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Spatial behaviour and population dynamics of woodland rodents

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Population dynamics and spatial behaviour of the vole *Clethrionomys glareolus* (Schreber, 1780) and the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) were studied for 7 years in woodland of Kampinos National Park, Poland. Mice were more mobile and less site-tenacious than voles. Annual peaks ranged from 9 to 104 voles and from 4 to 62 mice per ha. The highest densities of both species were preceded by winter breeding. The greatest movement range and the longest distance moved were observed in the years of low density, whereas in the high density year both species were least mobile and most site-tenacious. Intensive movements in the low density years led to early maturation, high turnover rates, and probably increased mortality. Low mobility and high site tenacity in the high density year enhanced population growth and suppressed maturation. Increasing density and cessation of breeding accounted for declining juvenile recruitment. Differences in movement patterns between years of low and high density were coupled with differences in the autumn age structure and winter mortality of both species.

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Introduction

Animal densities are usually higher in resource rich habitats (Pimm and Rozenzweig 1981). A local increase in the available food supply often causes an influx of immigrants (Andrzejewski 1963, 1975, Hansson 1971, Flowerdew 1976, 1985, Boutin 1990, Brandt 1992, Löfgren *et al.* 1996). As a result of heavy seed crops or supplying additional food, rodent densities are high in the following years (Zejda 1962, Bujalska 1975, Andrzejewski and Mazurkiewicz 1976, Jensen 1982a, Mazurkiewicz and Rajska-Jurgiel 1987, Pucek *et al.* 1993). Spatial distribution of many species depends thus on the distribution of necessary resources, although this need not be only food but can be the abundance of shelters (Mazurkiewicz 1984, 1994). Long-term population dynamics of various rodent species largely reflects the dynamics of their resources, at least in temperate environment (Flowerdew 1985, Pucek *et al.* 1993, Jędrzejewski and Jędrzejewska 1996, Wolff 1996).

In contemporary fragmented landscapes, the abundance of animals primarily depends on the availability of suitable habitats. However, to predict the chance of species survival in changing landscapes we must also know their spatial behaviour that will determine the minimum patch size of these habitats and their acceptable level of isolation. Especially disturbing today is forest fragmentation. In isolated, small woodlots, densities of the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834) were always higher than densities of the bank vole *Clethrionomys glareolus* (Schreber, 1780) (Rajska-Jurgiel and Mazurkiewicz 1988, Rajska-Jurgiel 1992), although in extensive forests bank voles are typically several times more abundant (Mazurkiewicz and Rajska-Jurgiel 1978, 1987). The effect of isolation and habitat fragmentation on vole abundance was also found by Gliwicz (1989) and van Apeldoorn *et al.* (1992). More rapid colonization of woodlots by mice than by voles was observed by Kozakiewicz and Jurasińska (1989). The abundance of voles on woodland edges is lower and that of mice is similar or higher than in forest interior (Mazurkiewicz and Rajska-Jurgiel 1987).

The biology of the bank vole and the yellow-necked mouse is fairly well known (Golley *et al.* 1975, Petrusewicz 1983, Flowerdew *et al.* 1985). Their optimal habitats in central Europe are fertile deciduous and mixed-deciduous forests (Pucek 1983, Flowerdew *et al.* 1985). The two species differ in food habits and anti-predator adaptation. Mice are granivorous and the seeds of forest trees are their predominant food resource (Drożdż 1966, Zemanek 1972, Jensen 1982a). Bank voles are folivorous-granivorous (Holišova 1971, Gębczyńska 1976, 1983). Both species supplement their diet with invertebrates. However, the potential food spectrum of voles is much wider than that of mice. List of food items taken by voles covers most of those eaten by mice, although many food species eaten by voles are not touched by mice (Hansson 1985). Thus, the two species depend on resources of different availability. Spatial and temporal distribution of food resources is also more variable for mice than for voles. Mice with their large eyes and ears, nocturnal activity and powerful escape leaps are better equipped than voles to detect and avoid predation (King 1985, Ylönen *et al.* 1992). Active during daytime and slowly moving voles, with little possibility to escape predation, are more dependent on cover than mice. Mice are habitat specialist restricted mainly to mature woodland (Montgomery 1979, 1980, Gurnell 1985, but see Adamczewska-Andrzejewska *et al.* 1981). Voles are habitat generalist, inhabiting practically all types of forests (Pucek 1983), with a preference for dense ground cover (Jensen 1982b, Wiger 1982, Mazurkiewicz 1984, 1986, 1991, 1994, Chętnicki and Mazurkiewicz 1994).

Spatial behaviour may translate to population dynamics (Wiens *et al.* 1993). Despite much research there remain large gaps in our knowledge of movement patterns of the bank voles and especially of the yellow-necked mouse. The bank vole is considered to be a species which is site-tenacious (Nikitina 1970, Mazurkiewicz 1971, Löfgren 1995) and less mobile than the yellow-necked mouse (Bergstedt 1966, Mazurkiewicz and Rajska-Jurgiel 1987, but see Andrzejewski and Babińska-Werka 1986, Kozakiewicz and Szacki 1995, Liro and Szacki 1995).

In forests of central Europe, population dynamics of both the bank vole and the yellow-necked mouse are characterized by regular annual cycles and irregular long-term fluctuations (Alibhai and Gipps 1985, Flowerdew 1985). High numbers following winter breeding occur in both species in the years preceded by a heavy mast crop (Zejda 1962, Smyth 1966, Bäumler 1981, Jensen 1982a, Mazurkiewicz and Rajska-Jurgiel 1978, 1987, Pucek *et al.* 1993). The age structure of the spring population at high abundance differs from that at moderate or low abundance and breeding is terminated already in mid-July (Adamczewska 1961, Jensen 1982a).

Differential food abundance from year to year may influencenot only the density but also the spatial behaviour of rodents. The choice between staying in the natal site or dispersal can significantly affect the fates of individuals and be of great importance to regulation of the population density. There is a large literature about processes and features besides resources that may affect population dynamics. Here we are concerned with resource availability and movement patterns of temperate forest rodents. The objectives of this study were: (1) to compare spatial behaviour of two rodent species, the bank vole and yellow-necked mouse, in their natural habitats in continuous forests, and (2) to analyse the relationship between spatial behaviour of these rodents and their population dynamics and structure. We predict that: (1) species living on more limited food resources should hold larger home ranges, (2) home range size of such species should be more affected by changes in food supply, (3) maturation rates of species restricted in maturation by vacant space supply rather than by food availability should be more affected by density, (4) if competition for food resources is the main reason for dispersal then species depending on scarcer resource should be more prone to disperse, (5) if competition for place to breed is the main reason for dispersal then dispersal rates of species with lower maturation rates should be more affected.

Study area, material, and methods

The study area was located in the Kampinos Forest which is a large forest complex (225 km^2) near Warsaw (52°20'N, 20°51'E). In 1982–1985 the study was carried out on a 3.5-ha plot with 8 lines of 16 live-traps 15 m apart. In 1984–1985, the plot was extended to 12 ha by adding 8 lines of 16 live-traps 15 m apart that paralleled longer sides of the grid. Distances between lines varied from 15 to 90 m. The reason was to estimate whether the rodents were prevented from expressing their normal ranges by the uniform distribution of closely spaced trap. In 1987–1989, the study was conducted on a 6-ha plot (15 lines of 16 traps at 15 m intervals) situated about 1200 m from the earlier plot. The plots were located in a mosaic of mixed coniferous forest and deciduous forest.

Each year, four trapping sessions (each lasting 7 days) were carried out at 6-week intervals. The capture-recapture method (CMR) was used. All rodents were individually marked. Traps were checked twice daily. At each capture we noted the rodent species, its number, trap location, sex and reproductive condition (closed or perforated vagina in females, testes abdominal or scrotal in males), body weight and age (based on the body size and pelage color; see Mazurkiewicz and Rajska-Jurgiel 1987, Rajska-Jurgiel 1992).

Densities per ha were estimated by common census method for each trapping session on plots covered with trap grids. The abundance of rodents was also estimated as numbers of rodents trapped per 100 trap-days in each trapping sessions on each of the plots. The mean number of mature and immature males and females per trapping session in the period May–August was calculated for each year. Percentages of the trap stations occupied, number of rodents per trap station and total captures were calculated for each trapping session.

Home range sizes and geometric centres of activity of rodents were estimated in particular trapping sessions on every plot. As an index of home range size we used the maximum distance in metres between captures of an individual (Observed Range Length = ORL), with the smallest distance between trap points (15 m) added. This analysis was done only for individuals caught at least 4 times as (1) the distance between captures did not show a significant increase with successive captures, and (2) distributions of the number of captures of these individuals did not differ significantly among plots and between high and low population density. For all individuals present in 2 or more trapping sessions we estimated the total observed range of movements (TRL) as the maximum distance between their captures over the time of their presence on the plot. To analyse the effect of the length of observation period on the estimate of movement range of rodents, 3 groups of individuals were distinguished with respect to the time on the plot (1, 2, and 3 or more trapping sessions).

For individuals present in at least 2 trapping sessions, we analysed the home range shifts between two consecutive trapping sessions. The shift was estimated as (1) the distance between the last capture in the preceding trapping session and the first capture in the next session (LFD), and (2) the distance between geometric centres of home ranges in two successive trapping sessions (CCD). Winter shifts of home ranges (between the autumn and spring trapping sessions) are excluded from this analysis. For individuals present in at least 3 trapping sessions, we calculated the total distance of their shift between the first and the third trapping session. For individuals present in at least two trapping sessions, we compared their CCD with their ORL in the preceding trapping session. Individuals that shifted the centres of their home ranges to a distance shorter than ORL were designated as remaining within the boundaries of their earlier home range. Individuals that shifted the centres of their home ranges to a distance longer than ORL were designated as abandoning their home ranges.

Residency of rodents was estimated as the percentage of individuals present on the plot for a given number of trapping sessions (1, 2, 3, or more). Mean loss rates were estimated as percentage of rodents disappearing between particular trapping sessions. To distinguish between emigration and mortality, we calculated emigration rates of recruits assuming their 30% monthly mortality (French *et al.* 1975). To compare the relative age structure of the population, the distributions of body mass and the distributions of numbers of individuals marked in different seasons of the year were used.

The measures of movements were compared between years as well as between species by Kolmogorov-Smirnov two-sample test (*K-S*). We felt that comparisons of percentage distributions rather than averages would be more informative and logical, when distributions were mostly skew.

Results

Population density and structure

The data set comprised 10259 captures of 1579 bank voles, and 3900 captures of 1314 yellow-necked mice. Additionally, 120 striped field mice *Apodemus agrarius* and a few root voles *Microtus oeconomus* were also captured. The most of striped field mice were trapped only once. None of them were present for longer than one trapping session in August or October. Being highly mobile, striped field mice invade woodlands after harvesting in the crop fields (Mazurkiewicz and

Rajska-Jurgiel 1987). Twenty five percent of yellow-necked mice and 18% of bank voles were trapped only once.

In particular trapping sessions, the abundance of rodents (numbers of individuals trapped per 100 trap-days) varied from 0.25 to 30.5 for voles and from 0.1 to 19.5 for mice. Per ha densities were positively correlated with the abundance of rodents on the grids (voles: $r = 0.995$, df = 26, $p < 0.001$; mice: $r = 0.997$, df = 26, $p < 0.001$). The abundance of rodents trapped in particular trapping sessions on 8 trap-lines paralleling the 3.5-ha grid in 1984–1985 was positively correlated with the abundance on the grid (voles: $r = 0.955$, df = 7, $p < 0.001$; mice: $r = 0.934$, df = 7, $p < 0.001$). The abundance of rodents on trap-lines was slightly higher than that on the grid and increasing with the distance to nearest line (E. Rajska-Jurgiel and M. Mazurkiewicz, in prep.). Mean numbers of rodents trapped on the grid and mean numbers of rodents trapped on the lines per trapping session (21.6 ± 16 and 25.6 ± 21 for voles; 9 ± 5.4 and 10 ± 7 for mice) did not differ significantly (One-way ANOVA; voles: $F = 0.182$, df = 15, $p = 0.681$; mice: $F = 0.109$, df = 15, $p = 0.750$). A crude index was used as the goal was to make comparison, not to measure density. However, population densities over the 12-ha plot with uneven distribution of trap stations were similar to those on the 3.5 ha plot.

Over the seven years of the study, early-spring population densities varied from 1 to 30 inds/ha for voles and from 1 to 25/ha for mice (Fig. 1). Except in 1983 and 1989, only single juveniles were captured. In 1989, unusually early spring and accelerated growth of the vegetation resulted in an early beginning of breeding (Rajska-Jurgiel 1992). Some juveniles up to 17 g in voles and up to 24 g in mice were captured. However, high spring densities did not result in high annual peaks (Fig. 1). In 1983, heavy seed crop of deciduous trees resulted in winter breeding (Pucek *et al.* 1993). Spring populations were five times those in previous autumn (Fig. 1). The distributions of body mass of unmarked rodents differed between 1983 and 1989 (*K-S* test; voles: $D = 0.405$, $p < 0.001$; mice: $D = 0.628$, $p < 0.001$). In 1983 60% of the unmarked voles were already fully-grown adults with body mass more than 20 g. Also 50% of the unmarked mice were adults with body mass more than 27 g.

Annual peak densities varied from 9 to 104/ha for voles and from 4 to 62/ha for mice (Fig. 1). The highest densities of both species were preceded by winter breeding. In the remaining years, neither annual peaks depended on the spring density (voles: $r = 0.460$, df = 5, $p = 0.358$; mice: $r = 0.510$, df = 5, $p = 198$), nor October density did (voles: $r = -0.249$, df = 5, $p = 0.533$; mice: $r = 0.501$, df = 5, $p = 203$). In 1983, peak population density was 10 times those in 1982, 1984, and 1985 for voles and 6 times those in 1982, 1984, 1985, and 1988 for mice. The remaining study years, that is 1987–1989 for voles and 1987 and 1989 for mice, were the years of moderate density (at the end of August, the density of each species was 2–3 times those in the low density years (Fig. 1). Winter mortality varied from 40% in 1982 to 95% in 1983 in voles and from 33% in 1988 to 93% in

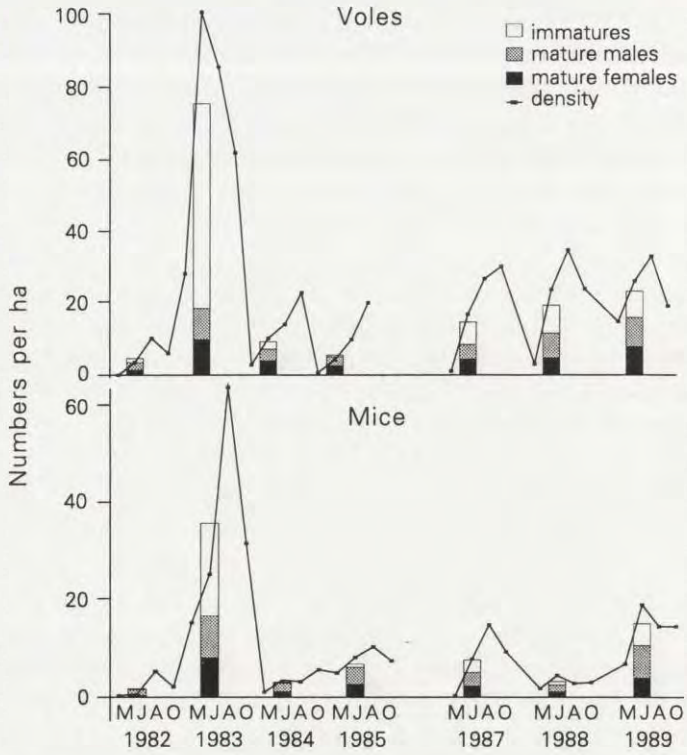

Fig. 1. Changes in population density and breeding structure (mean number of mature males and females and immature individuals per trapping session in the period May–August) for voles and mice.

1983 in mice. Thus, the lowest winter mortality for both species was coupled with low, and the highest with high autumn numbers.

Year-to-year differences were found in the maturation rate of year born young. The proportions of young maturing by autumn in the years of low, moderate, and high density were 85, 55, and 20%, respectively, for voles and 90, 70, and 50%, respectively, for mice. Thus, differences in population density were coupled with differences in the proportions of breeders in both species. In the low density years the populations consisted mainly of mature individuals, whereas in the high density year immature individuals prevailed (Fig. 1). Although the proportions of breeders in the populations of both species were lowest in the year of high density, their numbers were the highest (Fig. 1).

Percentages of the trap stations occupied by rodents as well as mean numbers of rodents per trap station varied in particular trapping sessions with changes in density (Fig. 2). The total space occupied in successive years of the study was 88, 100, 98, 94, 98, 95, and 95% trap stations for voles and 32, 100, 50, 83, 90, 77, and 95% trap stations for mice.

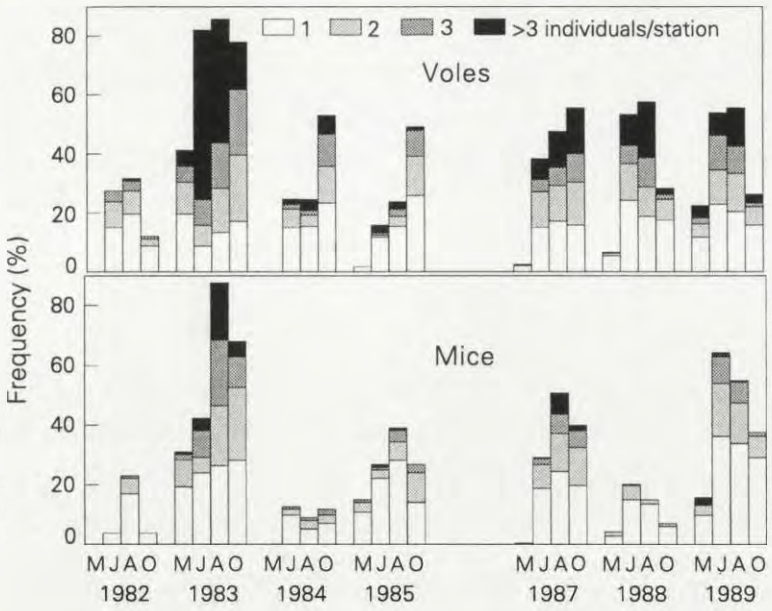

Fig. 2. Percentages of occupied trap stations in successive trapping sessions and their frequency distributions in relation to the number of individuals trapped.

Movement range

The maximum Observed Range Length (ORL) was over 400 m in both species. However, most individuals of the two species had ORL's below 100 m at high and low population densities on all the study plots. At the same time, ORL's smaller than 30 m were not observed, except in 1983. In both species, the ORL varied greatly during the study. This variation was a result of year-to-year differences in ORL, although in all the study years ORL's were smaller in late autumn than in the breeding season (two-way ANOVA, voles; year-to-year effect: $F = 47.8$, df = 1685, $p < 0.001$; seasonal effect: $F = 8.0$, $p < 0.01$; mice, year-to-year effect: $F = 34.5$, df = 742, $p < 0.001$; seasonal effect: $F = 3.2$, $p < 0.05$). Mean ORL in different trapping sessions varied from 35 to 100 m in voles and from 50 to 140 m in mice (Fig. 3). The mean ORL was correlated with the annual peak density (whole data set, voles: $R^2 = 64\%$, df = 25, $p < 0.001$; mice: $R^2 = 65\%$, df = 25, $p < 0.001$; May–August trapping sessions, voles: $R^2 = 78\%$, df = 19, $p < 0.001$; mice: $R^2 = 83\%$, df = 19, $p < 0.001$).

Total captures in a trapping session ranged from 3 to 48% of the possible capture opportunities (Fig. 3). To find out whether the estimate of ORL was influenced by the level of trap saturation, we compared frequency distributions of ORL between trapping sessions with different trap saturation in the high density year (1983) as well as between trapping sessions with a similar trap saturation

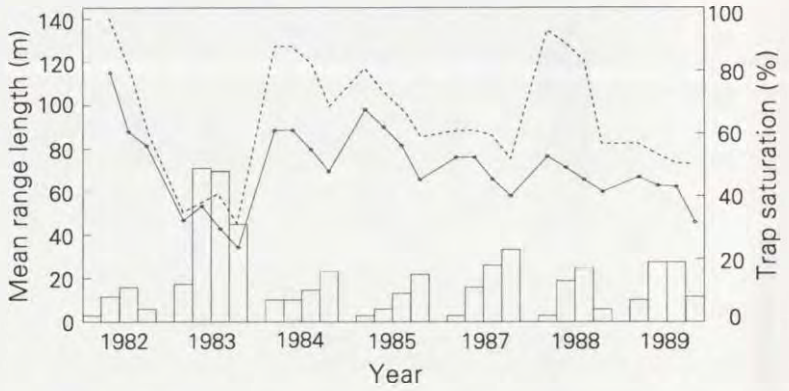

Fig. 3. Percentages of trap saturation (bars) and average home range lengths of voles (solid line) and mice (broken line) in succesive trapping series.

in different years (May 1983, July 1987, July 1988, October 1984 and October 1985; see Fig. 3). No significant differences were found for any species between May and July 1983. (*K-S* test; voles: $D = 0.147$, $p = 0.55$; mice: $D = 0.246$, $p = 0.35$). Independent of the level of trap saturation both species supported similar home ranges. Significant differences were found between August and October, ORLs in October being shifted towards smaller sizes (*K-S* test; voles: $D = 0.294$, $p < 0.001$; mice: $D = 0.298$, $p < 0.01$), in spite of better capture opportunities. ORL's of both species were significantly smaller in May 1983 than in July 1987 (*K-S* test; voles: $D = 0.375$, $p < 0.001$; mice: $D = 0.502$, $p < 0.001$), July 1988 (voles: $D = 0.328$, $p < 0.001$; mice: $D = 0.557$, $p < 0.001$), October 1984 (voles: $D = 0.273$, $p < 0.001$; mice: $D = 0.536$, $p < 0.01$), and October 1985 (voles: $D = 0.271$, $p < 0.01$; mice: $D = 0.333$, $p < 0.05$). Independent of the similar level of trap saturation both species hold smaller home ranges in 1983 than in other years. In a step wise multiple regression of the mean range length on: (1) the annual peak density, (2) density in a trapping session in question, (3) percentage of trap saturation, and (4) an index of the season (May, June, August and October) only annual peak density and the index of the season entered the model (voles: $R^2 = 79\%$, df = 25, $p < 0.001$; mice: $R^2 = 84\%$, df = 25, $p < 0.001$).

In different years, the mean ORL varied from 45 to 95 m for voles and from 55 to 125 m for mice. As no significant differences were found on the 6-ha and 12-ha plots, the material from each of these plots was combined for all the study years, whereas the material from the 3.5-ha plot was analysed separately for the year of high density (1983) and for the low density years (1982, 1984, 1985).

To find out whether the estimate of ORL was influenced by the plot size, we compared frequency distributions of ORL between 3.5-ha and 12-ha plots. Although the maximum ORL was higher on the 12-ha plot, no significant effect of plot size were found for either species (Table 1), (*K-S* test; voles: $D = 0.135$,

Table 1. Percentage distributions of observed home range length (ORL) for voles and mice on different plots at different population densities. Differences between distribution at low and high density were significant (*K-S* test; voles: $D = 0.387$, $p < 0.001$; mice: $D = 0.251$, $p < 0.05$). n – sample sizes.

Species	Plot (ha)	Density	n	Home range length (ORL)				
				50	100	150	200	> 200 m
Voles	3.5	High	464	74.6	18.0	4.7	2.3	0.4
		Low	368	37.2	40.2	9.4	8.7	4.5
	6	Moderate	854	51.6	32.5	9.9	3.8	2.3
	12	Low	428	42.4	33.3	9.5	7.1	7.6
Mice	3.5	High	199	60.0	26.3	10.5	2.6	0.5
		Low	181	14.9	47.5	22.6	9.4	5.5
	6	Moderate	363	28.3	53.3	12.5	3.3	2.5
	12	Low	256	14.5	42.2	20.5	12.0	10.8

$p = 0.093$; mice: $D = 0.153$, $p = 0.338$). Only 14% of voles and 16% of mice among those trapped on the 3.5 ha plot were also trapped outside that plot. Most of them were mature adult males (E. Rajska-Jurgiel and M. Mazurkiewicz, in prep.).

To examine whether ORL varied significantly with years of different population density, we compared frequency distributions of ORL's on the 3.5-ha plot between the high density year (1983) and the low density years (1982, 1984, 1985). ORL's for both species were significantly smaller at high than at low density (Table 1). The proportions of individuals with large ORL (more than 100 m) at low, moderate, and high densities were 22–24, 16, and 7%, respectively, in voles and 38–44, 18, and 13%, respectively, in mice. The proportion of individuals with smallest ORL (less than 40 m) increased with population size from 22 to 45% in voles and from 8 to 42% for mice (Table 1). Both voles and mice hold larger home ranges in the years of low density and smaller in the year of high density. Significant differences were found between the two species, ORL's of mice being shifted towards larger sizes (*K-S* test; high density: $D = 0.255$, $p < 0.001$; moderate: $D = 0.190$, $p < 0.001$; low: $D = 0.255$, $p = 0.02$, 3.5-ha plot; $D = 0.249$, $p < 0.001$, 12-ha plot). Thus, independent of the population density, mice supported larger home ranges than did voles (Table 1).

ORL was estimated with short, 7-day trapping sessions. The total observed range of movements (TRL) calculated as the maximum distance between captures of an individual over the time of its presence on the plot varied in particular years from 56 to 160 m for voles and from 70 to 170 m for mice. Plot size (3.5 and 12 ha) had no significant effect on the estimate of TRL (*K-S* test; voles: $D = 0.152$, $p = 0.129$; mice: $D = 0.196$, $p = 0.388$). TRL was larger in the years of low than of high densities (voles: $D = 0.437$, $p < 0.001$, mice: $D = 0.540$, $p < 0.001$). The proportion of individuals with TRL exceeding 100 m decreased with population size. For voles it was 45–38% at low, 35% at moderate, and 12% at high density.

The respective values for mice were 65–60, 45, and 20%. TRL was significantly smaller for voles than for mice on all the plots (high density: $D = 0.29$, $p < 0.001$; moderate density: $D = 0.21$, $p < 0.001$; low density: $D = 0.25$, $p = 0.04$ on 3.5-ha plot, $D = 0.18$, $p = 0.03$ on 12-ha plot). Differences between ORL and TRL were higher in the low density years than in the year of high density. The TRL increased with the length of time on the plot (Fig. 4). This increase was highest at low population density and lowest, not significant in voles, at high population density. TRL can be an effect of home range shifts by individuals, or an effect of different number of captures, or differential ORL of individuals with different lengths of time on the plot when marked. The original ORL (at the first capture after marking) for individuals with different lengths of time on the plot did not show significant differences. Instead, TRL depended on the length of time on the plot, rather than on the number of captures. Two-way ANOVA gives the following effects

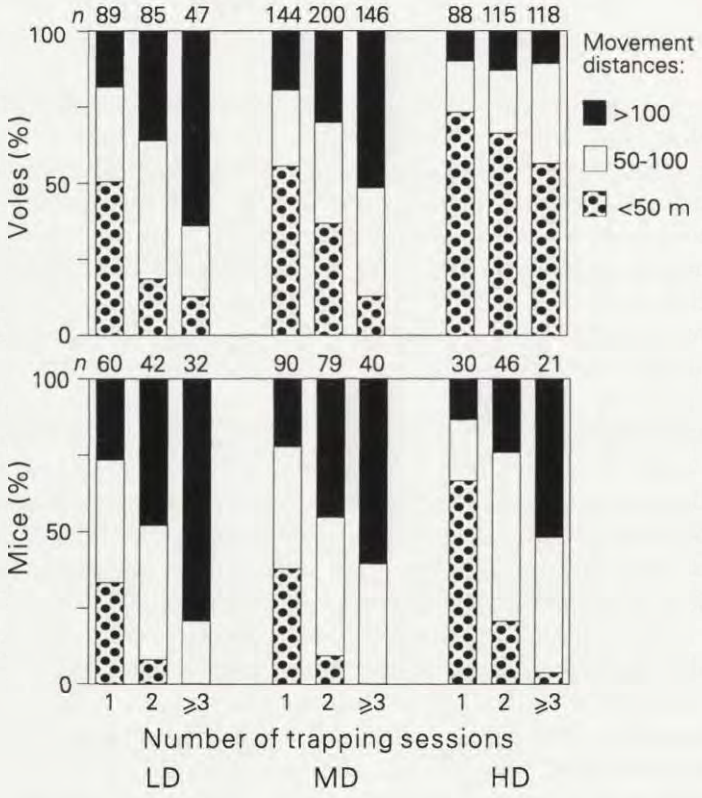

Fig. 4. Percentage distributions of the total movement distance of individuals present on the study plots over 1, 2, and 3 or more trapping series in the years of low (LD), moderate (MD) and high (HD) population densities. Numbers above bars indicate sample sizes. Significant increases in the movement distance with time: voles, moderate density: $\chi^2 = 45.84$, $p < 0.001$, low density: $\chi^2 = 38.20$, $p < 0.001$; mice, high density: $\chi^2 = 12.12$, $p = 0.02$, moderate density: $\chi^2 = 24.58$, $p < 0.001$, low density: $\chi^2 = 17.78$, $p < 0.001$.

for voles at low, moderate and high densities: time: $F = 15.6$, df = 220, $p < 0.001$; $F = 22.3$, df = 489, $p < 0.001$; $F = 0.42$, df = 320, $p = 0.661$; captures: $F = 1.13$, $p = 0.335$; $F = 0.54$, $p = 0.658$; $F = 3.8$, $p = 0.011$. For mice, time: $F = 10.9$, df = 133, $p < 0.001$; $F = 10.2$, df = 208, $p < 0.001$; $F = 3.4$, df = 136, $p = 0.035$; captures: $F = 1.49$, $p = 0.223$; $F = 1.52$, $p = 0.216$; $F = 2.5$, $p = 0.04$.

Home range shift

The distance between the last and the first capture (LFD) as well as the distance of the shift of home range centre between successive trapping sessions (CCD) varied during the study with density of rodents (One-way ANOVA; voles: $F = 12.5$, df = 817, $p < 0.001$ for LFD, $F = 14.5$, $p < 0.001$ for CCD; mice: $F = 3.5$, df = 299, $p < 0.03$ for LFD, $F = 3.0$, $p = 0.04$ for CCD). The LFD can be an effect of a change in location of individuals as well as an effect of differences in home range size. It was found that LFD were correlated with CCD (for voles at low, moderate and high densities: $r = 0.941$, df = 154, $p < 0.001$; $r = 0.909$, df = 404, $p < 0.001$; $r = 0.885$, df = 327, $p < 0.001$, respectively; and for mice: $r = 0.936$, df = 63, $p < 0.001$; $r = 0.908$, df = 149, $p < 0.001$; $r = 0.818$, df = 80, $p < 0.001$) and not with home range sizes (voles: $r = 0.144$, $p = 0.171$; $r = 0.095$, $p = 0.55$; $r = 0.123$, $p = 0.34$; mice: $r = 0.153$, $p = 0.227$; $r = 0.110$, $p = 0.177$; $r = 0.177$, $p = 0.117$).

The mean LFD in different trapping sessions varied from 19 to 70 m in voles and from 35 to 82 m in mice. The mean CCD varied from 16 to 60 m in voles and from 31 to 80 m in mice. In a step wise multiple regression of mean CCD on: (1) the annual peak density, (2) density in a trapping session in question and (3) the index of season (May, June, and August), annual peak density entered the model first (voles: $R^2 = 82\%$, df = 19, $p < 0.001$; mice: $R^2 = 73\%$, df = 19, $p < 0.001$). Only addition of the index of season increased the coefficient of determinant (by 2% for voles and by 6% for mice).

The analysis of home range shifts calculated by using both indices did not show a signifcant effect of the plot size on the estimate of the shift of home anges of both rodents (*K-S* test; voles: $D = 0.116$, $p = 0.999$ for LFD, $D = 0.113$, $p = 0.999$ for CCD; mice: $D = 0.154$, $p = 0.999$ for LFD, $D = 0.139$, $p = 0.999$ for CCD). Most voles and mice shifted their home ranges by significantly shorter distances in the high than in the low density years (Tables 2 and 3). As the density increased, the proportion of individuals with a home range shift greater than 100 m declined from 14 to 1% in voles and from 19 to 6% in mice (Tables 2 and 3). Concurrently, the proportion of individuals with home range shift less than 15 m (not shifting their hone ranges?) increased from 18 to 55% in voles and from 14 to 19% in mice. Mice shfted their home ranges to greater distances than did voles (*K-S* test; for LFD: $D = 0.292$, $p < 0.001$ at high, $D = 0.219$, $p < 0.001$ at moderate, $D = 0.336$, $p = 0.02$ at low density on 3.5-ha plot, and $D = 0.240$, $p < 0.001$ at low density on 12-ha plot; and for CCD: $D = 0.385$, $p < 0.001$ at high, $D = 0.160$, $p < 0.001$ at moderate, $D = 0.207$, $p = 0.02$ at low density on 3.5-ha plot, and $D = 0.186$, $p = 0.03$ at low density on 12-ha plot) (Tables 2 and 3).

Table 2. Percentage distributions of the shifts of home ranges calculated as a distance between the site of the last capture in the preceding trapping series and the site of the first capture in the next trapping series (LFD) at different population densities on plots of different sizes. Differences between distribution at low and high density were significant (*K-S* test; voles: $D = 0.495$, $p < 0.05$; mice: $D = 0.485$, $p < 0.05$). n – sample sizes.

Species	Plot	Density (ha)	n	Shifts of home ranges (LED)						
				25	50	75	100	125	150	> 150 m
Voles	3.5	High	327	74.6	19.9	1.5	1.5	1.2	0.9	0.3
		Low	101	30.3	39.4	13.6	3.0	4.5	1.5	7.6
	6	Moderate	390	49.5	25.8	7.0	8.0	3.3	2.3	4.3
	12	Low	157	29.7	31.0	14.8	7.7	3.2	2.6	11.0
Mice	3.5	High	82	48.8	37.5	7.5	2.5	0.0	0.0	3.8
		Low	69	15.9	26.1	17.4	14.5	13.0	4.4	8.7
	6	Moderate	150	29.3	31.3	14.7	7.3	7.3	4.7	5.3
	12	Low	104	21.1	28.2	16.9	9.9	7.0	2.8	14.1

Table 3. Percentage distributions of home range shifts calculated as a distance between geometric centres in two successive trapping series (CCD), at different population densities on plots of different sizes. Differences between distribution at low and high density were significant (*K-S* test; voles: $D = 0.532$, $p < 0.001$; mice: $D = 0.309$, $p < 0.05$). n – sample sizes.

Species	Plot	Density (ha)	n	Shifts of home ranges (CCD)						
				25	50	75	100	125	150	> 150 m
Voles	3.5	High	327	82.3	14.7	1.5	0.6	0.3	0.3	0.3
		Low	101	37.9	30.3	15.2	3.0	4.5	1.5	7.6
	6	Moderate	390	52.3	26.8	9.5	4.3	2.3	1.0	4.0
	12	Low	157	43.9	21.9	14.8	5.8	5.8	2.7	5.2
Mice	3.5	High	82	48.8	35.4	7.3	2.4	2.4	1.2	2.4
		Low	69	34.8	26.1	13.0	8.7	7.2	3.0	7.2
	6	Moderate	150	42.0	26.0	13.3	6.7	4.7	4.0	3.3
	12	Low	104	32.4	23.9	16.9	7.0	4.2	2.8	12.7

Shifts of home ranges between successive trapping sessions can be directional or non-directional and rodents may remain longer at the same sites. The summation of directional shifts of home ranges, even if these are small shifts, causes that rodents leave the study area which may be their natal sites and become emigrants. The total distance of the shifts, calculated for individuals present in at least 3 trapping sessions, was shorter at high than at low densities (*K-S* test; voles: $D = 0.389$, $p < 0.001$; mice: $D = 0.563$, $p = 0.03$). At high density, mice moved longer distances than voles ($D = 0.449$, $p = 0.04$) (Fig. 5). The total distance of shift was significantly higher than shift between successive trapping sessions, in

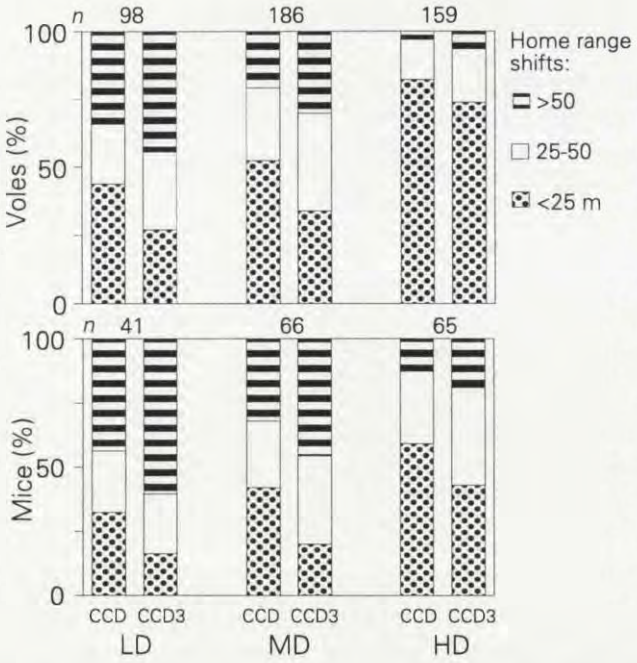

Fig. 5. Comparison of percentage distributions of home range shifts (CCD) between successive trapping series (1 and 2, 2 and 3) and the total distance of shift between trapping series 1 and 3 (CCD3). Numbers above bars indicate sample sizes. The total distance of the shift was significantly longer than the shift between successive trapping series at low (LD) and moderate (MD) densities (*K-S* test; voles: $D = 0.242$, $p < 0.001$ and $D = 0.208$, $p < 0.001$, respectively; mice: $D = 0.356$, $p < 0.05$ and $D = 0.303$, $p < 0.05$). HD – high density of populations.

the years of low and moderate population densities. In the high density year, the total distances of shift did not significantly differ from the shifts between successive trapping sessions (Fig. 5). To estimate whether home range shifts occur at random or directionally, we compared home range shifts of individual rodents between successive trapping sessions with the total distance of their shift. A net shift longer than 75% of the sum of successive shifts was considered as a directional shift. When shifts between successive trapping sessions were longer than the total shift, we considered them to involve occasional sallies. In the years of low and moderate densities, about 15% of voles and 20% of mice temporarily shifted home range centres by more than 50 m and finally returned to their previous home ranges. Such sallies practically did not exist in the high density year (0.5% in both species). Nonetheless, 60% of the voles and 70% of the mice at low density, and 50% of the voles and 65% of the mice at moderate density, but only 20% of the voles and 30% of the mice at high density moved directionally within the study area. Thus, in the high density year, home range shifts of both species were not only shorter but also non-directional.

Site tenacity and dispersal

Differences in the spatial behaviour of rodents observed between the years of low and high densities concerned both the distance of home range shift and the size of home ranges. Thus, the absolute distance of the shift of a home range centre alone does not provide evidence for abandoning the home range. Only individuals that shifted the centres of their home ranges to a distance longer than ORL in the preceding trapping session were designated as abandoning their home ranges. In both species the proportion of individuals abandoning their home ranges was higher in the low density years than in the high density year and these differences were larger for voles than for mice (Table 4).

Table 4. Proportions of individuals staying in the same home range, partly shifting it, and abandoning it. Differences between distribution at low and high density were significant (voles: $\chi^2 = 70.4$, $p < 0.001$; mice: $\chi^2 = 11.7$, $p < 0.001$). n – sample sizes.

Species	Density (ha)	n	Percentage		
			Staying	Shifting	Abandoning
Voles	High	327	84	9	7
	Low	157	50	12	38
	Moderate	400	57	19	24
Mice	High	82	54	30	16
	Low	86	45	15	40
	Moderate	132	53	17	30

As a result of differential tendencies to abandon their home ranges observed in the years of high and low densities, rodents can move deferentially beyond the study plot. Between successive trapping sessions 60% of the voles disappeared in the years of low density and 44% in the year of high density. The respective figures for mice were 70 and 60%. Among the rodents disappearing from the study plot new individuals prevailed. The proportion of new individuals that disappeared declined with increasing density, and it was lower in voles than in mice (Fig. 6). Differential mobility of rodents in the years of low and high densities can be accompanied by differential frequency of immigration to the study plots. In each trapping session, among individuals trapped for the first time there were not only young weaned between trapping sessions but also adult individuals, more than 2-month old. These individuals were considered as immigrants. The proportion of immigrants in the total number of individual s appearing between successive trapping sessions in the vole population was 34% in the years of low and 14% in the year of high density. The respective figures for the mouse population were 40 and 30% (Fig. 6).

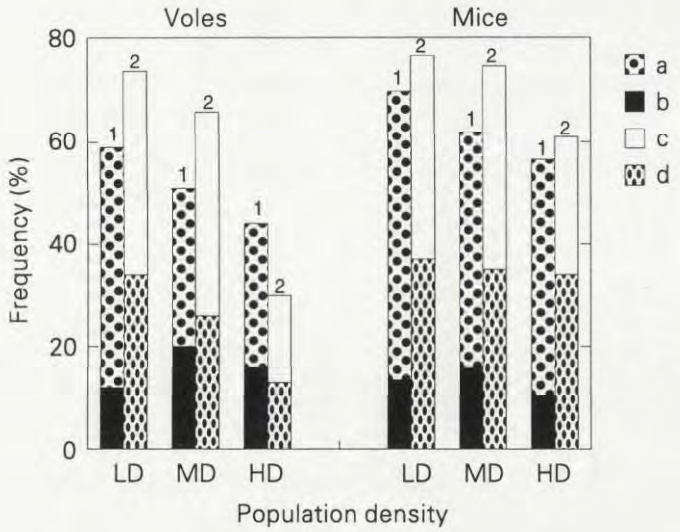

Fig. 6. Percentages of disappearing individuals (1) subdivided into those captured for the first time (a) and those already marked (b) in populations. Percentages of individuals recruited to the population (2) subdivided into those born between successive trapping series (c) and immigrants (d) in populations. See Fig. 4 for explanation of population density symbols.

Table 5. Percentage distributions of May–August recruits with various length of time on the plot. The lenght of time on the plot was expressed as numbers of trapping sessions. The proportion of recruits that emigrated after marking was significantly higher in mice than in voles (at high density: $\chi^2 = 19.68$, $p < 0.001$, at moderate density: $\chi^2 = 30.06$, $p < 0.001$, at low density: $\chi^2 = 4.60$, $p < 0.05$ on 3.5-ha plot and $\chi^2 = 4.78$, $p < 0.05$ on 12-ha plot).

Species	Plot	Density (ha)	n	Numbers of trapping sessions		
				1	2	3 or more
Voles	3.5	High	415	23.0	41.0	36.0
		Low	118	38.0	45.0	17.0
	6	Moderate	600	33.0	40.0	27.0
	12	Low	230	39.0	43.0	19.0
Mice	3.5	High	243	46.5	43.0	10.5
		Low	85	50.0	37.0	13.0
	6	Moderate	288	47.5	34.5	18.0
	12	Low	133	49.0	33.0	18.0

Loss rates measure both, the mortality and emigration of rodents. Emigration rates of recruits were higher in mice than in voles (Table 5). Voles remained on the plot for a longer time than mice. Moreover, the residency of voles increased

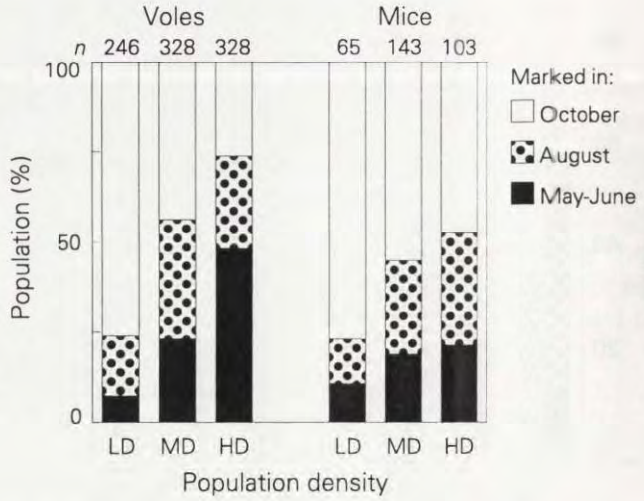

Fig. 7. Age structure of the population in autumns of the years with different population densities. Numbers above bars indicate sample sizes. Age of rodent populations was significantly "older" at high than at low population densities ($\chi^2 = 155.75$, $p < 0.001$ for voles, $\chi^2 = 12.32$, $p < 0.001$ for mice). See Fig. 4 for explanation of population density symbols.

with the population density (Table 5). Comparing the presence of the same individuals between the 3.5-ha plot and the 12-ha plot, only 20% of the mice and 25% of the voles classified as emigrants on the 3.5-ha plot settled in the nearby neighbourhood (on the 12-ha plot), whereas the other individuals disappeared.

Differences in emigration rate between the years of high and low densities may cause differences in the age structure of the population on the plot, and if it is assumed that emigrants incur higher mortality, also in the whole forest. The age structure of the populations of both species was estimated in the autumns of the years with different population densities. The proportions of individuals marked in early and late summer and in autumn showed significant differences between the years of high and low densities (Fig. 7). Distributions of body mass also varied with density in both species, being shifted towards higher body mass at high density (*K-S* test; voles, low-high density: $D = 0.444$, $p < 0.001$; medium-high density: $D = 0.410$, $p < 0.001$; low-medium density: $D = 0.267$, $p < 0.001$; mice, low-high density: $D = 0.413$, $p < 0.001$; medium-high density: $D = 0.404$, $p < 0.001$; low-medium density: $D = 0.230$, $p = 0.05$). The proportions of voles with body mass less than 17 g, at low, moderate, and high densities were 66–51%, 48–40%, and 23%. The proportions of mice with body mass less than 25 g, were, respectively, 80–60%, 51–45%, and 21%. Thus the proportion of young decreased with population size. With increasing population density, low mobility and high site tenacity delayed the maturation of young individuals and reduced recruitment of new individuals, and the populations of both species grew older.

Discussion

Food supply frequently limits population density and reproduction, at least in temperate environment (Flowerdew 1985, Boutin 1990, Pucek *et al.* 1993, Jędrzejewski and Jędrzejewska 1996, Wolff 1996). Indeed, we found that numbers of breeding males and females were highest in the high density year and lowest in the low density years. High numbers of rodents in 1983 were preceded by heavy mast crop and by winter breeding, also observed in other parts of Europe, and numbers of these species in the other years were also correlated with food abundance (Pucek *et al.* 1993). In 1983, spring numbers of mice and voles were high. However, population of voles grew faster and reached a higher and earlier annual peak suggesting a stronger effect of kinship and familiarity on population dynamics (Ylönen *et al.* 1995) in voles than in mice. High spring numbers in 1989 was caused by early breeding following an unusually early spring and accelerated growth of vegetation (Rajska-Jurgiel 1992). The onset of breeding coincides with the beginning of phenological spring (Bujalska 1983, 1985, Rajska-Jurgiel 1992), and the survival of spring generations depends on food supply (Bujalska 1975, Banach 1986). However, annual peak densities did not depend on the spring density, except in 1983. Instead, annual peaks were correlated with spring--summer home range sizes and home range shifts. Although the food availability and predation are the ultimate factors that determine the level of species abundance, the pattern of changes in numbers and winter mortality rates are not fully explained by food supply and predation alone (Pucek *et al.* 1993, Jędrzejewski and Jędrzejewska 1996).

Movement patterns of both species varied over the study period. Changes in mobility were associated with long-term rather than seasonal changes in numbers of rodents. The largest home ranges for both species were observed in the years of low numbers. The year-to-year changes in the home range size concerned mature males and females, as well as immature individuals of both species (E. Rajska-Jurgiel and M. Mazurkiewicz, in prep.). Changes in home range sizes with variation in the density of forest rodents were observed by many authors (Zejda and Pelikan 1969, Mazurkiewicz 1981, Wolff 1985, Adler and Wilson 1987, Johnson 1988, Bujalska and Grüm 1989). Both, home range size and the population density are related to the resource abundance, however defined (Attuquayefio *et al.* 1986, Bondrup-Nielsen 1986, Boutin 1990, Jones 1990). Spatial behaviour of animals primarily depends on the availability of necessary resources. A strategy increasing fitness (survival and breeding) is to possess the largest amount of resources within the smallest area. That minimizes the time spent outside the nest, risk of predation and infanticide (Schoener 1971, Krebs 1980, Wolff and Cicirello 1989, Wolff 1993). In resource rich patches, where rodent densities are typically higher, the home ranges can be smaller (Karaseva and Ilyenko 1957, Lavrova and Andreeva 1960, Nikitina and Merkova 1963, Wolff 1985, Attuquayefio *et al.* 1986, Jones 1990). Home range size declines with a food addition (Smith 1971, Bujalska 1975, 1985,

Andrzejewski and Mazurkiewicz 1976, Ims 1987, Boutin 1990). With resource deficiencies, however defined, there is an increase in the home range size and mobility of rodents (Bondrup-Nielsen and Karlsson 1985, Attuquayefio *et al.* 1986, Bondrup-Nielsen 1986, Korn 1986, Wolff and Cicirello 1990, Rajska-Jurgiel 1992, Salsbury and Armitage 1994).

Year-to-year changes in home range sizes were accompanied by changes in the distance of home range shifts. In the low density years, the total range of movements significantly increased with time. Both the shifts between successive trapping sessions and the total distance of shift increased with increasing home range sizes, and were highest in the low density years. Year-to-year changes in the home range shift concerned mature males and females, as well as immature individuals (E. Rajska-Jurgiel and M. Mazurkiewicz, in prep.). More rodents abandoned their home ranges in the years of low than in the year of high density. In non-cyclic populations, the rate of dispersal is typically higher at low than at high densities (Mazurkiewicz and Rajska-Jurgiel 1975, Jannett 1978, Jones *et al.* 1988, Wolff *et al.* 1988, Bujalska and Grüm 1989, Jones 1989, Wolff and Cicirello 1990, Hansson 1991, Chistova 1995, Lukyanov 1995), as a consequence of resource limitation as well as competition for mates or space to breed. Dispersal rates decline with increasing availability of resources. Superabundant food supply (seed crop, supplemental feeding) inhibit emigration and allow for immigration into food rich patches (Boutin 1990, Brandt 1992, Löfgren *et al.* 1996). As the territory size is a function of habitat quality (Bujalska 1975, 1985, Ostfeld 1985, Bondrup--Nielsen 1986, Jones 1990), good food conditions relax competition for space (Ims 1987, Ylönen *et al.* 1988). Dispersal distance depends on the home range size and exploration rates (Johnson 1988, Jones 1989, Wegner and Merriam 1990). Resource deficiency, however defined, causes an increase in dispersal rates (Jones *et al.* 1988, Wolff and Cicirello 1990, Brandt 1992). Although dispersal increases the risk of predation, the chance of finding resources is also increased. If densities reflect the food conditions, high dispersal rates at low density may be a strong stabilizing factor against food shortage. Another explanation is that at low numbers rodents disperse just because they can (Bujalska and Grüm 1995, Grüm and Bujalska 1995, Plesner-Jensen 1996).

We conclude that the spatial behaviour of both, the bank voles and the yellow--necked mice is highly flexible and can change under various environmental conditions. At high density, movement ranges of voles were similar to those found in confined populations (Ylönen *et al.* 1988, Bujalska and Grüm 1989). At low density, they were similar to those observed in the patchy field-forest landscape (Kozakiewicz and Szacki 1995).

Assuming that the spatial behaviour of a single individual depends on the available resources, a question arises whether spatial behaviour of rodents can be responsible for determining population dynamics? The choice: stay in the natal area or leave it can be of crucial importance to the regulation of population numbers. Local population density largely depends on residency of rodents

(Andrzejewski 1963, Petrusewicz 1983, Mazurkiewicz and Rajska-Jurgiel 1987, Gliwicz 1989). We have shown that site tenacity of the two species varied with changes in home range size. As the mobility increased, the number of rodents disappearing from the study area increased, although free space was more available. High rate of movements and dispersal observed at low densities can increase mortality from predation (Erlinge *et al.* 1984, Hansson and Henttonen 1988), and affect the total numbers over larger forest areas. Low mobility of rodents led to their increased site tenacity and to a rapid increase in the density of, at least, local populations.

Resource deficiency accounts for increased mobility, aggressiveness and territorial tendencies in animals (Bondrup-Nielsen 1985, Ims 1987, Ostfeld 1985, Anderson 1989, Hansson 1991, Brandt 1992). High mobility of rodents caused high emigration rates and early juvenile maturation. At low density, dispersers can easily find a place to breed because of a good supply of vacant space and frequent movements of residents. Low mobility and high site tenacity inhibited juvenile maturation. At high density, early juvenile maturation is suppressed (Adamczewska 1961, Bujalska 1970, Bobek 1971, Montgomery 1980, Gipps 1985, Montgomery and Gurnell 1985, Bujalska and Grüm 1989). High spring numbers of breeding females give rise to recruitment of large numbers of juveniles and rapid filling of vacant space early in the season. High densities of the year-born young inhibit their dispersal (Mazurkiewicz and Rajska 1975, Goundie and Vessey 1986, Bujalska and Grüm 1995, Grüm and Bujalska 1995). As a result of lack of vacant space and high site tenacity of residents, a chance for finding a place for breeding is small. The recruitment of young declines in summer with increasing population numbers and cessation of breeding.

Both, population density and maturation rates were effects of changing movement patterns of rodents. Reduced mobility, increased site tenacity, and increased population density accounted for cessation of breeding and reduced juvenile recruitment in late summer. As a result, local populations showed different age structures in autumn. "Old age structure" may account for high winter mortality observed in the high density year. Under different environmental conditions, the same species of rodent can show "cyclic" or "non-cyclic" population dynamics (Hansson and Henttonen 1985, Henttonen *et al.* 1985, Taitt and Krebs 1985). One of these species is the bank vole. The direct proximate reasons for the peak and crash years are still under debate (Hornfeldt 1994, Körpimaki *et al.* 1994, Löfgren 1995, Jędrzejewski and Jędrzejewska 1996, Hanski and Henttonen 1996, Krebs 1996). However, changes in the proportion of breeders, maturation rates, shortening of the breeding season, lack of juvenile recruitment, and old age structure, are surprisingly similar to those described above.

Independent of their population densities, voles and mice differed in their spatial behaviour. Species living on more limited food resources should hold larger home ranges. Home ranges of mice were larger than those of voles. Home range size of the species living on more limited food resources should be more affected

by changes in food supply. We found that year-to-year differences in home range size were greater for mice, more dependent on specific food resources (Angelstam *et al.* 1987) than for less food selective voles. Maturation rates of the species restricted in maturation by vacant space supply rather than by food availability should be more affected by density. We found that year-to-year differences in maturation rates were greater for voles than mice. If competition for food resources is the main reason for dispersal then species depending on scarcer resource should be more prone to disperse. Mice moved longer distances and more often abandoned their home ranges than did voles. Also more mice than voles emigrated from and immigrated into the study plots. If competition for place to breed is the main reason for dispersal then dispersal rates of species with lower maturation rates should be more affected. Year-to-year differences in the magnitude of home range shifts and in site tenacity were larger in voles than mice. Increase in the time of residency and inhibition of juvenile maturation as a result of the low mobility of rodents in 1983, were much greater in voles than in mice. However, mice were only locally abundant and patchily dispersed over the forest. In another locality of the same forest, the density of voles was equally high and the density of mice was much lower (Mazurkiewicz and Rajska-Jurgiel 1987). In the low density year mice, but not voles, were almost absent from that plot. Thus, according to habitat saturation hypothesis (Bujalska and Grüm 1995, Grüm and Bujalska 1995, Löfgren 1995, Plesner-Jensen 1996) mice simply "could" move farther than voles, at least into a dispersal sink.

The natural heterogeneity of each landscape, even of continuous forests, and habitat selection of animals means that the environment of the species is heterogeneous. Patchy distribution of resources results in increasing animal mobility (Merriam and Lanoue 1990, Wegner and Merriam 1990, Szacki and Liro 1991, Rajska-Jurgiel 1992, Kozakiewicz and Szacki 1995) which increases the chance of encountering resources, although increases the predation risk through exposure. Under circumstances of spatial and temporal variability in the habitat quality, natural selection favours exploration and dispersal behaviour (Stenseth and Lidicker 1992). Natural fragmentation of the forest habitat, resulting from spatial heterogeneity of plant cover, means that the spatial distribution of food resources is more uneven for seed-eating mice than for voles. It is also probably more patchy in poor than in good food years. The availability of shelters, important to bank voles, is less variable in time. Nonetheless spatial differentiation of the habitat in terms of the availability of good vacant shelters and nest places is higher at low than high density. Differences in food requirements and in predictability of the resource distribution have an effect on site tenacity and dispersal of the two species. Narrow food/habitat preference in mice is offset by their lower vulnerability to predation. High mobility in search of food, frequent shifting of home ranges, and high dispersal capabilities are adaptations to natural fragmentation of the habitat and a specific preadaptation of this species to landscape fragmentation.

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