. The existence of contrasted genetic differentiation within the same population owing to age or sex structure or to fluctuating population dynamics altogether suggests that sampling consideration could account for the observed variability, which calls for caution when interpreting differences across studies.

In addition, differences in the genetic structure of a given species could be attributed to variation in demographic processes and flexible dispersal strategies. In particular, we reported above on clear demonstrations of negative density-dependent dispersal, which suggests that differences in population densities or dynamics should influence genetic differentiation. Berthier *et al.* (2005) revealed genetic discontinuities between areas with contrasting density in fossorial water voles, but only one study compared spatial genetic differentiation across different population dynamics. Ehrich *et al.* (2009) found for cyclically fluctuating *Myodes* popula-

Table 3 Spatial genetic structure and inferences on dispersal patterns within wild populations of arvicoline rodents

Species identity	Study location and scale	Genetic marker	Reported patterns	References
Microtus arvalis	Europe (1600 km, 8 pops)	mtDNA	High genetic differentiation for mtDNA	Heckel et al. (2005)
	Switzerland (200 km, 5 pops)	microsatellites	Moderate genetic differentiation for microsatellites Significant genetic isolation by distance for both markers Male-biased dispersal	Hamilton et al. (2005)
	Poland (18 km, 8 sites)	Microsatellites	Low, significant genetic differentiation No significant genetic isolation by distance Genetic maps reveal a potential barrier to dispersal	Ratkiewicz & Borkowska (2006)
	France (30 km, 193 sites)	Microsatellites	Significant genetic isolation by distance Significant genetic correlations below 2–3 km Indirect dispersal distance of 88 m	Gauffre et al. (2008)
	France (24 km, 10 sites)	Microsatellites	Significant relatedness in females below 100–200 m Significant male-biased dispersal at a local scale No sex-biased dispersal at a global scale	Gauffre et al. (2009)
Microtus californicus	USA (5 km, 7 sites)	Microsatellites mtDNA	Significant genetic isolation by distance Weak genetic correlations Indirect dispersal distance between 10 and 24 m	Adams & Hadly (2010)
	USA (5 km, 11 sites)	Microsatellites mtDNA	Moderate genetic differentiation Significant genetic isolation by distance	Neuwald (2010)
Myodes glareolus	Norway (256 km, 31 sites)	mtDNA	Moderate genetic differentiation Significant genetic isolation by distance Significant genetic correlations below 5 km	Stacy et al. (1997)
	Norway (10 km, 31 sites)	mtDNA	Significant genetic isolation by distance Significant genetic correlations below 2 km	Aars et al. (1998)
	Denmark (10 km, 5 sites)	Microsatellites	Low, significant genetic differentiation No significant genetic isolation by distance	Redeker et al. (2006)
	France (80 km, 10 sites)	Microsatellites	Low, significant genetic differentiation Significant isolation by distance in hedge networks No significant isolation by distance in forests Significant relatedness at scales below 100–200 m	Guivier et al. (2011)
Myodes rufocanus	Japan (100 m, 1 pop)	mtDNA	Matrilineal kin structures in spring Genetic isolation by distance in females	Ishibashi et al. (1997)
	Japan (300 m, 1 pop)	Microsatellites	Maternal families in winter	Ishibashi et al. (1998)
	Japan (300 m, 1 pop)	Microsatellites	Male-biased social dispersal	Ishibashi & Saitoh (2008)

Table 3 *Continued*

Species identity	Study location and scale	Genetic marker	Reported patterns	References
Arvicola terrestris	Scotland (25 km, 9 inland sites)	Microsatellites	Low-to-moderate genetic differentiation	Stewart *et al.* (1999)
			Significant genetic isolation by distance	
	Scotland (6 km, 15 islands)	Microsatellites	High genetic differentiation	Telfer *et al.* (2003a)
	Scotland (10 km, 5 metapopulations)	Microsatellites	Moderate genetic differentiation in juveniles	Aars *et al.* (2006)
			Low genetic differentiation in adults	
			Significant genetic correlations below 3 km	
	France (163 km, 23 sites)	Microsatellites	Low, significant genetic differentiation	Berthier *et al.* (2005)
			Significant genetic isolation by distance	
			Significant genetic correlations below 20–30 km	
	France (13 km, 7 sites)	Microsatellites	Low, significant genetic differentiation	Berthier *et al.* (2006)
			Significant genetic isolation by distance	
			Weaker genetic differentiation during peak years	
			Stronger isolation by distance during peak years	

We report data from species for which several studies were available. For each study, we indicate the study location and scale (continent or country, number of sampling sites or populations), the genetic marker (mtDNA = mitochondrial DNA, microsatellites = nuclear microsatellite markers). Raw data are provided in Table S1 (Supporting information).

tions that spatial genetic differentiation declined with the amplitude of the population cycle (i.e. temporal population variability). It was suggested that increased dispersal owing to more extinction–colonization dynamics was the underlying cause.

Our computation of standardized genetic dissimilarity values (G'_{ST}) for all populations and molecular markers [allozyme: three studies, mitochondrial DNA (mtDNA) control region: 17 studies, mtDNA RFLP: two studies, nucDNA AFLP: one study and microsatellites: 40 studies] indicated a mean of 0.41 (median = 0.27) at a median spatial scale of investigation of 10 km (see Table S1 for raw data, Supporting information). We compared estimates of G'_{ST} across studies using only mtDNA control region and nuclear microsatellite data. G'_{ST} was influenced by the genetic marker, spatial scale and number of demes, but not by landscape geometry (mixed-effect linear model after square-root transformation to ensure normality, genetic marker: $F_{1,42} = 25.9$, $P < 0.0001$, spatial scale: $F_{1,42} = 11.1$, $P = 0.002$, number of demes: $F_{1,42} = 8.67$, $P = 0.005$, landscape geometry: $F_{2,42} = 0.52$, $P = 0.6$). G'_{ST} increased with the spatial scale of the study and with the number of demes and was stronger for maternally inherited mitochondrial markers than for nuclear markers. When controlling for these factors, G'_{ST} varied little and not significantly between species (random, $\chi^2 = 0.25$, d.f. = 1, $P = 0.62$). These results are consequences of the relatively modest dispersal abilities of these species, of the predominant female philopatry (Hamilton *et al.* 2005) and smaller effective population of mtDNA markers and of the significant sensitivity of dispersal to landscapes' features in microtine rodents.

Synthesis and conclusion

Our statistical analyses revealed substantial, unexplained variation between species for dispersal distances and a strong variation within species for both dispersal distance and emigration fraction. However, we must acknowledge that our comparison is subject to strong caveats because estimates were collected with different methods and different samples in separate locations for the same species. These methodological aspects consistently explained much of the variation in dispersal fractions, dispersal distances or genetic dissimilarity across studies, which cautions against interspecific comparisons that do not control for them. In addition, serious methodological limitations could bias systematically our quantitative estimates of dispersal. To address this issue, we suggest that future approaches of dispersal should be conducted at larger spatial scales, should try to incorporate data on all age classes and cohorts (see also Box 1), and should also account for unequal capture rates with distance (Telfer *et al.* 2003b). One promising

way to accurately measure dispersal could be to combine mark–recapture and genetic assignment methods where a sufficiently portion of individuals can be sampled (Paetkau *et al.* 2004). These approaches may, however, be difficult to perform in spatially continuous and high-density populations of arvicoline rodents because of the magnitude of the sampling effort required. In these cases, direct observations of dispersal by means of telemetry could still be an option.

Our comparative analysis portrays species with frequent short-distance dispersal events (of the order of hundreds of metres) and extremely flexible dispersal strategies at these short distances. However, most species are also capable of dispersing long distances (on the order of kilometres) under some circumstances. Female arvicolines are more philopatric relative to males, but we could not find a significant association between the mating system and the degree of male-biased dispersal across species. The absence of a relationship with the mating system may be a consequence of the small number of species included and of a substantial variation in social organization within some species. Future studies of sex-biased dispersal would therefore benefit from including more species and/or from quantifying social and mating systems of each study population independently. An interesting result was the occurrence of sexual differences in condition-dependent dispersal. Sexes thus differed not only in their dispersal abilities but also in their dispersal plasticity, a fact that has rarely been accounted for in previous reviews of sex-biased dispersal.

The analysis of condition dependence shows that dispersal is a response to various proximate and ultimate factors, including competition, inbreeding avoidance, mate searching, habitat quality and the costs of transience and settlement. This result is in line with the dispersal patterns reported for mammals and birds investigated so far (Clobert *et al.* 2004, 2009). In particular, our review suggests that costs and benefits experienced during transience and during settlement are prime determinants of condition dependence; for example, dispersal is influenced by landscape geometry and habitat quality while prospecting, by predation risks during exploration and by the social conditions experienced during settlement. This indicates that our understanding of dispersal would benefit from more studies of the transience and settlement stages. Condition dependence results primarily from direct effects of current environmental conditions rather than delayed life history effects or indirect inductions through other phenotypic changes (see Fig. 1). We found no common patterns of phenotype-dependent dispersal in the few studies published so far, except for a widespread association between an exploration-activity syndrome and natal dispersal. Clo-

bert *et al.* (2009) also raised the issue of idiosyncratic dispersal syndromes. They suggested that it could be explained by interactions between condition-dependent and phenotype-dependent dispersal such that different individuals dispersed in different contexts, but this explanation was not supported by our comparative analysis. We instead suggest that it might be more worthwhile to pursue molecular studies to unravel the genetic architecture of condition-dependent behaviour.

Acknowledgments

References

Aars J, Ims RA (2000) Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. *The American Naturalist*, **155**, 252–265.

Aars J, Ims RA, Liu HP, Mulvey M, Smith MH (1998) Bank voles in linear habitats show restricted gene flow as revealed by mitochondrial DNA (mtDNA). *Molecular Ecology*, **7**, 1383–1389.

Aars J, Johannesen E, Ims RA (1999) Demographic consequences of movements in subdivided root vole populations. *Oikos*, **85**, 204–216.

Aars J, Dallas JF, Piertney SB *et al.* (2006) Widespread gene flow and high genetic variability in highly fragmented populations of water voles *Arvicola terrestris*. *Molecular Ecology*, **15**, 1455–1466.

Adams RI, Hadly EA (2010) High levels of gene flow in the California vole (*Microtus californicus*) are consistent across spatial scales. *Western North American Naturalist*, **70**, 296–311.

Anderson PK (1989) *Dispersal in Rodents: A Resident Fitness Hypothesis*. American Society of Mammalogists, Provo.

Andreassen HP, Gundersen G (2006) Male turnover generates population decline: an enclosure experiment on voles. *Ecology*, **87**, 88–94.

Andreassen HP, Ims RA (2001) Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology*, **82**, 2911–2926.

Andreassen HP, Bjornbom E, Carlsen RG, Gundersen G, Gundersen H (1998a) Visual cues as determinants of perceptual range in root voles *Microtus oeconomus*. *Acta Theriologica*, **43**, 371–378.

Andreassen HP, Hertzberg K, Ims RA (1998b) Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology*, **79**, 1223–1235.

Andreassen HP, Stenseth NC, Ims RA (2002) Dispersal behaviour and population dynamics of vertebrates. In: *Dispersal Ecology* (eds Bullock JM, Kenward RE and Hails RS), pp. 237–256. Blackwell, Oxford.

Arnaud CM, Dobson FS, Murie JO (2011) Philopatry and within-colony movements in Columbian ground squirrels. *Molecular Ecology*, doi: 10.1111/j.1365-294X.2011.05219.x.

Beacham TD (1979) Dispersal tendency and duration of life of littermates during population fluctuations of the vole *Microtus townsendii*. *Oecologia*, **42**, 11–21.

Berthier K, Galan M, Foltete JC, Charbonnel N, Cosson JF (2005) Genetic structure of the cyclic fossorial water vole (*Arvicola terrestris*): landscape and demographic influences. *Molecular Ecology*, **14**, 2861–2871.

Berthier K, Charbonnel N, Galan M, Chaval Y, Cosson JF (2006) Migration and recovery of the genetic diversity during the increasing density phase in cyclic vole populations. *Molecular Ecology*, **15**, 2665–2676.

Bollinger EK, Harper SJ, Barrett GW (1993) Inbreeding avoidance increases dispersal movements of the meadow vole. *Ecology*, **74**, 1153–1156.

Bondrup-Nielsen S (1992) Emigration of meadow voles, *Microtus pennsylvanicus*: the effect of sex ratio. *Oikos*, **65**, 358–360.

Bondrup-Nielsen S (1993) Early malnutrition increased emigration of adult female meadow voles, *Microtus pennsylvanicus*. *Oikos*, **67**, 317–320.

Boonstra R, Krebs CJ, Gaines MS, Johnson ML, Craine ITM (1987) Natal philopatry and breeding systems in voles (*Microtus spp.*). *Journal of Animal Ecology*, **56**, 655–673.

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Review*, **80**, 205–225.

Boyce CK, Boyce JL (1988) Population biology of *Microtus arvalis*. II. Natal and breeding dispersal of females. *Journal of Animal Ecology*, **57**, 723–736.

Clobert J, Ims RA, Rousset F (2004) Causes, mechanisms and consequences of dispersal. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski I and Gagiotti O), pp. 307–335. Elsevier, Academic Press, London.

Clobert J, Le Galliard J-F, Cote J, Massot M, Meylan S (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, **12**, 197–209.

Clutton-Brock TH, Lukas D (2011) The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, doi: 10.1111/j.1365-294X.2011.05232.x.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 4065–4076.

Crone EE, Doak D, Pokki J (2001) Ecological influences on the dynamics of a field vole metapopulation. *Ecology*, **82**, 831–843.

Davis-Born R, Wolff JO (2000) Age- and sex-specific responses of the gray-tailed vole, *Microtus canicaudus*, to connected and unconnected habitat patches. *Canadian Journal of Zoology*, **78**, 864–870.

Diffendorfer JE, Gaines MS, Holt RD (1995) Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology*, **76**, 827–839.

Ebenhard T (1990) A colonization strategy in field voles (*Microtus agrestis*): reproductive traits and body size. *Ecology*, **71**, 1833–1848.

Ehrich D, Stenseth NC (2001) Genetic structure of Siberian lemmings (*Lemmus sibiricus*) in a continuous habitat: large patches rather than isolation by distance. *Heredity*, **86**, 716–730.

Ehrich D, Krebs CJ, Kenney AJ, Stenseth NC (2001) Comparing the genetic population structure of two species of arctic lemmings: more local differentiation in *Lemmus trimucronatus* than in *Dicrostonyx groenlandicus*. *Oikos*, **94**, 143–150.

Ehrich D, Yoccoz NG, Ims RA (2009) Multi-annual density fluctuations and habitat size enhance genetic variability in two northern voles. *Oikos*, **118**, 1441–1452.

Ergon T, Lambin X, Stenseth NC (2001) Life-history traits of voles in a fluctuating population respond to the immediate environment. *Nature*, **411**, 1043–1045.

Fisher DO, Lambin X, Yletyinen SM (2009) Experimental translocation of juvenile water voles in a Scottish lowland metapopulation. *Population Ecology*, **51**, 289–295.

Fortier GM, Tamarin RH (1998) Movement of meadow voles in response to food and density manipulations: a test of the food-defense and pup-defense hypotheses. *Journal of Mammalogy*, **79**, 337–345.

Francl KE, Glenn TC, Castleberry SB, Ford WM (2008) Genetic relationships of meadow vole (*Microtus pennsylvanicus*) populations in central Appalachian wetlands. *Canadian Journal of Zoology*, **86**, 344–355.

Gauffre B, Estoup A, Bretagnolle V, Cosson JF (2008) Spatial genetic structure of a small rodent in a heterogeneous landscape. *Molecular Ecology*, **17**, 4619–4629.

Gauffre B, Petit E, Brodier S, Bretagnolle V, Cosson JF (2009) Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3487–3494.

Getz LL, Cole FR, Gates DL (1978) Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy*, **59**, 208–212.

Getz LL, McGuire B, Hofmann JE, Pizzuto T, Frase B (1994) Natal dispersal and philopatry in prairie voles (*Microtus ochrogaster*)—settlement, survival, and potential reproductive success. *Ethology, Ecology & Evolution*, **6**, 267–284.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Guillot G, Leblois R, Coulon A, Frantz AC (2009) Statistical methods in spatial genetics. *Molecular Ecology*, **18**, 4734–4756.

Guivier E, Galan M, Chaval Y *et al.* (2011) Landscape genetics highlights the role of bank vole metapopulation dynamics in the epidemiology of *Puumala hantavirus*. *Molecular Ecology*, **20**, 3569–3583.

Gundersen G, Andreassen HP (1998) Causes and consequences of natal dispersal in root voles, *Microtus oeconomus*. *Animal Behaviour*, **56**, 1355–1366.

Gundersen G, Moe JA, Andreassen HP, Carlsen RG, Gundersen H (1999) Intersexual attraction in natal dispersing root voles *Microtus oeconomus*. *Acta Theriologica*, **44**, 283–290.

Gundersen G, Johannesen E, Andreassen HP, Ims RA (2001) Source-sink dynamics: how sinks affect demography of sources. *Ecology Letters*, **4**, 14–21.

Gundersen G, Andreassen HP, Ims RA (2002) Individual and population level determinants of immigration success on

local habitat patches: an experimental approach. *Ecology Letters*, **5**, 294–301.

Hamilton G, Currat M, Ray N *et al.* (2005) Bayesian estimation of recent migration rates after a spatial expansion. *Genetics*, **170**, 409–417.

Hanski I, Eralahti C, Kankare M, Ovaskainen O, Siren H (2004) Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters*, **7**, 958–966.

Heckel G, Burri R, Fink S, Desmet JF, Excoffier L (2005) Genetic structure and colonization processes in European populations of the common vole, Microtus arvalis. *Evolution*, **59**, 2231–2242.

Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution*, **59**, 1633–1638.

Heller R, Siegismund HR (2009) Relationship between three measures of genetic differentiation G_{st}, D_{st} and G'_{st}: how wrong have we been? *Molecular Ecology*, **18**, 2080–2083.

Heske EJ, Ostfeld RS (1990) Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *Journal of Mammalogy*, **71**, 510–519.

Hestbeck JB (1982) Population regulation of cyclic mammals: the social fence hypothesis. *Oikos*, **39**, 157–163.

Holekamp KE, Smith JE, Strelioff CC, Van Horn RC, Watts HE (2011) Society, demography and genetic structure in the spotted hyena. *Molecular Ecology*, doi: 10.1111/j.1365-294X.2011.05240.x.

Hoset KS, Le Galliard J-F, Gundersen G, Steen H (2008) Home range size and overlap in female root voles: effects of season and density. *Behavioral Ecology*, **19**, 139–145.

Ims RA, Andreassen HP (1991) Does kinship influence space use and dispersal in male gray-sided voles? *Oikos*, **62**, 216–220.

Ims RA, Andreassen HP (2000) Spatial synchronization of vole population dynamics by predatory birds. *Nature*, **408**, 194–196.

Ims RA, Andreassen HP (2005) Density-dependent dispersal and spatial population dynamics. *Proceedings of the Royal Society of London B*, **272**, 913–918.

Ims RA, Hjermann DO (2001) Condition dependent dispersal. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA and Nichols JD), pp. 203–216. Oxford University Press, Oxford.

Ims RA, Yoccoz NG (1997) Studying transfer processes in metapopulations: emigration, migration, and colonization. In: *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds Hanski IA and Gilpin ME), pp. 247–265. Academic Press, San Diego.

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? *Biological Conservation*, **63**, 261–268.

Ims RA, Henden JA, Killengreen ST (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79–86.

Ishibashi Y, Saitoh T (2008) Role of male-biased dispersal in inbreeding avoidance in the grey-sided vole (*Myodes rufocanus*). *Molecular Ecology*, **17**, 4887–4896.

Ishibashi Y, Saitoh T, Abe S, Yoshida MC (1997) Sex-related spatial kin structure in a spring population of grey-sided voles Clethrionomys rufocanus as revealed by mitochondrial and microsatellite DNA analyses. *Molecular Ecology*, **6**, 63–71.

Ishibashi Y, Saitoh T, Abe S, Yoshida MC (1998) Kin-related social organization in a winter population of the vole Clethrionomys rufocanus. *Researches on Population Ecology*, **40**, 51–59.

Jacquot JJ, Solomon NG (2004) Experimental manipulation of territory occupancy: effects on immigration of female prairie voles. *Journal of Mammalogy*, **85**, 1009–1014.

Kawata M (1987) The effect of kinship on spacing among female red-backed voles, *Clethrionomys rufocanus bedfordiae*. *Oecologia*, **72**, 115–122.

Kawata M (1989) Growth and dispersal timing in red-backed voles Clethrionomys rufocanus bedfordiae. *Oikos*, **54**, 220–226.

La Polla VN, Barrett GW (1993) Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecology*, **8**, 25–37.

Lambin X (1994a) Litter sex-ratio does not determine natal dispersal tendency in female Townsend voles. *Oikos*, **69**, 353–356.

Lambin X (1994b) Natal philopatry, competition for resources, and inbreeding avoidance in Towsend's voles (*Microtus townsendii*). *Ecology*, **75**, 224–235.

Lambin X (1994c) Territory acquisition and social facilitation by litter-mate Towsend's voles (*Microtus townsendii*). *Ethology, Ecology & Evolution*, **6**, 213–220.

Lambin X (1997) Home range shifts by breeding female Townsend's voles (*Microtus townsendii*): a test of the territory bequeathal hypothesis. *Behavioral Ecology and Sociobiology*, **40**, 363–372.

Lambin X, Yoccoz NG (1998) The impact of population kin-structure on nestling survival in Towsend's voles, *Microtus townsendii*. *Journal of Animal Ecology*, **67**, 1–16.

Lambin X, Yoccoz NG (2001) Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. *Journal of Animal Ecology*, **70**, 191–200.

Lambin X, Elston DA, Petty SJ, MacKinnon JL (1998) Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **265**, 1491–1496.

Lambin X, Aars J, Piertney SB (2001) Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt A and Nichols JD), pp. 110–122. Oxford University Press, Oxford.

Lambin X, Aars J, Piertney SB, Telfer S (2004) Inferring patterns and process in small mammal metapopulations: insights from ecological and genetic data. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski IH and Gagiotti E), pp. 515–540. Elsevier, London.

Lambin X, Le Bouille D, Oliver MK *et al.* (in press) High connectivity despite high fragmentation: iterated dispersal in a vertebrate metapopulation. In: *Dispersal and Spatial Evolutionary Ecology* (eds Clobert J, Baguette M, Benton TG and Bullock JM),. Oxford University Press, Oxford.

Lawson Handley LJ, Perrin N (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, **16**, 1559–1578.

Le Galliard J-F, Ferrière R, Clobert J (2003) Mother-offspring interactions affect natal dispersal in a lizard. *Proceedings of the Royal Society of London B*, **270**, 1163–1169.

Le Galliard J-F, Gundersen G, Andreassen HP, Stenseth NC (2006) Natal dispersal, interactions among siblings and intrasexual competition. *Behavioral Ecology*, **17**, 733–740.

Le Galliard J-F, Gundersen G, Steen H (2007) Mother-offspring interactions do not affect natal dispersal in a small rodent. *Behavioral Ecology*, **18**, 665–673.

Leblois R, Rousset F, Estoup A (2004) Influence of spatial and temporal heterogeneities on the estimation of demographic parameters in a continuous population using individual microsatellite data. *Genetics*, **166**, 1081–1092.

Lidicker WZJ (1985) Dispersal. In: *Biology of New World Microtus* (ed. Tamarin RH), pp. 725–778. American Society of Mammalogists, Lawrence, Kansas.

Lin Y-TK, Batzli GO (2001a) The influence of habitat quality on dispersal, demography, and population dynamics of voles. *Ecological Monographs*, **71**, 245–275.

Lin YK, Batzli GO (2001b) The effect of interspecific competition on habitat selection by voles: an experimental approach. *Canadian Journal of Zoology*, **79**, 110–120.

Lin Y-TK, Batzli GO (2002) The cost of habitat selection in prairie voles: an empirical assessment using isodar analysis. *Evolutionary Ecology*, **16**, 387–397.

Lofgren O, Hornfeldt B, Eklund U (1996) Effect of supplemental food on a cyclic *Clethrionomys glareolus* population at peak density. *Acta Theriologica*, **41**, 383–394.

Lucia KE, Keane B, Hayes LD et al. (2008) Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioral Ecology*, **19**, 774–783.

Madison DM (1990) Social organizational modes in models of microtine cycling. In: *Social Systems and Population Cycles in Voles* (eds Tamarin RH, Ostfeld RS, Pugh SR and Bujalska G), pp. 25–34. Birkhauser, Basel.

Mazurkiewicz M, Rajska E (1975) Dispersion of young bank voles from their place of birth. *Acta Theriologica*, **20**, 71–81.

McGuire B, Lowell LL (1995) Communal nesting in prairie voles (*Microtus ochrogaster*)—an evaluation of costs and benefits based on patterns of dispersal and settlement. *Canadian Journal of Zoology*, **73**, 383–391.

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. *Behavioral Ecology and Sociobiology*, **32**, 293–302.

McShea WJ (1990) Social tolerance and proximate mechanisms of dispersal among winter groups of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, **39**, 346–351.

Morris DW, MacEachern JT (2010) Active density-dependent habitat selection in a controlled population of small mammals. *Ecology*, **91**, 3131–3137.

Neuwald JL (2010) Population isolation exacerbates conservation genetic concerns in the endangered Amargosa vole, Microtus californicus scirpensis. *Biological Conservation*, **143**, 2028–2038.

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*, **13**, 55–65.

Peles JD, Barrett GW (1996) Effects of vegetative cover on the population dynamics of meadow voles. *Journal of Mammalogy*, **77**, 857–869.

Pinheiro JC, Bates DM (2000) *Mixed-effect Models in S and S-plus*. Springer, New York.

Pita R, Beja P, Mira A (2007) Spatial population structure of the Cabrera vole in Mediterranean farmland: the relative role of patch and matrix effects. *Biological Conservation*, **134**, 383–392.

Pugh SR, Tamarin RH (1991) A comparison of population characteristics and reproductive success of resident and immigrant meadow voles. *Canadian Journal of Zoology*, **69**, 2638–2643.

Rajska-Jurgiel E (1992) Demography of woodland rodents in fragmented habitat. *Acta Theriologica*, **37**, 73–90.

Rajska-Jurgiel E (2000) Breeding dispersal in *Clethrionomys glareolus* females. *Acta Theriologica*, **45**, 367–376.

Ratkiewicz M, Borkowska A (2006) Genetic structure is influenced by environmental barriers: empirical evidence from the common vole *Microtus arvalis* populations. *Acta Theriologica*, **51**, 337–344.

Redeker S, Andersen LW, Pertoldi C et al. (2006) Genetic structure, habitat fragmentation and bottlenecks in Danish bank voles (*Clethrionomys glareolus*). *Mammalian Biology*, **71**, 144–158.

Rémy A, Le Galliard J-F, Gundersen G, Steen H, Andreassen HP (2011) Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent. *Journal of Animal Ecology*, **80**, 929–937.

Robinson GR, Holt RD, Gaines MS et al. (1992) Diverse and contrasting effects of habitat fragmentation. *Science*, **257**, 524–526.

do Rosario IT, Mathias MD (2007) Post-fire recolonisation of a montado area by the endangered Cabrera vole (*Microtus cabrerae*). *International Journal of Wildland Fire*, **16**, 450–457.

Rousset F (1997) Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Saitoh T (1995) Sexual differences in natal dispersal and philopatry of the grey-sided vole. *Researches on Population Ecology*, **37**, 49–57.

Schooley RL, Branch LC (2009) Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecological Applications*, **19**, 1708–1722.

Schradin C, Lindholm AK, Johannesen JES et al. (2011) Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology*, doi: 10.1111/j.1365-294X.2011.05256.x.

Schweizer M, Excoffier L, Heckel G (2007) Fine-scale genetic structure and dispersal in the common vole (*Microtus arvalis*). *Molecular Ecology*, **16**, 2463–2473.

Selonen V, Hanski IK (2010) Condition-dependent, phenotype-dependent and genetic-dependent factors in the natal dispersal of a solitary rodent. *Journal of Animal Ecology*, **79**, 1093–1100.

Sherratt TN, Lambin X, Petty SJ et al. (2000) Use of coupled oscillator models to understand synchrony and travelling waves in populations of the field vole *Microtus agrestis* in northern England. *Journal of Applied Ecology*, **37**, 148–158.

Smith JE, Batzli GO (2006) Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. *Oikos*, **112**, 209–217.

Smith FA, Lyons SK, Ernest SKM et al. (2003) Body mass of late quaternary mammals. *Ecology*, **84**, 3403.

Solomon NG (2003) A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy*, **84**, 1182–1197.

Solomon NG, Richmond AR, Harding PA *et al.* (2009) Polymorphism at the avpr1a locus in male prairie voles correlated with genetic but not social monogamy in field populations. *Molecular Ecology*, **18**, 4680–4695.

Stacy JE, Jorde PE, Steen H *et al.* (1997) Lack of concordance between mtDNA gene flow and population density fluctuations in the bank vole. *Molecular Ecology*, **6**, 751–759.

Steen H (1994) Low survival of long-distance dispersers of the root vole (*Microtus oeconomus*). *Annales Zoologici Fennici*, **31**, 271–274.

Steen H (1995) Untangling the causes of disappearance from a local population of root voles, *Microtus oeconomus*—a test of the regional synchrony hypothesis. *Oikos*, **73**, 65–72.

Stenseth NC (1999) Population cycles in voles and lemmings: density dependence and phase dependency in a stochastic world. *Oikos*, **87**, 427–430.

Stenseth NC, Lidicker WZ (1992) *Animal Dispersal: Small Mammals as a Model*. Chapman and Hall, London.

Stewart WA, Dallas JF, Piertney SB *et al.* (1999) Metapopulation genetic structure in the water vole, *Arvicola terrestris*, in NE Scotland. *Biological Journal of the Linnean Society*, **68**, 159–171.

Stoddart DM (1970) Individual range, dispersion and dispersal in a population of water voles (*Arvicola terrestris* (L.)). *Journal of Animal Ecology*, **39**, 403–425.

Telfer S, Dallas J, Aars J *et al.* (2003a) Demographic and genetic structure of fossorial water voles *Arvicola terrestris* on Scottish islands. *Journal of Zoology*, **259**, 23–29.

Telfer S, Piertney S, Dallas J *et al.* (2003b) Parentage assignment detects frequent and large-scale dispersal in water voles. *Molecular Ecology*, **12**, 1939–1949.

Watts CHS (1970) Long distance movement of bank voles and wood mice. *Journal of Zoology*, **161**, 247–256.

Whitlock MC (2011) G'_{st} and D do not replace F_{st}. *Molecular Ecology*, **20**, 1083–1091.

Wilson DE, Reeder DM (2005) *Mammal Species of the World. A Taxonomic and Geographic Reference*, p. 142. Johns Hopkins University Press.

Witt WC, Huntly N (2001) Effects of isolation on red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) in a sage-steppe matrix. *Canadian Journal of Zoology*, **79**, 1597–1603.

Wolff JO, Sherman PW (2007) *Rodent Societies—An Ecological and Evolutionary Perspective*, p. 610. University of Chicago Press, Chicago, Illinois.

Wolff JO, Schauber EM, Edge WD (1997) Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology*, **11**, 945–956.

J.-F. is an evolutionary ecologist with broad interests in dispersal behaviour, life history strategies and population dynamics. This study forms part of a collaborative project during the doctoral research of A.R. at Hedmark University College. R.I. studies processes affecting the dynamics and structure of boreal communities, with a special emphasis on small mammals. X.L. is an ecologist interested in complex temporal and spatial population dynamics and host-parasite interactions.

Data accessibility

All data used in the analyses are available in the Supporting information and on Dryad at doi:10.5061/dryad.71p127f8.

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Supporting information on data set, study variables, and species description.

Table S1 Estimates of genetic structure in microtine rodents' populations.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.