

## Breeding dispersal in *Clethrionomys glareolus* females

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Spatial behaviour of female voles *Clethrionomys glareolus* (Schreber, 1780) was studied for 7 years in woodland of Kampinos National Park, Poland. Annual peaks ranged from 25 to 40 voles per ha. Twenty-six percent of newly marked females were already fully-grown adults. Immature females were slightly less site-tenacious than mature ones. The total movement range does not differ much between immature and mature recruits. Home range shifts between successive trapping sessions were the longest in maturing females but also prevalent in pregnant or lactating ones. Non-maturing females as well as mature but not breeding ones were the least mobile and the most site-tenacious. The home range length and between-capture distances were greater for pregnant than for immature females. They were also greater for transients than residents. Extensive movements of reproducing females suggests that breeding dispersal may thus be much more widespread amongst *Clethrionomys* females than previously thought.

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### Introduction

To predict the chance of species survival in changing landscapes we must know their spatial behaviour as individual movements may translate into patterns of population distribution (Wiens 1997). Colonization of habitat patches in which species have gone extinct is more rapid if mature or even pregnant females disperse during the reproductive season. Such presaturation dispersal (*sensu* Lidicker 1975, Stenseth and Lidicker 1992) is an ecological mechanism for increasing total population size in both fragmented and continuous habitats. Also heterozygosity levels strongly depend on genetic rescue effects mediated by dispersal.

The bank vole *Clethrionomys glareolus* (Schreber, 1780), is a native woodland species that is potentially endangered by habitat fragmentation (Rajska-Jurgiel and Mazurkiewicz 1988, Rajska-Jurgiel 1992). The life history of this folivorous-granivorous species, inhabiting various kinds of forests with a good ground cover (Mazurkiewicz 1984, Chętnicki and Mazurkiewicz 1994), is fairly well-known (Petrušewicz 1983, Flowerdew *et al.* 1985, Tamarin *et al.* 1990). Active during daytime and slowly moving voles, with little possibility to escape predation, are considered to be a site-tenacious species (Bergstedt 1966, Mazurkiewicz 1971, Mazurkiewicz and Rajska-Jurgiel 1987, Löfgren 1995, but see Andrzejewski and Babińska-Werka 1986, Kozakiewicz and Szacki 1995).

A choice between staying in the well-known home site or dispersal can significantly affect the fates of individuals. Little is known about hazards involved in rodent dispersal in general. Because of a lower risk of predation amongst dispersing adults than among juveniles, adult females sometimes can leave their territories to daughters. So adult and even pregnant females disperse between litters in some species (Cockburn 1992). Bank voles disperse as immatures (Watts 1970, Mazurkiewicz and Rajska-Jurgiel 1975, Bujalska and Grüm 1989, Gliwicz 1989, 1992, Viitala *et al.* 1994). As claimed by Bondrup-Nielsen and Karlsson (1985), Viitala *et al.* (1994) and Löfgren (1995) breeding dispersal is improbable or at least uncommon in bank vole females (but see Gliwicz 1989, Rajska-Jurgiel 1992). Spatial behaviour of rodents is highly flexible and can change under various environmental conditions (Mazurkiewicz and Rajska-Jurgiel 1998). Thus large data sets from natural habitats in continuous forests should be used for a study of dispersal and not brief experiments or trappings, especially those done in enclosures or crowded populations.

Despite much research there remain large gaps in our knowledge of movement patterns of bank voles, especially at low density. A social system of adult female territoriality causes young females to delay maturation if vacant breeding sites are not available (Bujalska 1970) and an important opportunity for their establishment is to reach an empty site (Bujalska and Grüm 1989). Although sexual maturation has a major effect on movement in rodents, daughters are more philopatric than sons (Stenseth and Lidicker 1992). Yet, only 10–30% of the young females matured near the natal site in several *Microtus* species (Boonstra *et al.* 1987). The same was true for the bank vole (Gliwicz 1989). Distances moved by juveniles at weaning do not differ much between males and females (Mazurkiewicz and Rajska-Jurgiel 1975). Young females can be also over-represented among immigrants (Gliwicz 1992, Rajska-Jurgiel 1992). At high density, however, immature females are philopatric (Bujalska and Grüm 1989, 1995).

The objective of this study was to compare movement patterns of mature and immature *Clethrionomys glareolus* females in their natural habitats in continuous forests at low or moderate densities. I predicted that if breeding dispersal is uncommon in mature bank voles then: (1) movement patterns and disappearance rates of immature and mature females should differ greatly, (2) most female recruits should be young, immature individuals.

### Study area and methods

The study area was located in the Kampinos National Park which is a large forest complex (350 km<sup>2</sup>) near Warsaw (52°20'N, 20°51'E). The woodland was a patchy area of various forest habitats: rich deciduous forest, mixed coniferous forests, pine forests, flood plain forests, bog alder forests and swamps. Data collected on large trapping plots at low to moderate densities were used. In 1970–1971, the study was conducted on 15 × 15 m grid covering a 6-ha plot (see Rajska-Jurgiel 1976). In 1984–1985, the study was carried out on a 12-ha plot with 16 lines of 16 live-traps 15 m apart. Distances between lines varied from 15 to 90 m, but inner lines formed a 3.5-ha grid (15 × 15 m). The rationale was to estimate whether the rodents were prevented from expressing their normal ranges by closely spaced

trap (see Mazurkiewicz and Rajska-Jurgiel 1998). In 1987–1989, the study was conducted on  $15 \times 15$  m grid covering 6-ha plot (see Chętnicki and Mazurkiewicz 1994). As bank voles avoid swamps and dry pine forests, all plots were located in a mosaic of deciduous forest, mixed coniferous forest, flood plain forests and bog alder forest. Trapping was performed four times a year for seven days, the midpoints of the trapping sessions being 11 May, 1 July, 17 August, and 7 October. The capture-recapture method was used. All rodents were individually marked. Traps were checked twice daily. At each capture we noted the rodent number, trap location, reproductive status, body weight and age (based on the body size and pelage color; see Mazurkiewicz and Rajska-Jurgiel 1987, Rajska-Jurgiel 1992). Females were classified as immature (closed vagina), mature (perforated vagina), pregnant (visible pregnancy) or lactating (lactation). Densities per ha were estimated as the minimum number present for each trapping session on plots covered with trap grids. Densities over the 12-ha plot with uneven distribution of trap stations were similar to those on the inner 3.5-ha grid (Mazurkiewicz and Rajska-Jurgiel 1998).

I measured the extent of movements as the maximum distance in meters between captures of a female (Observed Range Length). The extent of movements was analyzed over the entire time a female remained on the plots, during the breeding season it was marked [hereafter called the Total Range Length = TRL; for details see Mazurkiewicz and Rajska-Jurgiel (1998)]. Winter movements were excluded from the analysis. For each female, all captures were plotted and geometric centers of activity in particular trapping sessions were calculated. For all females present in at least 2 trapping sessions, I analyzed the home range shifts between 2 consecutive trapping sessions. A shift was estimated as the distance between geometric centers of home ranges in 2 successive trapping sessions (Center-to-Center Distance = CCD), and as the Maximum Distance Moved between 2 successive trapping sessions (MDM). As dispersal movements may occur both between trapping sessions and within a short 7 day trapping session, I also measured the extent of short time movements within single trapping sessions (hereafter called the Home Range Length = HRL). In each trapping sessions, Between-Captures Distances (BCD) were also calculated. Females that moved their capture locations on the plots and never returned were designated as abandoning their previous home ranges. Measures of movements were compared between groups by Kolmogorov-Smirnov two-sample test (K-S). Averages are also given to allow for comparison with another data on bank vole movements.

## Results

The data set comprised 5476 captures of 1100 female bank voles. Additionally, 1135 male voles were captured as well as 705 yellow-necked mice *Apodemus flavicollis*, 145 striped field mice *A. agrarius* and a few root voles *Microtus oeconomus*. Over the 7 years of the study, low or moderate numbers of bank voles were recorded on the study plots. Spring population densities varied from 1 to 14 per ha and annual peak densities from 25 to 40 per ha. The densities were several times lower than at high density when more than 100 voles per ha were recorded (Mazurkiewicz and Rajska-Jurgiel 1998). In particular trapping sessions, per ha densities of female voles varied from 1 to 18 for immature, from 1 to 12 for mature and from 1 to 9 for pregnant and/or lactating females (Fig. 1).

Twenty-six percent of females marked in May–August were already fully-grown adults with body mass more than 22 g (Table 1). In July they were mainly overwinterers. In August there were also early-spring born females among them. Thirty percent of the recruits were pregnant or lactating females (Table 1). In total, 44% of females marked in spring-summer period were transients that were present in one trapping session only (Table 1). Sixty-one percent of mature but only 51% of immature female recruits were present in at least 2 or more trapping sessions

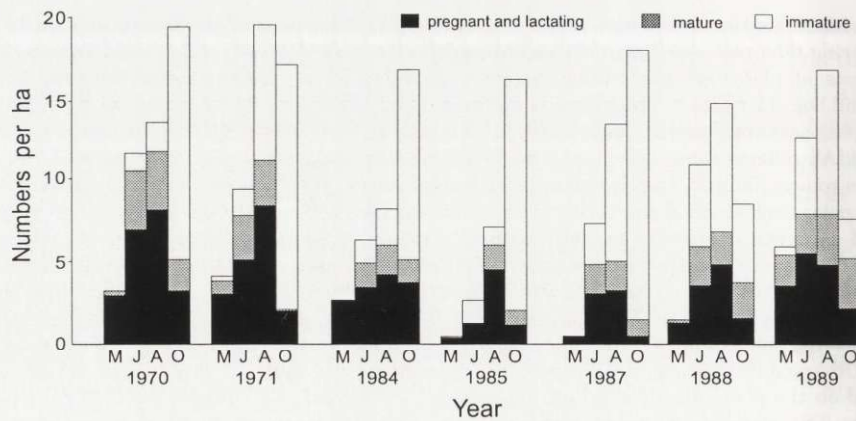


Fig. 1. Density and breeding structure of female bank voles in May, July, August and October in the Kampinos National Park.

(Chi-square test:  $\chi^2 = 6.52$ ,  $p = 0.010$ ). Mean disappearance rates between 2 successive trapping sessions were 45, 39 and 44% for breeding, non-breeding mature and immature females, respectively.

The total observed range length (TRL) was estimated for all females that were marked in May–August and were present in at least 2 trapping sessions. The mean TRL was 105 m. In different years, it varied from 90 to 115 m. As no significant differences were found (ANOVA:  $F = 0.629$ ,  $p = 0.706$ ), the material was combined for all years of study. The maximum TRL was over 400 m. However, 60% of females had TRLs less than 100 m and the proportion of females with large TRL (more than 150 m) was only 25%. To analyze the effect of the reproductive status of recruits at marking on their total range length in the breeding season, 3 groups of recruits were distinguished: immature, mature without any visible signs of pregnancy or lactation (hereafter called mature) and those already pregnant or lactating when marked. The mean TRL did not differ much either among cohorts or with reproductive status of female at marking (Fig. 2). However, TRLs of spring recruits were greater than those of late summer recruits (Fig. 2). TRLs of both mature and breeding females were greater than those of immature recruits (Fig. 2). The maximum TRL for a female that was already breeding when marked was 340 m.

Table 1. Description of newly marked female bank voles; years combined.

Season	<i>n</i>	Percent of:			
		adults	mature	pregnant or lactating	transients
May	146	29	70.5	37	38
July	259	32.5	69.5	39	42
August	357	18	43	21	47
October	338	10	17	6	–

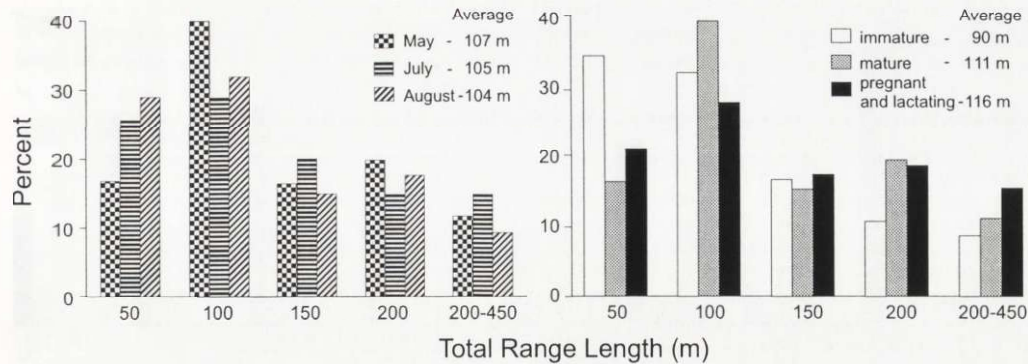


Fig. 2. Percentage distributions and averages of the Total Range Length (TRL) of May, July and August female recruits (left) and of females that were immature, mature or already breeding when marked (right). TRLs of spring recruits were greater than those of late summer recruits (K-S test:  $D = 0.28$ ,  $p < 0.001$ ). The TRL of both mature and pregnant/lactating females was significantly longer than that of immatures (K-S test:  $D = 0.31$ ,  $p < 0.001$  and  $D = 0.25$ ,  $p < 0.001$ , respectively).

For females present in at least 2 trapping sessions, I analyzed the home range shifts as the distance of the shift of home range center (CCD), and as the maximum distance moved (MDM). The mean CCD was 41 m and the mean MDM was 89 m. To examine whether the home range shifts varied with reproductive status of females, 4 groups of females were distinguished: non-maturing immature, maturing between successive trapping sessions, mature and pregnant or lactating females. Both the CCD as well as MDM were the longest for maturing females (Fig. 3). However, shifts were much longer for previously breeding females, ie pregnant or lactating, than for nonbreeding mature or immature ones (Fig. 3). The maximum CCD for a female that was previously breeding was 280 m and the maximum MDM was 340 m. All females that moved their centers more than 75 m, never have returned. The MDM depended on the CCD ( $r = 0.945$ ,  $p < 0.001$ ) rather than on the home range length of females ( $r = 0.310$ ,  $p = 0.201$ ). Some females were, however, observed to shift their ranges during trapping sessions.

Short-time movements were analyzed as the maximum distance moved by a female within single 7 day trapping sessions (hereafter home range length or HRL) as well as the mean distance between successive captures (BCD). The mean HRL was 60 m and the mean BCD was 15 m. To analyze the effect of the reproductive status on the short time movement of females, 4 groups of females were distinguished: immature, mature, pregnant and lactating. Short-time movements were estimated separately for transients and residents, that is females present on the plot for only 1 and more than 1 trapping sessions. The longest HRLs were observed for mature nonbreeding females, the shortest for lactating ones (Fig. 4). HRLs were significantly shorter for pregnant, than for mature females but significantly longer for pregnant than for both lactating and immature females (Fig. 4). HRLs were also significantly longer for transients than residents among pregnant, mature, and

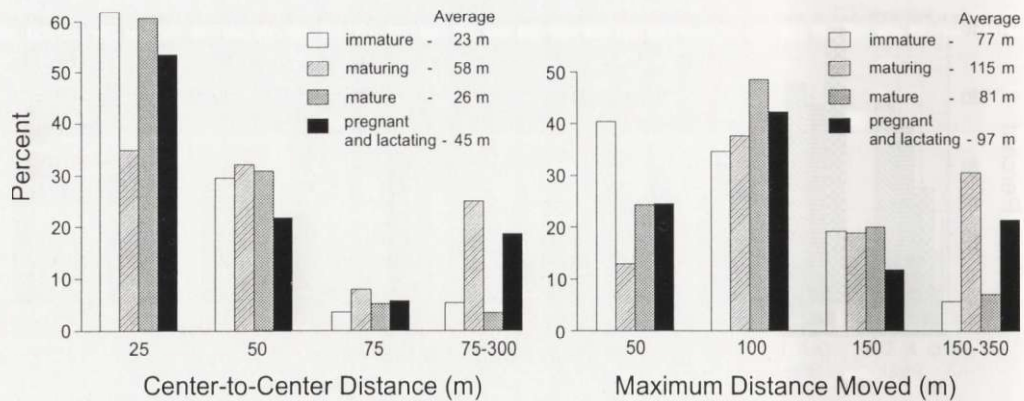


Fig. 3. Percentage distributions and averages of the shifts of home ranges calculated as the distance between geometric centers of home ranges in two successive trapping sessions (CCD; left) and as a Maximum Distance Moved between 2 successive trapping series (MDM; right). CCD was significantly longer for maturing than breeding females, and significantly shorter for both immature and nonbreeding than for breeding females (K-S test:  $D = 0.20$ ,  $p < 0.01$ ;  $D = 0.30$ ,  $p < 0.001$ ;  $D = 0.19$ ,  $p < 0.01$ , respectively). MDM was significantly longer for maturing than breeding females, and significantly shorter for both immature and nonbreeding than for breeding females (K-S test:  $D = 0.19$ ,  $p < 0.01$ ;  $D = 0.41$ ,  $p < 0.0001$ ;  $D = 0.23$ ,  $p < 0.01$ , respectively). Sample sizes for nonmaturing, maturing immatures, mature, and previously pregnant or lactating females were 103, 162, 113, and 241.

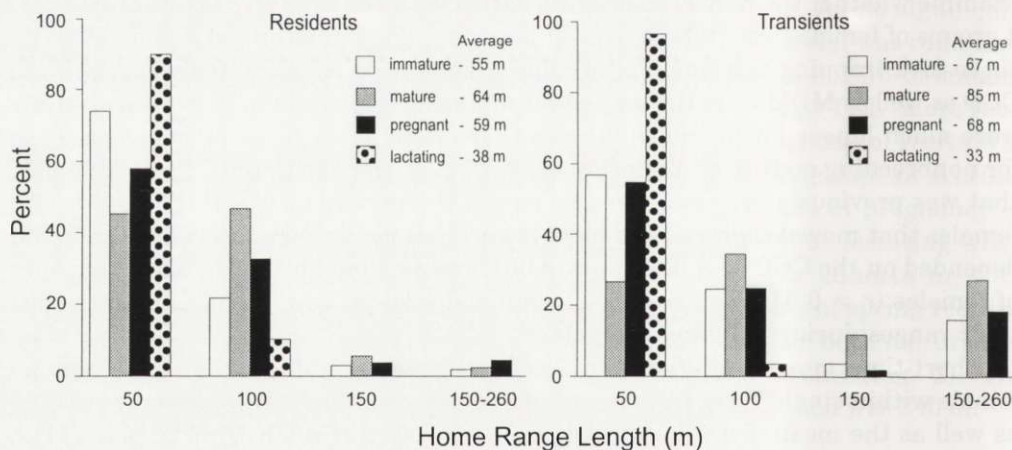


Fig. 4. Percentage distributions and averages of the Home Range Length (HRL) for residents (left) and transients (right). HRL was significantly shorter for pregnant than mature females, and significantly longer for pregnant than both lactating and immature females (K-S test:  $D = 0.33$ ,  $p < 0.001$ ;  $D = 0.48$ ,  $p < 0.001$ ;  $D = 0.22$ ,  $p < 0.001$ , respectively). HRL was significantly longer for transients than residents (K-S test:  $D = 0.29$ ,  $p < 0.01$ ;  $D = 0.32$ ,  $p < 0.05$ ;  $D = 0.26$ ,  $p < 0.01$  for pregnant, mature and immature females, respectively). HRL was significantly shorter for pregnant than mature females, and significantly longer for pregnant than both lactating and immature females (K-S test:  $D = 0.30$ ,  $p < 0.01$ ;  $D = 0.48$ ,  $p < 0.001$ ;  $D = 0.20$ ,  $p < 0.01$ , respectively for residents and  $D = 0.51$ ,  $p < 0.05$ ;  $D = 0.46$ ,  $p < 0.01$ , respectively for transients). Sample sizes for immature, mature, pregnant and lactating females were 223, 143, 336 and 161 for residents, and 136, 76, 96 and 31, respectively for transients.

immature females, respectively (Fig. 4). The longest BCDs were observed for mature nonbreeding females, the shortest ones for lactating ones (Fig. 5). BCDs were significantly shorter for pregnant than mature females. Again, BCDs were significantly longer for pregnant than for both lactating and immature females (Fig. 5). BCDs were also significantly longer for transients than residents among pregnant, mature and immature females, respectively (Fig. 5). The maximum HRL for a transient pregnant female was 260 m and the maximum BCD was 220 m. The maximum HRL for a resident pregnant female that shifted the home range during a trapping session was 240 m and the maximum BCD was 170 m. However, such shifts were seldom observed and none of mature or pregnant females was observed to move long distances in 2 successive trapping sessions.

I roughly estimated that 5% of immature, 7% of mature, 8% of pregnant and 0% of lactating residents, and at least 10, 19, 15 and 0%, respectively, of transients moved their home ranges to another locations on the plots during short, 7 day trapping sessions. Corresponding rates of home range abandoning between 2 successive trapping sessions were 17% for nonmaturing and 40% for maturing young. Also 24% of females that were pregnant of lactating in a previous trapping and 11% of mature nonbreeders moved their home ranges and never returned. The mean distance of the shift of home range center was 111 m but varied from 40 to 290 m.

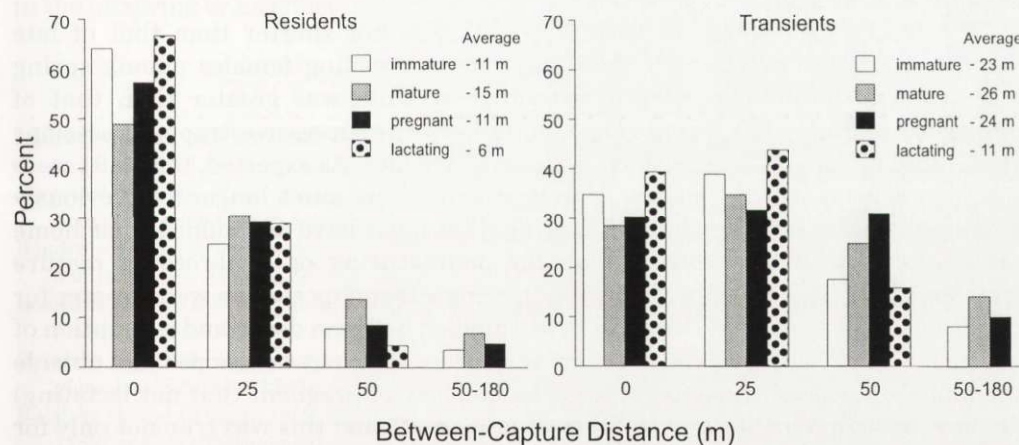


Fig. 5. Percentage distributions and averages of the Between-Capture Distance (BCD) for residents (left) and transients (right). BCD was significantly shorter for pregnant than mature females, and significantly longer for pregnant than both lactating and immature females (K-S test:  $D = 0.46$ ,  $p < 0.001$ ;  $D = 0.57$ ,  $p < 0.001$ ;  $D = 0.48$ ,  $p < 0.001$ , respectively). BCD was significantly longer for transients than residents (K-S test:  $D = 0.57$ ,  $p < 0.001$ ;  $D = 0.5$ ,  $p < 0.001$ ;  $D = 0.62$ ,  $p < 0.001$  for pregnant, mature and immature females, respectively). BCD was significantly shorter for pregnant than mature females, and significantly longer for pregnant than both lactating and immature females (K-S test:  $D = 0.57$ ,  $p < 0.001$ ;  $D = 0.66$ ,  $p < 0.001$ ;  $D = 0.62$ ,  $p < 0.001$ , respectively for residents and  $D = 0.31$ ,  $p < 0.001$ ;  $D = 0.41$ ,  $p < 0.001$ ;  $D = 0.35$ ,  $p < 0.001$ , respectively for transients). Sample sizes as in Fig. 4.

### Discussion

Dispersal in rodents as well as methods of its study is a complex phenomenon and a subject of profound interest (Hansson 1991, Stenseth and Lidicker 1992, Ims and Yoccoz 1997). In this paper I focused on presaturation dispersal by breeding females of *Clethrionomys glareolus*. The absolute values given here should be treated with caution because of highly flexible spatial behaviour that may change under various environmental conditions (Mazurkiewicz and Rajska-Jurgiel 1998). Yet, to my knowledge, this is the first attempt to describe and compare various measures of movement patterns in immature and mature females of bank voles in large natural habitats in continuous forests at low or moderate densities.

I predicted that if breeding dispersal is improbable or at least uncommon in mature bank voles then movement patterns and disappearance rates of immature and mature females should differ greatly and that the most of female recruits should be young, immature voles. However, 26% of females marked in spring-summer were already fully-grown adults. These females were certainly not visitors but adult immigrants that moved from outside and settled on the plot (E. Rajska-Jurgiel, unpubl.). Also the transients were movers (immigrants and emigrants) rather than visitors to the plots (E. Rajska-Jurgiel, unpubl.). There were more transients among immature than mature recruits. However, disappearance rates were similar for immature and mature females and thus it was opposite to that which was expected.

The total range length of spring recruits was not shorter than that of late summer recruits even though there were more breeding females among spring recruits. The total range length of mature recruits was greater than that of immature recruits. The home range shifts between successive trapping sessions varied significantly with reproductive status of females. As expected, the shifts were the longest for maturing females. However, shifts were much longer for previously breeding females (ie pregnant or lactating, that must have abandoned their home ranges to their weaned litter) than for nonmaturing or nonbreeding mature females. Short time movements during the single trapping session were greater for transients than residents. It is hard to distinguish between death and emigration of the individuals. At least some of them are shifters that may be trapped just outside the plot (E. Rajska-Jurgiel, unpubl.). The mobility of pregnant (but not lactating) females was greater than the mobility of immatures and this was true not only for transient but also for resident females. Long distances moved in trapping sessions measured home range shifts by pregnant females, that found on an excursion a better place to raise their young, rather than home range lengths. To sum up, the mature, breeding, females were not more site-tenacious than immature and again it was opposite to that which was expected. The home ranges of females were greater than reported for isolated or crowded populations (Bujalska and Grüm 1989, Löfgren 1995), as some of them measured home range shifts rather than actual home range lengths and this was especially true for transients. Thus, at least at low density bank vole females in open habitats may shift their home ranges frequently.



Presaturation dispersal seems to be favoured by natural selection under circumstances of spatial and temporal variability of patch suitability, close proximity of highly suitable patches and spatial asynchrony in site quality (Stenseth and Lidicker 1992). According to Olivieri and Gouyon (1997), the optimum dispersal rate is the one which maximizes the proportion of habitat occupied. Reasonable high dispersal rates are probably beneficial in most species (Olivieri and Gouyon 1997). The woodland was a patchy area of various forest habitats. Although bank voles avoid large patches of too dry or too wet habitats, such a habitat mosaic offers high quality living conditions for the species. Yet, due to asynchronous vegetation dynamics of plant communities (Falińska 1986), spatial patterns of food resources change seasonally. So "greener pastures" may attract females and motivate them to move.

At high density dispersal rates and distances are reduced (Mazurkiewicz and Rajska-Jurgiel 1975, 1998). Dispersal distances are also shorter in enclosure populations (Boonstra *et al.* 1987). Thus dispersal by mature females may not occur in enclosures or crowded populations (Viitala *et al.* 1994, Löfgren 1995) once a population has inhabited all the available space. However, extensive movements of reproducing females as described above suggest that breeding dispersal may be much more widespread amongst *Clethrionomys* females than it is commonly believed. Such dispersal may explain a rapid recolonization of previously empty habitat patches in both continuous forests and woodlots. Whether this is a form of parental investment in the offspring or an effect of spatial asynchrony in site quality remain to be studied.

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