

# Spacing behavior and key resources: an experiment on seasonal preference of male bank voles, *Clethrionomys glareolus*, for food and females

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We studied experimentally male distribution in relation to key resources, food and females, during winter and at the onset of breeding in eight enclosure populations of the bank vole *Clethrionomys glareolus*. In the experiment we manipulated the social environment of individuals under thick snow cover. After we had determined the male movements in a mixed population of both sexes all females of each enclosure were captured and kept in a cage at one end of the enclosure while food was offered in the opposite end. Male movements between these two patches were monitored by life-trapping under the snow. We found a seasonal pattern in the distribution of males in relation to key resources. 1) During the non-breeding season the manipulation of female and food distribution did not affect the male movements significantly, but 2) as expected, at the onset of breeding females were the preferred resource for the males. The results are discussed in the light of survival and mating strategies of males.

## 1. Introduction

A number of empirical and theoretical papers have dealt with the question of spacing behaviour of individuals in animal populations in relation to key resources (Ostfeld 1985, 1986, Ims 1987, 1988, 1990). Ostfeld (1985) argued that spacing behaviour of female voles is determined by food distribution and that of males by the female distribution, so that males would be non-territorial when females were more evenly distributed and should defend territories if females were clumped in space. Most

studies on spacing behaviour have been focusing on individuals in breeding condition, only. Seasonal shifts in space use of rodents have not been studied much in relation to resource distribution (see, however Montgomery et al. 1991). As far as we know our study is the first one to manipulate experimentally the social environment and resource distribution of free-ranging voles both in winter under snow and during the onset of breeding.

The spatial organisation of the bank vole (*Clethrionomys glareolus*), a common rodent of boreal and central European forests, is character-

ised by strict female territoriality during the breeding season (e.g. Bujalska 1973). Social organisation changes to inter-sexual aggregations during late autumn and this lasts through the winter until the onset of breeding (Ylönen 1990, Ylönen et al. 1995). Males are organised hierarchically during the breeding season, are aggressively competing for mates and have large overlapping home ranges (Gipps 1985). For the winter males join the overwintering aggregations (Karlsson 1988, Ylönen & Viitala 1991). Both seasonal social systems in the bank vole can be affected by the food distribution (Ylönen et al. 1988, Ylönen & Viitala 1991).

In large outdoor enclosures we conducted an experiment lasting throughout the winter until the beginning of the consecutive breeding season. We let free-ranging males to choose between distinct patches of females and food. Ylönen and Viitala (1991) found out that both sexes were concentrated around the best overwintering patches during winter (c.f. Ostfeld 1986). At the onset of breeding females move to more or less exclusive breeding territories (Ylönen et al. 1988, 1995). When offering the males only one food patch during the mid-winter we predicted that the male movements would be directed towards this point more pronounced than e.g. towards a female aggregation. However, attaining breeding condition should change the behaviour of males in favour of seeking sexually receptive females. Males come to breeding condition earlier than females, which still can be living in groups during early spring (e.g. Ylönen et al. 1988). When we offered males a choice between a food patch and a female group after the onset of breeding we predicted that the movements of males should be directed towards the group of females (Ostfeld 1985, Davis 1991).

## 2. Methods

We conducted the study at the Konnevesi Research Station of the University of Jyväskylä in central Finland during the winter and spring 1990–91. Eight populations of bank voles consisting of ten males and five females each were introduced into eight 0.25 ha enclosures on November 7th. Voles originated from the populations of the previous summer's experiment in the enclosures and from additional captures in ten different locations around the research station. Voles in each enclosure were unfamiliar with each other at the onset of the experiment. In the end of October the enclosures were

emptied of previous residents by intensive live-trapping. The habitat of the enclosures was abandoned field with meadow vegetation and some bush pockets. This habitat allowed the formation of even and protective snow cover of 70 cm on average during the mid-winter. Snow cover lasted from November to April. Each enclosure had 25 Ugglan Special live-traps in a 10 × 10 m grid and each trap was covered with a trap chimney of 50 × 50 × 50 cm to allow live-trapping under the snow (see Ylönen & Viitala 1991 for details). Populations were left undisturbed until the end of January when the first live-trapping took place. The uneven sex-ratio of 2:1 in favour of males was created in order to study male-male competition at the onset of breeding. Poor survival of the populations made this impossible, however.

Both winter and spring trappings consisted of two parts. Before the experimental manipulation the populations were monitored for five days. During this time we checked the traps eight times and used normally baited (oats and sunflower seeds) traps in order to determine male distribution in mixed populations (see Ylönen & Viitala 1991). After the manipulation male movements were monitored for two days using unbaited live-traps. The key resource manipulation was made as follows: at the end of the first part of the trapping all female voles were captured and placed in a wooden two-floor chamber of 40 × 40 × 40 cm, which was placed in a trap chimney under the snow at one corner of the enclosure. The average number of captured females was five in winter and three in spring. The chamber consisted of an upper nest compartment filled with hay, a lower compartment provided with food and water, and had four 3 × 20 cm windows covered with wire mesh. Male voles could enter the trap chimney and have olfactory contacts through the wire mesh with the females inside the chamber but did not have access to females nor to food. At the opposite corner of the enclosure there was a similar wooden feeding station where sunflower seeds and oats were offered for the males *ad libitum*. The consecutive trapping period, with only free-ranging males, lasted for two days with three trap controls in three-hour intervals both days. The short trapping period was in order to avoid stress in the captured females. A similar two-part trapping session was conducted at the onset of breeding in the end of April. The corners where food and female patches were located were chosen randomly for both winter and spring manipulations.

During the mid-winter trapping we got data from all eight enclosures. End of April we got data only from four enclosures. During the January trapping the average density of females was 4.6 voles/enclosure (*S.D.* = 0.3, *N* = 8) and that of males 6.4 ± 0.9 (*N* = 8). In April the densities had decreased to 3.0 ± 0.8 females and 2.5 ± 0.3 males/enclosure (*N* = 4, both). This resembles a normal spring decline during the cyclic population decline phase (e.g. Ylönen et al. 1988). Before and after the manipulation the movement centres of males (averages of eight enclosures, including 33 males in winter and of four enclosures including 11 males in spring) were calculated as arithmetic means of *x*- and *y*-co-ordinates of each capture point. Changes in males' movement centres were determined in metres from the diagonal of the encl-

sure to either "Female" or "Food" corner of each enclosure before and after the manipulation. The radius of male movements (see Ylönen & Viitala 1991) allows each male to visit both female and food corners between two trap controls. Thus male preference for either of the resource spots can be determined from the trapping data after the manipulation. Overlap of male movements was determined as a percentage of traps used by two or more males from the total number of traps used (Ylönen et al. 1988). Trappability was calculated as the percentage of captures of each individual of the total number of trap checkings during each trapping period. During the winter trapping all individuals were in non-breeding condition. In spring trapping all males had scrotal testis and all females were in breeding condition. To ensure independent replication we used mean values of enclosures in all statistical analyses. All significance values are two-tailed.

### 3. Results

The removal of the females to the chambers did not affect male trappability during winter nor during spring trappings. The average trappability in the winter was 41.5% (*S.D.* = 7.3) before the manipulation and 40.6% (*S.D.* = 8.3) after the manipulation, (Mann-Whitney  $U = 32.0$ ,  $p = 0.95$ ,  $N = 8$ ). In the spring the average trappability of males seemed to increase when the females were held in captivity, from 56.2% (*S.D.* = 21.6) before to 92.5% (*S.D.* = 17.8) after the manipulation ( $N = 4$ ,  $U = 14.0$ ,  $p = 0.083$ ).

In winter after the manipulation male movement centres shifted only by 1.45 metres (Range -3.3–3.0) (Fig. 1) (Paired  $t$ -test,  $t = -1.59$ ,  $p = 0.157$ ,  $N = 8$ ), towards the Food corner of the enclosure. In seven out of eight enclosures the slight shift was towards the "Food" corner. In spring the manipulation caused in all four enclosures a change of male movement centres towards the corner where the females were held in captivity (change 4.8 metres (Range 3.0–8.0),  $t = 4.47$ ,  $p = 0.021$ ) (Fig. 1). The difference in male movements in favour of females between winter and spring is significant (Mann-Whitney  $U = 32.0$ ,  $p = 0.008$ ).

The degree of overlap of male movements was high before the female manipulation:  $44.8 \pm 11.2\%$  ( $N = 8$ ) in winter and  $29.6 \pm 11.0\%$  ( $N = 4$ ) in spring ( $U = 33.0$ ,  $p = 0.27$ ). After the manipulation the degree of overlap decreased nearly significantly from winter ( $40.3 \pm 4.1\%$ ,  $N = 8$ ) to the breeding season ( $19.3 \pm 9.5\%$ ,  $N = 4$ ,  $U = 39.0$ ,  $p = 0.06$ ).

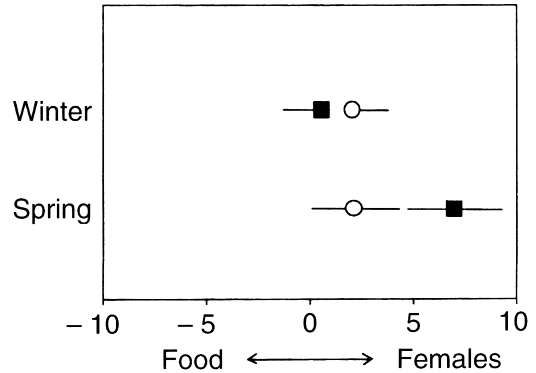


Fig. 1. Change of the centers of male movements in January (average of eight enclosures) and April (four enclosures) between the pre-manipulation trapping (open circles) and the male trapping after the females were captured in one corner of the enclosure (filled circles). The change is expressed in metres ( $\pm$  *S.E.*) in relation to the enclosure diameter (= 0) and the resource manipulation corners "Food" or "Females".

### 4. Discussion

We expected a clearer preference of males for the food resource during the non-breeding season than we got in our experiment. The short trapping time after the manipulation could have affected the small change. Orientation of voles during this short time under the snow could be more difficult than in the same time period during the snow-free season. The other possibility is that the high overlap in male movements during winter indicates aggregative social way of overwintering in order to save heat and energy (Vickery & Millar 1984, Ylönen & Viitala 1985, 1991, Karlsson 1988) and therefore the males did not respond in the short time in moving further away from their group nest sites towards the food aggregation. The strong overlap of male and female movements (72.2% of the traps used before manipulation in January were used by both sexes) could be a result of winter sociality, too. Montgomery et al. (1991) showed that the effect of tree seed production (food) and the presence of opposite sex on the numbers of *Apodemus sylvaticus* on their study grids was very different between years. The models and empirical tests of space use have previously dealt with territoriality in relation to food and females as a basis of different mating

systems (Ostfeld 1985, 1986, Ims 1987, 1988, Davis 1991). Heat saving due to huddling in intersexual groups during harsh weather periods has been considered as a "resource" only in few studies (e.g. West & Dublin 1984, Vickery & Millar 1984, Ylönen & Viitala 1985, 1991).

At the onset of breeding the location of the group of females in breeding condition seemed to be more important in determining male movements than the food corner. This was expected on the basis of previous empirical and theoretical studies (Kawata 1988, Ims 1988, 1990, Davis 1991). The decreased overlap of male movement in spring, when the females were held captive in a single spot of each enclosure, could indicate a formation of male hierarchy and increasing competition between males in monopolising the aggregation of receptive females (Ostfeld 1985, Ims 1987).

Our results suggest that males cannot respond rapidly to changes in the food distribution during the winter with thick snow cover. At the onset of breeding during the snow-free period the response to female distribution was stronger and clear already in the short two-day trapping period. Probably heat-saving by huddling affects individual voles' space use during the long-lasting cold season, despite of its risks in terms of securing food for the whole winter (West & Dublin 1984). Further, our experiment supports the previous hypothesis by Ostfeld (1985), Ims (1987) and the review by Davis (1991) of the importance of female distribution as a key resource in determining male space use during the breeding season.

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