Intersexual attraction in natal dispersing root voles
Microtus oeconomus

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By an enclosure experiment we tested whether natal dispersing root voles *Microtus
oeconomus* (Pallas, 1776) were prevented from colonising already occupied habitat
patches or if they were attracted to habitat patches by potential mates. The treatment
consisted of manipulating the presence of animals in immigration patches, either with
the presence of a solitary sexually mature male or female, whereas empty patches were
used as a control. Immigration patches were separated from a patch used for release of
a matriline (mother with her newly weaned litter) by a semipermeable fence allowing
only interpatch movements of young animals. We predicted that either a social fence
would prevent immigration to treatment patches, or that potential mates would attract
dispersing individuals. In particular we expected fewer dispersing males to colonise
male occupied patches, and fewer dispersing females to colonise female occupied
patches due to intrasexual competition, ie an intrasexual social fence. We found that a
higher proportion of females settled in male treatment patches than in female patches,
whereas male dispersal was unaffected by treatment. Thus, the observed female
immigration pattern appeared to be an attraction to patches occupied by the opposite
sex. We found no sign that immigration was prevented by a social fence.

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Introduction

Dispersal as a demographic parameter may affect the size of populations (eg
Stenseth 1983, Hastings 1990), and it is a key parameter in spatially structured
population models, eg metapopulation dynamics (Ims and Yoccoz 1997). However,
the role of dispersal in population dynamics is difficult to grasp without an
understanding of the mechanisms triggering or preventing dispersal. In the last
decades, small mammals have been extensively used as model organisms in studies
of dispersal (Stenseth and Lidicker 1992), which have resulted in the identification
of a variety of proximate factors causing dispersal. To a large extent, the proximate
causes for dispersal have been connected to the natal environment, such as

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maternal condition (Bondrup-Nielsen 1993), litter characteristics (Ims 1987, 1989, 1990, Jacquot and Vessey 1995) and changes in population density or composition of the kin group (Christian 1970, Lidicker 1975, Bekoff 1977, Krebs 1978, Hestbeck 1982, McShea 1990, Wolff 1992, 1993, 1994, Bollinger *et al.* 1993, McGuire *et al.* 1993).

All studies mentioned above have been designed to study the mechanisms which repel individuals from their natal area, whereas the motivating mechanisms which may attract individuals to particular areas, and their success of settlement have not been investigated. However, habitat choice and the ability to settle down in a novel area are important aspects for the understanding of population development (see Smith and Peacock 1990, Reed and Dobson 1993). Thus, it should be essential to unravel the behavioural mechanisms involved both in the emigration as well as in the immigration processes of dispersal (Ims and Yoccoz 1997).

We designed an experiment where root voles *Microtus oeconomus* (Pallas, 1776) were given the option to colonise empty habitat patches (controls), or habitat patches occupied either by a sexually mature female or male (treatments). This experiment was done to test whether already occupied patches acted to prevent (eg as a social fence, Hestbeck 1982), or attract (eg to maximise reproduction, Dingle 1972) dispersing individuals. We chose sexually mature animals as the experimental unit because they are most prone to show aggressive behaviour and exclude intruders, eg function as a social fence, or become potential mates.

We made the following predictions: (1) Given that young voles are attracted to potential mates we predicted that dispersing voles would immigrate more often into patches containing opposite-sex individuals compared to empty (ie control) patches. (2) If dispersing voles were avoiding resource or reproductive competition (see eg Dobson 1982, Pusey 1987), they would settle more often in empty patches compared to patches with same-sex individuals, ie reflecting the effect of an intrasexual social fence.

Material and methods

Origin of the experimental animals

Animals used in the present study were laboratory raised root voles originating from Valdres in the southern part of Norway (see Ims *et al.* 1993, Ims 1997). To randomize between-litter variation (eg genetic variation) and to standardize litter characteristics between treatments, eg litter size and sex ratio, we attempted to cross-foster most of the litters (ie exchanging parents for the whole litter) at an age of 7 days ± 2 days. Twenty-eight litters were successfully cross-fostered. To increase the sample size, 18 additional litters (not cross-fostered) were included to make a total of 46 litters. Cross-fostered and not cross-fostered litters were randomly allocated to treatments. The average litter size and sex ratio (number of females / litter size) was 5.30 (SE = 0.18) and 0.45 (SE = 0.03), respectively.

Experimental procedure

This experiment was conducted in six 50×16.7 m^2 "vole proof" enclosures at Evenstad Research Station, SE Norway (Hedmark), between July 1 and December 18, 1995. The whole study area was surrounded by a 1.5 m high chicken wire fence to prevent mammalian predation.
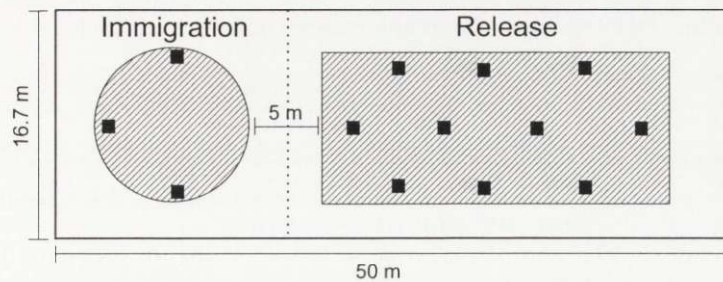
Fig. 1. One of the experimental enclosures with the release and immigration patches (hatched), semipermeable fence (dotted line) and position of live traps (black squares).

Within each of the six enclosures we established two habitable meadow patches embedded in a matrix where the vegetation was removed completely by herbiciding (Fig. 1). These two patches were separated by 5 m and a semipermeable barrier, made out of chicken wire fence (mesh size: 11 mm), which prevented interpatch movement of animals larger than 30 g. One patch (28 m × 13 m), hereafter termed the *release patch*, was colonised at the onset of each trial by releasing a root vole female and her newly weaned litter (18 d old). The other habitat patch, termed *treatment patch*, was circular (50 m², ca. the size of a female root vole core area (Andreassen *et al.* 1998) and was used for the experimental manipulation. In the treatment patch we released either a sexually mature female which had previously given birth to one litter, a sexually mature male (ie scrotal), or left the patch empty. Hence, there were 3 treatment levels, hereby called *female, male* and *control* treatment, respectively. A total of 9 different females were used to colonise female patches with a mean weight of 43.6 g (SE = 0.9) and a total of 15 different males were used to colonise male patches with a mean weight of 51.6 g (SE = 1.4). Thus, the semipermeable fence was a barrier for all treatment animals, except for the young animals which on average weighed 13.1 g (SE = 0.3) and 13.8 g (SE = 0.3), females and males respectively, at the time of release.

The release patch was empty of other voles. Before release, weight and sex were recorded and each individual was uniquely marked by toe clipping. Each trial lasted for 16 days whereafter the surviving animals were removed by live trapping (Ugglan multiple capture traps) which lasted for two days. Moreover, we also performed live trapping sessions, which lasted for 24 hours (2 trap checks), 4 and 9 days after release. All traps were baited with potatoes and whole grained oats and were checked twice daily (see Fig. 1 for trap location). For each captured individual we recorded toe code, sex, weight and trap station. At the end of a trial the animals were killed by cervical dislocation and autopsied (see Gundersen and Andreassen (1998) for ethical considerations). Pregnancy and presence of *tubuli epididymus* were recorded for females and males, respectively, and have here been used to define sexual maturation.

We performed 6 experimental trials (one in each enclosure) during 9 consecutive periods. For each period the location of the three treatment levels were randomized between the six enclosures, with the restriction that the subsequent treatments in each enclosure should differ. Lack of appropriate animals forced us to exclude female treatment the last 3 periods. A total of 9, 18 and 19 trials were performed for female, male and control treatments, respectively.

Analyses

Natal dispersal in voles appears shortly after weaning (Boonstra *et al.* 1987, Ims 1990, Lambin 1994). The 16 day long period of each trial should therefore suffice to observe natal dispersal and settlement triggered by factors in the life history of the individuals. We defined dispersers as young animals recaptured in the immigration patch at the end of a trial, assuming that they had succeeded in settling down in the immigration patches.

Table 1. Description of the litter specific responses analysed in the present study.

Response	Description
Survival	The proportion of same sex individuals in a litter released that were recaptured
Dispersal	The proportion of same sex individuals in a litter recaptured in the immigration patch at the end of a trial
Female sexual maturity	The proportion of pregnant females among the littermates (from autopsy data)
Male sexual maturity	The proportion of males with visible *tubuli epididymus* among the littermates (from autopsy data)
Growth	The growth in grams (averaged over same-sex individuals in a litter) from release to recapture

The binomial responses; like survival, dispersal, and sexual maturation (see Table 1 for description of the responses), were analysed by logistic regression, whereas growth rate of young was analysed by the use of ANCOVA. All analyses were performed for the sexes in each litter separately, (ie proportion of females/males in the litter in logistic regression, and mean for females/males in the litter in ANCOVA). Preliminary analyses showed only minor ($p > 0.10$) effects of possible covariables, such as litter characteristics (litter size, sex ratio and mean body mass at time of release) and maternal characteristics (body mass and survival), and were therefore excluded from further analysis. However, we included period as a covariable in the analyses of treatment effects, whenever it was significant ($p < 0.05$).

Results

The proportion of individuals in litters that survived the 16 days of the experimental trial averaged 0.81 (SE = 0.03) and was not significantly affected by treatment (Table 2). There was significant treatment effects on female dispersal, but not on male dispersal (Table 2). A higher proportion of females in a litter settled in patches occupied by a sexually mature male than in patches occupied by a female (Fig. 2). The proportion of sexually mature females in a litter was largest in male

Table 2. Statistics for sex specific test for treatment effects in logistic models. See Table 1 for a description of responses.

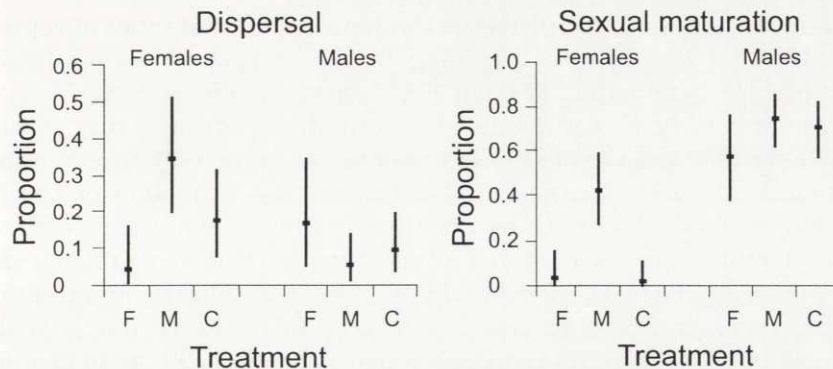| Response	Sex	χ^2 (df = 2)	p
Survival	Females	2.02	0.364
	Males	5.11	0.078
Dispersal	Females	9.95	0.007
	Males	2.24	0.326
Sexual maturation	Females	25.92	< 0.001
	Males	2.27	0.322

Fig. 2. Proportion ($\pm 2 \times$ SE) of females and males in a litter that dispersed and attained sexual maturation during a trial in the 3 treatments (F – female patches, M – male patches, C – control patches). See Table 1 for a description of variables.

treatment compared to the other two treatment levels, whereas we found no effect of treatment on male sexual maturation (Table 2, Fig. 2).

The mean body growth rate of individuals in a litter decreased throughout the season both among females ($\beta = -0.97$, SE $= 0.31$, $F_{1,38} = 9.81$, $p = 0.003$) and among males ($\beta = -1.38$, SE $= 0.24$, $F_{1,42} = 34.66$ $p < 0.001$). The mean body growth rate of males in a litter was not affected by the treatment ($F_{2,37} < 1,69, p > 0.120$), but females grew faster in male treatment plots compared to the other two treatment plots ($F_{2,33} = 3.29$, $p = 0.049$; period as a covariat: $F_{1,33} = 12.95$, $p = 0.001$). Increased growth rate among females was probably due to a higher pregnancy rate in male treatment, and using the proportion of pregnant females in the litter as a cofactor ($F_{1,32} = 7.42, p = 0.010$) removed treatment effects of female growth ($F_{2,32} = 0.61$, $p = 0.551$).

Discussion

We have presented the results of an experiment in which we used root vole litters as the observational unit to test whether conspecifics in neighbouring patches inhibited or promoted natal dispersal in root voles. We found that a higher proportion of females immigrated to male patches than to female patches, whereas males were unaffected by treatment. Consequently, our results show a different dispersal pattern for the sexes. However, because dispersal of females did not differ between female and control treatment (see Fig. 2), the dispersal pattern appeared not to be caused by an intrasexual defence of habitat patches. On the contrary, our results suggest intersexual attraction to be a mechanism of habitat choice and settlement in young female root voles. The higher proportion of pregnant females in male treatments show that female dispersal events were not only occasionally sallies, but resulted in mating and probably settlement. The intersexual attraction

observed in the present study increased the reproductive potential of reproducing females as would be expected according to the ontogenetic-switch-hypotheses (Dingle 1972, Holekamp and Sherman 1989, see also Lidicker 1985).

Our results must be viewed in light of the unnatural setting of the experimental design. The factors observed to affect dispersal did so in very simple, controlled circumstances. Even though we found an intersexual attraction in the present setting, this might not come to be expressed within a population with a more complicated level of organisation and a multitude of influencing factors. A social fence mechanism (Hestbeck 1982) could be a factor inhibiting immigration in a population were a social group acts as the social fence. For instance, males and females may be more disposed to defend a patch if they had a mate or a litter to defend. The absence of intrasexual defence of immigration patches was anyway quite surprising as the immigration patches were small, about the size of a female root vole core area (Andreassen *et al.* 1997), and thus with no surplus of resources.

Furthermore, dispersal distance was limited in the enclosures. It may even be argued that the short distance between patches could hardly be called dispersal. However, an interpatch distance of 4 m limit mature male root vole movement in unfamiliar areas (Andreassen *et al.* 1996), and interpatch distances between 4 and 9 m hinder female root voles to include multiple habitat fragments within their home range (Berg 1995). Our discrete habitat patches separated by 5 m in addition to the semipermeable fence should therefore represent a situation where young animals that settle in the immigration patches no longer have any contact with the natal area (dispersal *sensu* Stenseth and Lidicker 1992). Due to the short distance between release and immigration patches (5 m), however, young animals released might have been attracted to disperse because they smelled or heard animals in the immigration patches. However, during the phase of dispersal individuals finally choose a habitat patch according to some cues. Such cues might be the presence of conspecifics (Stamps 1988), or intersexual conspecifics as suggested in the present study.

We found a higher proportion of females to be pregnant in male treatment compared to female and control patches. The lack of an experienced mate for the young females in the release patch may have forced females to disperse more than would be expected in the presence of an adult male. Young females in control and female treatments could only have mated with their brothers which were not sexually mature at the time of release, although a high proportion of the young males were sexually mature at removal. Thus, low pregnancy rates in control and female treatments could have been due to the absence of large, experienced males. However, low pregnancy rates may also have been an avoidance of kin mating. Santos *et al.* (1995) did show some degree of inbreeding depression in laboratory experiments on the same strain of root voles as the one used in this study.

Although the experimental design may limit the generality of our results, it still gives a novel insight to microtine natal dispersal. Possible proximate factors for explaining natal dispersal have previously been examined from the perspective of

the natal environment (eg Ims 1987, 1989, 1990, McShea 1990, Wolff 1992, 1993, 1994, Bondrup-Nielsen 1993, Jacquot and Vessey 1995). These studies have focused on mechanisms that stimulate voles to leave their natal area, rather than on what may attract them to a new area. As far as we know, the present study is the first in the microtine literature suggesting that dispersal might appear as an attraction towards voles of the opposite sex in the neighbourhood.

In conclusion, we were not able to confirm that root vole colonisation is prevented by conspecifics. Our results instead suggest that in the absence of potential mates in the natal area, there may be an intersexual attraction mechanism of natal dispersal in root voles as an adaptation to accelerate mating in females. Thus, with the constraints of the present experimental setting, we found natal dispersal to be in accordance with the ontogenetic switch hypothesis (Dingle 1972, Holekamp and Sherman 1986). In accordance with previous studies (Ims 1989) we found the ontogenetic switch to be more flexible in females than in males.

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