

**DISPERSAL: TRIGGERS, TRAITS, AND FITNESS
CONSEQUENCES IN COMMON VOLES (*MICROTUS ARVALIS*)**

Dissertation

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GENERAL INTRODUCTION**State of the art – what is known?**

Human activities have been causing extensive landscape fragmentation (Forman and Godron 1986), which results in habitat reduction, segregation, and isolation of populations. The chance of population extinction increases as the size of a habitat patch decreases (Hastings and Wolin 1989, Ferrière and Galliard 2001), and small and isolated populations are at risk of losing genetic variation through genetic drift. The negative effects of fragmentation on populations can be counteracted by dispersal, defined as an “one-way movement of individuals away from their home range site” (Lidicker and Stenseth 1992). Dispersal is considered a link between otherwise isolated populations, and it plays a major part in the demography of populations as well as in their genetic composition (see Andreassen and Ims 2001, Clobert et al. 2001a, Lidicker 2002, Bowne and Bowers 2004, Aars et al. 2006). As a consequence, an extensive system of corridors, connecting small habitat patches, is being established in order to facilitate a disperser-mediated link and gene flow between populations (Gilpin 1991, Whitlock 2001).

Dispersal may be seen as composed of three sequential phases: emigration, travel and immigration (see Andreassen et al. 2002). While emigration of individuals might prevent overpopulation, immigration can lead to large-scale persistence of small populations (i.e. rescue-effect; Hanski 2001) or prevent deleterious effects of inbreeding (Aars and Ims 1999, Aars et al. 2006). From the individuals’ perspective dispersing, or, conversely, remaining behind, will affect both fitness-relevant parameters, reproduction and survival (Clobert et al. 2001b). While dispersers are known to have a high risk of starvation or of being preyed upon (Andreassen and Ims 2001, Smith and Batzli 2006; but see McGuire et al. 1993), philopatry carries a potential cost of intraspecific competition, as well as a risk of inbreeding (Clobert et al. 2001b, Lambin et al. 2001, Aars et al. 2006, Höner et al. 2007, Lawson Handley and Perrin 2007). Although dispersal is a high-risk strategy (Lidicker 1975) it might enhance fitness due to a release of competition, a reduced risk of inbreeding, and/or an increase in the reproductive success in the new population (c.f. Jack and Fedigan 2004). Dispersal, therefore, has major consequences for individuals as well as for both, the population which is left (i.e. the *natal population*) and the *new population* into which a disperser immigrates.

It is hypothesized that dispersers are not a random subset of a population, but morphologically and/or genetically different from residents (O’Riain et al. 1996, Clobert et al. 2001b, Cote et al. 2007). In 2002 we conducted morphological studies with male common voles and compared various biometric data between residents and dispersers (E. Kammerer, unpublished data). While residents had a higher body-length, dispersers exceeded residents in terms of fat-depots, weight of liver, testes, specific muscles, and weight of seminal vesicles, indicating that male dispersers are “prepared” for emigration. Still, the possibility that dispersers may constitute a morphologically distinct group is discussed contradictory and the hypothesis that they might be genetically distinct from residents has long been the subject of

speculation and investigation (e.g. Lidicker 1975, Gaines and McClenaghan 1980, Keith and Tamarin 1981, Waser and Jones 1989, Krebs 1992, Boonstra and Hochachka 1997, Roff and Fairbairn 2001).

Which sex predominantly disperses depends on the relative costs and benefits of dispersal and this seems to be closely linked to the mating system (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). Polygyny, as found in most mammals, is typically associated with male-biased dispersal (but see Nagy et al. 2007). While females' reproductive success is primarily dependant on food availability, males have to compete for the access to females (Ostfeld 1985, Bondrup-Nielsen 1993). Although sex-biased dispersal *per se* has frequently supposed to reduce the risk of inbreeding (*inbreeding avoidance hypothesis*; Viitala et al. 1994, Gundersen and Andreassen 1998), it is important to consider the age at emigration. Individuals emigrate either prior to their first reproduction (hereafter termed *natal dispersal*) or leave their home after having reproduced (hereafter termed *breeding dispersal*). The latter might implicate that the home range is passed on to the offspring. To avoid inbreeding, however, animals have to be natal dispersers.

Dispersal is a heterogeneous phenomenon encompassing a variety of timings, motivations, and consequences (Lidicker 1985), and there are various hypotheses for the causes of dispersal (Lidicker and Stenseth 1992). In order to disentangle these hypotheses it is important to discriminate ultimate causes, which account for the establishment of a behavior as an evolutionary stable strategy (ESS), and proximate triggers, defined as those external stimuli which directly initiate or maintain biological processes. Ultimate causes for dispersal are explained by the competition for food and mates, as well as by inbreeding avoidance (Liberg and von Schantz 1985, Gandon and Michalakis 2001, Lambin et al. 2001). Inbreeding avoidance was supported by a sex-biased dispersal rate (Greenwood 1980, Dobson 1982, Wolff 1992, Bollinger et al. 1993, Gundersen and Andreassen 1998), the dependency between dispersal distance and social structure (Jacquot and Vessey 1995, Gundersen and Andreassen 1998), as well as by the preference to mate with non-related partners (Lidicker and Stenseth 1992). In contrast to the relatively well established ultimate causes a large, and controversially discussed, array of proximate triggers has been proposed (Waser and Jones 1989, Lidicker and Stenseth 1992, Andreassen and Ims 2001, Clobert et al. 2001b). These triggers are ranging from social factors, temporal and spatial variation in habitat quality and habitat structure, to interspecific interactions such as predation and parasitism (see Andreassen and Ims 2001 and references therein).

The probably most investigated proximate trigger for emigration is population density (e.g. Wolff 1992, Aars and Ims 2000, Andreassen and Ims 2001, Ferreras et al. 2004), which is directly correlated with resource competition in the natal population. Here, Lidicker (1975) defined two different types of dispersers. Those that emigrate before the maximum population density is reached (hereafter termed *presaturation dispersers*) and individuals that leave their natal population at or after population maxima (hereafter termed *saturation dispersers*). While saturation dispersers are proposed to be competitively inferior and evicted by conspecifics, presaturation dispersers are probably risk prone individuals that leave their natal population voluntarily.

Although it is widely accepted that dispersal plays a major part in population dynamics and population genetics, dispersal and associated consequences still constitute a big gap in our knowledge and remain one of the most studied, yet least understood concepts in ecology and conservation biology (Clobert et al. 2001b). This is mainly due to the difficulties in obtaining robust field data which is reflected in predominantly anecdotal or theoretical works (Mossman and Waser 1999, Kenward et al. 2002).

Methodical approaches and associated problems

Dispersal is a seldom event and, under natural conditions, it is impossible to predict in advance which individual will emigrate, when it will emigrate, and where it will go. The location and timing of a disperser's activity is surely not arbitrary, but to reduce competition and predation risk an adaptation of the dispersers' spatial and temporal behavior likely. Here, immigration phenomena are especially difficult to study since movements through unfamiliar and unsuitable areas are known to heavily increase mortality rates of dispersers (Andreassen and Ims 2001, Smith and Batzli 2006), which reduces the number of animals arriving in a new population. It is often impossible to distinguish in the field between individuals that have entered a population due to birth or immigration. It is even harder to distinguish between individuals that disappeared because of death versus those that emigrated, and in the past dispersal was often taken as an indistinguishable component of "gross mortality" for which it is irrelevant if an individual dispersed or fell prey to a predator (Lidicker 1975, 1985). Manipulating emigration and immigration would, therefore, be the most powerful approach we know for studying the demographic as well as the population genetic aspects of dispersal (Aars and Ims 2000).

A widely used technique to study dispersal was to trap out an area and then assume that individuals caught subsequently are dispersers (Myers and Krebs 1971, Gaines et al. 1979, Keith and Tamarin 1981). This, however, poses several sources of error (for an overview see Lidicker 1985). For example, it is extremely difficult to trap out an area and, if empty, habitat patches might attract individuals that otherwise would not have dispersed. Some workers (Tamarin 1980, Hestbeck 1982) have attempted to provide barriers or poor habitat strips that are trespassed only by those individuals with a particularly high motivation to disperse. Furthermore, investigations in small mammals have been conducted in semi-natural enclosures, while dispersers were defined as those individuals that changed adjacent populations by using exit doors (Gaines et al. 1979) or one-way tubes (Viitala et al. 1994).

Recent studies have used genetic markers to identify immigrating small mammal dispersers and to ascertain the proportion of new animals in the populations examined (Mossman and Waser 1999, Schweizer et al. 2007). However, in such studies it remains unclear, how many of these immigrants actually reproduce in the new populations and which factors determine their establishment. Lambin (1994) proposed that an effective disperser must not only complete emigration and travel successfully, but also immigration (i.e. settle and/or reproduce). Only reproducing immigrants will have a genetic impact on the new population and dispersal will not result in gene flow unless individuals become part of the new

breeding population (Schweizer et al. 2007).

The establishment of a disperser can be thought of in two ways: First, by simply integrating its home range into an existing social structure. This is possible at relative low population densities when sites to settle are still available or by a decrease of the residents' home range. Second, when population density is high, by repelling a resident off its home range. The latter scenario is only possible if dispersers are highly competitive and this might have profound effects on the quality and quantity of gene flow between populations. For a successful establishment of a disperser a former resident would have to emigrate, which may lead to a *domino-effect* if the repellence continues.

Agenda – what I did

In this study I used semi-natural enclosures as an experimental model system (EMS; Wiens et al. 1993) and the common vole, *Microtus arvalis* (Pallas), as a model organism. The appeal of the EMS approach is that it allows a relative precise study of biological processes by creating a simplified abstraction of nature (Bowers and Dooley 1999, see DISCUSSION). Voles are particularly suitable as a model organism since they have been the subject of numerous experimental field investigations in which individual, population-level, and community-level responses to various factors have been quantified. We know the biology and natural histories of most vole species, we can individually mark voles and therefore monitor and track them (Szacki et al. 1993). They live in relatively small spatial areas, have short lives, a high reproductive output, and are relatively easy to trap and handle (Niethammer and Krapp 1982). Dispersers were identified by their trapping history and emigration and immigration was manipulated in the populations by a one-way transfer of dispersers. I transferred the dispersers manually and, hence, excluded high mortality rates during travel, which surely increased the sample size of immigrants compared to investigations under complete natural conditions. Since demographic changes are inevitably linked with changes in the population genetic structure I combined classical capture-mark-recapture methods and genetic analyses. The latter were done by using microsatellite-analyses which allows the computation of various population genetic parameters like heterozygosity, relatedness, or inbreeding coefficients, as well as precise assignments of newborns to their parents (Marshall et al. 1998, Slate et al. 2000, Zande et al. 2000, Belkhir et al. 2002, Jones and Ardren 2003, Aars et al. 2006). Additionally, I conducted intensive radio tracking sessions and used devices for automatic activity recording to investigate the dispersers' spatio-temporal behavior in their natal populations (i.e. *emigrants*) as well as in the new populations (i.e. *immigrants*). In particular I wanted to ascertain:

- If dispersers constitute a morphologically and/or behaviorally distinct group and whether the dispersal behavior is genetically inheritable.
- The spatio-temporal behavior of emigrants and immigrants and potential strategies by the voles in avoiding both intraspecific competition and predation risk.
- What factors motivate emigration. Here, I predominantly concentrated on proximate factors.

- The reproductive success of dispersers in the natal as well as in the new populations, consequences for their survival rate, and factors for a successful establishment.
- Demographic, genetic, and behavioral implications of emigration and immigration on resident populations.
- Differences between population-genetic models with simple immigration versus those that assume a *domino-effect*.

Although studies to some of the points mentioned above already exist, associated investigations are predominantly theoretical, based on anecdotal events, and/or controversially discussed. Statistically reliable results, especially for the establishing success of dispersers, will have practical use for natural conservation in planning and realizing corridors that connect otherwise isolated habitat patches.

GENERAL METHODS

Field side and trapping

The investigation was conducted at the Remderoda field station which is located near Jena, Germany (50°55'N, 11°35'E). The station comprises six 50 x 50 m outdoor enclosures (Figure 1) that were separated from each other by metal plates insurmountable for voles. The enclosures were additionally surrounded by a two meters high fence which prevented ground predators to enter the station. Avian predation, however, was allowed in order to avoid overpopulation and to maintain predation pressure. Enclosures were covered with natural meadow vegetation (mainly consisting of *Calamagrostis sp.*, *Festuca rubra*, *Cirsium arvense*, *Convolvulus arvensis*, and *Crepis biennis*) which was left untouched during the experiments (hereafter termed *habitat*) except for a 2.5 m wide frequently mown strip along the edges of each enclosure (hereafter termed *matrix*). Each enclosure's habitat patch was covered with a grid of 25 Oos live traps (Oos, Germany) which were modified by an additional wooden box providing shelter from rain and insulation on hot or cold days (Halle 1994). The Oos live-traps were spaced 10 m apart. For the spatial behavior of the voles (see SPATIO-TEMPORAL BEHAVIOR, this volume) the outer 16 trap stations were part of the section defined as habitat edge, while the inner nine Oos traps belonged to the interior (Figure 1). Additionally, eight multiple-capture Ugglan live traps (Grahnb, Sweden) were distributed in the corners of each enclosure's matrix and in the middle in between in order to get information on individuals moving in the matrix (see below).

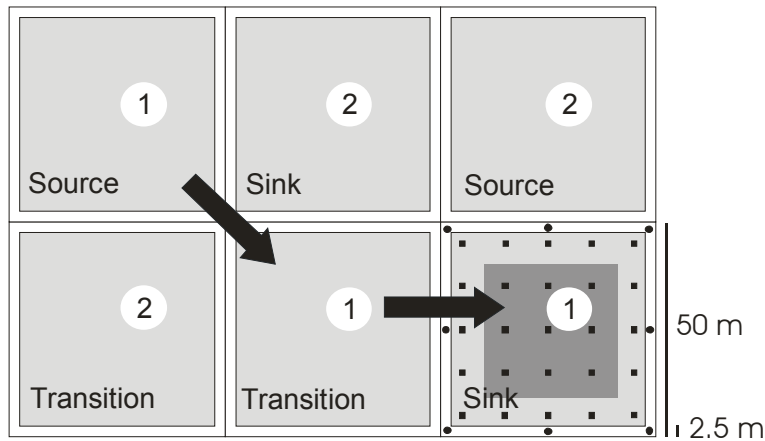


FIGURE 1 Experimental setup of the six semi-natural enclosures. Grey areas represent habitat patches consisting of naturally occurring meadow vegetation. For the spatial behavior of the voles (see SPATIO-TEMPORAL BEHAVIOR, this volume) we distinguished between habitat interior (dark gray; exemplified for one enclosure) and habitat edge (light gray). White surroundings indicate a frequently mown strip, representing the risky matrix. The positions of live traps are indicated by black squares (Oos) and circles (Ugglan) for one enclosure only. Arrows indicate the one-way-direction of transfer of dispersers from source to transition and sink enclosures for one of the two separate experimental systems.

The common vole, *Microtus arvalis*, is a very wide-spread small mammal throughout most of Europe and typically abundant in open meadow habitats (Mitchell-Jones et al. 1999, Heckel et al. 2005). Common voles are territorial and have home ranges of about 100-200 m² with wide overlap between related females and between sexes (Jacob and Hempel 2003, Briner et al. 2005, E. Heinze et al., unpublished data). They have short lives, high reproductive output and often disperse from their natal areas (Boyce and Boyce 1988a, b, Szacki et al. 1993). The individuals occupying a colony constitute a family. This is usually a female, or several females, with the young from one or sometimes several litters. Males are more loosely connected with their colony and home ranges are more extensive as they mate with a large number of females (i.e. polygynous mating system; Mackin-Rogalska 1979).

In June 2004, three males and five females were released into each of the six enclosures. Founding voles were trapped at different locations in the region of Jena. Individuals trapped at the same site were put into different enclosures to account for potential family structures in the original population (see Schweizer et al. 2007). In May 2005 and June 2006, I released 12 and 22 additional voles into the enclosures to compensate for population crashes in April and May, respectively.

I conducted weekly live-trapping with all habitat traps throughout 2004 and in spring 2005 and 2006 to get detailed information on all population founders. During treatment periods the habitat was trapped bi-weekly. Treatment periods of the experiments started in July (week 28 in 2005 and week 30 in 2006) with the appearance and transfer of the first dispersers (see Results) and ended in early November 2005 and end of October 2006 when the voles terminated reproduction. At all trapping sessions the live-traps were activated for two days and two nights. The traps were left open deactivated on all other days. For each vole, the trapping location, sex, body-weight, and the reproductive state was recorded at every capture. For the latter I distinguished between enlarged and non-visible testes in males, and between closed vagina, open vagina, pregnancy, and lactation in females. A vole was considered to be adult/mature as soon as

testes were enlarged in males or as soon as a perforation of the females' vagina (open vagina) or any sign of pregnancy was observed (i.e. pregnant or lactating). Additionally, I noted any biting wounds and scars of the voles which were most probably induced by aggressive encounters of conspecifics. All voles weighing 10 g or more were individually marked by passive integrated transponders (PIT; Trovan® Electronic Identification System). The voles were anaesthetized with ether for PIT tagging and at the same time a tissue sample from the tip of the tail was taken and stored in 70% ethanol for genetic analyses. Voles below 10 g body-weight were marked by fur cut to prevent double counting within a trapping session.

Population densities were measured with the minimum number of animals alive technique (MNA; Krebs 1989). For calculations of MNA, PIT-tagged individuals were assumed to have been present in an enclosure between the first and the last capture because voles were not able to deliberately move between enclosures. To account for voles which were too light for PIT tagging the number of new fur cuts per fortnight was added to the calculated MNA.

Identification of dispersers

Identification of dispersers was based on the repeated trapping of individuals in the coverless and therefore unsuitable matrix of the enclosures. Areas with short vegetation cover are typically avoided by voles due a high predation risk and low food abundance (Bowers and Dooley 1993). Pilot studies in the enclosures between 2001 and 2003 have shown that (i) repeated trapping of a vole (ii) in at least two different matrix traps and (iii) within a short time period is suitable to identify individuals that are likely to leave the populations if they were unfenced. In the 2003 field season, a score system was established for the identification of dispersers in their natal populations by comparing actual dispersers with their preceding trapping history in the matrix. By connecting adjacent enclosures the number of dispersed individuals was recorded (about 9% dispersal rate) and subsequently the best fitting score system established which embraced 90% of the actual dispersers. The score system has following conditions:

$$G*V>13 \quad (1)$$

$$T<2*G \quad (2)$$

$$V>1 \quad (3)$$

This means that voles were identified as dispersers if the total number of captures G in the matrix traps multiplied by the number of different matrix traps V an individual entered exceeded 13. Furthermore, the number of days T from the first matrix capture to the actual date must not have exceeded twice the total number of captures, and a disperser had to be trapped in at least two different matrix traps. The onset of emigration was retroactively defined as the first day when a disperser entered a matrix trap, since I assume that the “decision” to emigrate was taken by a vole before it was scored as a disperser.

I defined residents as adult voles which were never or seldom trapped in the matrix traps and stayed in the relative safety of the habitat patches. Throughout the treatment periods in 2005 and 2006, in total 78% ($n = 176$) of the residents never entered any matrix trap, and 91% ($n = 207$) of them had a $G*V$ score of equal or below 13. The remaining 9% ($n = 20$) of residents exceeded the $G*V$ score of 13, but entered

the matrix traps over a time period longer than $2 \cdot G$ and, therefore, missed the threshold for identification as disperser.

The experiment was conducted in parallel in two separate enclosure systems (system 1 and system 2) with three different randomly chosen enclosure treatments within each system (Figure 1). The enclosure systems were not altered in 2005 and 2006, and trapping sessions during the treatment periods were conducted alternately in system 1 and system 2. Matrix traps were checked opportunistically until first voles began to enter the matrix in June 2005 and 2006, respectively. Thereafter, the matrix traps were checked daily.

Transfer of dispersers

To investigate immigration processes (see SPATIO-TEMPORAL BEHAVIOR, ESTABLISHMENT AND FITNESS CONSEQUENCES, and DEMOGRAPHIC AND GENETIC IMPLICATIONS, this volume), dispersers were transferred during field seasons 2005 and 2006. In 2004 no dispersers were transferred and enclosure populations, therefore, were completely isolated. The dispersers were transferred by hand as soon as they exceeded the threshold of disperser identification. The time lag from the first capture in a matrix trap to the transfer of a vole was seldom longer than a week. I transferred dispersers in one direction only from source to transition, and from transition to sink enclosures (Figure 1). If a disperser from a source enclosure did not establish in the transition enclosure and was identified as a disperser again, it was further transferred to the sink enclosure. Dispersers which were born in or transferred into a transition enclosure were only transferred to the corresponding sink enclosure, and dispersers born in sink enclosures were not transferred at all. I refer to the latter as frustrated dispersers (Lidicker 1975, see Johnson and Gaines 1987) because they were forced to stay in their natal population despite the obvious affinity to leave.

Molecular analyses

I extracted DNA from tissue samples using a standard phenol-chloroform protocol (modified by Sambrook et al. 1989). Vole samples were analyzed for the following 13 microsatellite loci multiplexed in two sets: Set 1: MM1, MM8, CRB5, MAG25, MAG6, MAR113; Set 2: MM2, MM6, Moe02, Mar049, MAR016, MAR 080, AVPRup (Heckel et al. 2005, Jaarola et al. 2007, Walser and Heckel 2008). I performed PCR amplifications with the Quiagen Multiplex kit using thermal cyclers PCR System 9700 (Gene Amp[®]) or PTC-100TM (MJ Research Inc.). Final PCR-programs for both multiplex sets consisted of a denaturation step at 94°C for 5 min, 30 cycles of 94°C denaturation for 1 min, 1 min of primer annealing at 57°C, and 1.25 min of primer extension at 72°C. A final step at 72°C for 10 min was used to complete primer extension. Fragments were separated and detected on an ABI 3100 sequencer (Applied Biosystems), and fragment length was determined in comparison to an internal size standard using Genemapper[™] software version 3.7 (Applied Biosystems). I re-amplified and scored previously genotyped individuals independently to ensure accuracy and consistency of genotyping across experiments (repetitions: Set 1: 165 individuals (13.1 % of 1255), Set 2: 193 (15.4% of 1255)).

EMIGRATION IN COMMON VOLE DISPERSERS: TRIGGERS AND TRAITS

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rodents

Abstract

It is widely accepted that dispersal plays a major part in population dynamics as well as in population genetics. Still, dispersal and its associated consequences constitute a big gap in our knowledge, which is mainly due to the difficulties in obtaining robust field data. In this study we used an experimental approach in semi-natural enclosures with individually marked common voles, *Microtus arvalis*. We combined classical capture-mark-recapture studies with molecular analyses to ascertain what proximate factors emigration trigger, and investigated morphological characteristics of dispersers as well as a potential genetic predisposition for the dispersal behavior. Males predominantly emigrated prior to the maximum population densities (i.e. as presaturation dispersers) and their dispersal rate was positively correlated with density increase. This surely enhances the success of male dispersers in finding reproductively active mates and still vacant sites to settle. The dispersal rate of females was associated with the proportion of residents in a population indicating that the propensity of females to disperse is dependant on social interactions. The male-biased dispersal rate and the relative high proportion of natal dispersers supported the inbreeding avoidance hypothesis. Based on the trapping history and reproductive state, three groups of voles were differentiated. Residents, defined as mature and stationary individuals, were the heaviest and reproductively most successful individuals. Philopatrics were stationary voles but never reached sexual maturity. They comprised the lightest individuals. While philopatric females might participate in nursing or defense against intruders, males may wait to sneakily mate as soon as the more competitive residents are absent or die. Male dispersers predominantly delayed the onset of reproduction and accelerated maturation at the time of emigration. This surely decrease agonistic interactions with residents in the natal population. Female dispersers showed a high dichotomy in their body-weight at emigration indicating that individuals eventually reach an age when their relatives' contribution to inclusive fitness is greater than their own. Despite various speculations of a genetic predisposition we missed to find any hint for a genetic inheritance of the dispersal behavior. Hence, dispersal seems to be a flexible behavior conducted by a morphologically distinct group of animals that is triggered by extrinsic factors rather than induced by a specific "dispersal gene". While females seem to increase inclusive fitness, male dispersers are likely to enhance individual reproduction in new populations.

Introduction

Dispersal, defined as an one-way movement of individuals away from their home range site (Lidicker and Stenseth 1992), has been considered a “glue” linking otherwise isolated populations, and it plays a major part in the demography of populations as well as in their genetic composition (e.g. Andreassen and Ims 2001, Clobert et al. 2001b, Lidicker 2002, Bowne and Bowers 2004, Aars et al. 2006). Dispersal may be seen as comprising three sequential, but behaviorally different, phases: emigration, travel and immigration (see Andreassen et al. 2002). The phase of emigration initiates the dispersal process as the dispersing individuals leave their area of residence. From the individuals’ perspective, emigration, or, conversely, remaining behind, will affect both fitness relevant parameters, reproduction and survival (Clobert et al. 2001a). While dispersers are known to have a high risk of starvation or of being preyed upon (Andreassen and Ims 2001, Smith and Batzli 2006; but see McGuire et al. 1993), philopatry carries a potential cost of intraspecific competition, as well as a risk of inbreeding (Clobert et al. 2001b, Lambin et al. 2001, Aars et al. 2006, Höner et al. 2007, Lawson Handley and Perrin 2007).

To understand emigration, both the mechanisms that initiate dispersal (see below) as well as potential characteristics that differentiate dispersers from stationary individuals have to be considered. This combined approach is essential since initiating mechanisms will surely not induce all animals in a population to emigrate but individuals with a particular propensity to disperse. It is hypothesized that dispersers are not a random subset of a population, but morphologically and/or genetically different from residents (O’Riain et al. 1996, Clobert et al. 2001c, Cote et al. 2007), and the hypothesis that dispersers might be genetically distinct from residents has long been the subject of speculation and investigation (e.g. Lidicker 1975, Gaines and McClenaghan 1980, Keith and Tamarin 1981, Waser and Jones 1989, Krebs 1992, Boonstra and Hochachka 1997, Roff and Fairbairn 2001). Still, the possibility that dispersers constitute a morphologically and/or genetically distinct group remains speculative (Lidicker 1985).

Mechanisms that initiate dispersal have to be distinguished between ultimate causes, which require the establishment of a behavior as an evolutionary stable strategy (ESS), and proximate triggers, defined as those external stimuli which directly initiate or maintain biological processes. Ultimate causes for dispersal are explained by the competition for food and mates, being directly linked with the density in the natal population, as well as by an inbreeding avoidance (Liberg and von Schantz 1985, Gandon and Michalakis 2001, Lambin et al. 2001). Inbreeding avoidance was supported by a sex-biased dispersal rate (Greenwood 1980, Dobson 1982, Wolff 1992, Bollinger et al. 1993, Gundersen and Andreassen 1998), the dependency between dispersal distance and social structure (Jacquot and Vessey 1995, Gundersen and Andreassen 1998), as well as by the preference to mate with non-related partners (Lidicker and Stenseth 1992). In contrast to the relative well-established ultimate causes a large, and controversially discussed, array of proximate triggers has been proposed (Waser and Jones 1989, Lidicker and Stenseth 1992, Andreassen and Ims 2001, Clobert et al. 2001b). These range from social factors, temporal and spatial variation in habitat quality and habitat structure, to interspecific interactions such as predation and parasitism (see Andreassen et al. 2002 and references therein).

The most investigated proximate trigger for emigration is probably population density (e.g. Wolff 1992, Aars and Ims 2000, Andreassen and Ims 2001, Ferreras et al. 2004), which is directly correlated with resource competition. Here, Lidicker (1975) defined two different types of dispersers: those that emigrate before the maximum population density is reached (i.e. presaturation dispersers) and individuals that leave their natal population at or after population maxima (i.e. saturation dispersers). While saturation dispersers are thought to be competitively inferior and evicted, presaturation dispersers are probably risk prone individuals that leave their natal population voluntarily.

Despite the importance of dispersal, mechanisms that trigger emigration, and differentiating characteristics of dispersers, remain poorly understood (Wiens 2001). This is mainly due to the difficulties in obtaining empirical data (Kenward et al. 2002). Since it is impossible to know in advance what individual will emigrate, when it will emigrate, and where it will go, the study of dispersal remains difficult under completely natural conditions. As a consequence, works are often theoretical or based on anecdotal evidence.

In the present study experiments were conducted in an attempt to ascertain (i) what proximate factors (i.e. direct factors) might trigger emigration. Here, we concentrated on demographic parameters like fluctuating density, sex ratio, and proportion of residents, as these parameters will change the social interaction between conspecifics. Furthermore, we aimed to detect (ii) morphological differences between residents and dispersers, as well as to figure out if dispersal behavior is genetically inherited. The study was conducted in semi-natural enclosures with the common vole (*Microtus arvalis* Pallas) as a model organism and we combined classical capture-mark-recapture methods (triggers and morphological traits) with genetic analyse (genetic predisposition). For the identification of dispersers and stationary individuals, respectively, an established score system based on the trapping history of individually marked voles was used.

Methods

For field site and trapping, identification of dispersers, transfer of dispersers and molecular analyses see GENERAL METHODS.

Based on both, trapping locations and reproductive state, it was not only possible to distinguish between residents, that reached maturity, and dispersers (see GENERAL METHODS), but to define another stationary group that strictly avoided the matrix but did not reach sexual maturity at any time of the investigation. These individually marked voles included juveniles as well as subadults, latter suppressing maturation. This group was termed *philopatrics*.

For the calculation of body-weight increase only voles which were 15 g or lighter at first individual marking were tested. This was done to roughly estimate the voles' minimum age (Reichstein 1964) and to compare changes of reproductive state and body-weight between stationary individuals (i.e. residents and philopatrics) and dispersers.

Parentage assignment and statistics

To quantify natal and breeding dispersers and to ascertain a potential inheritance of dispersal behavior parentage assignments were attempted for a total of 1142 genetically analyzed voles in 2005 and 2006. For parentage assignments, genotypic information was employed in combination with observational data on trapping dates, trapping sites, body-weight, and reproductive states. Genetic assignments were performed by applying a combined strategy of parentage exclusion and the likelihood approach implemented in the program Cervus 3.0.3 (Marshall et al. 1998). For a more detailed description see ESTABLISHMENT AND FITNESS CONSEQUENCES (this volume and Heckel and von Helversen 2003). The mean allele number per locus over all years and enclosures was 9.2 ± 1.3 in 2005 and 9.9 ± 1.4 in 2006. The total exclusionary power with which the microsatellite loci excluded an unrelated candidate parent was, on average, $99.8\% \pm 0.2$. Simulations which are required for likelihood-based parentage assignments in Cervus were run with 10,000 cycles, a typing error rate of 0.01, and a proportion of 80% sampled candidate parents. The 80% proportion actually was a conservative estimate, because capture and recapture rates within the enclosures were high (see Results). The assignment rate which indicates the proportion of genotyped voles for which one univocal father or mother was determined was, on average, $61\% \pm 13.8$.

Further statistical analyses were done using SPSS for Windows 15.0.1. We applied Bonferroni-corrections whenever conducting multiple comparisons. If not stated otherwise, values are presented as means \pm one standard deviation (1 SD).

Results

During the 2005 and 2006 field seasons we individually marked 1630 voles. On average, the marked individuals were retrapped 9.6 ± 14.7 times. Including matrix traps, the bi-weekly recapture rates were significantly higher in males than in females ($92.1\% \pm 17.2$ vs. $91.5\% \pm 11.7$; Mann-Whitney-U; $z = -3$, $p = 0.003$) and higher in dispersers than in residents ($91.5\% \pm 11.7$ vs. $87.9\% \pm 15.3$; $z = -7.976$, $p < 0.001$). Densities in 2005 and 2006 were highest in September with 58 ± 19.9 voles per enclosure in 2005 ($286 \text{ individuals} \cdot \text{ha}^{-1}$) and 52.33 ± 15.3 individuals in 2006 ($258 \text{ individuals} \cdot \text{ha}^{-1}$; Figure 1A). We recorded lowest densities in April 2005 and May 2006 with five individuals and less in all enclosures except in one enclosure in 2005 (minimum 6) and one in 2006 (minimum 17; see ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume).

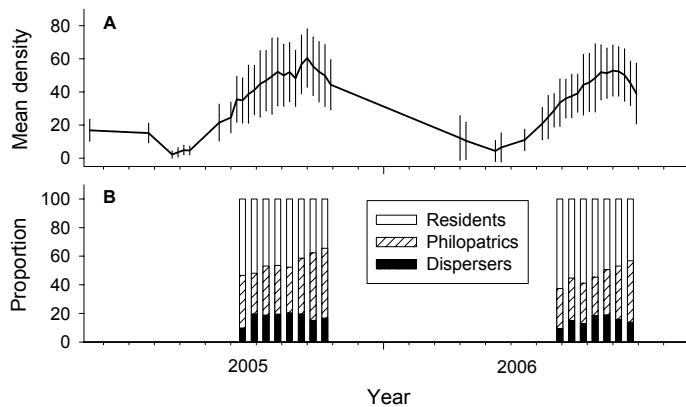


FIGURE 1 A: Mean density measured by MNA. Error bars show ± 1 SD. B: Mean proportions of residents, philopatrics, and dispersers during the disperser period displayed for intervals of two weeks. Residents were defined as stationary voles that reached maturity, whereas philopatrics were stationary but did not reach maturity at any time of the investigations. The latter group included juveniles as well as subadults.

In 2005 and 2006, the first dispersers appeared in July (week 28 in 2005 and week 30 in 2006; Figure 1B). In total, 132 dispersers were identified in 2005 and 93 dispersers in 2006. Towards the end of the field season we recorded a decreasing proportion of residents (i.e. stationary individuals that reached maturity) and an increasing proportion of philopatrics (i.e. stationary but immature voles; Figure 1B).

Proximate triggers for dispersal

The bi-weekly dispersal rate was significantly higher for males than for females (0.095 ± 0.095 vs. 0.045 ± 0.054 ; Mann-Whitney-U; $z = -3.83$, $p < 0.001$; Figure 2 A). To ascertain what factors trigger emigration male and female dispersal rate was correlated with population density, population increase/decrease (i.e. population change), sex ratio, and proportion of residents. We did not find any significant correlation between dispersal rate and population density (Pearson; males: $r = 0.093$, $p = 0.37$; females: $r = 0.192$, $p = 0.06$; Figure 2A). For male dispersers, however, presaturation dispersal (i.e. dispersers which emigrated before population maxima were reached) was higher than saturation dispersal (0.11 ± 0.1 vs. 0.07 ± 0.08 ; t-Test; $t = 2.013$, $p = 0.047$; Figure 2B). Females showed an opposite tendency, but this was not significantly different (0.039 ± 0.044 vs. 0.0533 ± 0.065 ; t-Test; $t = -1.256$, $p = 0.213$).

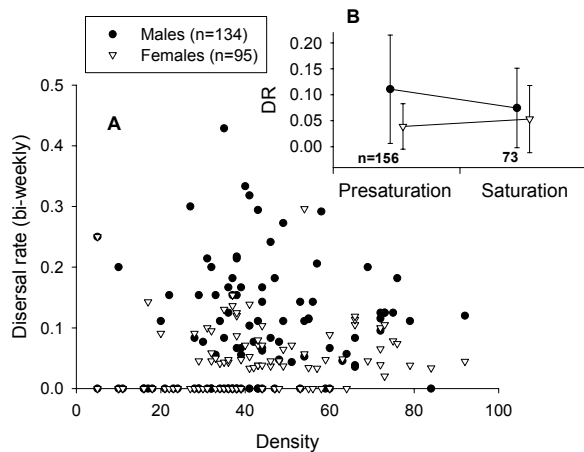


FIGURE 2 A: Bi-weekly dispersal rate of males and females over population densities. B: Bi-weekly dispersal rate (DR) for the period before maximum densities were reached (i.e. presaturation dispersal) and for the period at or after density maxima (i.e. saturation dispersal). Error bars indicate 1 SD over years 2005 and 2006 and enclosures.

As for the population density, no correlation was apparent between dispersal rate and sex ratio (Pearson; males: $r = 0.19$, $p = 0.064$; females: $r = -0.182$, $p = 0.075$). However, there was a positive non-linear correlation with population change for males ($r = 0.245$, $p = 0.018$; Figure 3) and a negative linear correlation with the proportion of residents for females ($r = -0.14$, $p = 0.036$; Figure 3).

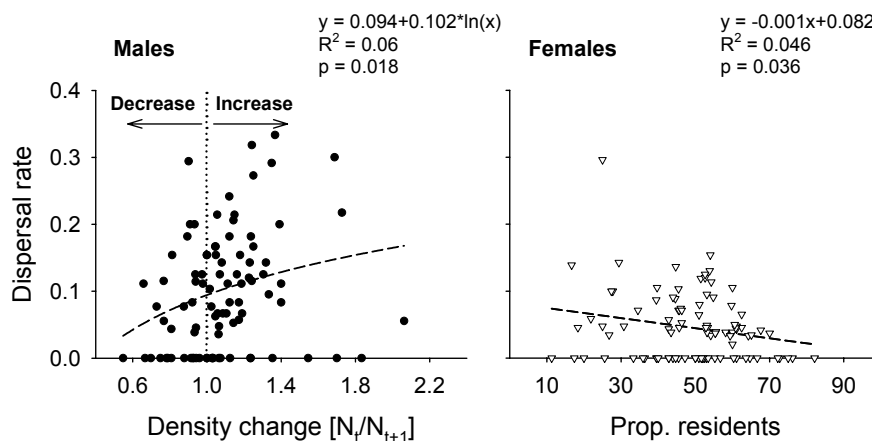


FIGURE 3 Correlation between bi-weekly dispersal rate and density change for males (left) and proportion of residents for females (right). Dashed lines show logarithmic and linear regression, dotted line in the male graph represents stable state of neither increase nor decrease.

Morphological traits of dispersers

Body-weights were significantly higher in residents than in dispersers during the week of emigration. This was true for males ($26.86 \text{ g} \pm 6.62$ vs. $24.31 \text{ g} \pm 6.16$; t-Test; $t = 3.56$, $p < 0.001$) as well as for females ($24.68 \text{ g} \pm 5.89$ vs. $20.75 \text{ g} \pm 6.09$; $t = 6.49$, $p < 0.001$). For females especially, we recognized a bimodality in the dispersers' body-weight distribution (Figure 4). Male presaturation dispersers were significantly heavier than saturation dispersers ($25.11 \text{ g} \pm 5.58$ vs. $22.43 \text{ g} \pm 7.31$; t-Test; $t = 2.264$,

$p = 0.025$; Figure 4). In contrast, female presaturation dispersers were somewhat lighter than saturation dispersers, but this difference was not significant ($20.82 \text{ g} \pm 5.88$ vs. $21.64 \text{ g} \pm 6.92$; $t = -0.636$, $p = 0.526$).

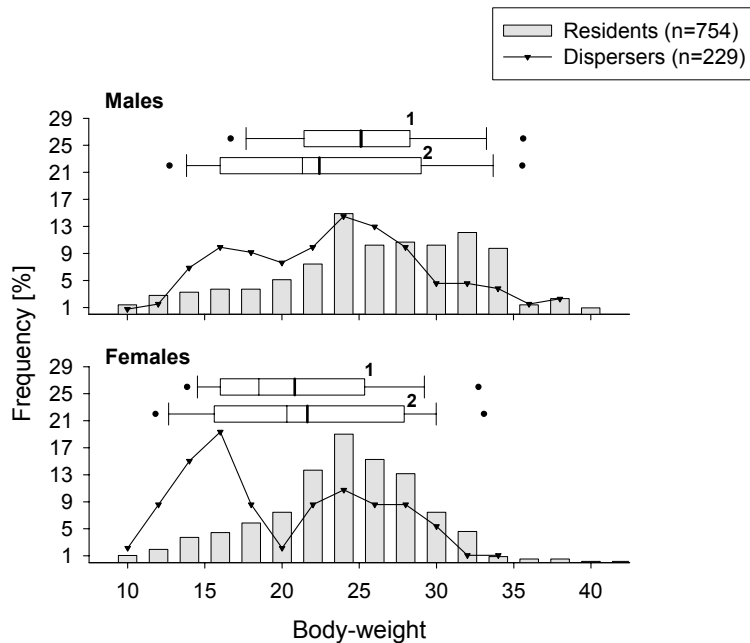


FIGURE 4 Body-weight distribution for residents (bars) and dispersers (lines) separated for males and females. Residents were defined as stationary adults, i.e. voles that did not disperse and that had reached maturity. Values for residents are means of individually marked voles over the entire field seasons 2005 and 2006. Body-weights of dispersers are given for the week of dispersal. Box plots above the graphs represent body-weight for male and female dispersers separated between presaturation dispersers (1) and saturation dispersers (2). Boundaries of the boxes are 25th and 75th percentiles; the whiskers represent 10th and 90th percentiles, and outliers show 5th and 95th percentiles. Thin lines in the box plots represent medians, bold lines are mean values.

Most male and female dispersers were mature at a minimum age of 29 days, whereas most stationary male individuals were still immature at an age of 43 days (i.e. philopatric; Figure 5 A). Female dispersers and residents showed an almost linearly increasing proportion of mature individuals. Male dispersers, on the other hand, heavily accelerated maturation between the 15th and 29th day. The sudden maturation coincided with emigration (c.f. Figure 4 and Figure 5 B). For both males and females, we found the three groups residents, philopatrics, and dispersers to have significantly different body-weights. In most age classes residents showed highest body-weights, whilst the lowest were found in philopatrics (ANOVA; all p after Bonferroni-correction < 0.001 ; Figure 5 B). Differences in the body-weight between the three groups were increasingly large over the individuals' age.

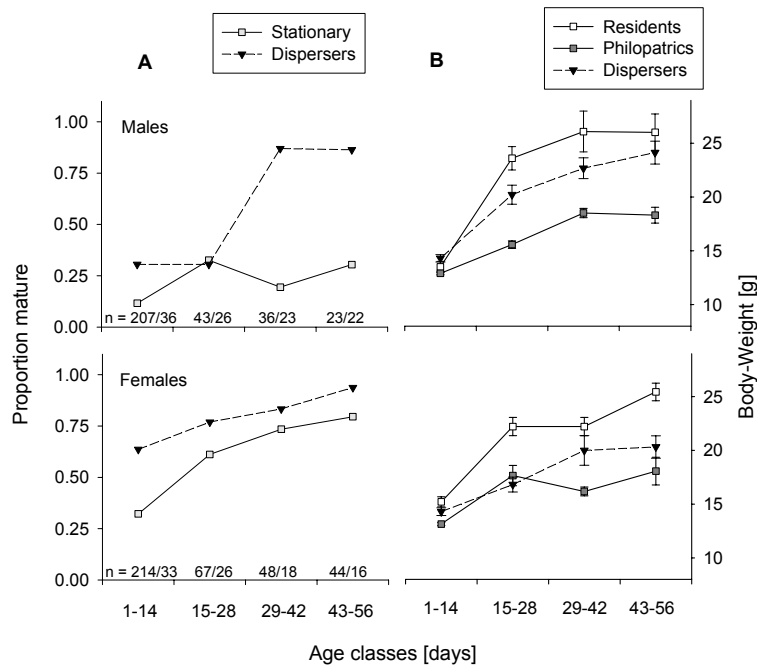


FIGURE 5 A: Proportion of mature, i.e. adult individuals over minimum age, separated for males and females and for stationary voles and dispersers. Within the stationary group, y-values indicate residents, 1-y are philopatrics. First number at the bottom represent the number of stationary individuals, the second number are the numbers of dispersers. B: Development of body-weight for males and females and separated for residents, philopatrics, and dispersers. For calculations, only voles with a body-weight of 15 g or lighter at first individual marking were considered. Error bars show 1 SE. All body-weights between groups and within each age class were significantly different after Bonferroni-correction (all $p < 0.001$).

Reproductive and genetic traits of dispersers

Altogether 44 of initially 1142 genotyped voles had the same genetic identity. This was most probably due to a 4% loss of PITs and, therefore, due to a double sampling of individuals. These 44 voles were excluded from the entire data set and analyses, respectively. The residual 1098 genotyped voles correspond to 67.4% of all 1630 marked individuals. Sixteen percent of the genotyped voles were dispersers (178 of 1098), and 15% residents, based on their trapping history (163 of 1098). The remaining 69% (757 of 1098) were immature philopatrics. Although the mean number of alleles considerably varied over loci, no significant differences were observed among years (Kruskal-Wallis; $\text{Chi}^2 = 3.193$, $p = 0.203$). This was due to the introduction of new genetic variation by the release of additional voles in spring 2005 and 2006 (see DEMOGRAPHIC AND GENETIC IMPLICATIONS, this volume).

Genetic assignment analyses revealed that 64.4% of the residents (105 of 163) and 28.1% of the dispersers (50 of 178) reproduced in the natal populations, with a relative higher proportion of breeding dispersers in females (Figure 6). We also found relatively more breeding dispersers within individuals that emigrated before maximum population density was reached (i.e. natal dispersers). Natal dispersers were significantly lighter than breeding dispersers during the week of emigration. This was true for males ($22.821 \text{ g} \pm 5.495$ vs. $29.562 \text{ g} \pm 6.769$; t-Test; $t = -4.958$, $p < 0.001$) and females ($18.136 \text{ g} \pm 4.669$ vs. $25.919 \text{ g} \pm 3.959$; t-Test; $t = -7.186$, $p < 0.001$).

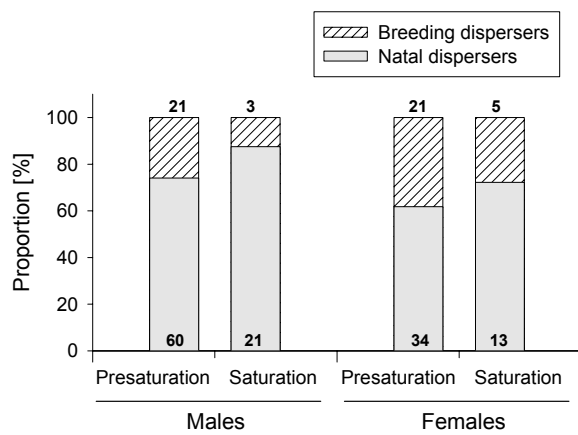


FIGURE 6 Proportions of breeding and natal dispersers within presaturation and saturation dispersers and separated for males and females. The numbers above and at the bottom of the bars are total numbers of breeding and natal dispersers, respectively. Natal dispersers were significantly lighter than breeding dispersers (see text).

If emigration behavior is strictly inherited a relative higher dispersal tendency in dispersers' offspring compared to residents' offspring would be expected. However, assignment analyses revealed that the proportion within dispersers' and residents' offspring was not significantly different (0.19 ± 0.3 vs. 0.14 ± 0.24 ; Mann-Whitney-U; $z = -0.699$, $p = 0.484$; Figure 7; power analysis; $1 - \beta = 0.106$). Again, this was true for males ($z = -0.073$, $p = 0.942$) and females ($z = -1.034$, $p = 0.301$).

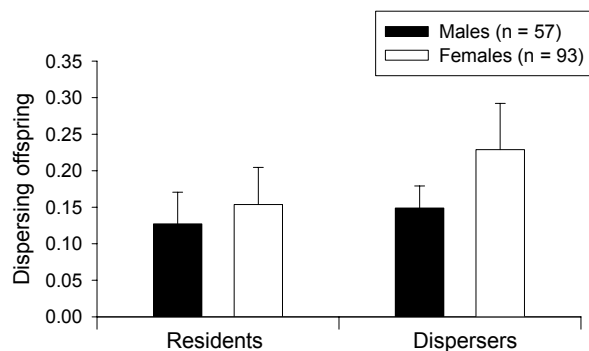


FIGURE 7 Proportion of residents' and dispersers' offspring that were defined as dispersers. If strictly inherited a much higher dispersal tendency of dispersers' offspring would be expected. Error bars indicate 1 SE

Discussion

The investigation of common voles (*Microtus arvalis*) in semi-natural enclosures combined with extensive capture-mark-recapture data revealed proximate triggers which seemingly caused emigration, as well as morphological characteristics that differentiated dispersers from stationary individuals. No evidence was found, however, for a genetic inheritance of dispersal behavior. While male emigration propensity seems to be affected by changes in density, female emigration rate was associated with the proportion of residents in the population. Morphological differences between dispersers and stationary

individuals were apparent in early age classes, already manifested prior to maturation. As we found no evidence for a genetic inheritance of emigration behavior it is highly likely that the dispersal probability is dependant on early morphological condition of individuals. Such individuals should be especially prone to those demographic triggers that initiate dispersal.

Emigration triggers

In contrast with other small mammal studies, neither male nor female dispersal rates significantly correlated with density in this investigation (Aars and Ims 2000, Hanski 2001, Gundersen et al. 2002, Smith and Batzli 2006; but see Gaines and McClenaghan 1980, Gaines and Johnson 1984, Sandell et al. 1991). Dispersal rates in males, however, were positively correlated with density increase. Increasing population densities surely enhance intraspecific competition and, as Hahne et al. has shown (see ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume), agonistic encounters were especially high in male dispersers. This could well be due either to active evictions by superior conspecifics or to a higher interaction with residents as a consequence of the propensity to disperse. In any case, dispersers clearly had a lower reproductive success in their natal populations and a comparatively lower body-weight than residents. Enhanced dispersal rates during population increase, combined with the present finding of a significantly higher presaturation dispersal, should increase males' success in finding reproductively active mates and still vacant sites to settle, respectively (see Gaines and McClenaghan 1980). Dispersal clearly relieves competition in the natal populations and increases the chances of successful reproduction in new populations, particularly when dispersal is conducted before maximum densities are reached (i.e. presaturation dispersal). Additionally, the chance of a successful establishment seems to be higher in presaturation dispersers as these were significantly heavier at the time of emigration compared with saturation dispersers. Hence, dependant on the strength of competitive interactions in the natal population, early dispersal can outweigh the high risk during the travel phase.

Females, however, emigrated about equally as presaturation and saturation dispersers and their dispersal rate was found to be negatively correlated with the populations' proportion of residents. Thus, dispersal in females seems to be predominantly dependant on the voles' social interactions. Boyce and Boyce (1988a) found female common voles to form social clusters of related individuals and they showed dispersal only in solitary breeding individuals. Females in clusters may gain fitness benefits as a result of cooperative foraging and feeding, group defense and assistance in thermoregulation, which thereby promotes philopatry (Gaines and McClenaghan 1980, Hayes 2000, Ylönen and Horne 2002, Le Galliard et al. 2006, Lawson Handley and Perrin 2007). If residents constitute the social center of a cluster, a relative decrease of residents should lead to a higher dispersal motivation among females (c.f. McGuire et al. 1993).

The dispersal rate in this study was heavily male-biased, a fact undoubtedly due to the polygynous mating system which is prevalent in most mammalian species (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). While female reproductive success is primarily dependant on food availability,

males have to compete for access to females (Bondrup-Nielsen, 1993, Aars and Ims 2000). To avoid inbreeding, males should emigrate before reproducing in their natal population (i.e. as natal dispersers). The relative high proportion of male natal dispersers seems to support such a view of inbreeding avoidance. It is doubtful, however, that inbreeding avoidance can increase the motivation of dispersers to emigrate (see Perrin and Goudet 2001). It is more likely that the relative low reproduction rate of dispersers prior to emigration was due to a high intraspecific competition in the natal population.

Morphological traits of dispersers

Based on the spatial behavior and reproductive state, three groups of voles were defined which significantly differed in their body-weight. It is likely that these groups follow different social and reproductive strategies to optimize their direct and inclusive fitness, respectively.

A high, but fluctuating proportion of individuals that resided in the populations stayed reproductively immature. We termed these individuals philopatrics in order to show their stationary behavior and to differentiate them from residents which were defined as voles that participated in reproduction. Residents and philopatrics significantly differed in their body-weight with much heavier residents, whereas the body-weight of male and female dispersers was in-between residents and philopatrics in most age classes (c.f. Gaines and McClenaghan 1980, Aars and Ims 2000, Gundersen et al. 2002). Male dispersers predominantly delayed the onset of reproductive activity and they accelerated maturation at the time of emigration. By not participating in reproduction, dispersers surely reduced agonistic encounters with residents in their natal population.

The body-weight of all three groups differed already at an early stage in the voles' life and these differences increased with the age of the individuals concerned. This might have been due either to extrinsic factors like variations in nutrition or stress, or was genetically determined. Either way, comparatively high body-weights and high reproductive rates, respectively, indicate that resident voles are competitively superior. As female voles were described to form kin clusters (Boyce and Boyce 1988a, Ishibashi 1997) philopatric females may participate in nursing or defense against intruders and, therefore, increase their inclusive fitness. Male voles, in contrast, are more loosely connected with their colony (Mackin-Rogalska 1979), and philopatric males might wait for a chance to sneakily mate as soon as the more competitive residents are absent or die.

Dispersers obviously take the risk of travel which may pay off in high reproductive success when establishment is successful. The dichotomy which was especially apparent in female dispersers' body-weight might occur because parents eventually reach an age when their progeny's contribution to inclusive fitness is greater than their own (Morris 1982). Hence, the benefits of each group are a dynamic trade-off in the life history of an animal being dependant on the proportion of individuals in the respective other groups. An individual should, therefore, disperse as soon as the expected fitness (i.e. survival and reproduction) is greater than staying in the natal population and consequently being suppressed by the more competitive residents (Morris 1982, Wolff 1992; c.f. Krebs 1978). Here, male dispersers seem to be

more concerned about individual reproduction in the new populations while females may predominantly gain by inclusive fitness.

Genetic traits of dispersers

Despite widespread speculations of a genetic predisposition (Waser and Jones 1989, Krebs 1992, Boonstra and Hochachka 1997, Roff and Fairbairn 2001) no hint of a genetic predisposition of dispersal behavior was found. Rather, the offspring of dispersers did not have a higher tendency to emigrate than the offspring of residents. This is in accordance with studies by Boonstra and Hochachka (1997) on the collared lemming *Dicrostonyx groenlandicus* who also found no additive genetic inheritance of dispersal behavior. If this is so, dispersal is context dependant whilst emigration is a flexible behavior conducted by a morphologically distinct group of animals triggered by extrinsic factors as discussed above. Whilst females seem to increase inclusive fitness, males are likely to enhance individual reproduction.

SPATIO-TEMPORAL BEHAVIOR OF COMMON VOLE DISPERSERS

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**Key words: Dispersal, common vole, emigration, immigration, *Microtus arvalis*, rodents,
radio tracking, passage counter**

Abstract

During the last decades much effort was devoted to the investigation of dispersal, defined as an “one-way movement of individuals away from their home range site”. Still, dispersal and associated phenomena remain poorly understood. In this study we used an experimental approach in semi-natural enclosures with individually marked common voles (*Microtus arvalis*). Classical capture-mark-recapture studies and intensive radio tracking of 55 voles revealed the spatio-temporal behavior of dispersers in their natal populations (i.e. emigrants) and in new populations (i.e. immigrants). The data highly suggest that voles’ spatio-temporal behavior reflects a balance between the avoidance of intraspecific competition and an avoidance of predation risk. Several studies have stated an increased risk of predation at habitat edges which was supported by an overall preference of the habitat interior and an avoidance of edge sections, respectively. A predominant use of interior sections by dispersers, however, went along with a highly asynchronous activity with resident conspecifics. This temporal avoidance surely implicates a reduced participation in social and reproductive activity. While emigrating males predominantly used the habitat interior, female emigrants were mainly found at edge sections. It is, therefore, likely that female emigrants rather take the risk of being preyed upon than not taking part in social interactions. A use of more risky edge sections surely enhances the predation risk but decreases intraspecific competition. The spatio-temporal behavior was reverse in immigrating dispersers. While female immigrants preferred habitat interior, male immigrants predominantly used edge sections, indicating different motivations and strategies in male and female dispersers. Female immigrants apparently avoided predation risk and male immigrants may try to take part in reproductive activity. Dispersers left the habitat patches and entered the matrix synchronously at dawn and dusk. Following the “safety in numbers”-hypothesis this should reduce predation risk during travel. Dispersers’ activity were generally enhanced, especially when entering a new population. Over the three days of radio tracking immigrants maintained an increased activity-level. This indicates low establishing success, and might lead to high dispersal distances. Although the resident populations were not affected by dispersal in their temporal behavior, a high turnover of dispersers seem to cause shifts in the residents’ activity range.

Introduction

During the last decades much effort has been devoted to the investigation of dispersal, defined as an one-way movement of individuals away from their home range site (Lidicker and Stenseth 1992, Clobert et al. 2001, Gundersen et al. 2002). Dispersal has received particular attention with regard to habitat fragmentation because of its ability to link otherwise isolated populations (Gaines and McClenaghan 1980, Wiens 2001). Human activities have to an increasing extent resulted in a more extensive landscape fragmentation (Forman and Godron 1986) with presumed negative consequences for the affected organisms (Hovland et al. 1999). Although it is widely accepted that dispersal plays a major part in the life history of a species as well as in population regulation (Gundersen et al. 2002, Lidicker 2002) dispersal remains one of the most studied yet least understood concepts in ecology and conservation biology (Clobert et al. 2001). This is mainly due to the difficulties in receiving reliable field data on the behavioral strategies of dispersers (Aars and Ims 2000, Kenward et al. 2002). Dispersal is a seldom event and it is impossible to predict in advance which individual will disperse and where it will go. Although a large body of literature exists concerning animal movements, studies are predominantly theoretical, based on anecdotal observations, or focused on dispersal emigration as a mechanism of population regulation (Sandell et al. 1991). Because of the severe methodical problems empirical work on the individual behavior of dispersers are still rare (but see Höner et al. 2007).

Considering the tremendous mortality risk of up to more than 90% during dispersal (Andreassen and Ims 2001, Smith and Batzli 2006; but see McGuire et al. 1993) it is most likely that emigration from the natal population is not a simple *ad hoc* decision, but rather has to balance the costs and benefits of dispersal in terms of fitness consequences. It is heavily debated if dispersal proneness is due to a genetic predisposition of the individual, or if it is triggered by extrinsic factors like intraspecific competition in particular (Keith and Tamarin 1981, Waser and Jones 1989, O'Riain et al. 1996, Boonstra and Hochachka 1997). Even if not generally weak or socially outcast (see ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume) we assume that dispersers might actively avoid interference with residents. Emigration was found to be density dependant in several studies (Gaines et al. 1979, Gaines and McClenaghan 1980, Andreassen and Ims 2001) and we frequently observed lesions in dispersers in our experiment (see ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume), so competition with residents is most likely to play a major part for the dispersers' propensity to emigrate from their natal population.

Enhanced competition between residents and dispersers can be avoided in two different ways. First, habitat sections could be used differentially in order to avoid competitive interactions locally. If so, the spatial behavior of residents and dispersers might conceptually be interpreted in terms of an ideal free distribution (IFD; Fretwell and Lucas Jr 1970) which assumes that individuals are free to choose locations such that they optimize fitness relevant parameters like survival and reproduction. The fitness of an individual is, therefore, determined by both its phenotype, and the environment it experiences (McPeck and Holt 1992). Dispersers that occupy habitat edges, for example, adjoin fewer territorial boundaries from residents than in the interior of sections, which could reduce competition (Bowers and Dooley

1999). Groups of individuals with different social states like residents and dispersers might, therefore, occupy different sections within habitat patches. Second, activity timing is a relatively flexible behavior in many species (Meyer and Valon 1999). To avoid competition with conspecifics, individuals might adapt their activity pattern in order to minimize antagonistic interactions (Halle and Stenseth 2000). If, for example, residents are active during daytime, dispersers may shift their main activity phase into the night and vice versa. There might also be an interaction between spatial and temporal activity (Meyer and Valon 1999). Individuals that occupy habitat edges are more exposed to predation (Andr en 1995 and references therein, Brand and George 2000). Daily variation in predation risk may, therefore, affect the activity behavior of the potential prey. Predator avoidance is especially important for dispersers at the time of dispersal as they typically leave safe habitat patches and pass hostile and risky areas, which is generally assumed to cause the much higher mortality rates in comparison to stationary individuals (Gaines and McClenaghan 1980, Lidicker 1985, Johnson and Gaines 1990, Andreassen and Ims 2001, Smith and Batzli 2006; but see Boyce and Boyce 1988a). Hence, it is not only crucial for an individual where to be active, but also when the activity is performed.

The dispersal process itself is governed by a high amount of activity. This will result in more frequent interactions between dispersers and residents and might lead to increased antagonistic behavior especially in the new population. Residents may try to exclude dispersers because they compete for resources as well as opportunities of reproduction, and may even kill unrelated offspring in an attempt to establish their own territories (Hayes et al. 2004). As a consequence, residents may adapt temporal behavior to defend their territory, or frequent disturbances by dispersers might force them to shift or even leave their home range. Moreover, competitive interactions within natal activity ranges are probably different in quality and quantity than in foreign ones, especially when assuming that dispersers in natal populations are more related to the local residents. This might be reflected in the spatio-temporal behavior of dispersers in their natal populations (i.e. as emigrants) on the one hand, and in the new populations (i.e. as immigrants) on the other hand. It is reasonable, therefore, to distinguish between behavioral patterns prior to or during the phase of emigration, and the spatio-temporal activity during the phase of immigration, i.e. during the attempts to establish in a foreign social environment.

Since we are far from having a comprehensive understanding of the role of space in individual dynamics (Clobert et al. 2001b) scrutinizing activity behavior can give hints on spatio-temporal attraction or avoidance of locations or conspecifics. The study of travel and settlement processes of dispersers hence provides a better understanding of how dispersers behave spatio-temporally, which has important implications for other fields of study such as conservation biology (Peles 1999).

In this study we wanted to reveal (i) the space use pattern of dispersers and their activity timing within natal and new populations, and (ii) their temporal behavior compared to resident conspecifics. As a potential effect of disperser attendance we also investigated (iii) the spatio-temporal behavior of residents. We used common voles, *Microtus arvalis* (Pallas), in semi-natural enclosures as a model system and

combined standard capture-mark-recapture methods with intensive radio tracking and automatic activity recording.

Methods

For field site and trapping, identification of dispersers, and transfer of dispersers see GENERAL METHODS.

Activity recording

Most small mammals are secretive and/or nocturnal in habits, making observation of dispersal difficult. The only means to monitor the movements of individuals directly involves radio tracking (Getz et al. 1992). Between August and October 2005 and 2006 (Figure 1) we radio tracked altogether 13 residents, 14 dispersers in their natal populations (behaviorally categorized as emigrants), and 28 dispersers which we transferred into a new enclosure population (categorized as immigrants; Appendix). For radio tracking we used two different types of tags to assure that transmitters never exceeded 10% of the body weight of voles (in accordance with the guidelines of the American Society of Mammalogists 1987). Individuals heavier than 20 g were fitted with a 2 g radio-collar (TW-4, Biotrack), while young that were lighter than 20 g got a small 0.8 g collar (Pip, Biotrack). Both types of radio-collars were fixed to the neck using a cable tie. During the radio tracking sessions, which lasted for three days each, live trapping was paused. For localization of the collared voles we used point antennas, consisting of a modified 5 m long fishing rod with a fixed coaxial cable. The long fishing rod allowed us to reach each point of the enclosure from one of five defined pathways within the habitat patches. The paths were also used for checking the traps to avoid extensive trampling of the vegetation. Radio tracking fixes were taken every 30 min. and control dummies which were hidden into the habitat vegetation revealed an average precision of ± 1 m. After radio tracking, trapping was continued and radio-collars were removed at the next capture.

For automatic recording of above-ground movements we used "passage counters", placed in the voles' surface runways. Passage counters consist of a 5 cm long PVC pipe with a wire gate hinged to the top (Lehmann and Sommersberg 1980, Halle and Lehmann 1987). When an animal moves through a counter, the wire gate is pushed upwards and activates a reed switch by an attached magnet. The initiated short current impulses were recorded with "Miniscript event-recorders" (Metrawatt, Germany) on time-labeled paper stripes and counted for 30 min. intervals. Fifteen passage counters were distributed in each of the six enclosures' habitat patches from August 22 to October 15. For each enclosure we separately summed up the activity counts for five consecutive ten-day periods. Between October 19 and October 29 we moved the passage counters of two enclosures into the matrix area while the passage counters of four enclosures were left in the habitat patches.

Between July and October 2005 and 2006 we calculated shifts of activity range centers of resident voles. For the computation of the activity centers we used resident individuals which were trapped at least three times within a month. Activity centers were then calculated by the Kernel center of the minimum convex polygon (MCP) spanned by each voles' trapping locations (see below). Activity centers were

calculated for each month separately and distances between centers were determined.

Statistics

Home range is the area that an animal uses for its normal activities. Since dispersal does not belong to an everyday routine activity, we defined the area that is traversed at dispersal as activity range instead of home range, and for consistency, we will also use this more broad term for resident individuals. We calculated activity ranges, activity centers, Jacob's indices, and running distances of the radio tracked voles by using the software package Ranges VI (Kenward et al. 2003). Activity ranges were estimated by MCPs (95%) and Kernel (95%) method (Worton 1989). We used the Jacob's index (Jacobs 1974) to quantify spatial attraction or avoidance of the voles towards the enclosure sections interior, edge, and matrix:

$$D = \frac{r - p}{(r + p - 2 \cdot r \cdot p)} \quad (1)$$

in which r is the proportion of location fixes within the respective section, and p depicts the proportion of the section at the entire habitat (including matrix).

To support radio tracking data of potential section attraction or avoidance, we additionally calculated the relative use of interior and edge traps for each individual and for residents and dispersers separately. Due to the different number of interior and edge traps we z-transformed the entire data set (Bortz, 1999), receiving a relative measure of edge affinity. Positive numbers mean, in our case, a relative attraction towards the edge, while negative values state a relative avoidance of the edge and attraction to the interior, respectively.

We used the mean running distances per 1/2 h from the radio tracking sessions 2005 and 2006 and the passage counter data from 2006 to calculate an index of diurnality as well as an index of crepuscularity (Halle 1995, Halle and Weinert 2000). The diurnality index (I_D) compares the number of counts recorded by passage counters during daytime ($\sum cL$) with the number of counts recorded during the night ($\sum cD$):

$$I_D = \left(\frac{\sum cL/hL}{\sum cL/hL + \sum cD/hL} \right) 2 - 1 \quad (2)$$

The length of day (hL) and night (hD) in hours were defined by the periods between sunrise and sunset. I_D is positive when diurnal activity prevails (+1 for total diurnality), and negative when nocturnal activity prevails (-1 for total nocturnality). To exclude activity bouts during twilight, 30 minutes prior and subsequent to sunrise and sunset, respectively, were not taken into account (i.e. altogether three 1/2 h intervals = 1 1/2 hours).

Crepuscular activity (I_C) weights activity at sunrise and sunset as compared with the average activity over a 24-h period as given by:

$$I_c = \log \cdot \left(\frac{\sum c_{SR} + \sum c_{SS} / \sum c_{48}}{6/48} \right) \quad (3)$$

where $\sum c_{SR}$ and $\sum c_{SS}$ are the sums of counts during, in this case, the 30-min intervals prior and subsequent to sunrise (SR) and sunset (SS), respectively, and $\sum c_{48}$ is the total number of counts during the entire day. I_c is positive when crepuscular activity is greater than the average activity, and negative when it is lower.

Further statistical analyses were done using SPSS for Windows 15.0.1. We applied Bonferroni post-hoc testes when multiple comparisons were necessary. If not stated otherwise values are presented as means \pm one standard deviation (1 SD). Each of the main factors of interest had three levels, and data analysis was designed to reveal possible interactions among the three main factors and additional factors like sex and time (Table 1)

TABLE 1 Overview of the factors of interest in the data analysis. The main question was how individuals from the different behavioral categories use the different habitat sections, and how this affected enclosure treatment. Each of the factors had three levels as explained in the text.

behavioral category	habitat section	enclosure treatment
immigrants	interior	source
emigrants	edge	transition
residents	matrix	sink

Results

Densities during the field seasons 2005 and 2006 fluctuated, reaching highest values in September with 58.00 ± 19.93 voles per enclosure in 2005 (286 individuals * ha^{-1} when regarding habitat patch area only) and 52.33 ± 15.27 in 2006 (258 individuals * ha^{-1} ; Figure 1). We recorded lowest densities in April 2005 and May 2006 with five individuals and less in all enclosures except in the source enclosure 1 in 2005 (minimum of six individuals) and in the transition enclosure 1 in 2006 (minimum of 17 individuals). The sex ratio in all enclosures was female biased with an overall proportion of $59.4 \pm 8.4\%$ (one-sample t-test; $t_{113} = 11.901$, $p < 0.001$). In both years first dispersers were observed in July (week 28 in 2005 and week 30 in 2006). In total, we classified 132 dispersers in 2005 and 93 dispersers in 2006 with a significantly higher dispersal rate for males (0.095 ± 0.095) than for females (0.045 ± 0.054 ; Mann-Whitney-U-test; $z = -3.83$, $p < 0.001$). The unidirectional transfer of altogether 128 dispersers (2005 and 2006) from source over transition to sink enclosures resulted in significantly different proportions of dispersers among treatments (source: $12.24 \pm 6.38\%$, transition: $15.35 \pm 7.52\%$, sink: $22.10 \pm 7.37\%$; Kruskal-Wallis-test; $Chi^2 = 2.16$, $p < 0.001$) and significantly different population densities (source: 37.13 ± 8.28 ind. * $encl.^{-1}$; transition: 50.97 ± 23.35 ind * $encl.^{-1}$; sink: 53.93 ± 13 ind * $encl.^{-1}$; $Chi^2 = 17.94$, $p < 0.001$). The eight radio tracking sessions in 2005 and 2006 were conducted at population densities between 23 and 92 individuals per enclosure (Figure 1). Automatic activity recording

yielded altogether 19,337 activity counts for the relevant periods (see Table 3) between August and October 2006.

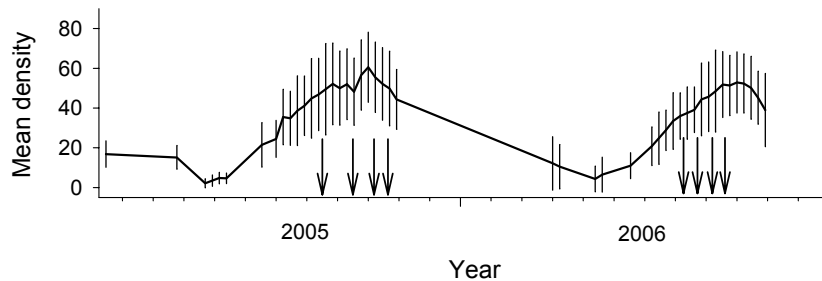


FIGURE 1 Mean density measured by MNA. Error bars show ± 1 SD. Arrows indicate radio tracking sessions. Sessions in chronological order 2005: Aug. 11-14, Sept. 8-11, Oct. 6-9, Oct. 27-30; 2006: Aug. 10-13, Aug. 24-27, Sept. 7-10, Sept. 21-24.

Spatial distribution and activity

Activity ranges of the radio tracked voles as measured by MCP were somewhat larger ($872.3 \pm 812.3 \text{ m}^2$) than those calculated by the Kernel method ($676.2 \pm 768.7 \text{ m}^2$; Table 2). The differences were, however, not statistically significant (t-test; $t_{108} = 1.3$, $p = 0.196$). We, therefore, used the more precise Kernel method for further analyses (Briner et al. 2005). Activity ranges significantly decreased among the behavioral categories immigrants (i.e. dispersers in the new population), emigrants (i.e. dispersers in their natal population), and residents (ANOVA; $F_{2,49} = 13.23$, $p < 0.001$; Table 2). There was no significant difference between males ($710 \pm 712.8 \text{ m}^2$) and females ($632.4 \pm 849.2 \text{ m}^2$; $F_{1,49} = 0$, $p = 0.989$), and we found no interaction between category and sex ($F_{2,49} = 0.093$, $p = 0.911$).

The Jacob's index (D) revealed significantly highest attraction of radio tracked voles towards the habitats' interior ($D = 0.176 \pm 0.654$) and highest avoidance towards the coverless matrix area ($D = -0.687 \pm 0.43$), while the edge of the habitat patches was intermediate and almost neutral ($D = -0.068 \pm 0.643$; ANOVA; $F_{2,162} = 31.785$, $p < 0.001$; Table 2). The differences were true for all tested section comparisons (Bonferroni post-hoc test; all $p \leq 0.03$). The attraction or avoidance of the habitat sections interior and edge neither differed significantly between males and females, nor among the three behavioral categories (all $p > 0.334$; Table 2). Most interestingly, however, habitat edges were most used by male immigrants in new populations, and most avoided by male emigrants in their natal populations. Female dispersers, on the other hand, showed the opposite tendency (interaction between sex and disperser category with residents excluded: $F_{1,38} = 5.445$, $p = 0.025$). The coverless matrix area was most avoided by residents and least so by immigrants in new populations ($F_{2,49} = 5.638$, $p = 0.006$). There were no differences in matrix avoidance between males and females ($F_{1,49} = 0$, $p = 0.989$), and we also found no interaction between sex and behavioral category ($F_{2,49} = 0.103$, $p = 0.902$).

TABLE 2 Activity ranges measured by the 95% minimum convex polygon and 95% Kernel. The Jacob's index indicates relative preference (positive values) or avoidance (negative values). "Immigrants" mean transferred dispersers in new populations, "emigrants" mean dispersers radio tracked in their natal population before the transfer. Residents were defined as adults which did not leave their natal population. Deviations show 1 SD over radio tracked individuals.

	MCP [m ²]	Kernel [m ²]	Jacob's index (D)		
			Interior	Edge	Matrix
Males:					
Immigrants	1505.7 ± 761.3	1110 ± 739.3	-0.03 ± 0.6	0.09 ± 0.56	-0.47 ± 0.51
Emigrants	361.2 ± 332.5	226.8 ± 210.3	0.46 ± 0.64	-0.34 ± 0.66	-0.82 ± 0.28
Residents	297.8 ± 171.6	215.4 ± 125.9	0.49 ± 0.45	-0.19 ± 0.64	-0.98 ± 0.03
Females:					
Immigrants	1349 ± 773.5	1210.4 ± 983.9	0.31 ± 0.57	-0.25 ± 0.56	-0.53 ± 0.47
Emigrants	272.5 ± 198.7	209.8 ± 137.1	-0.14 ± 0.73	0.35 ± 0.49	-0.75 ± 0.41
Residents	185.4 ± 128.5	123.5 ± 87.1	0.07 ± 0.82	0.08 ± 0.84	-0.97 ± 0.04

Additional calculation of the relative affinity to either edges or the interior sections based on trapping data revealed no significant difference between male and female residents (t-test; $t_{700} = -1.640$, $p = 1.02$; Figure 2). Male dispersers, however, had a higher relative affinity to the interior sections of the habitat patches than females (ANOVA; $F_{1,208} = 7.734$, $p = 0.006$). The relative affinity to habitat edges did not statistically differ between dispersers in new populations (i.e. immigrants) and dispersers in their natal populations (i.e. emigrants; $F_{1,208} = 0.576$, $p = 0.449$). While male emigrants showed a higher relative affinity to the habitat interior than male immigrants, female dispersers again showed the opposite tendency (interaction sex * disperser group: $F_{1,208} = 3.275$, $p = 0.072$).

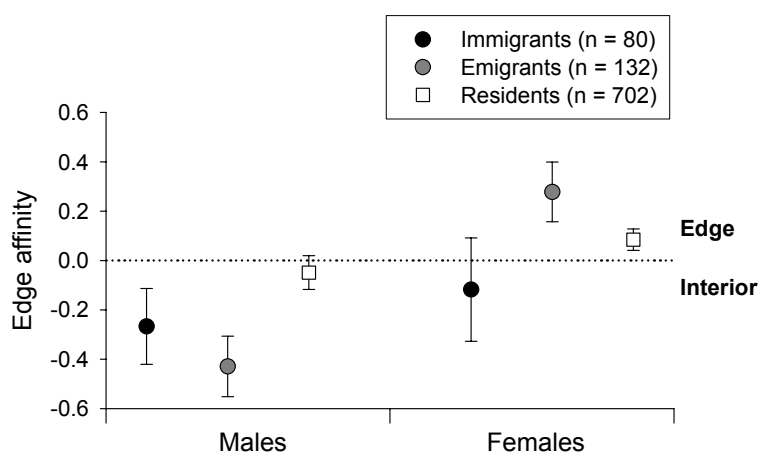


FIGURE 2 Relative edge affinity based on trapping data 2005 and 2006. "Immigrants" mean transferred dispersers in new populations, "emigrants" mean dispersers radio tracked in their natal population before the transfer. Residents were defined as adults which did not leave their natal population. Data were standardized by z-transformation. Values above the dotted line mean relative affinity to edge traps, values below relative affinity to interior traps. Shown are residents and dispersers from the time of first matrix capture. Dispersers which were only trapped in the matrix traps are not included. Error bars show ± 1 SE.

Mean running distances of radio tracked voles were significantly larger for males (6.84 ± 10.58 m) than for females (5.85 ± 9.31 m; ANOVA; $F_{1, 7846} = 4.879$, $p = 0.027$; Figure 3). For both sexes immigrants was the behavioural category with the largest mean running distances, and the shortest were measured for residents (behavioural category: $F_{2, 7846} = 132.952$, $p < 0.001$; interaction behavioural category * sex: $F_{2, 7846} = 1.414$, $p = 0.243$). The post-hoc test revealed that the difference in mean running distances was significant for all tested comparisons of the behavioural categories immigrants (8.39 ± 12.44 m), emigrants (4.87 ± 7.19 m), and residents (3.8 ± 4.62 m; Bonferroni post-hoc test; all p -values ≤ 0.002). Immigrants showed the highest running distances during the first day in a new population, while emigrants as well as residents did not considerably change their activity over the three days of observation (factor time: $F_{2, 7846} = 9.920$, $p < 0.001$; interaction time * disperser category: $F_{4, 7846} = 13.082$, $p < 0.001$; Figure 3).

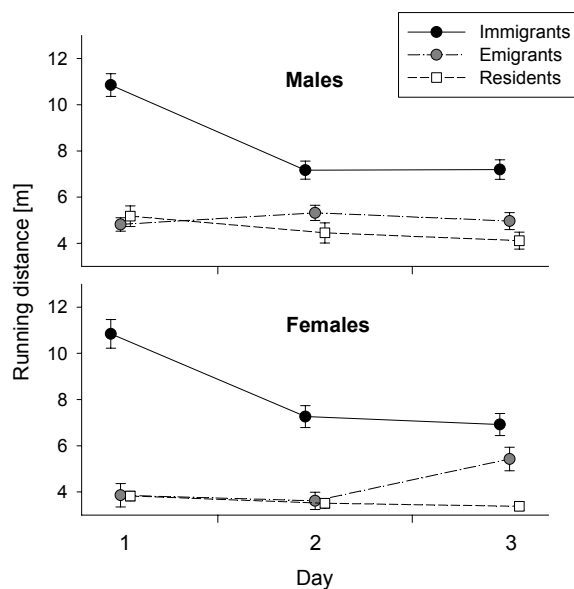


FIGURE 3 Mean running distances per 1/2 h for males and females based on eight radio tracking sessions 2005 and 2006 which lasted for three days each. Error bars show ± 1 SE.

Temporal avoidance and emigration timing

The diurnality index (I_D) did not significantly differ between the three days of radio tracking (ANOVA; $F_{2, 147} = 0.946$, $p = 0.391$; Figure 4), and we also found no difference between males (-0.11 ± 0.34) and females (0.00 ± 0.32 ; $F_{1, 147} = 1.415$, $p = 0.236$). However, I_D values indicated a temporal avoidance among the behavioural categories immigrants, emigrants, and residents (Figure 4): residents tended to be more active during daytime, while dispersers were more active at night (ANOVA; $F_{2, 147} = 3.179$, $p = 0.045$). The temporal avoidance of residents was most prominent in male emigrants and female immigrants. The interaction between sex and behavioural category was, however, not statistically significant ($F_{2, 147} = 1.053$, $p = 0.352$).

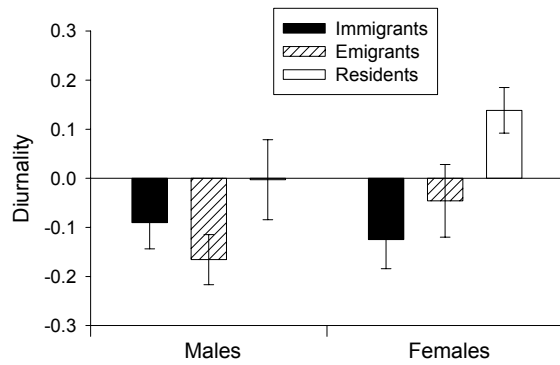


FIGURE 4 Diurnality indices based on mean running distances during radio tracking sessions. We excluded values 30 minutes prior and subsequent to sunrise and sunset, respectively. Error bars show ± 1 SE.

Data from automatic activity recording showed that voles within the habitat patches were most active during daytime, while the matrix area was preferably used at night (Figure 5 and Table 3). The difference in activity phase was, however, not statistically significant between habitat patches and matrix (t-test; $t_3 = 1.69$, $p = 0.19$). In the matrix we recorded remarkably high activity bouts at twilight, resulting in a significant difference of the crepuscularity index between habitat patches and matrix ($t_3 = -3.32$, $p = 0.045$).

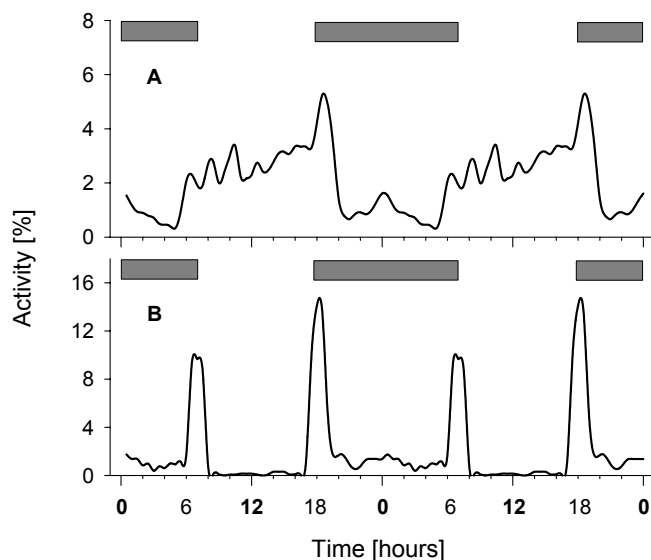


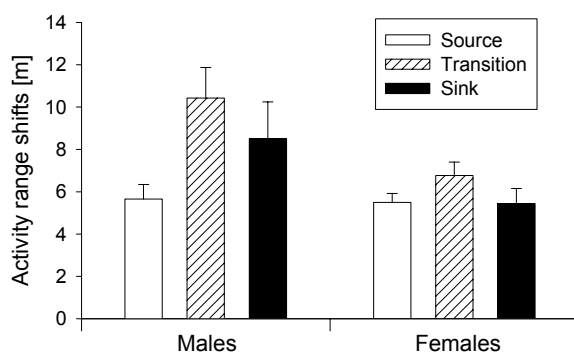
FIGURE 5 Activity patterns for habitat patches (A) and matrix (B) recorded by passage counters and summed up for four enclosures in A and two enclosures in B. 10-day periods of recording (from October 19 to October 29) are plotted. The patterns show the relative distribution of activity in 1/2-h intervals over 24 hours (=100%). For clarity each 24-h pattern is plotted twice. Data were smoothed by a running mean of 3 intervals. The gray bars indicate nighttime defined by sunset and sunrise.

TABLE 3 Diurnality and crepuscularity indices in habitat and matrix (see Figure 6) and different enclosure treatments, i.e. source, transition, and sink. Deviations show 1 SD.

	Diurnality (I_D)	Crepuscularity (I_C)
Oct.19 – 29:		
Habitat	0.275 ± 0.298	0.267 ± 0.074
Matrix	-0.403 ± 0.634	0.505 ± 0.087
Aug. 22 – Oct. 15:		
Source	0.164 ± 0.340	0.127 ± 0.162
Transition	0.506 ± 0.282	0.238 ± 0.176
Sink	0.498 ± 0.241	0.111 ± 0.065

Effects on resident population

Monthly shifts of the activity range centres of residents were larger for males than for females (Mann-Whitney-U-test; $z = -2.717$, $p = 0.007$; Figure 6). There was a tendency of largest activity shifts in the transition enclosures which, however, marginally missed the significance threshold (Kruskal-Wallis-test; $\text{Chi}^2 = 5.325$, $p = 0.07$). We found no effect of dispersal on the populations' diurnality index (rm-ANOVA; enclosure treatment: $F_2 = 4.293$, $p = 0.323$; time: $F_4 = 1.417$, $p = 0.372$; Table 3) and the crepuscularity index (enclosure treatment: $F_2 = 0.405$, $p = 0.743$).

**FIGURE 6** Monthly shifts of residents' activity range centres based on trappings between July and October 2005 and 2006. Error bars show ± 1 SE.

Discussion

By combining classical capture-mark recapture methods with intensive radio tracking and automatic activity recording we were able to reveal the spatial and temporal behavior of residents, dispersers in their natal populations before they left the home patch (i.e. emigrants), and dispersers in new populations at the phase when they tried to establish in a foreign social environment (i.e. immigrants). Dispersers were defined by a score system based on the individual trapping history in the coverless and therefore risky matrix. The basic assumption of this approach is a general avoidance of the matrix section, which was ascertained by the radio tracking data. We are aware of missing individuals with a lower motivation for

dispersal or even of some false disperser classifications. However, currently there is no better way to quantify dispersal motivation in free-living small rodents. By using the score system in combination with the semi-natural enclosure set-up we were able to classify dispersers and transferred them by hand. The separation of dispersal into its components of emigration and immigration may involve very different behavioral patterns and decisions that are still rarely taken into account in empirical studies (Lawson Handley and Perrin 2007). Differences between residents and dispersers in their morphological conditions (see TRIGGERS AND TRAITS, this volume), in their reproductive success (see ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume), and differences in their activity behavior (this study) indicate that the score system is at least able to identify individuals with an obviously high motivation to leave a population.

Spatio-temporal activity

Habitat edges have frequently been found to bear higher predation risk than interior sections because they are more exposed to predators from the outside (Andr n 1995 and references therein, Stevens and Husband 1998, Hovland et al. 1999, Brand and George 2000; but see Ibarzabal and Desrochers 2001). To reduce predation and, hence, increase individual fitness, voles should prefer habitat interiors (Andreassen and Ims 1998; but see Bowers et al. 1996). Our findings support this view by an overall attraction of radio tracked voles towards the habitat interior, which was most prominent in male residents. It is, therefore, reasonable to assume that habitat patches become at first occupied in the interior sections until limiting space force subordinate individuals towards the more risky edges. Subordinates occupying habitat edges must cope with a higher risk of being preyed upon, but have the advantage that they border fewer territorial boundaries from residents. Radio tracked female residents, however, used interior and edge sections almost equally. This might have been due to the more restricted territoriality of resident females which can lead to a social fence phenomenon (Hestbeck 1982, Ostfeld 1994), i.e. an establishment of barriers by conspecifics which results in a limited movement ability of female voles (c.f. Sandell et al. 1991, Smith and Batzli 2006). Males, on the other hand, showed a significantly higher mobility than females and are certainly more “free” in their movements and choice of section, respectively. Higher mobility found in resident males as well as in male and female dispersers may reflect an ideal free distribution type of behavior (Fretwell and Lucas Jr 1970) in order to balance competition and predation risk.

Comparatively large activity ranges as well as large mean running distances affirm the lack of spatially restricted home ranges in dispersers (Hayes et al. 2004). When entering a new population, particularly high running distances were observed during the first day of immigration, but decreased over the following days. Immigrating male and female dispersers obviously surveyed the new populations quickly and, afterwards, maintained a still increased activity level. The latter indicates that residents might largely prevent immigrants from settling (Mackin-Rogalska 1979, Lambin et al. 2001, Gundersen et al. 2002), which decreases the chance of successful dispersal (see ESTABLISHMENT AND FITNESS

CONSEQUENCES, this volume) and causes dispersers to continue their search further than expected (Szacki et al. 1993).

The onset of emigration was strongly synchronized among dispersers as voles left the relative safe habitat patches and entered the coverless matrix predominantly at dawn and dusk, whereas voles in the habitat patches were most active throughout daytime. We suggest that predation risk of dispersers is somewhat reduced by synchronized emigration at twilight, because the activity bursts reduce the relative vulnerability of an individual (“safety in numbers”; Daan and Slopsema 1978). Twilight does not seem to be considerably risky, which was stated by Halle (1993) who showed that predation risk for arvicoline rodents is almost evenly distributed over the 24-h day.

Spatio-temporal avoidance

We showed that edges are avoided by male emigrants and predominantly used by female emigrants, indicating different motivations for males and females to emigrate (Figure 8). The well-established sex-bias in dispersal proneness depends on the relative costs and benefits of dispersal and philopatry, which appears to be closely linked to the species’ mating system (Greenwood 1980, Dobson and Jones 1985, Lawson Handley and Perrin 2007). Like most mammalian species, *Microtus arvalis* has a polygynous mating system, and consequently, we found a highly male-biased dispersal rate. We have shown that most male emigrants are relatively young, classified as natal dispersers (i.e. which have not bred in their natal population before), and emigrate at an early stage of population increase, while female emigration seems to be correlated with a decline in familiarity (see TRIGGERS AND TRAITS, this volume). We suggest that male dispersers are highly viable individuals (Gundersen et al. 2002), which suppress reproductive activity in their natal populations and stay in the safer interior sections in order to reduce predation risk until they decide to actually leave the home patch. Female dispersers on the other hand seem to rely on social interactions but are competitively inferior and, therefore, have to avoid highly competitive interior sections (see below).

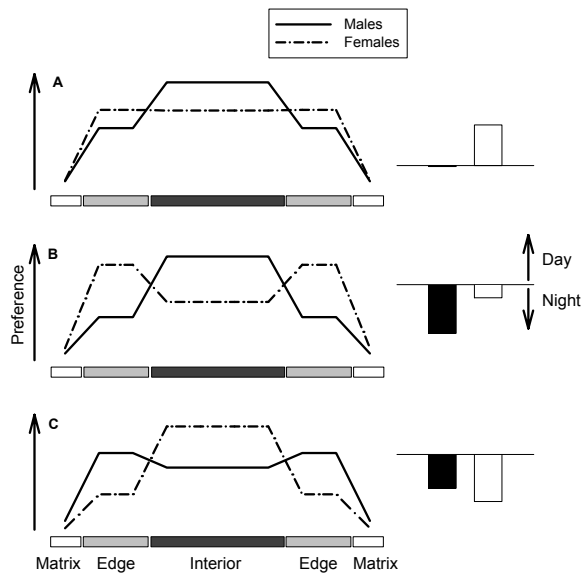


FIGURE 8 Left: relative preference of the different habitat sections matrix, edge, and interior, separated for males and females. A: residents; B: emigrants in natal populations; C: immigrants in new populations. Right: the use of more preferred interior sections by dispersers went along with a higher temporal avoidance of residents (black bars: males; white bars: females).

The sex-differences in habitat use were reversed in immigrants, i.e. in dispersers entering a new population. Both radio tracking and trapping data revealed a relatively higher use of edges by male immigrants, and a relatively higher attraction of interior sections by female immigrants. From that we concluded that male and female dispersers not only have different motivations to emigrate, but also follow different spatio-temporal strategies in natal as well as in new populations. While both male and female dispersers tried to temporally avoid residents, this avoidance was most prominent in male emigrants and in female immigrants. It seems that the use of the safer and, therefore, more preferred interior sections go along with a higher temporal avoidance of residents and vice versa (Figure 8). Females appear to be more concerned about social associations and kin alliances in their natal populations (see Ishibashi et al. 1997, Ishibashi et al. 1998). This behavioral strategy probably promotes the weaning success of young and/or helps to build up a collective defense against aggressive or infanticidal behavior by unfamiliar conspecifics (Fortier and Tamarin 1998, Ylönen and Horne 2002, Hayes et al. 2004, Le Galliard et al. 2006). Hence, females might rather take the risk in their natal populations of being preyed upon than to temporally avoid residents in the safer interior sections. In new populations, however, female dispersers seem to predominantly avoid predation, while male immigrants are more risk prone and simultaneously active with resident individuals in order to sneak into reproduction. The two different strategies in male and female immigrants may also be the proximate reason for different dispersal distances as found in several mammalian species (see Künkele and von Holst 1996, Murrell et al. 2002, Kozakiewicz et al. 2007).

Effects on resident population

In the literature it has widely been discussed what ultimate and proximate factors might trigger emigration and immigration. Only few studies, however, explicitly investigated spatio-temporal activity of resident individuals being affected by immigration and emigration of dispersers, respectively (but see Hayes et al. 200). Although residents did not seem to change their temporal activity in the presence of dispersers, we found a tendency for larger shifts of resident activity centers in the transition enclosures with both immigration and emigration. Hence, the relatively high turnover of dispersers, which is closest to the natural situation, seem to decrease the spatial anchorage of residents. The effort of immigrants to establish might even force residents into dispersal, which would have disruptive effects on the resident population in general (Gaines and McClenaghan 1980). As a consequence, vacant sites emerge that can be reoccupied by neighboring residents or dispersers. The situation when the establishment of a disperser in the new population drives out a resident into dispersal is the so-called “domino-effect” (see THE DOMINO-EFFECT, this volume), which not only would have consequences for the demography and social structure of a population, but also might have long-term population genetic implications.

Appendix

Number of different animal groups radio tracked during 2005 and 2006 field sessions. “Immigrants” mean transferred dispersers in new populations, “emigrants” mean dispersers radio tracked in their natal population before the transfer. Residents were defined as adults which did not leave their natal population.

Session	2005				2006				Total
	1	2	3	4	1	2	3	4	
Males:									
Immigrants	2	2	2	4	2	2	2	1	17
Emigrants	-	-	-	-	2	2	5	2	11
Residents	-	-	-	-	-	1	2	-	3
Females:									
Immigrants	2	2	2	-	1	1	2	1	11
Emigrants	-	-	-	-	1	2	-	-	3
Residents	-	1	-	1	1	3	2	2	10
Total	4	5	4	5	7	11	13	6	55

ESTABLISHMENT AND FITNESS CONSEQUENCES OF IMMIGRATING VOLE DISPERSERS

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Abstract

Dispersal is one of the most important yet least understood phenomena of ecology, behavior, and evolution. Causes and consequences of dispersal are difficult to study in natural populations since dispersers can typically only be identified *a posteriori*, and most work on dispersal is either of theoretical nature or based on anecdotal observations. We investigated the fitness trajectories of residents and dispersers in their natal and new populations by using an individual-based experimental approach in semi-natural enclosures with individually marked common voles (*Microtus arvalis*). Our study combines life history information with genetic data on the reproductive success of 1255 individuals. Dispersal was highly male-biased and, as lesions showed, most probably induced by the agonistic encounters of conspecifics. We suggest that these encounters often involved relatives, and the induction of dispersal may therefore contribute to the avoidance of inbreeding and reduction of kin competition. Although nearly 26% of the dispersers reproduced in their natal populations before leaving only seven percent of them reproduced in the new populations, showing the relative low establishing success of immigrants. Permanent settlement appeared to be a prerequisite for reproduction in both sexes and those that did not settle in a new population dispersed again predominantly on the same day of immigration. The probability of male dispersers for reproduction was highest at relatively low population densities and nearly all established immigrants were presaturation dispersers. Young and natal male dispersers had highest establishing success whereas most successful female immigrants were breeding dispersers. In conclusion, the effectiveness of vole dispersal depends to a high extent on demographic factors in the new population and it is most likely to be selected for in highly heterogeneous landscapes with low-density or unoccupied habitat patches. Dispersal, therefore, seems to be most successful in a fragmented landscape with high extinction and recolonization rates and the inability for establishment in moderate or high density populations might lead to genetic separation on a fine geographical scale.

Introduction

Dispersal, defined as an “one-way movement away from an individual’s home range site” (Lidicker and Stenseth 1992), has long been recognized to be an important process for both, the population which is left (i.e. the natal population) and the new population into which a disperser immigrates (Curtis 1956, Myers and Krebs 1971). Dispersal is not only known to have important demographic impacts (Wiens et al. 1993, Diffendorfer 1998) but it also implies a genetic connection between otherwise isolated populations (Aars and Ims 2000). Facilitating a disperser-mediated link and gene flow between populations has become even more important in an increasingly fragmented landscape in order to avoid population extinction or deleterious effects of inbreeding (Aars and Ims 1999, Aars et al. 2006). High extinction rates, high costs of inbreeding as well as spatially and temporally heterogeneous landscapes should, therefore, select for dispersal (Hastings 1983, Gandon and Michalakis 2001). Vice versa, dispersal seems to enhance both diversity and productivity of communities over evolutionary timescales (Venail et al. 2008).

Despite the importance of dispersal, most work is either of theoretical nature or based on anecdotic dispersal observations. The lack of empirical studies for many organisms can be attributed to the difficulty in obtaining field data (Stenseth and Lidicker 1992, Aars and Ims 2000). Dispersal is a seldom event and, under natural conditions, it is impossible to predict in advance which individual will go where. Movements through unfamiliar and unsuitable areas are known to heavily increase mortality rates of dispersers (Andreassen and Ims 2001, Smith and Batzli 2006) which reduces the number of immigrants. It is often difficult to distinguish in the field between individuals that have entered a population due to birth or immigration. It is even harder to distinguish between individuals that disappeared because of death versus those that emigrated. Dispersal is, therefore, one of the most important, yet least understood, features of ecology, population genetics, behavior, and evolution (Wiens 2001).

Recent studies have used genetic markers to identify immigrating small mammal dispersers and to ascertain the proportion of new animals in the populations examined (Mossman and Waser 1999, Schweizer et al. 2007). However, in such studies it remains unclear, how many of these immigrants actually reproduce in the new populations and which factors determine their establishment. Lambin (1994) proposed that an effective disperser must not only have completed emigration and travel successfully, but also immigration (i.e. settled and/or reproduced). Only reproducing immigrants will have a genetic impact on the new population and dispersal will not result in gene flow unless individuals become part of the new breeding population (Schweizer et al. 2007).

Dispersal patterns, especially the frequent sex bias in dispersal, are believed to be influenced by the avoidance of inbreeding (Bollinger et al. 1993, Jacquot and Vessey 1995, Aars and Ims 1999). The sex that predominantly disperses depends on the relative costs and benefits of dispersal and this seems to be closely linked to the mating system (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). Polygyny, as found in most mammals, is typically associated with male-biased dispersal (but see Nagy et al. 2007), and to avoid breeding with close relatives, males should be natal dispersers (i.e. should not have mated in their natal population before). As a consequence of inbreeding avoidance, immigrating dispersers

might have a high reproductive success due to an enhanced preference of residents to mate with unfamiliar immigrants (Höner et al. 2007) and give birth to offspring that may enjoy a fitness advantage from hybrid vigor (Ingvarsson and Whitlock 2000, Ebert et al. 2002, Kozakiewicz et al. 2007). On the other hand territoriality may prevent immigrants to settle and high densities in the new populations should force immigrating dispersers to keep on traveling (Andreassen and Ims 2001, Gundersen et al. 2002, Smith and Batzli 2006). It is likely that dispersers which are not capable to establish themselves will have lower survival rates due to increased stress, decreased food availability, or higher predation risk.

Although dispersal is a high-risk strategy it might enhance fitness due to a release of competition between dispersers and relatives in their natal population and/or an increase in the reproductive success in the new population. This study aims to directly measure the fitness consequences of dispersal for individuals remaining in their natal populations versus those that immigrate into new populations. In particular, we ascertain on an individual basis (i) the proportion of spatially as well as genetically established immigrants, (ii) the overall reproduction and survival rates of dispersers and residents, and (iii) the factors which might determine an establishing success of the dispersers. We used common voles, *Microtus arvalis* (Pallas) in semi-natural enclosures as an experimental model system (EMS; Wiens et al. 1993) and a combination of classical capture-mark-recapture methods (spatial establishment) and genetic analyses (genetic establishment). This comprehensive approach allowed us to gather precise information on individual dispersers as well on their natal as on the new population which would not be possible under completely natural conditions.

Methods

For field site and trapping, identification of dispersers, transfer of dispersers and molecular analyses see GENERAL METHODS.

We calculated survival rates for intervals of two week periods by using the MNAs. For this we divided the number of animals which were still alive at the end of a period by the number of animals being present at the beginning (Krebs 1989). We treated residents and dispersers, and males and females separately. Different recapture rates between these groups may have an effect on the calculation of their survival rates. Therefore, we calculated the recapture rates (RR) by dividing the actual number of captures per fortnight by the corresponding MNA (see Ylönen et al. 1990) and survival rates (SR) were then corrected by:

$$SR^* = SR + (1 - RR) \quad (1)$$

Parentage assignment

We attempted parentage assignments for altogether 1255 genetically analyzed voles. We genotyped all adult voles present in 2004 (n=157) and all additionally released individuals in 2005 and 2006. Parentage analyses concentrated on the periods when potential offspring of transferred dispersers could have emerged from burrows in transition and sink enclosures. This included all newly trapped voles which appeared after

week 32 in 2005 ($n = 618$) and after week 34 in 2006 ($n = 480$). Additionally, we genetically analyzed all transferred dispersers ($n = 128$), 50 frustrated dispersers from sink enclosures, and all other voles which showed evidence of reproductive activity over at least two consecutive captures.

For parentage assignments we used genotypic information in combination with observational data on trapping dates, trapping sites, body-weight, and reproductive states. Genetic assignments were performed by applying a combined strategy of parentage exclusion and the likelihood approach implemented in the program Cervus 3.0.3 (Marshall et al. 1998). We first excluded all candidate parents that did not share at least one microsatellite allele at all but one locus with the offspring in question. We allowed for one mismatch at one locus per parent-offspring pair to account for possible mutations or genotyping errors. We then determined the most likely parent among the remaining candidates. As candidate parents we considered all voles in the enclosure in question. As putative offspring we tested all voles in an enclosure except for the population founders. The mean allele number per locus over all years and enclosures was 9.1 ± 1.53 (1 SD; Appendix) and we obtained, on average, 97.3% of the genotypes at each locus for all voles analyzed. The total exclusionary power with which the microsatellite loci excluded an unrelated candidate parent was, on average, $99.83\% \pm 0.15$ (1 SD; Appendix). The simulations which are required for likelihood-based parentage assignments in Cervus were run with 10,000 cycles, a typing error rate of 0.01, and a proportion of 80% sampled candidate parents. The 80% proportion actually was a conservative estimate, because capture and recapture rates within the enclosures were high (see Results).

All genetic assignments were verified with observational data on the trapping history of the individuals. Parentage was not assigned when genetic analysis and data on the trapping history of the individuals did not match (e.g. when a putative parent was younger than the offspring). When two or more adults were still compatible with an offspring after using genetic and observational data, parentage was assigned to the most likely individual based on the likelihood-score in Cervus. We performed parentage assignment for putative mothers first, and genotypic information on unequivocally assigned mothers was used for genetic assignment of fathers (see Heckel and von Helversen 2003).

Parentage assignment aimed at a quantification of the reproductive success of immigrated vole dispersers in comparison to the residents present in the same enclosures. To account for changes in reproduction during the field seasons we compared dispersers only with residents which were present in the populations at the same time window of investigation, i.e. which were trapped before the first dispersers appeared and which lived at least until the onset of the treatment period (i.e. around week 28 in 2005 and week 30 in 2006). Statistical comparisons were done using SPSS for Windows 15.0.1 and S-Plus for Windows 6.1. All values are presented as means \pm one standard deviation (1 SD).

Results

Demographic changes in enclosures

All populations in 2004 reached maximum densities in October with 30.2 ± 6.34 voles per enclosure (149 individuals* ha^{-1} ; Figure 1). In the following years, maximum densities were reached in September with

58 ± 19.93 individuals per enclosure in 2005 ($286 \text{ individuals} \cdot \text{ha}^{-1}$) and 52.33 ± 15.27 animals in 2006 ($258 \text{ individuals} \cdot \text{ha}^{-1}$). Densities in the peak months differed significantly between years (densities log-transformed; ANOVA; $F_{2,42} = 24.48$, $p < 0.001$). We recorded lowest densities in April 2005 and May 2006 with five voles and less in all enclosures except in the source enclosure 1 in 2005 (minimum 6) and in the transition enclosure 1 in 2006 (minimum 17). To compensate for the low densities we released additional voles into the enclosures (see Methods).

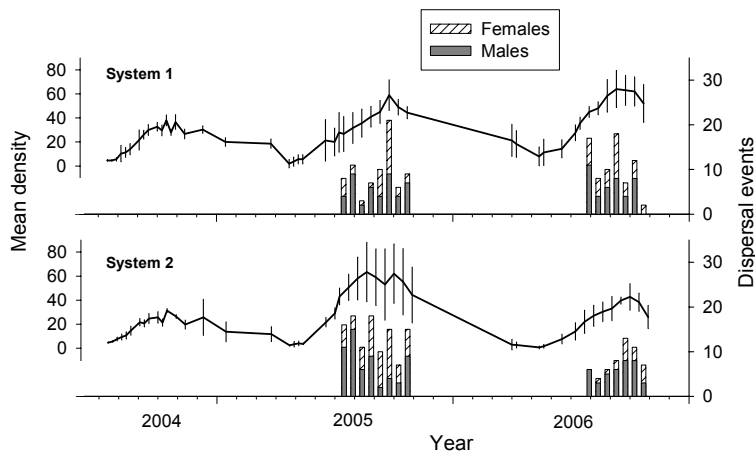


FIGURE 1 Mean density (lines) measured by MNA and number of dispersal events (stacked bars). Error bars indicate ± 1 SD over enclosures. The number of dispersal events (right x-axis) is displayed for intervals of two weeks and for all three enclosures within a system.

In both years the first dispersers appeared in July (week 28 in 2005 and week 30 in 2006; Figure 1). We detected in total 187 dispersal events in 2005 and 129 in 2006. These numbers include individuals from sink enclosures as well as voles that were repeatedly identified as dispersers after transfer. The bi-weekly dispersal rate of 0.095 ± 0.095 was significantly higher for males than for females with 0.045 ± 0.054 (Mann-Whitney-U; $z = -3.83$, $p < 0.001$) while we found no significant differences in the overall dispersal rate between the enclosures (Kruskal-Wallis; $\text{Chi}^2 = 2.65$, $p = 0.75$). Sixty-eight percent of the dispersal events took place before maximum densities were reached (68.4% in 2005 and 67.4% in 2006). Hence, 32% of the dispersal occurred during or after maximum population densities.

In 2005 and 2006 we transferred a total of 128 dispersers in the week when they reached the score threshold. Thirty-three of these individuals were transferred twice, because they repeatedly entered the matrix traps in the transition enclosures (Table 1). After transfer, we trapped six males (7.7% of the 78 transferred males) and six female dispersers (12% of the 50 transferred females) in adjacent habitat traps over a period of at least two weeks. We consider these individuals as having settled. All six males settled after their first transfer whereas two females (4% of the 50) settled only after their second transfer. Forty-four (34.4%) of the 128 transferred voles were trapped too seldom in the new enclosures to define them as dispersers or residents.

TABLE 1 Number of dispersers transferred to transition or sink enclosures in 2005 and 2006. Numbers in parentheses give voles which were transferred twice and are already included in the numbers before.

	2005		2006		Total transfers	Dispersers total
	Transition	Sink	Transition	Sink		
Enclosure system 1:						
Males	10	13 (4)	7	18 (5)	48 (9)	39
Females	6	8 (3)	8	7 (1)	29 (4)	25
Enclosure system 2:						
Males	5	20 (4)	14	11 (7)	50 (11)	39
Females	12	16 (7)	4	2 (2)	34 (9)	25
Total	33	57 (18)	33	38 (15)	161 (33)	128

Considering only transition and sink enclosures, 74 individuals (57.8% of the 128 dispersers; 44 males and 30 females) were identified as dispersers again after their first transfer, 17 (51.5% of the 33 repeatedly transferred; 9 males, 8 females) after their second transfer. Repeated dispersal of voles occurred predominantly within the first days after transfer. Twenty-six (59.1%) males and 20 (66.7%) females were immediately trapped in the matrix traps after their first transfer and were identified as dispersers again during the following days. Females dispersed again slightly but not significantly earlier than males (females after 1.5 ± 0.94 days; males after 2.89 ± 3.38 days; Mann-Whitney-U; $z = -1.52$, $p = 0.13$).

During the treatment periods we found significant differences between source, transition, and sink enclosures in terms of mean population density (37.13 ± 8.28 vs. 50.97 ± 23.35 vs. 53.93 ± 13 ; Kruskal-Wallis; $\text{Chi}^2 = 17.94$, $p < 0.001$) and proportion of dispersers (12.24 ± 6.38 vs. 15.35 ± 7.52 vs. 22.10 ± 7.37 ; $\text{Chi}^2 = 2.16$, $p < 0.001$), which was most probably related to the unidirectional transfer of dispersers and the inability of voles in the sink enclosures to emigrate. We also found differences between the treatment enclosures in the overall sex ratio (37.13 ± 8.28 vs. 50.97 ± 23.35 vs. 53.93 ± 13 ; $\text{Chi}^2 = 13.695$, $p = 0.001$) but no significant difference was detected in the proportion of residents ($\text{Chi}^2 = 2.96$, $p = 0.228$).

Factors associated with dispersal

In order to ascertain potential factors for the establishing success of dispersers, we considered the demographic parameters population density, proportion dispersers, sex ratio, and proportion residents in the new populations as well as the mean body-weight and the approximate age of the dispersers during the week of transfer. The approximate age was estimated as the period from first capture of the individual to the date of transfer. Settled female dispersers differed for none of the mentioned parameters significantly from individuals that dispersed again (Wilcoxon rank-sum; all p -values > 0.09). Settled male dispersers, however, had been transferred into new populations with significantly lower densities than males that repeatedly dispersed (13.5 ± 6.06 vs. 54.11 ± 17.72 ; Wilcoxon rank-sum; $z = 3.92$, $p < 0.001$). Furthermore, the approximate age in the week of transfer was significantly lower in settled than in non-settled males (17.67 ± 13.92 vs. 37.05 ± 27.53 ; $z = 2.0$, $p = 0.045$). There was a trend that male settlement

was more likely in enclosures with comparatively low proportions of dispersers (11.38 ± 14.43 vs. 20.99 ± 7.63 ; $z = 1.78$, $p = 0.075$). All other parameters of male dispersers were not significant (all other p -values > 0.15).

The recapture rate during treatment periods 2005 and 2006 was $92.13\% \pm 17.21$ for males and $91.45\% \pm 11.7$ for females. This difference was statistically significant (Mann-Whitney-U; $z = -3.0$, $p = 0.003$). Additionally, residents had a significantly lower recapture rate than dispersers ($87.85\% \pm 15.26$ vs. $91.45\% \pm 11.7$; $z = -7.976$, $p < 0.001$). We took the differences in the recapture rates into account for the correction of the bi-weekly survival rates (see Methods). Bi-weekly survival rates were significantly higher for females than for males (0.89 ± 0.18 vs. 0.78 ± 0.29 ; Mann-Whitney-U; $z = -3.682$, $p < 0.001$; Figure 2 A). This sex difference was true within residents (Mann-Whitney-U; $z = -3.31$, p after Bonferroni-correction = 0.003) and frustrated dispersers ($z = -2.28$, p after Bonferroni-correction = 0.044). We did not find any significant difference, however, between the survival rates of transferred male and female dispersers ($z = -0.092$, p after Bonferroni-correction = 0.927). There was also overall no significant difference in the survival rates between residents, frustrated dispersers and transferred dispersers neither in males (Kruskal-Wallis; $\text{Chi}^2 = 2.026$, $p = 0.363$) nor in females ($\text{Chi}^2 = 4.674$, $p = 0.097$).

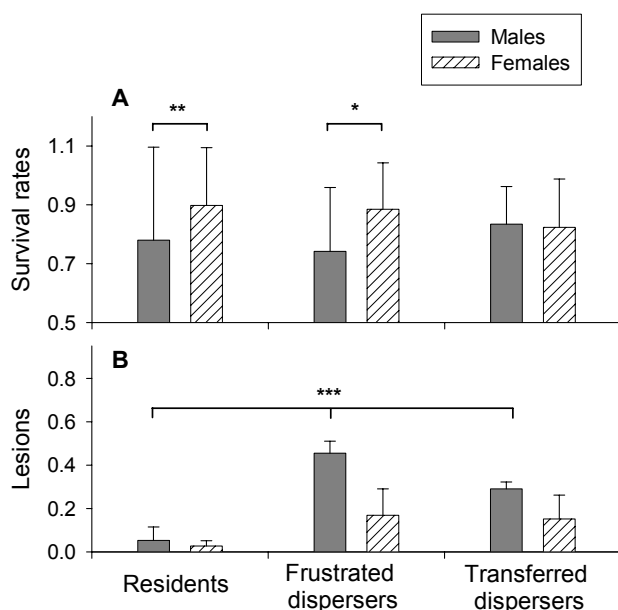


FIGURE 2 Survival and injuries of residents, frustrated dispersers and transferred dispersers. A: Bi-weekly survival rates for males and females. Error bars indicate 1 SD. “Frustrated dispersers” refers to voles which were born in the sink enclosures and were not transferred. Survival rates were corrected for different recapture rates (see Methods). B: Proportion of individuals with lesions (scars and wounds) induced by aggressive encounters of conspecifics. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$.

The occurrence of scars and wounds probably induced by aggressive encounters with conspecifics was significantly highest in frustrated male dispersers, followed by transferred male dispersers, and lowest in male residents ($\text{Chi}^2 = 15.04$, $p = 0.001$; Figure 2 B). The difference was significant for all tested combinations between the male groups (Mann-Whitney-U; all p after Bonferroni-correction < 0.021), but there was no significant difference between the three groups for females (Kruskal-Wallis; $\text{Chi}^2 = 4.83$,

$p = 0.09$). The proportion of lesions did not significantly differ between males and females overall (Mann-Whitney-U; $z = -1.7$, $p = 0.089$; Figure 2 B), but there were trends for more lesions in frustrated and transferred male dispersers than in the respective female individuals (Mann-Whitney-U; $z = -2.31$, p after Bonferroni-correction = 0.063; $z = -2.31$, $p = 0.058$).

Parentage assignment

The 1255 genetically analyzed voles corresponded to 69.3% of all common voles individually marked between 2004 and 2006 (total 1811 voles individually marked; Appendix). We genotyped 450 voles for which we assumed to have reproduced based on their trapping history. 372 voles in 2005 and 235 individuals in 2006 appeared first during the treatment periods and were analyzed as potential offspring of the dispersers or residents. The mean number of alleles per locus and enclosure population did not significantly change between years 2004 to 2006 (Kruskal-Wallis; $\text{Chi}^2 = 3.193$, $p = 0.203$) indicating that the release of additional voles not only compensated for low numbers of individuals but also maintained genetic variation in enclosure populations. On average we univocally assigned $62.73\% \pm 13.67$ of all potential offspring to a father and/or a mother. The overall assignment rate in 2005 and 2006 was 54% for the voles born before the treatment period began and 71% during the treatment period.

Resident individuals had an overall higher probability to reproduce than dispersers (Table 2). 53.8% of the resident males and 69.4% of the resident females reproduced whereas we found a reproduction rate of 33.3% for frustrated male dispersers and 34.8% for frustrated female dispersers. 19.2% of the transferred male and 36% of the transferred female dispersers reproduced already in their natal populations but, although relatively rare alleles of the immigrating dispersers facilitated assignments, we found only nine out of 128 (7%) transferred dispersers to have reproduced in the new populations (Table 2). Five of these were males (6.4% of the 78 males transferred) and four females (8% of the 50 transferred). Eight of these nine dispersers were presaturation dispersers, i.e. voles which dispersed before maximum densities in their natal populations were reached. One of the four reproducing female dispersers was transferred during the week of population maximum (i.e. saturation disperser), and only one female reproduced after its second transfer. All reproducing dispersers also settled in the new enclosures according to trapping data which indicates that reproduction depended on successful settlement. Hence, no offspring was detected in the transition enclosures for any of the repeatedly transferred dispersers. All five male dispersers which reproduced in the new populations were natal dispersers, i.e. voles which had not reproduced in their natal populations before. On the other hand, three of the four reproducing female dispersers were breeding dispersers. All four females reproduced with a male from the new population, i.e. none of them gave birth to offspring sired by a male from their natal population.

TABLE 2 Proportions of residents, frustrated dispersers (see text), and transferred dispersers to which offspring could be assigned in 2005 and 2006. The absolute numbers of voles that reproduced are shown in parentheses together with the total number of individuals in this category. “Overall” refers to transferred dispersers which reproduced in the natal population and/or in the new population. All male dispersers which reproduced in the new population were natal dispersers; three of four females that reproduced were breeding dispersers and were, therefore, listed twice, in the natal population, as well as in the new population.

	Residents		Frustrated dispersers		Transferred dispersers	
	Males	Females	Males	Females	Males	Females
Natal population	53.8% (28/52)	69.4% (77/111)	33.3% (9/27)	34.8% (8/23)	19.2% (15/78)	36% (18/50)
New population					6.4% (5/78)	8% (4/50)
Overall					25.6% (20/78)	38% (19/50)

Reproducing males had on average more offspring than reproducing females (6.44 ± 6.67 vs. 3.6 ± 2.77 ; Mann-Whitney-U; $z = -2.17$, $p = 0.03$; Figure 3) and more mates (2.75 ± 2.84 vs. 1.6 ± 0.9 ; $z = -3.64$; $p < 0.001$). Neither the mean number of offspring (Kruskal -Wallis; $\text{Chi}^2 = 0.5$, $p = 0.778$) nor the mean number of mates ($\text{Chi}^2 = 0.09$, $p = 0.954$) differed between residents, frustrated dispersers, and transferred dispersers. It is worth mentioning, however, that two of the five transferred male dispersers which reproduced in the new populations had an extraordinary high breeding success with 13 and 27 offspring, respectively.

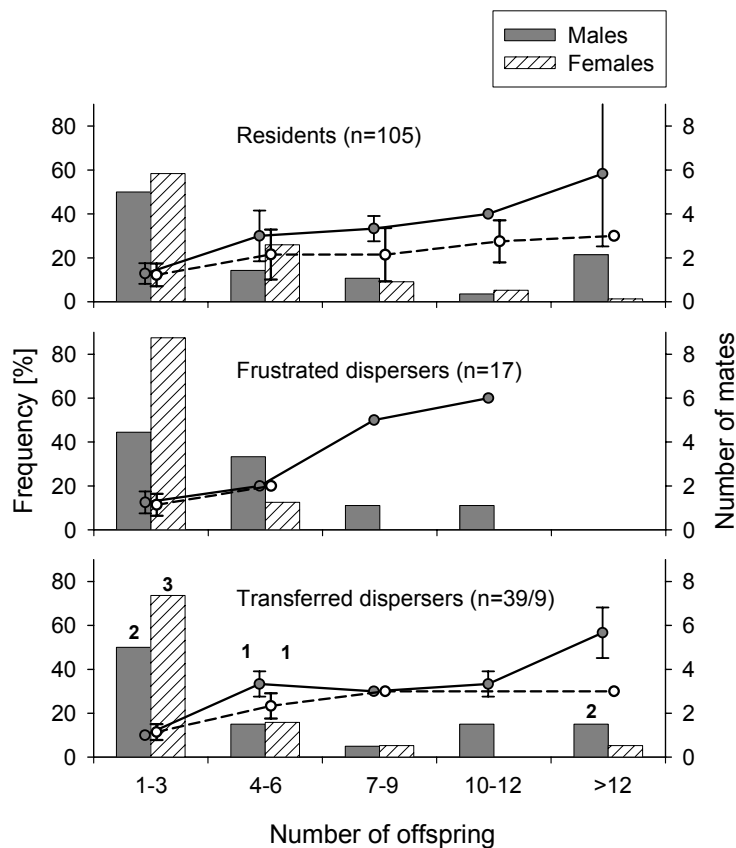


FIGURE 3 Frequency of the number of offspring (bars) and corresponding mean number of mates (lines) for voles that reproduced. We considered only residents which were present in the populations at the same time as dispersers for these comparisons. Frustrated dispersers refers to dispersers from sink enclosures which were not transferred. Transferred dispersers reproduced either in their natal population ($n=39$) or in the new population ($n=9$). The numbers above the bars of transferred dispersers represent the voles which reproduced in the new populations. Error bars show ± 1 SD.

Discussion

This study demonstrates that a combination of capture-mark-recapture data and extensive parentage analyses is able to resolve the pre- and post-dispersal history of common voles (*Microtus arvalis*) in semi-natural enclosures at the individual level. We detected differences between males and females in fitness-relevant life history traits such as lower survival and a lower proportion of successfully reproducing individuals in males. Both sexes dispersed but there was a strong male bias overall. This seems to be induced by the agonistic behavior of conspecifics since male dispersers had highest amounts of lesions. Dispersers were not generally subordinate in their natal population but had only a low establishing success in the new populations. Establishing success of immigrant males was related to age and population density, and settlement appeared to be a prerequisite for reproduction of both sexes.

Causes of dispersal

Our study shows that dispersers are not subordinate *per se* but are able to compete for reproduction in their natal populations. Although resident voles had highest reproductive rates with more than 64%, nearly 26% of the dispersers reproduced in their natal populations before transfer, and dispersers and reproducing

residents had similar numbers of offspring and mates. However, the comparatively low establishing success of immigrants (7%) makes dispersal apparently a very risky strategy for enhancing individual fitness. So the question arises why voles disperse at all.

Increasing densities during the reproductive season certainly increase competition and aggression in populations which has been taken as an explanation for density dependent dispersal in voles (Gaines and McClenaghan 1980, Gaines and Johnson 1984). The larger number of bite wounds and scars of actual (i.e. transferred) and frustrated male dispersers compared to residents shows that dispersers experienced a high level of aggression. This might have been either due to more territorial interactions caused by increased activity as a consequence of the propensity to disperse, or due to an active eviction from natal territories by resident conspecifics. The higher number of lesions of frustrated male dispersers which were forced to stay with their relatives in the natal populations compared to actual male dispersers indicates a role for relatedness. Since kin recognition is possible in many small mammal species including *Microtus arvalis* (McGuire et al. 1993, Mateo 2003) we hypothesise that male dispersers were actively evicted by related individuals. This surely resulted in an increased activity and consequently in more territorial interactions with residents. In any case, it seems likely that high levels of agonistic behavior may have contributed to prevent individuals from reproduction in their natal population and increase the motivation to emigrate.

Sex differences in dispersal

Our study shows male-biased dispersal in common voles associated with a polygynous mating system (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). The higher chance for reproduction in females was reflected by a higher number of mates and a higher offspring number in reproducing males. The higher intrasexual competition for mates among males (Gaines et al. 1979) most probably caused the lower survival rate in males overall. Males have much larger home range sizes than females (Niethammer and Krapp 1982) which will increase their stress and predation risk, respectively. It is important to note, however, that dispersal was not male-exclusive, but that females dispersed as well, although at a lower level (see also Schweizer et al. 2007). It seems likely that aggression is sex-specific and that female-female associations in the species contributed to overall lower levels of aggression towards females (Niethammer and Krapp 1982) and differences between the sexes in the propensity to disperse.

Liberg and Schantz (1985) and Wolff (1992) suggested that the decision to disperse in birds and mammals is rather mediated by the parents than the exclusive decision of the offspring. Expulsion of male offspring and tolerance of female immature descendants is a relatively simple strategy which avoids deleterious effects of inbreeding (Perrin and Goudet 2001) and increases inclusive fitness if females may inherit the breeding site from their mother (Hayes 2000, Hayes et al. 2004). Male-biased dispersal in *M. arvalis* (this study; Hamilton et al. 2005) is in accordance with many other small mammal studies suggesting that inbreeding avoidance can influence emigration (e.g. Bollinger et al. 1993, Jacquot and Vessey 1995, Aars and Ims 1999, Devillard et al. 2004, Lawson Handley and Perrin 2007). Inbreeding depression due to sib-sib mating has been detected by dosSantos et al. (1995) and results in reduced litter

size and pregnancy rates for voles under laboratory conditions. The extent of inbreeding and inbreeding depression in natural populations, however, is heavily debated and may largely depend on the taxon, the dispersal abilities, the extent of physical separation from other populations, and many other factors (Keller and Waller 2002).

The low sample size of five reproducing male immigrants and four reproducing females prevents further conclusions on the relative performance of each sex. However, established females were predominantly breeding dispersers (i.e. voles which had already reproduced) and all established males were natal and comparatively young dispersers which had not reproduced in the natal populations before. Thus, most successful female dispersers left their natal population and released the competition for resources between them and their offspring (i.e. resource competition hypothesis; Gundersen and Andreassen 1998), which may have enhanced their own inclusive fitness. In contrast, successful male dispersers did not breed with relative individuals in the natal populations, which is in agreement with the inbreeding avoidance hypothesis (Viitala et al. 1994). The sex difference in the survival rates was not detected in the actual (i.e. transferred) dispersers which may indicate that dispersal might be more rewarding for males than for females. We are aware, however, that our bi-weekly estimates of survival rates may not capture subtle differences within dispersers and the sample sizes for the comparison of male and females dispersers are considerably lower (see Results).

Immigration success and determining factors

All of the immigrating dispersers which reproduced also settled in the new populations, i.e. stayed within a relatively confined area and did not try to disperse again. Immigrants that did not establish either died or dispersed again, predominantly during the first day after transfer. Thus, settlement appears to be important for reproduction in *M. arvalis* even for males which do not show paternal care. Reproduction seems to be associated with settlement in other vole species as well (Telfer et al. 2003) although in *M. oeconomus* individuals may perform short-term mating excursions and return to their natal population (Aars and Ims 1999). Such mating excursions were impossible among the enclosures in our study and it is unknown if there are differences in mate choice behavior between the species which could require more familiarity or a pair bond among mating partners in *M. arvalis* (Fink et al. 2006, Heckel and Fink in press).

Population density and the availability of territories are apparently important factors for the establishment in new populations. Virtually all established immigrants were presaturation dispersers which left their natal populations before the maximum density was reached (Lidicker 1975) and we found establishment of *M. arvalis* males to be associated with population density. Although other studies reported that immigration is typically done into patches with a relative small number of individuals (Aars and Ims 2000, Andreassen and Ims 2001, Gundersen et al. 2002, Smith and Batzli 2006), we were able to quantify and statistically proof immigration success on an individual basis. High densities may therefore represent a “social fence” (Hestbeck 1982) for immigrants. This social fence may be fortified by the formation of family groups among female common voles and other species (E. Heinze et al., unpublished data; Ishibashi

et al. 1998). Female kin groups might help to prevent intruders additionally to settle and form a defense against aggressive or infanticidal behavior by unfamiliar males (Fortier and Tamarin 1998, Le Galliard et al. 2006).

Consequences of dispersal

Our study shows that dispersal might either be successful during phases of increasing populations numbers (Gaines and Johnson 1984) or in highly heterogeneous landscapes (Hastings 1983, Bondrup-Nielsen 1993, Gandon and Michalakis 2001) when breeding sites are still available. Presaturation dispersers may be predisposed for successful establishment as indicated by the extraordinary high reproductive success of two immigrating males (13 and 27 offspring). This suggests that abandoning the natal population and taking a chance by moving to a new habitat may actually pay off. However, some of the extreme variation in the reproductive success of dispersers may be due to the presence of two distinct types of dispersers, the ones which voluntarily disperse before the carrying capacities of populations are reached (i.e. presaturation dispersers; Lidicker 1975), and others which are evicted by conspecifics at maximum population densities (i.e. saturation dispersers). The prospectus of the latter for future reproductive output is low.

More heterogeneous conditions in terms of unoccupied breeding sites would probably have increased the establishing success of immigrating dispersers (Hastings 1983, Bondrup-Nielsen 1993, Gandon and Michalakis 2001). Dispersal might therefore be most successful in a proceeding landscape fragmentation, which results in small habitat patches with high extinction and recolonization rates. However, it is important in this respect to distinguish between the number of migrants and the fraction of them which actually reproduces in the new population (see Schweizer et al 2007). The simple number or proportion of individuals moving between adjacent demes or habitat patches (Slatkin 1981) will likely lead to an overestimation of the effective gene flow in many organisms.

Conclusion and prospects

Our study demonstrates the benefits of EMS approaches in combination with parentage analyses for the study of elusive phenomena like dispersal processes. We were able to show that dispersers are not inferior *per se* because they are able to compete successfully in their natal populations. Their relatively low reproductive success after immigration gives support to reports of genetic differentiation among adjacent populations despite frequent dispersal events (Schweizer et al. 2007). According to our results, successful male dispersers can be described as young natal dispersers at or near their maximal reproductive value (Dobson 1982, Morris 1982), which emigrated before the carrying capacities in the populations were reached. In contrast, successful female immigrants seem to be breeding dispersers, i.e. individuals which leave their first litter after weaning in order to breed a second time elsewhere. Very little is known about the proximate mechanisms that trigger dispersal but we suggest that agonistic behavior arising from sex-specific relatedness structures in populations is the most likely driver of dispersal. It remains further to be investigated whether presaturation and saturation dispersers differ morphologically or genetically from

each other and whether the same triggers for dispersal operate.

Appendix

Number of individuals genotyped between 2004 and 2006, mean number of alleles per locus, and results of paternity assignments. Numbers in parentheses represent voles which were individually marked with PITs. The exclusionary power gives the probability of excluding an unrelated individual as parent without assuming that the other parent was known. Assignment rates indicate the proportion of genotyped voles for which one univocal father (“males”) or mother (“females”) each was determined. Deviations show 1 SD over years and enclosures.

	Individuals typed	Mean No. alleles	Exclusionary power [%]	Assignment rate [%]
Enclosure system 1:				
Males	248 (436)	8.73 ± 1.4	99.83 ± 0.15	60.54 ± 13.57
Females	357 (381)			59.9 ± 17.44
Enclosure system 2:				
Males	263 (490)	9.48 ± 1.65	99.83 ± 0.17	63.21 ± 14.01
Females	351 (504)			67.46 ± 10.04
Total	1255 (1811)			

DISPERSAL: DEMOGRAPHIC AND GENETIC IMPLICATIONS IN ENCLOSED VOLE POPULATIONS

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Abstract

The increase in human-caused habitat fragmentation has profound effects on population extinction and it can reduce genetic diversity. Dispersal might counteract these negative impacts, as it implicates a transfer of animals and genes between otherwise isolated populations. An understanding of dispersal is, therefore, essential. However, due to difficulties in receiving robust field data dispersal and its consequences remain poorly understood. In this study we used an experimental approach in semi-natural enclosures with individually marked common voles (*Microtus arvalis*). The manipulation of emigration and immigration showed that dispersal can affect density and the sex-ratio of populations. The latter was due to a highly male-biased dispersal. An increase of disperser proportions enhanced aggressive encounters in the populations as it was apparent in the amount of lesions. We showed that dispersers can serve as a vector distributing parasites within and among populations. However, both increased agonistic encounters and high parasite infection rates did not apparently affect dispersal probability, survival and/or fecundity. The yearly population breakdown in early spring was associated with a genetic depletion. This indicates the necessity of dispersal in order to maintain genetic diversity over years. Despite frequent dispersal events populations remained genetically separated. This was most probably due to a low reproductive success of immigrating dispersers during the breeding period. Inbreeding coefficients were not considerably affected by an isolation of populations. Dispersal seems to have long-term effects in the maintenance of genetic diversity over years, while inbreeding avoidance might operate on the within-population-level by means of kin recognition.

Introduction

Habitat reduction, segregation, and isolation of populations into small habitat fragments have many harmful biological effects ranging from the genetic to the community level (Ims and Stenseth 1989, Aars and Ims 1999, Smith and Batzli 2006). The chance of population extinction increases as the size of a habitat patch decreases (Hastings and Wolin 1989, Ferrière and Galliard 2001), and small and isolated populations are at risk to lose genetic variation through genetic drift. Since human activity leads to increasing fragmentation of natural habitats, an understanding of associated phenomena is, therefore, vital.

The negative effects of fragmentation on populations can be counteracted by dispersal, which is generally defined as a transfer of individuals and genes (i.e. gene flow) among sites (c.f. Clobert et al. 2001b). Intrasexual competition for mates is more intense among males than among females in polygynous species and this is believed to trigger a predominantly male biased dispersal in mammals (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). Dispersal, therefore, has consequences for individuals as well as for populations and it is now widely accepted that dispersal plays a major role for the dynamics and the genetic makeup of populations (e.g. Aars and Ims 2000, Andreassen and Ims 2001, Clobert et al. 2001b, Lidicker 2002, Bowne and Bowers 2004, Aars et al. 2006). Density-dependent emigration can prevent overpopulation and immigration can lead to large-scale persistence of small populations (i.e. rescue-effect; Hanski 2001). The degree of demographic synchrony as well as the genetic similarity among populations may, therefore, be associated with the amount of dispersal.

Despite its importance, dispersal and associated consequences still constitute a big gap in our knowledge (Clobert et al. 2001a). This is mainly due to the difficulties in obtaining robust field data which is reflected in predominantly anecdotal or theoretical works (Mossman and Waser 1999, Kenward et al. 2002). Dispersal is a relative seldom event and to study the impact of dispersal on population dynamics and population genetics one has to monitor both the demography of the population which is left (i.e. the emigration processes) and the new population into which a disperser immigrates. This, however, is extremely difficult under completely natural conditions, and in the past dispersal was often taken as an indistinguishable component of “gross mortality” for which it not really matters if an individual dispersed or fell prey to a predator (Lidicker 1975, Lidicker 1985). Manipulating emigration and immigration is therefore a more powerful approach than field observations to study the demographic as well as the population genetic aspects of dispersal (Aars and Ims 2000).

In this study we used semi-natural enclosures as an experimental model system (EMS; Wiens et al. 1993) and the common vole, *Microtus arvalis* (Pallas), as a model organism. Dispersers were identified by their trapping history and we manipulated emigration and immigration in the populations by a one-way transfer of dispersers. Since demographic changes are inevitably intertwined with changes in the populations' genetic composition we combined classical capture-mark-recapture methods and genetic analyses. In particular we wanted to ascertain the effects of dispersal on (i) the demography of

populations and the social interactions between dispersers and residents as these might change local birth or death rates. We analysed the impact of dispersal on (ii) the genetic constitution within and among populations. Following the “one-migrant-per-generation”-rule immigrants should maintain genetic variability in populations or even enhance it, and reduce the risk of inbreeding. Furthermore, we hypothesised populations which are connected by frequent dispersal to loose genetic separation (Wright 1931).

Methods

For field site and trapping, identification of dispersers, transfer of dispersers and molecular analyses see GENERAL METHODS.

In June, August, and October 2006 voles were additionally trapped in the vicinity of the field station to compare genetic parameters of the semi-natural enclosures with a completely natural situation.

We calculated sex ratios as the proportion of males in each enclosure. Survival rates were calculated by using relative MNA losses per fortnight for males and females and for enclosures separately (finite survival rates; Krebs 1989). We defined reproduction rates as the number of lactating and pregnant voles relative to the total number of adult females, and calculated recruitment rates for each population as the number of juvenile voles (i.e. immature individuals with a body-weight below 20 g) relative to the number of adults. To investigate a potential impact of dispersal on ectoparasite affection rates we recorded the presence of fleas, mites, and botflies (*Oestromyia leporine*, Pallas) for each population during 2006. This was done for residents and dispersers, separately.

Statistical analyses

We wanted to ascertain if population densities in the treatment enclosures matched the expectations of simple disperser subtraction (i.e. source enclosures) or addition (i.e. sink enclosures) or if changes in birth or death rates compensated for emigration and immigration, respectively. Therefore, we took densities in the transition enclosures as a reference and subtracted removed dispersers for source enclosures and added introduced dispersers for sink enclosures.

To investigate the population genetic impacts of emigration and immigration, number of alleles, allelic richness (AR), heterozygosity levels (H_o), and inbreeding coefficients (F_{IS}) were computed for each population and we compared pairwise genetic distances (F_{ST}) among populations separately for enclosure populations and years by using Arlequin 3.11 (Excoffier et al. 2005). The F_{ST} and F_{IS} -values were statistically tested for deviations from zero with 10,000 permutations. Populations with free exchange of breeding individuals should be characterized by $F_{IS} = F_{ST} = 0$, given infinitely sized populations and random breeding within groups (Chesser 1991). Allelic richness is a measure of the number of alleles standardized for sample size (El Mousadik and Petit 1996). Hence, it allows comparing genetic variability between different sample sizes. We computed allelic richness using Fstat 2.9.3.2 (Goudet 2001).

Further statistical analyses were done using SPSS for Windows 15.0.1 and we applied Bonferroni-corrections whenever conducting multiple comparisons. If not otherwise stated values are presented as means \pm one standard deviation (1 SD).

Results

Demography and social interactions

Between 2004 and 2006 we individually marked altogether 1811 voles. On average, the marked individuals were retrapped 10.03 ± 14.42 times. In the 2004 field season maximum population densities were reached in October with 30.2 ± 6.34 voles per enclosure ($149 \text{ individuals} \cdot \text{ha}^{-1}$; Figure 1). In 2004 dispersers were not transferred and population densities between enclosures were overall not significantly different (Kruskal-Wallis; $\text{Chi}^2 = 4.297$, $p = 0.508$). Densities in the following years were highest in September with 58 ± 19.93 voles per enclosure in 2005 ($286 \text{ individuals} \cdot \text{ha}^{-1}$) and 52.33 ± 15.27 individuals in 2006 ($258 \text{ individuals} \cdot \text{ha}^{-1}$). We recorded lowest densities in April 2005 and May 2006 with five individuals and less in all enclosures except in the source enclosure 1 in 2005 (minimum 6) and in the transition enclosure 1 in 2006 (minimum 17).

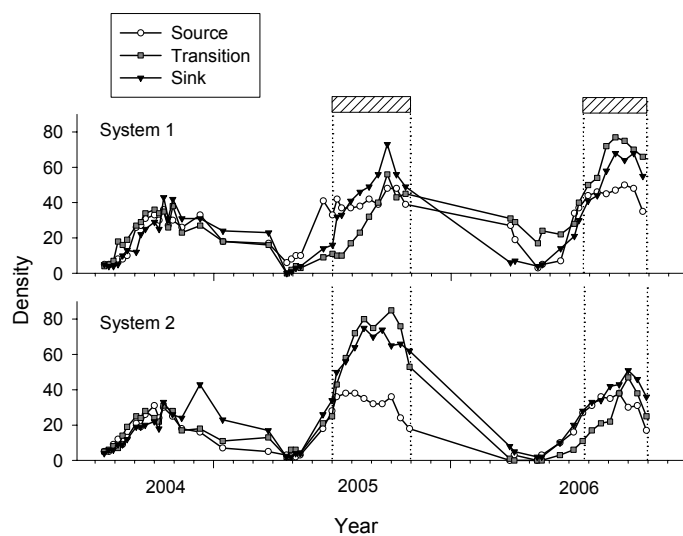


FIGURE 1 Mean densities in the two experimental systems and treatment enclosures, respectively. Dispersers were transferred in 2005 and 2006, but not in 2004. Bars above indicate the treatment periods which began with first dispersal events and ended with the termination of reproductive activity.

In 2005 and 2006 first dispersers appeared in July (week 28 in 2005 and week 30 in 2006). We refer to the following period when dispersers were transferred as the treatment period. Based on 187 dispersal events in 2005 and 129 in 2006 we calculated a bi-weekly dispersal rate of overall 0.07 ± 0.081 with significantly higher dispersal rates among males (0.095 ± 0.095 vs. 0.045 ± 0.054 ; Mann-Whitney-U; $z = -3.83$, $p < 0.001$). There was no difference in the dispersal rates, however, between the treatment enclosures source, transition, and sink (Kruskal-Wallis; $\text{Chi}^2 = 2.65$, $p = 0.75$). We transferred altogether 128 dispersers including 78 males and 50 females (Table 1). Fifty percent of the dispersers (33 of 66)

which were first transferred into the transition enclosures were repeatedly transferred into the sink enclosures because they apparently did not settle and entered the matrix traps again.

TABLE 1 Number of dispersers transferred to transition or sink enclosures in 2005 and 2006. Numbers in parentheses give voles which were transferred twice and are already included in the numbers before.

	2005		2006		Total transfers	Dispersers total
	Transition	Sink	Transition	Sink		
Enclosure system 1:						
Males	10	13 (4)	7	18 (5)	48 (9)	39
Females	6	8 (3)	8	7 (1)	29 (4)	25
Enclosure system 2:						
Males	5	20 (4)	14	11 (7)	50 (11)	39
Females	12	16 (7)	4	2 (2)	34 (9)	25
Total	33	57 (18)	33	38 (15)	161 (33)	128

We found a significantly increasing proportion of dispersers during the treatment periods 2005 and 2006 from source enclosures ($12.24 \pm 6.38\%$) over transition ($15.35 \pm 7.52\%$) and sink enclosures ($22.1 \pm 7.37\%$; Kruskal-Wallis; $\text{Chi}^2 = 22.162$, $p < 0.001$; Figure 2). Contrary, there was a decreasing tendency in the proportion of residents from source to sink enclosures ($50.48\% \pm 9.6$ vs. $48.72\% \pm 16.13$ vs. $43.83\% \pm 14.95$). This was, however, not statistically significant (Kruskal-Wallis; $\text{Chi}^2 = 2.955$, $p = 0.228$). Mean densities in the three treatment enclosures and during the treatment periods 2005 and 2006 differed with lowest values in the source and highest in the sink enclosures (37.13 ± 8.28 individuals*enclosure⁻¹ vs. 50.97 ± 23.35 vs. 53.93 ± 13 ; Kruskal-Wallis; $\text{Chi}^2 = 17.944$, $p < 0.001$; Figure 2). The mean densities in the source and sink enclosures matched our expectations of a simple numerical subtraction and adding, respectively (Mann-Whitney-U; Source: $z = -0.819$, $p = 0.413$; Sink: $z = -0.414$, $p = 0.679$; see Methods).

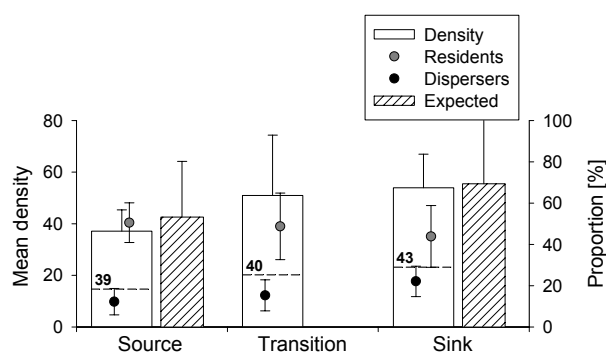


FIGURE 2 Mean densities, expected densities (left y-axis; see Methods), and proportion of residents and dispersers (right y-axis) during the treatment periods 2005 and 2006. Dashed lines with corresponding numbers indicate proportion of males. Error bars indicate 1 SD.

Bi-weekly survival rates of all individually marked voles in treatment periods 2005 and 2006 were not significantly different between source, transition, and sink enclosures (0.751 ± 0.233 vs. 0.757 ± 0.199 vs. 0.791 ± 0.181 ; ANOVA; $F_{2,369} = 1.402$, $p = 0.247$). There were also no differences between treatment enclosures neither in reproduction rates (0.419 ± 0.244 vs. 0.498 ± 0.223 vs. 0.466 ± 0.263 ; Kruskal-Wallis; $\text{Chi}^2 = 2.074$, $p = 0.355$) nor in recruitment rates (0.284 ± 0.185 vs. 0.309 ± 0.207 vs. 0.274 ± 0.218 ; Kruskal-Wallis; $\text{Chi}^2 = 0.655$, $p = 0.721$). We found, however, a significant difference between treatment enclosures in the sex ratio with lowest proportion of males in source and highest in sink enclosures ($0.388\% \pm 0.079$ vs. $0.395\% \pm 0.086$ vs. $0.433\% \pm 0.082$; ANOVA; $F_{2,111} = 3.369$, $p = 0.038$; Figure 3).

The proportion of lesions (scars and wounds) of all individually marked voles (including adults and juveniles) was significantly higher for males than for females (Mann-Whitney-U; $z = -2.45$, $p = 0.012$; Figure 3) and we found an increasing proportion of lesions from source (0.054 ± 0.042), over transition (0.089 ± 0.033), and sink enclosures (0.145 ± 0.025) in males. This difference was significant between the three treatment enclosures when immigrating dispersers were included in the calculation (Kruskal-Wallis; $\text{Chi}^2 = 7.654$, p after Bonferroni-correction = 0.044) and lesions in males showed an increasing tendency when immigrants were excluded ($\text{Chi}^2 = 6.552$, p after Bonferroni-correction = 0.076). There was no significant difference in the proportion of lesions between the treatment enclosures in females ($\text{Chi}^2 = 1.515$, $p = 0.469$).

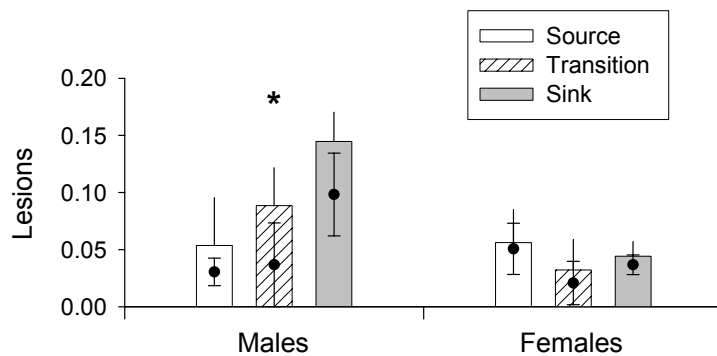


FIGURE 3 Proportion of voles with lesions (scars and wounds) induced by agonistic behaviour. Bars represent all marked animals during the treatment period, including immigrated dispersers. Dots are only voles born in the respective enclosure with immigrants excluded. Error bars indicate 1 SD. *: $p < 0.05$ between treatment enclosures.

During the treatment period in 2006 we found 13.4% of all individually marked voles with botflies and 23% of all individuals with fleas or mites. We did not find any significant difference in the overall proportion of ectoparasites neither between males and females (Mann-Whitney-U; $z = -0.16$, $p = 0.873$) nor between treatment enclosures (Kruskal-Wallis; $\text{Chi}^2 = 2.808$, $p = 0.246$). Males, however, showed highest proportions of ectoparasites in sink enclosures in system 1 as well as in system 2 (Appendix 1).

Genetic implications

Between 2004 and 2006 we genetically analysed altogether 1255 individuals from the enclosures which corresponds to 69.3% of all 1811 individually marked common voles. The number of alleles over all 13 loci and throughout 2004 and 2006 was 9.13 ± 1.53 on average. In 2005 and 2006 we released 12 and 22 additional voles into the enclosures to compensate for the population crashes which happened in April and May, respectively (Figure 2 and Figure 4). We did not release any additional voles, however, into the source enclosure 1 in 2005 because of a sufficient number of voles which survived over the winter. The allelic richness was not significantly different over the years, i.e. between 2004 and the periods before treatment started in 2005 and 2006 (ANOVA; $F_{2,231} = 0.345$, $p = 0.709$), and we found no difference before treatment between source, transition, and sink ($F_{2,231} = 1.308$, $p = 0.272$). During treatment periods 2005 and 2006, however, significant differences between treatment enclosures were found with lowest mean allelic richness in source and highest mean values in sink enclosures (ANCOVA with allelic richness before treatment as covariate; $F_{2,153} = 20.179$, $p < 0.001$; Table 2 and Figure 5). Allelic richness appeared to decrease throughout field seasons 2005 and 2006 in source as well as in transition enclosures, but increased in sink enclosures (Figure 5).

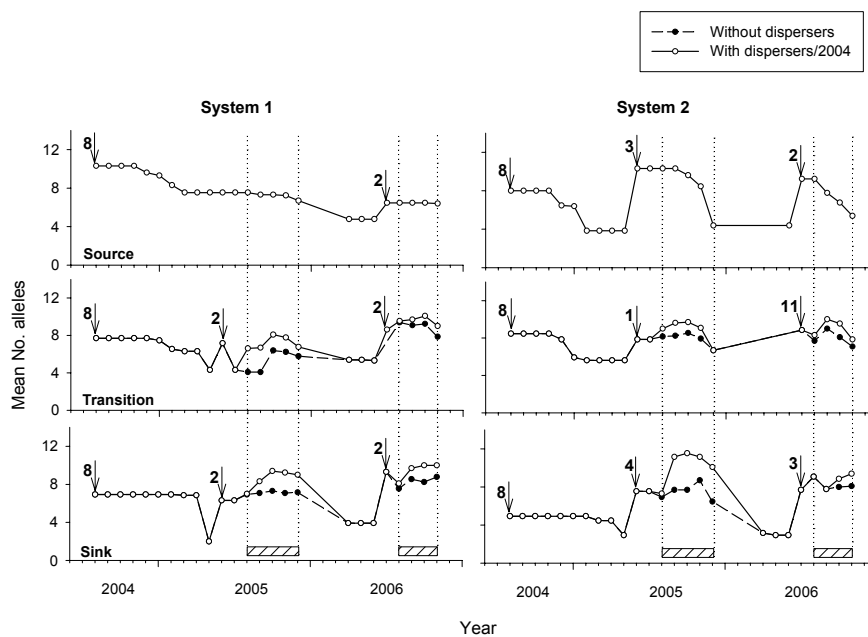


FIGURE 4 Mean number of alleles per locus. The calculations were done separately with and without immigrated dispersers. Arrows indicate date and number of released voles. Bars at the bottom line indicate treatment periods.

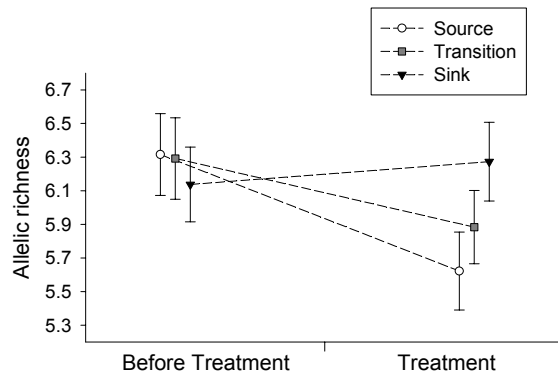


FIGURE 5 Allelic richness before treatment periods and during treatments 2005 and 2006. Error bars indicate 1 SE.

Changes in genetic diversity were rather due to the immigrants themselves than to their successful mating and fixation of new alleles, respectively. When excluding immigrants from the analyses we found significantly lower allele numbers during treatment periods compared to computations with immigrants included (7.568 ± 1.123 vs. 8.917 ± 1.295 ; Mann-Whitney-U; $z = -4.034$, $p < 0.001$; Figure 4).

During the treatment periods 2005 and 2006 the observed heterozygosity (H_o) ranged from 0.67 to 0.809 (Table 2). After sequential Bonferroni-correction, significant deviations from Hardy-Weinberg equilibrium were detected in 82 out of 156 tests (52.56%) for all loci, populations, and years. In the 2004 field season we found only one allele (two out of 117 = 1.71%) to deviate from Hardy-Weinberg expectations.

Inbreeding coefficients (F_{IS}) in the semi-natural enclosures ranged from -0.12 to 0.04 and some enclosures were inbred (Table 2). There was no trend, however, for any treatment enclosure to be especially prone for inbreeding.

TABLE 2 Genetic parameters for 2004 and treatment periods 2005 and 2006. Parameters include individuals born and marked in the year before and which were still alive in the next year's treatment period. Immigrated dispersers were included in the analyses. #: number of individuals genotyped; AR: allelic richness; H_O : mean observed heterozygosity over loci; F_{IS} : inbreeding coefficient. *: $p < 0.05$

	2004				2005				2006			
	#	AR	H_O	F_{IS}	#	AR	H_O	F_{IS}	#	AR	H_O	F_{IS}
Encl. system 1:												
Source	29	7.34	0.82	-0.02	50	5.85	0.80	-0.05*	49	5.12	0.78	-0.10*
Transition	35	6.12	0.87	-0.12*	96	5.63	0.78	-0.04*	152	5.35	0.76	-0.04*
Sink	22	6.12	0.80	-0.05	139	6.14	0.81	-0.06*	106	6.16	0.74	0.01
Encl. system 2:												
Source	27	6.56	0.81	-0.04	44	6.55	0.71	0.04	42	4.97	0.67	-0.02
Transition	34	6.78	0.84	-0.05*	189	6.03	0.78	-0.05*	78	6.52	0.77	0.00
Sink	10	5.78	0.78	-0.02	161	6.61	0.80	-0.02*	80	6.18	0.74	0.01
Free living:												
June									7	6.84	0.79	0.08
August									20	6.36	0.82	0.00
October									21	6.74	0.79	0.05

Despite the high number of immigrating dispersers (i.e. high gene flow) all treatment enclosures were significantly different during the treatment periods (Appendix 2). Pairwise genetic distances (F_{ST} -values) in 2005 and 2006 ranged from 0.068 to 0.137 and genetic distances were somewhat smaller between source and transition (0.094 ± 0.019) and transition and sink enclosures (0.084 ± 0.02) than between source and sink enclosures (0.115 ± 0.019 ; Kruskal-Wallis; $\chi^2 = 5.115$, $p = 0.077$).

In June, August and October 2006 we analysed 48 voles which were trapped in the vicinity of the field station to compare genetic parameters between semi-natural enclosures and complete natural conditions. Free living voles had on average 9.667 ± 3.651 alleles per locus. The allelic richness did not significantly change between June and October (ANOVA; $F_{2, 36} = 0.262$, $p = 0.771$). We found only one allele to deviate from Hardy-Weinberg expectation, and F_{IS} values indicated that the free living population was not significantly inbred to any time of the investigation (Table 2).

Discussion

Overall population densities reached 286 individuals* ha^{-1} in 2005 and 52 individuals* ha^{-1} in 2006 which corresponds to a medium density (Niethammer and Krapp 1982). A high trapping success of, on average, 10 retraps per vole is surely not achievable under complete natural conditions. Survival rates were higher for females than for males, whereas males showed significantly higher dispersal rates. Both lower survival rates and higher dispersal rates in males can be associated with the polygynous mating system as it is prevalent in most mammalian species (Greenwood 1988, Dobson 1982). Higher intrasexual competition for mates leads to larger home range areas, increases males' stress level, the risk of being

preyed upon, and eventually their motivation to disperse. Consequently, populations were overall female-biased.

Impact of dispersal

Dispersal affected population densities and we showed that male biased dispersal can change local sex ratios (see Myers and Krebs 1971). The extraordinary high proportion of lesions among male voles was most probably due to agonistic encounters between conspecifics (Le Galliard et al. 2005), and seemed not only to be increased by immigrants that entered the populations but also because of dispersers which were not able to emigrate (i.e. frustrated dispersers; *sensu* Hansson 1991, Aars and Ims 2000). The dispersers' increased activity surely enhanced the interactions with conspecifics which not only affected the amount of lesions but also promoted the transmission of parasites. Dispersal is likely to serve as a vector distributing parasites within and among populations. However, we missed to show any significant difference between treatment enclosures in the dispersal rates or in birth or death rates, indicating that aggression and parasite infection did not considerably affect emigration propensities or the populations' net increase. This is in contrast to Ylönen and Horne (2002) who proposed that intruders (i.e. immigrants) of *Myodes glareolus* committed infanticide and oppose the study by Lin et al. (2004) who showed that immigrating *Microtus ochrogaster* can reduce the proportion of juveniles.

Severe decreases in the mean allele number coincided with the yearly population breakdown in early spring, reflecting genetic drift and the necessity for dispersal between small and isolated habitat patches. We proved the occurrence of gene flow in natural systems by stable allelic richness between June and October 2006 (Aars et al. 2006, Schweizer et al. 2007). There was no significant difference in the allelic richness between years of investigation, which was surely due to the release of additional voles. Allelic richness, however, was significantly different between treatment enclosures with lowest values in source and highest in sink enclosures, whereas allelic richness increased during field seasons only in sink enclosures. This was surely due to the fact that sink enclosures "received" immigrants from two different populations and the other two treatment enclosures from no and only one population, respectively. The differences in gene diversity between the enclosure populations were mainly due to the dispersers themselves as we found a much lower genetic impact of dispersal when considering the natal individuals in the respective population, only. This indicates a relatively low reproductive success of immigrating dispersers and also explains that populations were still genetically separated despite frequent dispersal events (see Schweizer et al. 2007). Consequently, it is important to distinguishing between the number of dispersers and the fraction of them which actually reproduces in the new populations (i.e. effective dispersal; Wang 2004). Pairwise genetic differences were somewhat smaller between directly connected population enclosures, indicating isolation-by-distance patterns on a surprisingly fine spatial scale.

Application to natural systems

We termed enclosure populations from which dispersers were removed (i.e. emigrated) but no immigrants added, “source” enclosures. The term is derived from populations in which birth rates exceed death rates (Diffendorfer 1998). We, however, regard source enclosures as isolated and small populations with emigration but restricted immigration. This might resemble highly fragmented landscapes with inter-patch distances exceeding the normal movement ability of voles. For source enclosures as well as for the 2004 season we found significant inbreeding coefficients in only two out of six cases. This was not considerably different compared to the other treatment enclosures. At least within a field season it seems that “internal” inbreeding avoidance is more important than dispersal events. Voles might prevent inbreeding not only by dispersal but they also may recognize and avoid breeding with close kin within isolated populations (Mateo 2003, Le Galliard et al. 2006). Aars et al. (2006) found that populations living in patchy habitats can maintain high levels of genetic variability when only a few adults contribute to breeding in each colony. Still, we released additional voles into the enclosures prior to each field season and the negative effects of isolation surely would have been more intense over a longer period as it was apparent in the severe decrease of genetic diversity in spring. To avoid long term negative effects of isolation in natural systems it is advantageous that fragments are connected by narrow strips of habitat referred to as landscape corridors (Andreassen et al. 1996, Aars and Ims 1999). Hence, dispersal seems to have long-term effects in the maintenance of genetic diversity over years, while inbreeding avoidance might operate on the within population level by means of kin recognition.

Enclosure populations with both immigration and emigration processes were termed “transition” enclosures. Transition enclosures might resemble a natural condition with inter-patch distances manageable for dispersers without considerable barriers for emigration (e.g. social fence; see below). The rescue-effect, i.e. the positive effect of immigration on local population size, combines a reduced risk of becoming locally extinct with a low risk of genetic depletion (Aars et al. 2006). However, despite frequent immigration events we showed a relatively low genetic effect on the consecutive generations in the enclosure populations and successful settlement seems to be highest at low population densities in spring (c.f. Andreassen and Ims 2001). Fifty percent of transferred voles did not establish and appeared to disperse again, a large fraction of immigrants most probably died, and Hahne et al. (ESTABLISHMENT AND FITNESS CONSEQUENCES, this volume) showed a relatively low establishing success in immigrating vole dispersers during the breeding period. This suggests that immigrants have a limited opportunity for successful dispersal in populations at or near their carrying capacity (McGuire et al. 1993, c. f. Andreassen and Ims 2001).

In “sink” enclosures we allowed immigration but prevented emigration. This might be associated with the social fence hypothesis which is defined as a social barrier of unrelated conspecifics restricting emigration and which is believed to cause population buildups, local resource exhaustion, and population crash (Hestbeck 1982, Aars and Ims 2000, Smith and Batzli 2006, see Sandell et al. 1991, but see Ostfeld 1994). The high aggression and infection rates indicate poor conditions for individuals to live in

populations with a high proportion of dispersers. Although we missed to show any evidence in this study, high aggression and infection rates may affect dispersal, survival and/or fecundity as soon as densities reach higher values. Healey (1967) found that juvenile deer mice grew poorly when competing with aggressive adults and juveniles also disappeared rapidly from the experimental plots when the adult population was aggressive. Le Galliard et al. (2005) found that an excess of male lizards begets aggression towards adult females, whose survival and fecundity drop, along with their emigration rate.

Appendix

APPENDIX 1 Proportion of male and female voles with parasites in 2006. Numbers in parenthesis give overall numbers of parasitised individuals.

	Males			Females		
	Botflies	Fleas/Mites	Overall	Botflies	Fleas/Mites	Overall
Enclosure system 1:						
Source	13.6	27.3	38.6 (17/44)	17.4	34.8	45.7 (21/46)
Transition	8.7	23.2	30.4 (21/69)	14.3	21.4	34.5 (29/84)
Sink	14.8	27.8	40.7 (22/54)	20.9	23.9	41.8 (28/67)
Enclosure system 2:						
Source	4.9	24.4	29.3 (12/41)	10.9	17.4	28.3 (13/46)
Transition	14.6	19.5	34.1 (14/41)	13.9	8.3	22.2 (8/36)
Sink	15.8	23.7	39.5 (15/38)	9.8	21.3	31.1 (19/61)
Total	11.8	24.4	35.2 (101/287)	14.7	21.8	34.7 (118/340)

APPENDIX 2 Estimates of pairwise genetic distance (F_{ST}) for treatment periods 2005 and 2006 below diagonal and p values above diagonal. Estimates include individuals born and marked in the year before, which survived and were still alive in the next year's treatment period, and dispersers which immigrated. ***: $p < 0.001$.

	2005			2006		
	Source	Transition	Sink	Source	Transition	Sink
Encl. system 1:						
Source	-	***	***	-	***	***
Transition	0.078	-	***	0.108	-	***
Sink	0.091	0.072	-	0.113	0.112	-
Encl. system 2:						
Source	-	***	***	-	***	***
Transition	0.110	-	***	0.077	-	***
Sink	0.118	0.083	-	0.137	0.068	-

**THE IMPACT OF THE DOMINO-EFFECT ON DEMOGRAPHY AND
GENETIC HETEROZYGOSITY IN DIFFERENT TYPES OF
METAPOPOPULATIONS – A MODEL APPROACH**

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Introduction

The establishment of a disperser can be thought of in two ways: first, by simply integrating its home range into an existing social structure or, secondly, by repelling a former resident individual. The latter scenario results in a *domino-effect* if the repulsion continues, and might have profound effects for the demography and the genetic constitution of populations.

During intensive field studies in semi-natural enclosures with the common vole, *Microtus arvalis*, we manipulated emigration and immigration of dispersers and investigated the impact of dispersal on the spatio-temporal behavior of resident individuals. A high turnover of dispersers affected home range shifts of resident individuals (see SPATIO-TEMPORAL BEHAVIOR, this volume). Hence, dispersal might increase the residents' propensity to disperse and this might be an indication on the occurrence of domino-effects. We, therefore, modeled simple emigration vs. domino-effect to show potential differences between the two scenarios. Modeling approaches have several clear advantages. They force one to develop explicit hypotheses, organize existing knowledge, and estimate values from unknown parameters (Wiens 2001). Models of dispersal events, however, mostly investigate demographic changes and ignore genetic consequences.

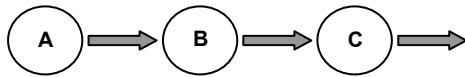
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Methods

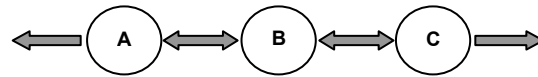
Model structure

The models were run with STELLA 8.1.1 software package (Constanza 1998). Three different metapopulation types were chosen consisting of three subpopulations each (Figure 1). In model 1 subpopulations were linearly connected by dispersal events, i.e. by strict movements of dispersers in one direction only. In model 2 we let back- and forward movements occur, but still without any connection between subpopulations A and C. Model 3 was based on a cyclic system of forward- and backward movements. In each subpopulation demographic and genetic changes were simulated, both affected by dispersal events.

Model 1



Model 2



Model 3

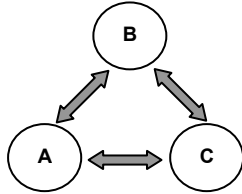


FIGURE 1 The three model types, reflecting different metapopulations, which increase in complexity: from one-way dispersal in a linear system (Model I) to back- and forward dispersal in a cyclic model (Model III). Each circle represents one subpopulation consisting of nine possible genotypes.

Population assumption/Demographic structure

The population development was density dependent by simulating intraspecific competition. This resulted in a decreasing growth rate (P 1):

$$\frac{dN}{dt} = 0.5 \cdot N \cdot \left(\frac{250 - N}{250} \right) \quad (1)$$

N represents the number of individuals within populations. This let the population densities level off into a plateau at a carrying capacity of 250 individuals. We assumed a species with overlapping, non-synchronous generation times and repeating reproduction (P 2). Time and population growth were chosen as being continuous. In the model runs sex was not considered (P 3). However, self-fertilization was assumed to be impossible for the alleles to be recombined (see assumptions for genetics). Furthermore, neither age nor season was taken into account (P 4). A stochastic element was not incorporated.

Dispersal assumptions

Disperser numbers were assumed to be positively density dependent on their natal population (D 1; Figure 2):

$$\left(\frac{1}{10} \cdot \text{Density original pop} + 0 \right) \cdot c, \quad (2)$$

whereas the coefficient c was to vary the proportion of individuals going into dispersal.

Establishing rates decreased with increasing densities in the target populations (D 2; Figure 2):

$$\left[\left(-\frac{1}{1000} \cdot \text{Density target pop} + 1 \right) \cdot \text{Disperser} \right] \cdot c \quad (3)$$

Here, the coefficient c was to vary the proportion of dispersers which successfully established. Emigrating animals which did not establish in the target population were assumed to die (Figure 2). The scenario of domino-effect was incorporated into the models by substituting a resident animal by a successful disperser. At the same time the evicted resident became a disperser.

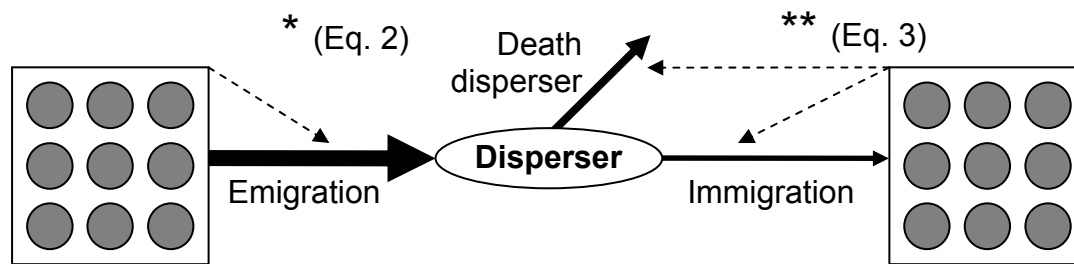


FIGURE 2 Schematic representation of the disperser model by showing two subpopulations. Emigration and immigration were dependent on the density of the original and the target population, respectively. The stars indicate model equations given and explained in the text. Dispersers which did not establish were supposed to die. The nine circles in each subpopulation (boxes) represent the nine possible genotypes of the animals (see text).

Genetic structure

All subpopulations consisted of nine different genotypes (G 1; Figure 2). This was possible by simulating diploid individuals with two loci and two different alleles per locus (A and a for locus one and B and b for locus two). The genetic recombination was done autosomal-recessive following Medelian rules (G 2):

$$\begin{array}{lll} aabb & aaBb & aaBB \\ Aabb & AaBb & AaBB \\ AA bb & AABb & AABB \end{array} \quad Z = \begin{bmatrix} Z_{00} & Z_{01} & Z_{02} \\ Z_{10} & Z_{11} & Z_{12} \\ Z_{20} & Z_{21} & Z_{22} \end{bmatrix} \quad (4)$$

The sum of Z_{ij} was always one and the sums of the lines give the proportions of the aa-, Aa-, and AA- genotypes of locus one. The sums of the columns give the proportions of the bb-, Bb-, and BB- genotypes of locus two.

Mutation, meiotic drive, selection, and genetic drift were ignored (G 3). To investigate the genetic effects of dispersal we chose *heterozygosity* H_0 as the measuring unit. Heterozygosity describes the relative proportion of heterozygous loci in the population and heterozygous animals are frequently described to have advantages over homozygous individuals. Heterozygosity values were investigated by, first, measuring the time when H_0 stabilized and, second, by the actual number reached at the end of each run.

The runs lasted until no more genetic variation occurred (i.e. the stable state). Heterozygosity values as well as demographic parameters were measured over the entire metapopulations.

As the final H_0 is dependant on the genetic constitution at the onset of each run (Figure 3), we varied initial genotype allocations in the metapopulations. We took account for lowest as well as for highest possible diversity-combinations and launched 18 initially different genetic combinations in each model type. All runs started with 5 animals per subpopulation.

ASSUMPTIONS FOR POPULATIONS

- (P 1) Density dependent growth rates
- (P 2) Species with overlapping, non-synchronous generation times and repeated reproduction
- (P 3) No sex differences, no self-fertilization
- (P 4) No age, no seasonality

ASSUMPTIONS FOR DISPERSAL EVENTS

- (D 1) Positively density dependent dispersal
- (D 2) Establishing rate negatively dependent on the density of the target population
- (D 3) The domino-effect could simply be activated and deactivated, respectively

ASSUMPTIONS FOR GENETICS

- (G 1) Nine different genotypes in all subpopulations
- (G 2) Inheritance autosomal-recessive following Mendelian rules
- (G 3) No mutation, meiotic drive, selection , and genetic drift

Results

To check if the genetic assumptions were correct we suppressed any dispersal event and varied the proportion of allele A in locus one (Figure 3). As expected, the amount of heterozygotes Aa changed with the variation in A, or, to put it the other way around, a slight variation of heterozygotes went along with a high divergence between the two homozygous loci AA and aa. The same was true for locus two (alleles B and b).

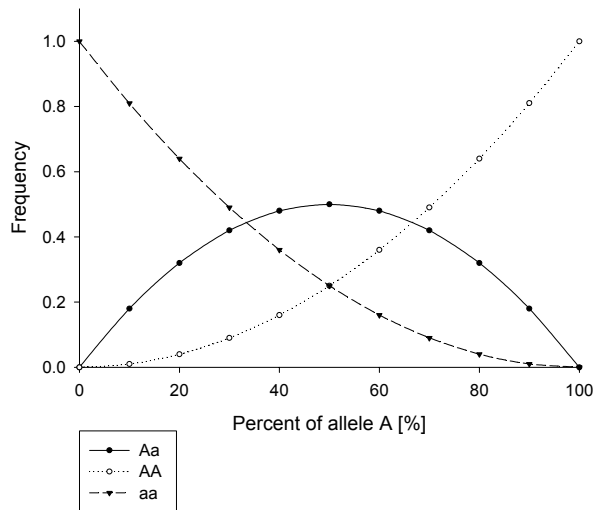


FIGURE 3 Test for the genetic validity of the subpopulations by suppressing any dispersal event. As expected, the amount of heterocytotes changed with the variation of allele A. The same was true for allele B. Initial genetic constitutions were, therefore, important for the outcome of heterozygosity values.

The number of dispersers as well as the number of successfully established dispersers grew with an increase in dispersal- and establishing rate, respectively (Figure 4 and Figure 5). Density in the different metapopulation types were negatively associated with the number of dispersers. A difference between the two scenarios - domino-effect vs. simple immigration - was shown in all three model types, with largest differences in the cyclic model 3. Here, we found up to four fold higher numbers of successfully established dispersers for the domino-effect compared to the scenario of simple immigration (240 vs. 54 successfully established).

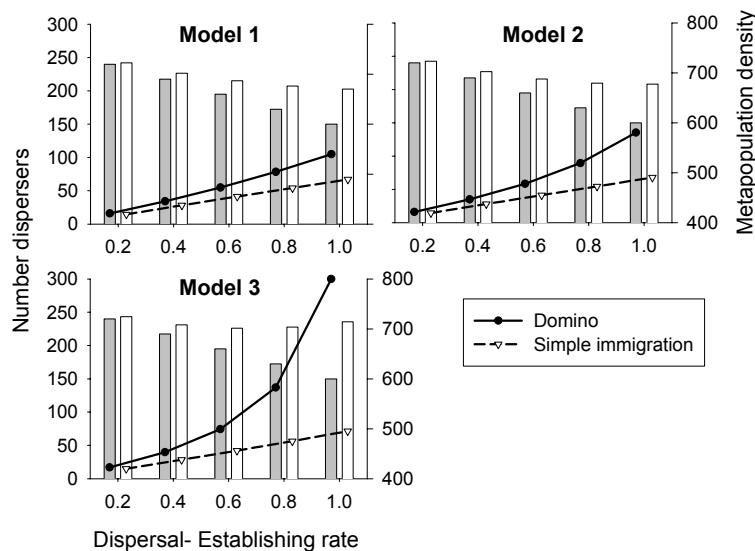


FIGURE 4 Total number of dispersers in the different model types (lines) and densities summed up for the three subpopulations (bars) by varying dispersal- and establishing rate. The values on the x-axis represent the variation in coefficient c (see text).

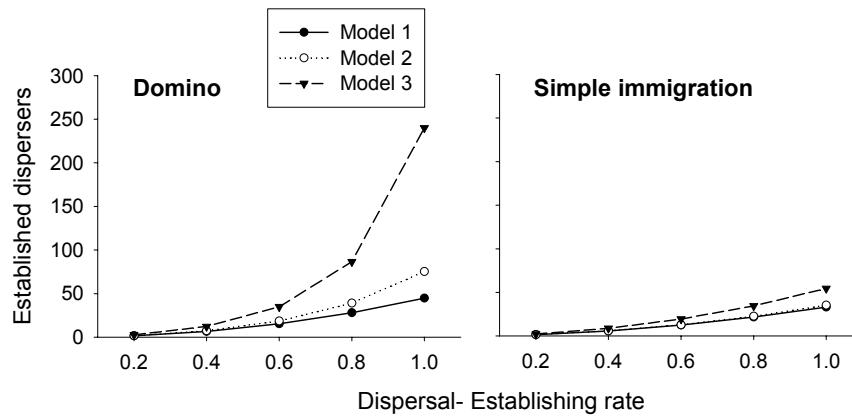


FIGURE 5 Total number of dispersers which successfully established in the new populations for the two scenarios and the different model types.

In all three model types the final value of H_0 was reached significantly faster with the domino-scenario compared to simple immigration (Figure 6A; Two-way ANOVA: d.f. = 1; $F = 14.2$; $p < 0.001$). Slowest development showed model 1, fastest was model 3 (d.f. = 2; $F = 38.2$; $p < 0.001$). There was no significant interaction of the two factors model type and dispersal scenario (d.f. = 2; $F = 0.521$; $p = 0.6$).

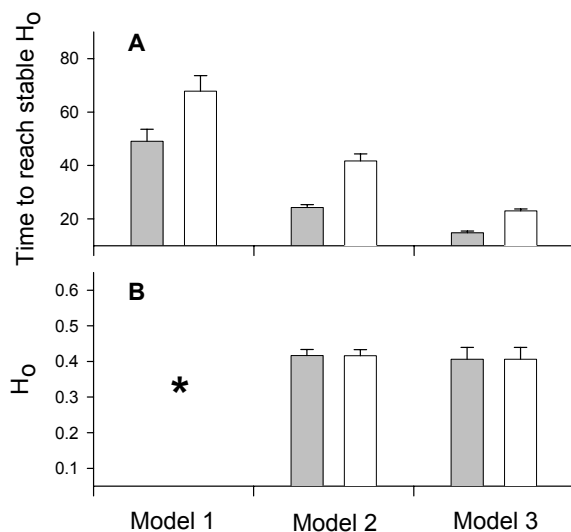


FIGURE 6 Heterozygosity H_0 measured by the time to reach stability (A) and by the final values shown at the end of each run (B). Grey bars: domino-effect; white bars: simple immigration. Error bars represent 1 SE which resulted from variations in initial genotype combinations (see text). Final values in model 1 were solely dependant on the initial genotype combinations in subpopulation A (See Figure 7).

We found no significant difference between domino-effect and simple immigration in the final values of H_0 (Figure 6B). Here, the initial combinations of genotypes had a much larger effect on the outcome of H_0 than the scenario-event itself. In model 1 final values of H_0 were solely dependent on the initial genotype combinations in subpopulation A (Figure 7). Homozygous dispersers from subpopulation A let the H_0 values drop down to zero. H_0 values reached 0.25 with one locus heterozygous in A and both loci

heterozygous let the final values reach 0.5. This was independent of genotype combinations whatsoever in subpopulations B and C.

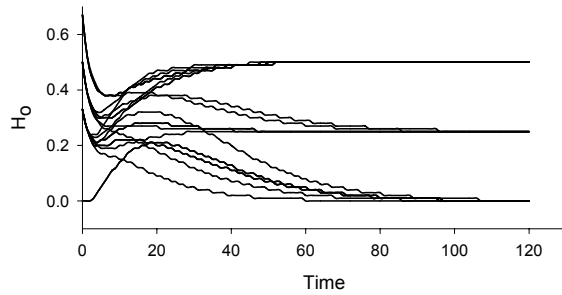


FIGURE 7 Development of heterozygosity H_0 over time. The three different final values were solely dependent on the initial genetic combinations in subpopulation A.

GENERAL DISCUSSION

In this study I used an experimental approach in semi-natural enclosures with individually marked common voles, *Microtus arvalis*. Here, classical capture-mark-recapture studies were combined with molecular analyses, intensive radio tracking, and an automatic activity recording. By using an experimental model system (EMS) I received data on altogether 1811 individually marked voles. Out of 225 defined dispersers 128 individuals were transferred into new populations to investigate the emigrants' and immigrants' spatio-temporal behavior, their establishment and fitness consequences, and the effect of dispersal on resident populations. The application of 13 polymorphic microsatellites on 1255 individuals gave extensive information on the reproductive success of residents and dispersers and on the impact of dispersal on population genetic changes.

Application of the experimental model system

The experiments were conducted in semi-natural enclosures with the common vole, *Microtus arvalis*, following the approach of an experimental model system. The appeal of an EMS is to simplify complex phenomena of natural systems in order to reduce unknown or to manipulate parameters, and to standardize and repeat experiments within a relative short time period (Wiens et al. 1993). Although we have to be cautious of applying all results of this study to larger scales and other organisms, respectively, it is likely that certain aspects of behavior can be used to predict another model system in a similar situation (see Ims et al. 1993). For instance, the sex-differences in dispersal, and certain aspects during the process of establishment are features that are likely to be common in many other territorial species.

Dedicated pilot studies in the experimental model system and detailed trapping data on individual voles during the experiment allowed to develop a score system for differentiating territorial residents from risk-prone dispersers. The detected differences in physical condition (lesions), in the reproductive success, and in behavior patterns suggest that this score system is at least able to identify individuals with a particularly high motivation to leave a population. Individuals with a lower motivation for dispersal may have been missed by this approach but there is currently no other way to quantify dispersal motivation in rodents and lower levels of motivation may be strongly context dependent (population density, kin structure, etc.). The score system in the EMS allowed to explicitly investigate the process and the consequences of emigration and immigration without additional loss of information due to the risky travel phase (Smith and Batzli 2006). The distinction between birth and immigration or death and emigration would hardly be possible for small mammals under completely natural conditions. For EMS studies, the logistically much simpler use of exit doors (Gaines et al. 1979) or one-way tubes (Viitala et al. 1994) may provide other means to identify dispersers. However, such approaches might lead to a false classification of individuals as dispersers which perform only a single excursion.

Emigration

The phase of emigration initiates the dispersal process as the individual leaves what used to be its area of residence (Andreassen et al. 2002). How far apart the previous and new home ranges must be for the movement to be classified as dispersal, is a matter of controversy. A general rule allowing several spatial scales is that the postdispersal home range does not overlap the predispersal home range (Stenseth and Lidicker 1992). This might implicate home range shifts within habitat patches. In this study, however, dispersal was defined as a behavior of an animal associated with a high motivation to leave the natal population and, hence, as a movement among habitat patches.

Morphological, behavioral, and genetic traits of dispersers

Based on the trapping history and reproductive state of individually marked voles, I differentiated three groups of animals which significantly differed in their body-weight already at an early stage of the individuals' life. Residents, defined as stationary and mature individuals were the heaviest and reproductively most successful individuals with an overall reproduction rate of 64%. It is, therefore, highly likely that residents constitute the competitively superior group of animals. Philopatrics were stationary individuals but did not become reproductively active, not even in high age classes. Philopatrics comprised the lightest voles with increasing weight-differences between the three groups over their age. Due to their morphological constitution it is most likely that philopatrics are subordinate individuals, and that a suppression of the reproductive activity reduced competitive interactions with residents. To enhance inclusive fitness philopatric females might participate in nursing a relatives' litter or in a defense against aggressive or infanticidal behavior by unfamiliar conspecifics. This behavioral strategy probably promotes the weaning success of young (Fortier and Tamarin 1998, Ylönen and Horne 2002, Hayes et al. 2004, Le Galliard et al. 2006, Lawson Handley and Perrin 2007). Subordinate males may wait to sneakily mate as soon as the more competitive residents are absent or dead.

Emigration clearly relieves the intraspecific competition in the natal population. However, as dispersal is a high risk strategy (Andreassen and Ims 2001, Smith and Batzli 2006; but see McGuire et al. 1993), emigration is surely not an *ad hoc* decision, but rather has to balance the costs and benefits of dispersal in terms of fitness consequences. An individual should, therefore, disperse as soon as the expected fitness (i.e. survival and reproduction) in the new population is greater than remaining in the natal population (Morris 1982, Wolff 1992, c.f. Krebs 1978). Small and subordinate philopatrics are not likely to be successful in new populations and probably do better when remaining in the natal population. The dispersers' body-weight, however, was in between the body-weight of residents and philopatrics. I found no significant difference in residents' and dispersers' survival rates, and their reproduction rate of overall 26% indicates that dispersers are not subordinate *per se*, but are able to compete for reproduction. Still, lesions, induced by agonistic interactions, indicate that male dispersers experienced overall high competition by residents, and dispersers might improve fitness when leaving the natal population. To reduce agonistic interactions in the natal population, male dispersers predominantly suppressed the onset

of reproduction and accelerated maturation as soon as they showed an increased motivation to emigrate. Female dispersers especially showed a high dichotomy in their body-weight at the time of emigration indicating that individuals eventually reach an age when their relative's contribution to inclusive fitness is greater than their own if the offspring inherit the breeding site from their mother (Hayes 2000, Hayes et al. 2004). This indicates that females might be more eager in increasing inclusive fitness, while male dispersers are likely to enhance individual reproduction in the new populations.

I suggest that the three groups residents, philopatrics, and dispersers, follow different social and reproductive strategies to optimize their direct and inclusive fitness, respectively. It is likely that the benefits of each group are a dynamic trade-off in a life history of an animal being dependent on the proportion of individuals in the respective other group. If, for example, intraspecific competition is low due to a low number of residents, young or otherwise subordinate individuals should try to participate in reproduction and stay rather than to suppress reproduction or taking the risk of dispersal. In accordance with studies by Boonstra and Hochachka (1997) on the collared lemming *Dicrostonyx groelandicus* I failed to find any hint for a genetic inheritance of the dispersal behavior. Hence, dispersal seems to be a flexible behavior, and conducted by a morphologically distinct group of animals that is triggered by extrinsic factors rather than induced by a specific "dispersal gene" (see below).

The present data highly suggest that dispersers' spatio-temporal behavior in the natal population reflects a balance between a competitive avoidance of residents and an avoidance of predation risk. Several studies have stated an increased risk of predation at habitat edges (Andr n 1995 and references therein, Brand and George 2000) which was reflected by an overall preference of the habitat interior and an avoidance of edge sections, respectively. The spatial behavior of residents and dispersers might conceptually be interpreted in terms of an ideal free distribution (Fretwell and Lucas Jr. 1970) which assumes that individuals are free to choose locations such that they optimize the fitness relevant parameters, survival and reproduction. It is, therefore, reasonable to assume that habitat patches become at first occupied in the interior sections until limiting space forces subordinate individuals towards risky edges. Subordinates occupying habitat edges must cope with a higher risk of being preyed upon but border fewer territorial boundaries from residents. I showed that edges are avoided by male emigrants but predominantly used by female emigrants, indicating different motivations for males and females to emigrate. The well-established sex-bias in dispersal proneness depends on the relative costs and benefits of dispersal and philopatry, which appears to be closely linked to the species' polygynous mating system (Greenwood 1980, Dobson and Jones 1985, Lawson Handley and Perrin 2007). I found a highly male-biased dispersal rate and showed that most male emigrants are relatively young, classified as natal dispersers (i.e. which have not bred in their natal population before). It is, therefore, likely that male dispersers are highly viable individuals (Gundersen et al. 2002), which suppress reproductive activity in their natal populations and stay in the safer interior sections in order to reduce predation risk until they decide to actually leave the home patch. Female dispersers, on the other hand, seem to rely on social

interactions but are competitively inferior and, therefore, have to avoid highly competitive interior sections (see below).

While both male and female dispersers tried to temporally avoid residents, this avoidance was most prominent in interior sections. It seems that the use of the safer and, therefore, more preferred interior sections go along with a higher temporal avoidance of residents and vice versa. The temporal avoidance of residents surely implies a reduced participation in social and reproductive activity. As female emigrants predominantly used habitat edges, they appear to be more concerned about social associations and kin alliances in their natal populations (see Ishibashi et al. 1997, Ishibashi et al. 1998). Hence, females might rather take the risk in their natal populations of being preyed upon than to enhance temporal avoidance of residents in the safer interior sections.

Dispersers left the habitat patches and entered the matrix synchronously at dawn and dusk. Following the “safety in numbers”-hypothesis (Daan and Slopsema 1978) these activity bursts should reduce predation risk during travel as they decrease the relative vulnerability of an individual. Predator avoidance is especially important for dispersers at the time of dispersal as they typically leave safe habitat patches and pass hostile and risky areas. This is generally assumed to cause much higher mortality rates in comparison to stationary individuals (Gaines and McClenaghan 1980, Lidicker 1985, Johnson and Gaines 1990, Andreassen and Ims 2001, Smith and Batzli 2006, but see Boyce and Boyce 1988a). Twilight does not seem to be considerably risky, which was stated by Halle (1993) who showed that predation risk for arvicoline rodents is almost evenly distributed over the 24-h day.

Triggers for dispersal

Dispersal was highly male-biased, a fact undoubtedly due to the polygynous mating system which is prevalent in most mammalian species (Greenwood 1980, Dobson 1982, Lawson Handley and Perrin 2007). As a consequence of intrasexual competition, males had overall lower survival rates compared to females. I showed that the higher chance for reproduction in females was reflected by a higher number of mates and a higher offspring number in reproducing males. As lesions indicated, male dispersers experienced a high level of aggression and emigration was most probably induced by the agonistic encounters of conspecifics. Liberg and Schantz (1985) and Wolff (1992) suggested that the decision to disperse in birds and mammals is mediated rather by the parents than by the decision of the offspring. I suggest that these encounters often involved relatives, and the induction of male-biased dispersal may, therefore, contribute to the avoidance of inbreeding and reduction of kin competition (Viitala et al. 1994, Perrin and Lehmann 2001). The males' relative high proportion of natal dispersers supported the inbreeding avoidance hypothesis (Bollinger 1993, Le Galliard 2006, Höner 2007, Lawson Handley 2007).

In contrast to other small mammal studies, neither male nor female dispersal rates significantly correlated with density in this investigation (Aars and Ims 2000, Hanski 2001, Gundersen et al. 2002, Smith and Batzli 2006, but see Gaines and McClenaghan 1980, Gaines and Johnson 1984, Sandell et al. 1991). Males, however, predominantly emigrated prior to the maximum population densities (i.e. as

presaturation dispersers) and their dispersal rate was positively correlated with density increase. This surely enhances the success of male dispersers in finding reproductively active mates and still vacant sites to settle (see Gaines and McClenaghan 1980). The chance of a successful establishment seems to be even higher in male presaturation dispersers as these were significantly heavier at the time of emigration than saturation dispersers. At least in males, presaturation dispersers are predisposed for successful dispersal while the prospectus of saturation dispersers for future reproductive output is surely low (see below). The dispersal rate of females, on the other hand, was associated with the proportion of residents in a population indicating that the propensity of females to disperse is dependant on the strength of social interactions. In contrast to the more loosely connected males (Mackin-Rogalska 1979) Boyce and Boyce (1988a) found female common voles to form social clusters of related individuals and they showed dispersal only in solitary breeding individuals. Females in clusters may gain fitness benefits as a result of cooperative foraging and feeding, group defense and assistance in thermoregulation, which thereby promotes philopatry (Gaines and McClenaghan 1980, Hayes 2000, Ylönen and Horne 2002, Le Galliard et al. 2006, Lawson Handley and Perrin 2007). If residents constitute the social center of a cluster, a relative decrease of residents should lead to a higher dispersal motivation among females (c.f. McGuire et al. 1993).

Immigration and consequences

The phase of immigration is typically considered as habitat selection following searching, entering, exploring, and, finally, the decision to settle in a new area (Andreassen et al. 2002). Due to methodical problems the immigration process is hardly ever studied empirically (see Stamps 2001). Information on the behavior of immigrants and their establishing success, however, is essential to understand demographic and genetic factors which are associated with metapopulation concepts.

Establishment and fitness of dispersers

Although nearly 26% of the dispersers reproduced in their natal populations before leaving only seven percent of them reproduced in the new populations, showing the relative low establishing success of immigrants. All of the immigrating dispersers which reproduced also settled in the new population, i.e. stayed within a relative confined area and did not try to disperse again. Those that did not settle in a new population dispersed again predominantly on the same day of immigration. Thus, settlement appears to be important for reproduction in *Microtus arvalis* even for males which do not show parental care (see Telfer et al. 2003). The probability of male dispersers for reproduction was highest at relatively low population densities and nearly all established immigrants were presaturation dispersers (Lidicker 1975). Population density and the availability of territories are apparently important factors for the establishment in new populations. High densities may therefore represent a “social fence” (Hestbeck 1982) for immigrants. This social fence may be fortified by the formation of family groups among female common voles and other species (Ishibashi et al. 1998, E. Heinze et al., unpublished data). Female kin groups might help to

prevent intruders to settle and form a defense against aggressive or infanticidal behavior by unfamiliar males (Fortier and Tamarin 1998, Le Galliard et al. 2006). Hence, the effectiveness of vole dispersal depends to a high extent on demographic factors in the new population and it is most likely to be selected for in highly heterogeneous landscapes with low-density or unoccupied habitat patches (Hastings 1983, Bondrup-Nielsen 1993, Gandon and Michalakis 2001). Presaturation dispersers are surely predisposed for successful establishment as indicated by the extraordinary high reproductive success of two immigrating males (13 and 27 offspring). This suggests that an early abandonment of the natal population and taking a chance by moving to a new habitat may actually pay off.

Young and natal male dispersers had highest establishing success whereas most successful female immigrants were breeding dispersers. Thus, most successful female dispersers left their natal population and released the competition for resources between them and their offspring (i.e. resource competition hypothesis; Gundersen and Andreassen 1998), which may enhance their own inclusive fitness (see above). A sex difference in the survival rates of immigrating dispersers was, in contrast to the overall higher survival rates in females, not detected. This might indicate that dispersal is more rewarding for males than for females. The low sample size of five reproducing male immigrants and four reproducing females, however, prevents further conclusion on the relative performance of each sex.

Dispersers' activity was generally enhanced, especially during the first day when immigrants entered a new population. This affirmed the lack of spatially restricted home ranges in dispersers (Hayes, 2004) and supported my argument that residents largely prevent immigrants from settling (Mackin-Rogalska 1979, Lambin et al. 2001, Gundersen et al. 2002). If so, dispersers have to continue their search further than expected, and dispersal distance should be positively correlated with an increase in local population densities. Long-distance dispersal surely decreases the chance of successful reproduction, as the risk of starvation or being preyed upon is heavily increased during travel (Andreassen 2001, Smith 2006). If successful, however, long-distance dispersal might have an even higher impact on the new population assuming that genetic distance is correlated with local distance (difference by distance), which means a comparatively high chance that new alleles are brought into the new population.

While edges were avoided by male emigrants and predominantly used by female immigrants in the natal population, the sex difference in the habitat use was reversed in immigrants, i.e. in dispersers entering a new population. Both radio tracking and trapping data revealed a relatively higher use of edges by male immigrants, and a relatively higher attraction of interior sections by female immigrants. Still, the use of interior sections went along with a higher temporal avoidance of residents. From that I concluded that male and female dispersers not only have different motivations to emigrate, but also follow different spatio-temporal strategies in natal as well as in new populations. In new populations female dispersers seem to predominantly avoid predation, while male immigrants are more risk prone and simultaneously active with resident individuals in order to reproduce. The two different strategies in male and female immigrants may also be the proximate reason for the sex difference in dispersal distance as found in several mammalian species (Künkele and von Holst 1996, Murrell et al. 2002, Kozakiewicz et al. 2007).

Demographic and genetic implications

The manipulation of emigration and immigration showed that dispersal has an effect on the density and the sex-ratio of populations (see Myers and Krebs 1971). The sex-ratio changed in accordance with the number of immigrants, as these were predominantly males. An increase in disperser proportions enhanced aggressive encounters in the populations, noticeable in the amount of lesions (Le Galliard et al. 2005). High aggressiveness among conspecifics was apparently not only due to immigrants but also because of an increased proportion of frustrated dispersers (*sensu* Lidicker 1975, see Johnson and Gaines 1987), i.e. dispersers which were prevented to emigrate. A restricted dispersal can be associated with the “social fence hypothesis” which is defined as a social barrier of unrelated conspecifics restricting emigration and which is believed to cause population buildups, local resource exhaustion, and population crash (Hestbeck 1982, Aars and Ims 2000, Smith and Batzli 2006). The dispersers’ increased activity is likely to enhance the interaction with conspecifics which not only affected the amount of lesions but also promoted the transmission of parasites. I showed that dispersers can serve as a vector distributing parasites within and among populations. However, both increased agonistic encounters and high parasite infection rates did not apparently affect dispersal propensity, survival and/or fecundity. This is in contrast to Ylönen and Horne (2002) who proposed that intruders (i.e. immigrants) of *Myodes glareolus* committed infanticide and oppose the study by Lin et al. (2004) who showed that immigrating *Microtus ochrogaster* can reduce the proportion of juveniles.

The yearly population breakdown in early spring was associated with a genetic depletion. This indicates the necessity of dispersal and gene flow, respectively, in order to maintain genetic diversity in small and isolated habitat patches (Aars et al. 2006). As immigrating dispersers showed relative high reproductive success in the early field season but comparatively low reproductive success during the breeding period, the increase in allele numbers was rather due to the immigrants themselves, than by the immigrants’ offspring. It is, therefore, important to distinguish between the number of dispersers and the fraction of them which actually reproduces in the new populations (i.e. effective dispersal; Wang 2004). The simple number or proportion of individuals moving between adjacent demes or habitat patches (Slatkin 1981) will likely lead to an overestimation of the effective gene flow in many organisms. An isolation of populations, and the relatively low reproductive success of immigrants, however, did not seem to considerably affect overall inbreeding coefficients. It seems that inbreeding avoidance is rather controlled by the recognition and avoidance of mating with close kin than by means of dispersal (Mateo 2003, Aars et al. 2006, Le Galliard et al. 2006). Hence, dispersal seems to have a long-term effect in the maintenance of genetic diversity over years, while inbreeding avoidance might operate on the within-population-level by means of kin recognition. To avoid long-term negative effects of isolation in natural systems it is advantageous that fragments are connected by narrow strips of habitat referred as landscape corridors (Andreassen et al. 1996, Aars and Ims 1999).

Although residents did not seem to change their temporal activity in the presence of dispersers, I found a tendency for larger shifts of resident activity centers in the transition enclosures with both immigration and emigration. Hence, the relatively high turnover of dispersers, which is closest to the natural situation, seems to decrease the spatial anchorage of residents. The effort of immigrants to establish might even force residents into dispersal, which would have disruptive effects on the resident population in general (Gaines and McClenaghan 1980). As a consequence, vacant sites emerge that can be reoccupied by neighboring residents or dispersers. The situation when the establishment of a disperser in the new population drives out a resident into dispersal is the so-called “domino-effect”, which not only would have consequences for the demography and social structure of a population, but also might have long-term population genetic implications.

Domino-effect vs. simple immigration

Most metapopulation models assume that immigrating dispersers are either repelled by residents or simply integrate their home range into an existing social structure. Intensive spatio-temporal investigations, however, indicate cases of domino-effects (see above). In order to compare the two scenarios, simple immigration vs. domino-effect, I used models of three different metapopulation types that varied in complexity (see THE DOMINO-EFFECT, this volume). To ascertain both demographic and genetic changes I incorporated realistic features of population ecology and population genetics.

Although not all model runs have been completed by the time of submission, I showed that the domino-effect results in lower metapopulation densities and higher rates of successful establishments. Densities and successful establishments were clearly due to an increased number of dispersers and, consequently, higher overall death rates, since dispersers’ survival was assumed to be negatively correlated with population densities. High numbers of established dispersers accelerated the time over which an allele was completely assimilated in a new population (i.e. the speed of gene flow). The outcome of the parameters disperser number, metapopulation density, and gene flow were heavily dependant on the metapopulation type. Final values of heterozygosity were not differently affected by the two scenarios but simply dependant on the initial genotype combinations at the time when the models were started.

I conclude that the domino-effect might not only have profound effects on the recolonization probability of extinct subpopulations but also can enhance a metapopulations’ ability to keep more stable densities. Furthermore, the domino-effect can speed up the spreading of rare or new alleles over space which should retain genetic variation in the face of genetic drift. If so, the domino-effect is particularly advantageous in highly fragmented landscapes consisting of small and isolated habitat patches that are at risk to suffer extinction and genetic depletion, respectively. According to Gilpin (1991), low extinction and increasingly high colonization probabilities will avoid metapopulation extinction and should result in patch coalescence, high levels of heterozygosity over metapopulations, or even panmixia. To illuminate purposes of evolutionary study and conservation managements, it is, therefore, important to take the occurrence of potential domino-effects into account.

SUMMARY

Human activities have been causing extensive landscape fragmentation which results in habitat reduction, segregation, and isolation of populations. Fragmentation can have severe effects on population extinction and genetic variation. Dispersal, defined as an “one-way movement of individuals away from their home range site”, can counteract the negative effects of fragmentation as it links otherwise isolated populations. Despite its widely accepted importance, dispersal remains one of the most studied yet least understood concepts in ecology and conservation biology. The lack of knowledge is mainly due to the difficulties in obtaining robust field data. This is reflected in works of theoretical nature or based on anecdotal dispersal observations. What is, therefore, needed are studies of dispersal that combine robust methodology with large sample sizes so to be able to draw firm conclusions.

In this study I used an experimental approach in semi-natural enclosures with altogether 1811 individually marked common voles, *Microtus arvalis*. I combined classical capture-mark-recapture methods, molecular analyses of 1255 individuals, intensive radio tracking, and methods for automatic activity recording. This resulted in a dataset which allowed me to ascertain what triggers emigration and immigration. It also allowed me to describe the morphological, genetic, and behavioral traits of dispersers as well as their fitness consequences. Finally I was able to find out the consequences of dispersal on the natal and new populations. Identification of dispersers was based on the trapping history of individually marked voles in the coverless and, therefore, unsuitable matrix area of the enclosures. A score system for disperser identification was established and intensively tested prior to the experiments. Out of 225 identified dispersers I manually transferred 128 dispersers in one direction only, thus creating three different treatment conditions with four replicates each in which populations were affected by emigration only, immigration and emigration, and immigration only. Furthermore, I modeled two different dispersal scenarios - simple immigration vs. domino-effect - to ascertain the impact of these two scenarios on the demography and genetic constitution on different metapopulation types.

Although the dispersers' body-weight was significantly lower compared to that of residents, dispersers showed an overall reproduction rate of 26% in their natal populations. This indicates that dispersers are not subordinate *per se* but able to reproductively compete with resident conspecifics. Still, lesions, induced by agonistic interactions, showed that dispersers experienced overall high competition. Lesions were highest in males. This was associated with a significantly lower survival rate as compared to females, which was undoubtedly due to the polygynous mating system. It is, therefore, likely that male dispersers especially improve their fitness when leaving, which was reflected in a highly male-biased dispersal rate. As lesions were most prominent for dispersers in natal populations it is likely that dispersal is predominantly induced by relatives, supporting the inbreeding avoidance hypothesis. To reduce competition male dispersers temporally avoided residents and suppressed their reproductive activity in the natal population. Male dispersers accelerated maturation, however, as soon as they showed an increased motivation to emigrate. Female dispersers had a comparatively higher reproduction rate in the natal population and showed a high dichotomy in their body-weight at the time of emigration. This indicates

that female dispersers eventually reach an age when their relatives' contribution to inclusive fitness is greater than their own. Hence, it is likely that female dispersers are more eager in increasing inclusive fitness by passing on their home range to their offspring, while male dispersers are highly viable animals, motivated to enhance individual reproduction in the new populations. This was reflected in the finding that male dispersers were relatively young individuals that predominantly emigrated during population increase, which should improve their chance of finding unoccupied sites to settle and reproductively active mates, respectively. Early emigration seems to be particularly successful in males as presaturation dispersers had a significantly higher body-weight than saturation dispersers. Female dispersal rate was associated with a low proportion of residents, indicating their dependency on social interactions. A sex-difference in the dispersal motivation was also prevalent in the spatio-temporal behavior of emigrants and immigrants, respectively. While male emigrants behaved to reduce predation risk females, again, were predominantly concerned about social associations and kin alliances in their natal populations. Male immigrants in new populations seem to accept predation risk in order to increase reproductive success. As I found no indication for a genetic inheritance of dispersal tendency, emigration seems to be a flexible behavior, conducted by a morphologically distinct group of animals that is triggered by extrinsic factors rather than induced by a specific "dispersal gene".

Although reproductively competitive in the natal population, dispersers showed a comparatively low reproductive success in the new populations with a reproduction rate of only seven percent. Permanent settlement was a prerequisite for reproduction and the availability of territories is apparently an important factor for the establishment in new populations. Hence, the effectiveness of dispersal is most probable in highly heterogeneous landscapes with low density and unoccupied habitat patches, respectively. Presaturation dispersers are surely predisposed for successful establishment and dispersal seems to be more rewarding for males than for females in a polygynous mating system.

Increased disperser proportions enhanced aggressive encounters in the populations and promoted the transmission of parasites. This, however, did not apparently affect overall survival and/or fecundity. Due to the relatively low reproductive success of immigrating dispersers populations remained genetically separated and the inability for establishment in moderate or high density populations might lead to a genetic separation on a fine geographical scale. Inbreeding coefficients were not apparently affected by isolation. Hence, dispersal seems to have long-term effects in the maintenance of genetic diversity in landscapes with high extinction and recolonization rates. Inbreeding avoidance, however, might operate on the within-population-level by means of kin recognition.

A high turnover of dispersers seems to decrease the spatial anchorage of residents which might lead to a domino-effect if the former residents become dispersers themselves. I showed that the domino-effect might not only have profound effects on the recolonization probability of extinct subpopulations but can also enhance a metapopulations' ability to keep more stable densities. Furthermore, the domino-effect can speed up the spreading of rare or new alleles over space which should retain genetic variation in the face of genetic drift.

ZUSAMMENFASSUNG

Die Fragmentation von Kulturlandschaften führt zunehmend zur Verkleinerung und Isolation von Habitaten. Dieses kann zum Aussterben lokaler Populationen und/oder zu einer Verarmung der genetischen Variabilität führen. Dispersal, definiert als ungerichtete Abwanderung aus einem angestammten Revier oder *Home range* und die dauerhafte Ansiedlung in einem neuen Lebensraum, kann den negativen Auswirkungen von Habitatfragmentation entgegenwirken, da durch Dispersal Habitatpatches miteinander verbunden werden. Obwohl Dispersal allgemein als überaus wichtig angesehen wird, sind dessen Prozesse und Auswirkungen noch sehr wenig verstanden. Diese Wissenslücke ist vor allem auf methodische Probleme zurückzuführen. Deshalb ist die Literatur zum Thema Dispersal überwiegend theoriebasiert oder es handelt sich um Einzelbeobachtungen, mit denen eine statistische Absicherung kaum möglich ist.

Für diese Studie benutze ich einen experimentellen Ansatz in halbnatürlichen Gehegepopulationen mit insgesamt 1811 individuell markierten Feldmäusen, *Microtus arvalis*. Dabei wurden klassische Fang-Wiederfang Methoden mit molekularen Analysen von 1255 Individuen, intensiver Radiotelemetrie und Methoden zur automatischen Aktivitätsregistrierung miteinander kombiniert. Ziel war es, Auslöser und Faktoren für die Aus- und Einwanderung von Dispersern zu finden, morphologische und genetische Qualitäten und spezielle Verhaltensweisen von Dispersern zu quantifizieren, ihre Fitnesskonsequenzen und Konsequenzen von Dispersal auf die Ursprungs- und Zielpopulation darzustellen. Die Identifizierung von Dispersern basierte auf der Fanghistorie von individuell markierten Feldmäusen im ungeeigneten und daher gemiedenen Matrixbereich. Ein Punktesystem für die Identifizierung von Dispersern wurde entwickelt und intensiv vor Beginn meiner Studie getestet. Von 225 identifizierten Dispersern wurden 128 per Hand in streng definierte Gehegepopulationen umgesetzt. So entstanden drei verschiedene Ansätze mit jeweils vier Replikaten, bei denen die Populationen nur durch Emigration, durch Immi- und Emigration oder nur durch Immigration beeinflusst wurden. Darüber hinaus modellierte ich den Einfluss von zwei verschiedenen Dispersalszenarien, einfache Einwanderung und Domino-Effekt, auf die Demographie und die genetische Konstitution unterschiedlicher Metapopulationstypen.

Obwohl Disperser signifikant leichter waren als residente Individuen, hatten sie eine Reproduktionsrate von 26% in ihrer Ursprungspopulation. Dies zeigt, dass Disperser nicht subdominant *per se*, sondern konkurrenzfähige Individuen sind. Dennoch deuteten Verletzungen an, dass Disperser allgemein einem hohen Konkurrenzdruck ausgesetzt sind. Verletzungen waren am häufigsten bei Männchen festzustellen. Diese zeigten auch eine niedrigere Überlebensrate als die Weibchen, was auf das polygyne Paarungssystem zurückzuführen ist. Es ist daher sehr wahrscheinlich, dass männliche Disperser am ehesten vom Verlassen der Ursprungspopulation profitieren, was sich in einer starken männlich-dominierten Dispersalrate widerspiegelte. Da Verletzungen am häufigsten bei Dispersern in ihrer Ursprungspopulation auftraten, ist es wahrscheinlich, dass Dispersal hauptsächlich von Verwandten erzwungen wird, was die Hypothese der Inzuchtvermeidung unterstützt. Um Konkurrenz zu verringern, zeigten männliche Disperser eine zeitliche Vermeidung zu residenten Individuen und unterdrückten die

reproduktive Aktivität in ihrer Ursprungspopulation. Männliche Disperser beschleunigten ihre reproduktive Reife jedoch ab dem Zeitpunkt, an dem sie Abwanderungsverhalten zeigten. Weibliche Disperser hatten eine vergleichsweise höhere Reproduktionsrate in ihrer Ursprungspopulation und zeigten bei Abwanderung eine deutliche Dichotomie im Körpergewicht. Dies deutet an, dass weibliche Disperser letztendlich ein Alter erreichen, bei dem der Beitrag ihrer Verwandten an ihre indirekte Fitness größer ist als ihre eigene. Während weibliche Disperser eher geneigt sind, ihre indirekte Fitness durch die Weitergabe ihrer *Home range* an ihre Nachkommen zu erhöhen, sind männliche Disperser wahrscheinlich höchst motiviert, sich in der neuen Population zu reproduzieren. Dies spiegelte sich darin wider, dass männliche Disperser relativ junge Individuen waren, die hauptsächlich während des Populationswachstums abwanderten, was ihre Chancen unbesetzte Lebensräume und reproduktive Weibchen zu finden sicherlich erhöht. Frühe männliche Abwanderer scheinen besonders erfolgreich zu sein, da ihr Körpergewicht signifikant größer war, als das später Abwanderer. Die weibliche Dispersalrate war korreliert mit einem niedrigen Anteil an residenten Individuen, was ihre Abhängigkeit von sozialen Strukturen verdeutlicht. Ein Geschlechtsunterschied bei der Dispersalmotivation konnte auch bei dem räumlich-zeitlichen Verhalten von Emi- bzw. Immigranten festgestellt werden. Während männliche Emigranten ein Verhalten zur Reduzierung von Prädationsrisiko zeigten, waren Weibchen in ihrer Ursprungspopulation eher um soziale Interaktionen bestrebt. Männliche Immigranten in neuen Populationen schienen ein hohes Prädationsrisiko für die Chance einer höheren Reproduktionsrate zu akzeptieren. Da ich keinen Hinweis auf eine genetische Vererbung von Dispersal gefunden habe, scheint Dispersal eine flexible Verhaltensweise zu sein, die eher von extrinsischen Faktoren beeinflusst, als durch ein spezielles „Dispersal-Gen“ hervorgerufen wird.

Obwohl konkurrenzfähig in ihrer Ursprungspopulation zeigten Disperser einen vergleichsweise geringen Reproduktionserfolg in einer neuen Population mit nur sieben Prozent Reproduktionsrate. Die Etablierung eines Reviers war Voraussetzung für eine erfolgreiche Reproduktion von Immigranten. Daher ist der Erfolg von Dispersal wahrscheinlich am größten in stark heterogenen Landschaften mit lokal geringen Populationsdichten bzw. unbesetzten Lebensräumen. Frühe Abwanderer sollten hierbei den größten Erfolg haben, wobei sich Dispersal in einem polygynen Paarungssystem eher für Männchen zu rentieren scheint.

Hohe Disperserzahlen waren mit einem erhöhten Aggressionsniveau und einer gesteigerten Übertragung von Ektoparasiten verbunden. Dies schien sich jedoch nicht auf das Überleben und/oder auf den Reproduktionserfolg der Feldmäuse auszuwirken. Aufgrund des relativ geringen Reproduktionserfolgs von Immigranten blieben die Gehegepopulationen genetisch voneinander getrennt, was auch in natürlichen Systemen zu einer genetischen Separation auf engstem Raum führen könnte. Trotz genetischer Isolation einiger Gehegepopulationen konnte ich keine erhöhten Inzuchtkoeffizienten feststellen. Es ist daher wahrscheinlich, dass Dispersal Langzeiteffekte bei der Erhaltung von genetischer Variabilität in Landschaften mit hohen Extinktions- und Rekolonisationsraten hat, und

Inzuchtvermeidung eher innerhalb der Populationen aufgrund von Verwandtschaftserkennung zu funktionieren scheint.

Eine hohe Fluktuation von Dispersern erhöhte die räumliche Aktivität von residenten Individuen, was zu einem Domino-Effekt führen könnte, wenn aus den ehemals residenten Tieren Disperser hervorgingen. Ich konnte zeigen, dass der Domino-Effekt nicht nur Einfluss auf die Rekolonisationswahrscheinlichkeit von Subpopulationen hat, und damit die Stabilität von Metapopulationen erhöhen kann, sondern auch, dass sich seltene oder neue Allele schneller über Subpopulationen hinweg verbreiten. Dies würde einer genetischen Drift entgegenwirken und die genetische Variabilität in Metapopulationen aufrechterhalten.

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Aug. 2000	Assistant at the limnology working group of Jill Lancaster (Edinburgh); field sampling and identification of freshwater invertebrates
2003 and 2004	Scientific assistant at <i>Dr. Knoell Consult GmbH</i> for two months each; small mammal and bird monitoring for <i>Bayer Crop Science</i>
June - Sept. 2004	Employment at the Max-Planck-Institute for Biogeochemistry in Jena; analyses of soil samples
2006 and 2007	Genetic analyses at the Computational and Molecular Population Genetics Lab (CMPG) in Bern for two months each; analyses of microsatellites and sequencing ^[2]
2005 – 2008	Supervision of four diploma students

Hobbies/Interests

Sport (Biking and Athletics) and Photography

Other skills

Foreign languages

English fluently
French basic

Computer skills

Microsoft office applications, SPSS, Cervus, Arlequin, Sigma Plot, Stella, Ranges, Photoshop, EndNote

Licenses

Driving: B, CE, L
Diving
Sailing

Publications

Papers

- Hahne, J. & Halle, S.: Edge effects reflected in the behaviour of the common vole *Microtus arvalis*. In prep for Can. J. Zoology
- Heinze, E., Heckel, G., Schmidt, K., Halle, S. & Hahne, J.: Spatial dynamics in a fluctuating vole population. In prep. for Oikos
- Hahne, J., Halle, S. & Heckel, G.: Establishment and fitness consequences of immigrating vole dispersers. Submitted to Ecology
- Hahne, J., Heckel, G. & Halle, S.: Dispersal: Demographic and genetic implications in enclosed vole populations. In prep. for Oikos
- Hahne, J., Heckel, G. & Halle, S.: Emigration in common vole dispersers: triggers and traits. In prep. for American Naturalist

Books

- Hahne, J. (2006): *Lepus europaeus*. In: Brockhaus-Redaktion (ed.) Faszination Natur - Tiere: Säugetiere I. Brockhaus, Mannheim. pp. 430-431.
- Hahne, J. (2006): *Lepus capensis*. In: Brockhaus-Redaktion (ed.) Faszination Natur - Tiere: Säugetiere I. Brockhaus, Mannheim. p. 432.
- Hahne, J. (2006): *Lepus timidus*. In: Brockhaus-Redaktion (ed.) Faszination Natur - Tiere: Säugetiere I. Brockhaus, Mannheim. p. 433.

Congress contributions

- Hahne J. & Halle S., (2003): The effect of habitat edges on daily activity patterns in small mammals: an experimental approach with the common vole (*Microtus arvalis*). In: Abstractvolume 4th European Congress of Mammalogy: 107.
- Hahne J. & Halle S. (2004): Testing for edge effects in the behaviour of the common voles (*Microtus arvalis*) - an experimental approach. In: Abstractvolume /Suppl. 10th International Behavioural Ecology Congress: 2.
- Halle S., Eccard J., Fuelling O. & Hahne J. (2006): Flexible, but not risk-sensitive: the paradox of arvicoline rodent activity. In: Abstractvolume 11th Congress of the international Society for Behavioral Ecology: 73.
- Hahne, J., Bitter, A., & Halle, S. (2007): Dispersal: Demographic and spatio-temporal implications in the common vole (*Microtus arvalis*). In: Abstractvolume 5th European Congress of Mammalogy: 99
- Heinze, E., Hahne J., & Halle, S. (2007): Spatial behaviour of female common voles at low density. In: Abstractvolume 6th International Zoo and Wildlife Research Conference on Behaviour, Physiology, and Genetics: 102
- Henning, A., Halle, S., & J. Hahne. (2008): Who Fears Most - Individual-Specific Registration Of Common Voles Foraging Under Predation Risk. In: Abstractvolume 4th Meeting Ecology and Behaviour: 38

References

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Jena, Januar 2009

Ich erkläre, dass ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

Jena, Januar 2009

Jörg Hahne