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Different dispersal in *Clethrionomys* and *Microtus*

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We studied dispersal in the bank vole (*Clethrionomys glareolus*), an omnivore, and the field vole (*Microtus agrestis*), a grazer, in two large outdoor enclosures in Konnevesi, central Finland to explore the causes of dispersal. The competition hypothesis — that superior animals oust the inferior ones from favoured resource — predicts that species living on more scarce resource (here bank vole) should be more prone to disperse. According to inbreeding avoidance hypothesis young animals should disperse to avoid mating with their parents and dispersal should be similar in both species. Two populations, one of each species, were introduced to separate 0.5 ha enclosures. The growth of the populations and dispersal of the animals through six one-way dispersal tubes were observed for three months. Both founder populations consisted of seven females and three males. The populations attained densities similar to those in previous experiments. Most bank vole dispersers left the area before maturation when about 30 days old, whereas almost all field vole dispersers were mature animals about 60 days old and all females were pregnant. Dispersal was not sex biased in either species. The different dispersal obviously reflects different life history strategies and supports the competition hypothesis of dispersal instead of the inbreeding avoidance one.

1. Introduction

The main hypotheses attempting to explain the causes of dispersal are (1) inbreeding avoidance and (2) competition for resources (Dobson 1982, Dobson and Jones 1985, Pusey 1987). Mates are sometimes also considered as a resource (Ostfeldt 1985). We suppose that if inbreeding avoidance is the main reason for dispersal then the timing and intensity of dispersal should be similar in related species, i.e. young maturing individuals should disperse regardless of the availability of resources. In contrast if competition for resources is the driving force then species depending on scarcer resource should be more prone to disperse. The main basis of inbreeding avoidance hypothesis is that in semelparous animals usually one sex — often males — is more prone to disperse (Greenwold 1980, Dobson 1982, Wolff 1992). Male dispersal promotes gene flow and inbreeding avoidance. However, in iteroparous animals inbreeding may take place between a philopatric young and its parent. If dispersal is mainly caused by resource competition, then species dependent on resources of different availability should have different dispersal patterns. Thus the causes of dispersal can be studied in closely related species that depend on resources of different availability.

Bank vole (*Clethrionomys glareolus*) is an omnivore of woods and bushy habitats, that feeds on scarce but high quality food such as berries, seeds, buds and other storage organs as well as green parts of herbs. Field vole (*Microtus agrestis*) is a grazer of old fields and other grasslands, feeding on abundant green parts of grasses, sedges and herbs (Hansson 1985). As the study area was old field with small bush pockets we assume that it was a good habitat for both species, as shown in an earlier study by Ylönen et al. (1988). The food supply for field vole was better since in addition to all the food items available to bank vole it also favours the abundant supply of grasses and sedges that are not consumed by bank vole (Hansson 1985).

Viitala (1977) provided field evidence that the basic behavioural patterns of *Clethrionomys* and *Microtus* are different and that dispersal may also play a different role in these species. The growth of a *Clethrionomys* population was limited by territorial behaviour of breeding females (but see Ylönen et al. 1988), and mostly post-juvenal, yet immature individuals dispersed in order to find breeding territories (e.g. Kalela 1957, Bujalska 1970, Viitala 1977, Saitoh 1981). The growth of many *Microtus* populations in productive habitats is not limited by territorial behaviour. Young females mature on home ranges greatly overlapping with those of old and other young females. A decrease of home range overlap during the breeding season (Viitala 1977) indicates dispersal.

In the present experiment we studied if animals reproduce in their natal area in spite of high chances of inbreeding with their parents. If inbreeding avoidance is of any importance, both male and female young should disperse before reproduction. The inbreeding avoidance hypothesis thus predicts that both sexes in iteroparous animals should disperse before maturation in order to avoid mating with their parents.

The competition hypothesis predicts that species living on resources of different availability should show different dispersal patterns. (1) Bank vole females living on more limited food supply should disperse before maturation to attempt to find resources (a territory) on which to breed. (2) Field vole females live on more abundant resources that allow the young born in early summer to stay and mature on the home range of the mother (Viitala 1977). Thus, they should disperse at an adult age and in breeding condition when competition for resources may become important. (3) For males the crucial resource is receptive females (Ostfeldt 1985). According to previous studies the mating system of both species is polygynous or promiscuous/polygynous (Viitala 1977, Greenwood 1980, Dobson 1982, Liberg & von Schantz 1985, Ims 1988, 1990, Boonstra et al. 1987, Ylönen et al. 1988, Sandell et al. 1990). Because of much greater home ranges of males than those of females there is strong competition for females and dispersal should be male biased in both species.

2. Material and methods

The study was carried out in two 0.5 ha (50 × 100 m) outdoor enclosures on an abandoned field in central Finland. For a detailed description of the bushy old field habitat and enclosure construction see Ylönen et al. (1990). Populations of bank vole and field vole, both consisting of seven females and three males, were introduced into the enclosures in the mid of June. All animals were mature.

Both populations were allowed to disperse through six one way dispersal tubes each five meters long (c.f. Gaines et al. 1979). Dispersal tubes were opened in mid July and remained open until the end of the experiment. Each dispersal tube ended in a chamber that was provided with food and nesting material. The chambers were checked every second or third day. There was an additional chamber half way along each tube that was not provisioned with food. From this chamber the voles had an opportunity to return back to the enclosure. Voles who entered the second chamber through an Ugglan Special trap which prevented the animals from returning were regarded as dispersers. All dispersers were killed and necropsied in the laboratory. Their ages were determined by tooth characteristics in

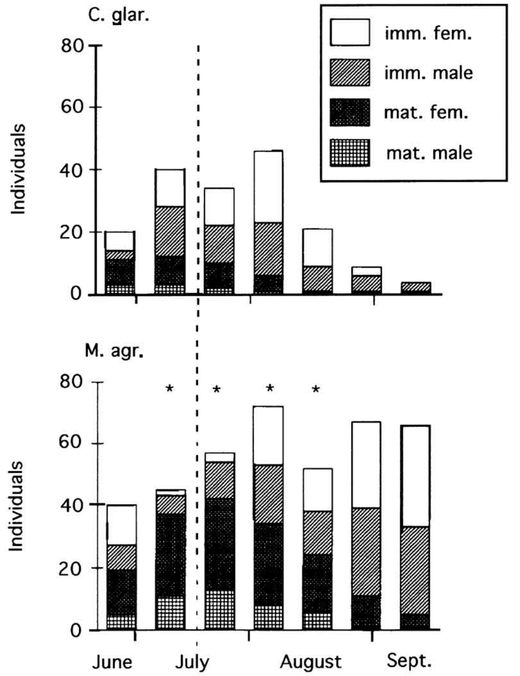

Fig. 1. Numbers of individuals known to be alive of different reproductive categories in enclosed populations of bank vole (C. glar.) and field vole (M. agr.) during different trapping sessions. Other explanatinos: imm. fem = non-breeding females, imm. male = non-breeding males, mat. fem. = breeding females and mat. male = breeding males. The dotted line gives the time of opening of the dispersal tubes. The asterisks above the bars denote interspecific differnce between proportions of functional groups during the trapping session ($P < 0.0001$).

the bank vole and by pelage in the field vole (Viitala 1977, 1981). Sexual status was determined by the size of testis in males and by the characteristics of the vagina (open vs. closed) and/or number of embryos and corpora lutea in females.

Both enclosures included 50 Ugglan Special traps arranged in a grid with ten meter intervals between traps. During the experiment both populations were live trapped for five days every third week. The traps were checked ten times during every trapping session. These data were used to estimate the minimum number of individuals alive (MNA) and social structure of the enclosed populations. For a more detailed description of the procedure see Ylönen et al. (1990).

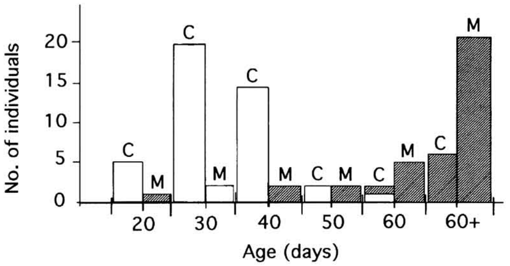

Fig. 2. Ages of dispersing individuals in bank vole and field vole. Shaded column = mature animal and open column = non-breeding. The letter above each column denotes the species (C = bank vole, M = field vole).

3. Results

In the beginning of August both populations reached a peak; bank vole of 46 sedentary individuals (92 voles/ha) and field vole of 70 individuals (140 voles/ha) (Fig. 1). The total numbers of individuals, i.e. both dispersers and residents included, produced, were 114 bank voles and 188 field voles. Fifty four bank voles and 32 field voles dispersed during the study ($\chi^2 = 32.09$; $P < 0.0001$; Fig 2). In bank voles 47 per cent of the losses from the population were due to dispersal but only 17 percent in field voles.

The mean age of dispersing bank voles was 30.3 days but that of field voles was 57.3 days (Mann-Whitney U = 261.5; $P < 0.001$; Fig. 2). There were only six sexually mature individuals among 54 dispersing bank voles but only two non-breeding individuals among the 32 dispersing field voles ($\chi^2 = 48.83$; $P < 0.0001$). All dispersing field vole females were pregnant. The mature dispersers among bank voles were five old introduced females that entered the dispersal tubes during the first days after their opening and one mature summer born female.

The proportion of reproducing bank voles did not differ significantly between residents and the dispersers (Fishers exact; $P = 0.107$). In the field vole the proportion of sexually mature animals was higher among dispersers than among residents (Fisher exact; $P < 0.001$). In July and August there were proportionally more mature individuals among resident individuals in field vole than in bank vole (Fig. 1), as expected on the basis of differences in spacing behaviour.

There was a significant difference in female home range overlap (measured as a number of trap stations used by at least two females) between bank vole and field vole from late July to late August (17.1% in bank vole, 38.5% in field vole, $\chi^2 = 19.91$; $P < 0.001$) but not during the first month of the experiment (field vole 26.9% and bank vole 16.5%; $\chi^2 = 2.62$; $P = 0.105$). Mature field vole males were less territorial than bank voles during the whole experiment: overlap of home ranges was in July 29.9 percent for the field vole and 7.9 percent for the bank vole ($\chi^2 = 15.99$; $P = 0.0001$) and in August 33.6 and 7.9 percent, respectively ($\chi^2 = 17.38$; $P < 0.0001$). The sex ratio of dispersers did not deviate from that of those who remained in the natal home range in either species (bank vole: $\chi^2 < 0.01$; $P > 0.95$; and field vole: $\chi^2 = 0.32$; $P = 0.571$).

4. Discussion

According to our predictions the interspecific difference in dispersal patterns, i.e. that bank voles left their natal home ranges earlier than did field voles, fits the competition hypothesis. Most bank vole dispersers were non breeding submatures whereas most field vole dispersers were already in breeding condition. Dispersal of bank vole could fit the inbreeding avoidance hypothesis, because the animals emigrated before maturity. We know from previous studies that young female bank voles tend to settle down as close to the natal home range as possible when maturing (Ylönen et al. 1988). Thus we believe that inbreeding avoidance may not have been important in bank vole, either.

Because field vole females as well as many other *Microtus* species, but not any *Clethrionomys*, mature on the maternal home range (Frank 1954, Viitala 1977, Bujalska 1970, Viitala 1977, 1987, Saitoh 1981) the timing of the dispersal must be different in these ecologically divergent species. This could also be the reason behind the observation that there were more dispersers in bank vole than in field vole. We argue that the ultimate reason for these interspecific differences is the different food source. The experiment lasted only about three months and most of the field vole voles did not reach the average dispersal age. A new field vole population may be established by one single pregnant female. This is important for annual colonisation of ephemeral habitats (Viitala 1977, Pokki 1982, Ylönen & Viitala 1987).

The sex ratio of the dispersers in either species did not deviate from that of resident populations. Thus, our results do not support the hypothesis that males are more prone to disperse than females — as was predicted on the basis of many earlier studies in these mainly polygynous or promiscuous species. However Pusenius & Viitala (1993) observed in *M. agrestis* an excess of males dispersing from the optimal field habitat into the suboptimal forest in late June. They explained it by competition between the highly aggressive breeding males. One explanation for our observation could be that in late summer young males may compete for food, but as socially subordinates not for mates (Hoffmeyer 1982). Their natal dispersal would therefore be similar to that of females and thus according to competition hypothesis. Previous studies have shown in field vole that long distance dispersal of both sexes occurs also during non-breeding season (Myllymäki 1977). In *Clethrionomys* species winter dispersal is male biased (Viitala 1987, Ylönen & Viitala 1991) except in *C. rutilus* the dispersal of which depends on cyclic population fluctuation (Viitala 1987). During low phases both sexes are involved but during high density winter dispersal is male biased. These winter movements could be due to inbreeding avoidance as there is no competition for mates between animals that are not in breeding condition, and food shortage is insufficient to explain the difference between the sexes.

Our results suggest that even though there is a tendency toward inbreeding avoidance (Dobson & Jones 1985, Pusey 1987, Wolff 1992) it is not of great importance during the short breeding season at high latitudes. Especially young field vole females maturing on the home range of their mother would most likely mate with the dominant male, i.e. with their father. The same applies also *Clethrionomys* females, that adopt a breeding territory as close to the natal home range as possible (e.g. Ylönen et al. 1988).

We suggest that the benefits of early reproduction obscure the obvious disadvantages of inbreeding in short lived iteroparous mammals like microtines, that live at high latitudes with a short breeding season. Thus during the breeding season, as in the present experiment, competition for mates or for other resources (Dobson & Jones 1985) should be the crucial factor generating dispersal. We also suggest that the excess of males observed among dispersers during breeding season (e.g. Dobson 1982, Sandell et al. 1990, Pusenius & Viitala 1993) could be due to the polygynous or promiscuous-polygynous mating system inducing strong competition among mature males.

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