Types of Ontogeny and Territorial Distribution of Small Rodents

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Abstract—In small rodents, differences in the average home range size, depending on the type of ontogeny and animal sex, have been revealed. The dynamics of changes in the spatial structure of populations during the breeding season are described.

The structure and dynamics of populations as indices characterizing their state in various animal species (Mezhzherin *et al.*, 2002) are closely related to changes in the spatial population structure. The spatial structure of a population manifests itself in a consistent distribution of individuals and their groups with respect to certain landscape elements and to each other, reflecting a species-specific type of area use. This distribution provides a foundation for all forms of the normal life activity of populations, ensuring the most efficient use of environmental resources (food supply, shelters, microclimatic conditions, etc.). In addition, spatial structuring is a basic condition for the maintenance of intraspecific (intrapopulation) contacts between individuals at an adequate level (Shilov, 1977).

Specific forms of the spatial distribution of animals in different seasons and years can noticeably change depending on environmental conditions. For instance, it has been shown that the home range size depends on animal body size (MacNab, 1963; Dol'nik, 1993, 1995), food supply (Harestad and Bunnel, 1979; Kryazhimskii, 1992; Dobrinskii *et al.*, 1994), population density (Okulova *et al.*, 1971), and a number of other factors. Moreover, individuals belong to different intrapopulation groups playing different roles in the integrated response of the population system to the state of its environment, and this fact must also be reflected in the pattern of area use. The structural inhomogeneity of small mammal populations is strikingly manifested in the existence of alternative ontogenetic pathways in rodents (Olenev, 2002).

The purpose of this work was to elucidate the role of ontogeny type in the formation of spatial population structure in small rodents and, in particular, in determining the size of their home ranges.

MATERIAL AND METHODS

Methodologically, this study was based on the concept of the functional approach (Olenev, 1981, 1989, 2002). Its essence is that the main criterion for distinguishing intrapopulation groups (structural units) is the functional state of individuals—specific features of growth, development, reproductive state, etc.—determining their functional unity corresponding to one of two pathways of ontogeny. On this basis, we proposed a scheme for distinguishing three main physiological functional groups (PFG), which is shown in Fig. 1. Each group consists of individuals that belong to several cohorts and are functionally united with respect to their role in reproduction.

The first ontogenetic pathway. *Monophasic growth. Young animals reproducing in the year of birth* (PFG3). They rapidly grow, mature, and usually die before the winter of the current year.

The second ontogenetic pathway. *The first phase. Young animals remaining nonreproductive in the year of birth* (PFG2). After a short period of growth in the first phase, the animals cease growing and remain in a "conserved" state, with a low metabolic rate, until the next spring.

The second phase. Overwintered animals (PFG1, formerly PFG2). After wintering and the spring period of intensive growth and maturation, most animals participate in reproduction.

A major advantage of the functional approach is that it offers the possibility of analyzing "pure" intrapopulation groups united by a certain functional role in the maintenance of their population. Such groups are easy to distinguish, which makes this analysis fairly simple, convenient, and logical.

This approach has been successfully used in a broad spectrum of population studies. For instance, the rodents following different ontogenetic pathways proved to be clearly differentiated with respect to time-
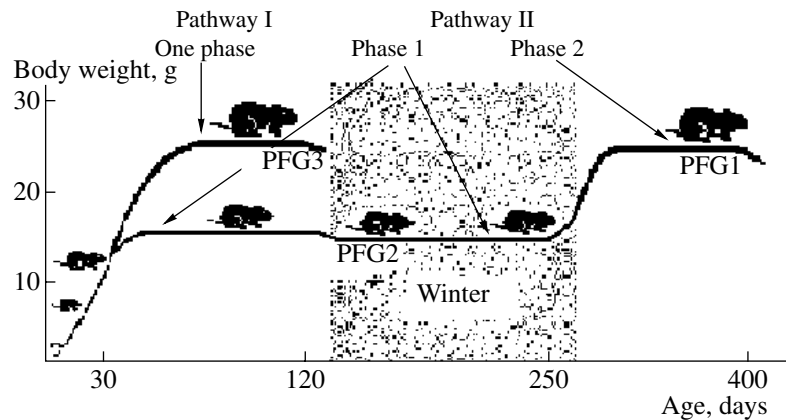
Fig. 1. Scheme of two ontogenetic pathways of murine rodents.

dependent changes in age markers (Olenev, 1989), the rates of metabolism and senescence, and life span (Olenev, 1981, 1991). Specific features of these two groups were traced at the tissue and biochemical levels (Gulyaeva and Olenev, 1979; Olenev *et al.*, 1983); differences between them in natural radioresistance (Olenev and Grigorkina, 1998), the rate of accumulation of heavy metals, and sensitivity to their toxic action were recorded (Bezel' and Olenev, 1989). These differences were often so obvious that there was no need to prove their statistical significance.

The bulk of material for this study was collected by G.V. Olenev in a 1.5-ha stationary marking plot located on a cape of Lake Bol'shoi Ishkul', in the Il'men State Nature Reserve (the Southern Urals). Monitoring studies on the rodent fauna, including the bank vole (*Clethrionomys glareolus* Schreber, 1780), were initiated in 1975 and are being continued today. In addition, we analyzed data on the northern red-backed vole (*Clethrionomys rutilus* Pall., 1779) collected by F.V. Kryazhimskii, Yu.M. Malafeev, and L.N. Dobrinskii in a 1.13-ha marking plot located in the Khadyta-Yakha River floodplain (Southern Yamal) in 1978.

In the study, conventional and original methods of field and laboratory studies were used. Most data on the spatial distribution of rodents were collected by the capture–mark–recapture (CMR) method (Petrusewicz and Hansson, 1975). As a measure of abundance, we used the total number of animals captured, i.e., the minimal number of animals living on a plot. The method of harmonic mean (Dixon and Chapman, 1980; Maklakov, 1998; Maklakov and Kryazhimskii, 2002) was used to reconstruct the configuration of home ranges and estimate their size from the coordinates of capture points. If an animal was captured only once, the size of its home range was estimated by the spherical model with a center in the capture point and a radius equal to the distance to the neighboring traps: 8 m in the Southern Yamal and 10 m in the Southern Urals (Fig. 2).

To analyze the role of different functional groups in the spatial organization of bank vole populations in the Southern Urals, we chose four years which present a striking contrast from the standpoint of population dynamics: 1975, an extremely arid season in which the structure of the bank vole population was abnormal; 1976, a season in which the population was restoring its size and structure after this anomaly; 1977, a typical season of high animal abundance; and 1981, a typical season of low abundance.

BANK VOLE POPULATION STRUCTURE AND ABUNDANCE IN THE SOUTHERN URALS DURING THE STUDY PERIOD

As a result of drought, the reproduction of overwintered animals in 1975 ceased as early as the beginning of July. Young of that year were not involved in reproduction, and all of them were the offspring of overwintered animals. Thus, no individuals belonging to PFG3 were found in 1975 (Fig. 3).

Weather conditions in 1976, the next year after depression, were close to the norm. Although the relative abundance of bank voles slightly increased after 1975, it remained low, averaging 23 individuals per 100 trap-days over the breeding season. The increase in abundance occurred mainly due to the reproduction of overwintered females: they produced five to six families of offspring each (instead of usual three to four), living to an age of 16 months. Although single overwintered females occurred until October, most representatives of PFG1 (mainly males) disappeared by late July (Fig. 3). Thus, overwintered females mated with overwintered males only until midsummer; thereafter, the remaining adult females were inseminated mainly by male young of the year of the first cohorts (PFG3); i.e., age crossing was observed. The females born at the beginning of the season had a negligible role in reproduction. The males of PFG3 could easily disperse almost immediately after their emergence (beginning from midsummer), occupying the area that became
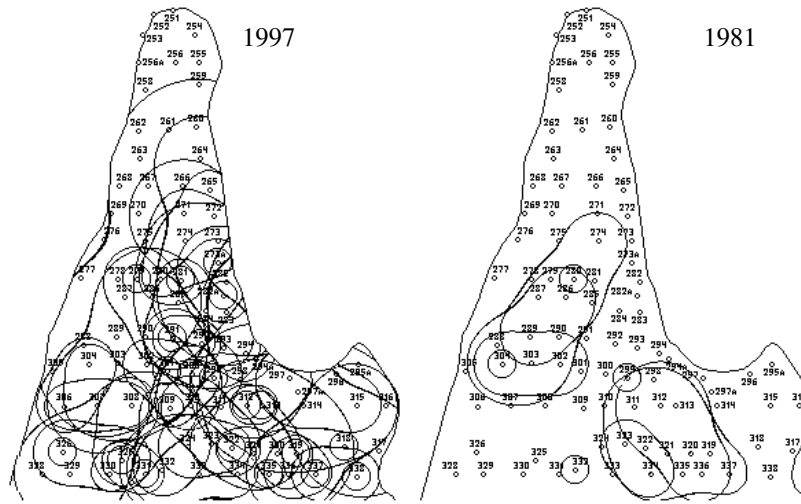
Fig. 2. Map of individual home ranges of bank voles in early August in the years with different population densities.
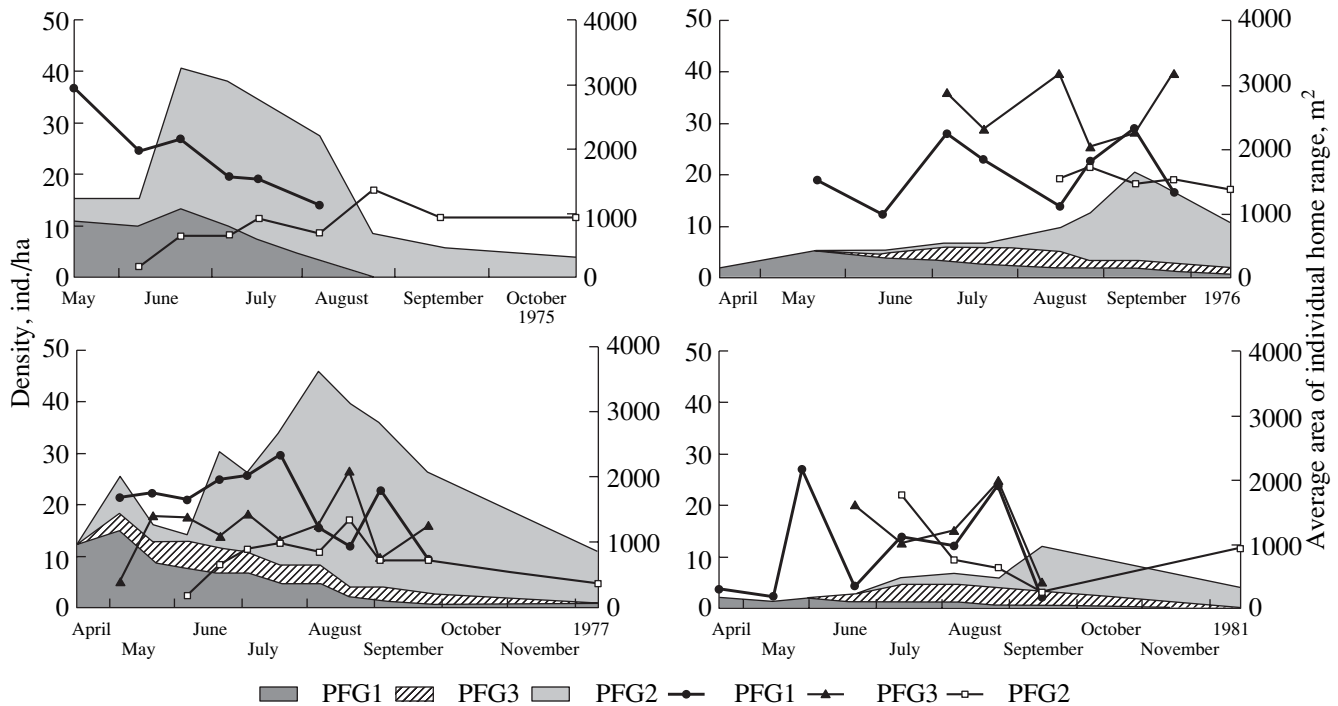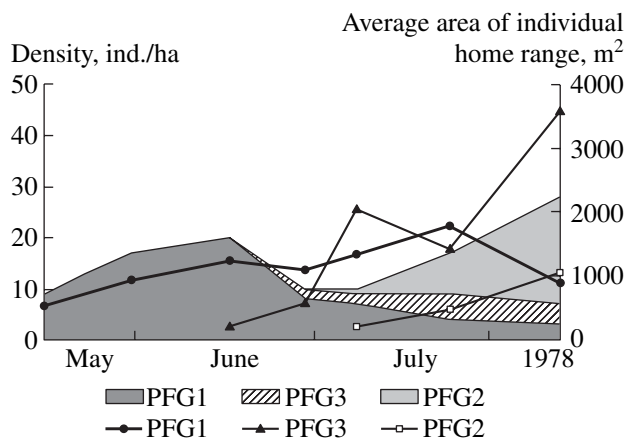

Fig. 3. Dynamics of population density (surface diagram) and average sizes of individual home ranges (linear diagrams) in bank voles differing in their functional status on Lake Ishkul'.

vacant after the disappearance of overwintered animals and, as noted above, performing their function.

In 1977, the seasonal average values of relative abundance reached 34.5 individuals per 100 trap-days; the highest abundance in the marking plot was 52 ind./ha (Fig. 3). The animals of PFG1 were fairly heterogeneous with respect to their origin (the group included representatives of all five cohorts born in the previous year). Upon maturation, both males and

females of PFG1 in that year had the maximum body weight (33.7 g). The shortest life span of some cohorts was also recorded in this group (Olenev, 1982). A fairly large proportion of young of the year (70% in June) reproduced and comprised PFG3 (Olenev, 2002).

In 1981, the highest population density in September reached only 10 ind./ha. All of the three groups were represented throughout the summer season, but in very small amounts (Fig. 3).

Fig. 4. Dynamics of population density (surface diagram) and average sizes of individual home ranges (linear diagrams) in northern red-backed voles differing in their functional status on the Khadyta-Yakha River in 1978.

Fig. 5. Sizes of individual home ranges (seasonal average values) of bank voles differing in their functional status (1975–1977 and 1981) and of northern red-backed voles (1978).

SPATIAL DISTRIBUTION

Figures 3 and 4 show changes in the size of home range of the voles belonging to different functional groups during the breeding seasons of 1975–1977 and 1981, and Fig. 5 shows the averaged home range size in each season. It can be seen that the home range size depends on the functional state of an animal: in any year, the sizes of home ranges were greater in the animals belonging to PFG1 and PFG3 (i.e., reproductive individuals) than in the animals of PFG2.

It is noteworthy that the sizes of home ranges in PFG3 (rapidly growing and maturing young of the year) were greater than in PFG1 (overwintered animals) in only two cases: the first is the restoration of population structure and abundance of the bank vole in the Southern Urals after drought (1976), and the second concerns the northern red-backed vole in the marking plot located in a floodplain meadow (Southern Yamal). In the latter case, northern red-backed voles colonized the biotope where root voles had always been dominant, coming there from the forest biotopes adjoining the marking plot. The abundance of root voles in this plot rapidly decreased throughout the summer of 1978 (Kryazhimskii *et al.*, 1985), which allowed northern red-backed voles to occupy parts vacated by the former species. The home ranges of colonizers expanded during the summer season, which indicated an increase in the number of "vacant places" (Fig. 4).

Thus, in both these cases, the home ranges of young animals proved to be greater than those of overwintered animals due to the increasing availability of vacant areas during the season. The situation with bank voles was explained by the weakening of intrapopulation competition; in the situation with northern red-backed voles, the main role apparently belonged to the weakening of interspecific competition for space.
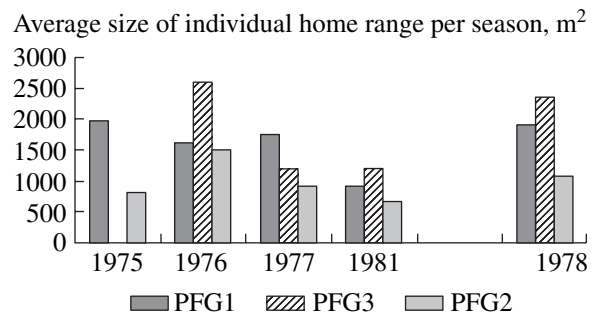
The significance of differences (Table 1) depends not only on the sizes of individual home ranges, but also on the number of animals comprising certain groups in catches. Large differences in the abundance of these groups (Fig. 3) can be seen in the earliest catches, i.e., in the period when young of the year (PFG2 and PFG3) begin falling into traps—and in the latest catches, in the period of mass mortality among reproductive overwintered individuals (PFG-1) and young of the year (PFG3). In the initial period of the breeding season, when the animals of PFG2 and PFG3 begin colonizing the area, their newly formed home ranges significantly differ in size from the previously established home ranges of individuals belonging to PFG1; the first two groups also differ in this parameter, but to a lesser extent. In general, the significance of these differences depends on the dynamics of population density during the season, being higher when reproductive and nonreproductive individuals are compared.

Single captures are apparently explained by the absence of home range. Such individuals have to be more mobile and enter the marking plot largely at random. We made calculations in two variants, with single captures and without them. In the latter variant, the significance of results was retained but became lower, which was additional evidence for the characteristic mobility of immature individuals. The data presented in this paper were obtained with regard to single captures.

The area of home ranges of young bank voles (PFG2 and PFG3) reached a peak in the year of low population density (1976) and was smaller in the year of high density (1977) (Figs. 3, 5). This fact is consistent with the aforementioned concept that the size of home range inversely depends on population density (Okulova *et al.*, 1971). The same trend was also manifested under unfavorable environmental conditions combined with a high spring abundance of overwintered animals, which resulted in the formation of an unusual population structure in the summer–autumn season of 1975. In this year, the home ranges of young bank voles also proved to be rather small (Figs. 3, 5).

Table 1. Significance of differences (Student's *t*-test) between individual home ranges of bank and northern red-backed voles differing in their functional status in individual catches and over the breeding season

| Species, region	Year	Groups	May beginning	May end	June beginning	June end	July beginning	July end	August beginning	August end	September beginning	September end	Total for the season
Bank vole, the Southern Urals	1975	PFG1 and PFG2				0.01*	0.04*	0.08	0.23				1.7e-6*
	1976	PFG1 and PFG2						0.38	0.27	0.44	0.12	0.43	0.37
		PFG1 and PFG3					0.37		0.09	0.35	0.47	0.17	0.04*
		PFG2 and PFG3							0.15	0.28	0.09	0.19	0.02*
	1977	PFG1 and PFG2			2.1e-4*	2.4e-3*	0.07	0.06	0.22				3.1e-6*
		PFG1 and PFG3	3.5e-3*	0.38	0.34	0.05	0.22	0.08	0.46				0.01*
		PFG2 and PFG3			0.03*	0.14	0.13	0.45	0.24				0.05*
	1981	PFG1 and PFG2					0.32		0.42				0.23
		PFG1 and PFG3				0.27	0.46		0.40				0.22
		PFG2 and PFG3					0.29		0.27	0.09	0.18		0.05*
Northern red-backed vole, Southern Yamal	1978	PFG1 and PFG2					0.03*		0.18	0.38			0.03*
		PFG1 and PFG3						0.31	0.25	0.16			0.31
		PFG2 and PFG3							0.30	0.18			0.09

* Differences are significant at $p \leq 0.05$.

The home range sizes estimated from the data on catches in traps distributed over a certain area depends on the probability of trapping, or capture rate, which in turn determines the frequency of trapping for each individual. We calculated the capture rate as the average number of captures of one individual per 100 trap-days. A comparison of functional groups (in all years) by this index showed, as expected, that the animals of reproductively active intrapopulation groups (PFG1 and PFG3) were trapped most frequently. The capture rate for the bank voles whose ontogenetic development followed the second pathway (PFG2 and PFG1) had the lowest value in 1981, at the lowest population density (Fig. 6). Apparently, this is why the estimated sizes of their home ranges in this year proved to be smaller than in other years. The fact that the home range size in a low-density year may be underestimated because of a low capture rate is confirmed by the results of our calculations: when single captures were excluded from analysis, the average sizes of home ranges increased by 400 m^2 for PFG1 and by 800 m^2 for PFG2.

After the death of overwintered individuals (PFG1), an increase in the area of home ranges is recorded in PFG2 (Figs. 3, 4), as young animals have an opportunity to occupy the place of adults in the territorial distribution. In the period of mass mortality among formerly reproductive individuals (PFG1 and PFG3) and before the animals belonging to PFG2 entered wintering, a noticeable expansion of their home ranges was recorded every year (Fig. 3). This could be explained by a decrease in total population density and an increase in the mobility of animals searching for the most favorable habitat for wintering. The same follows from the absence of such an expansion in 1976 (Fig. 3), when the animals involved in reproduction during the breeding season (PFG1 and PFG3) continued to appear in catches until winter.

When the home range areas were compared in males and females representing different ontogenetic pathways, the largest home ranges among overwintered individuals (PFG1, the second pathway) were recorded in males (Table 2). Thus, our data confirmed the widespread concept of a higher mobility of males. In PGF1, the home ranges of males were significantly larger than those of females throughout the breeding season. The same trend was observed in PFG3 (the first ontogenetic pathway), but the significance of the above difference for the entire season was insufficient because of continuing maturation of animals belonging to this group. In PFG2 (young of the year with a retarded growth and development), males and females did not differ in the sizes of home ranges. Thus, in addition to the relationship between the average areas of individual home ranges and the functional state of individuals, we revealed significant differences in the use of available area by animals of different sexes.

The analysis of animal distribution over the marking plot showed that, irrespective of annual variation in
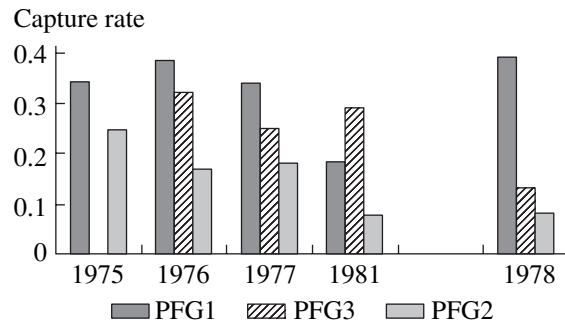
Capture rate

Fig. 6. Capture rates (numbers of captures of one individual per 100 trap-days) of bank voles differing in their functional status (1975–1977 and 1981) and of northern red-backed voles (1978).

population density and the number of captures, the animals were trapped most frequently in the same parts of the plot (indicated by dark shading in Fig. 7). These were the areas rich in the elements of microlandscape that could be used as shelters (fallen trees, abandoned burrows of beavers, stumps, stones, etc.). In the year of high population density, the animals were also caught at open, rocky and swamped sites offering poor shelter. It was mainly the intensity of area use that changed from year to year, whereas the location, configuration, and area of the most preferable habitats remained the same.

Table 2. Average areas of individual home ranges of male and female voles differing in their functional status and significance of differences between them (Student's t-test)

Species, region	Year	PFG	Home range area, m^2		p
			females	males	
Bank vole, the Southern Urals	1975	1	1585	2302	0.05*
		2	950	720	0.07
	1976	1	1570	1749	0.41
		2	1448	1544	0.40
		3	1837	2909	0.08
	1977	1	1331	2045	0.01*
		2	976	867	0.25
		3	1133	1314	0.31
	1981	1	624	1041	0.20
		2	651	674	0.48
		3	829	1547	0.07
Northern red-backed vole, Southern Yamal	1978	1	1446	2495	0.03*
		2	899	1223	0.32
		3	1833	5155	0.31

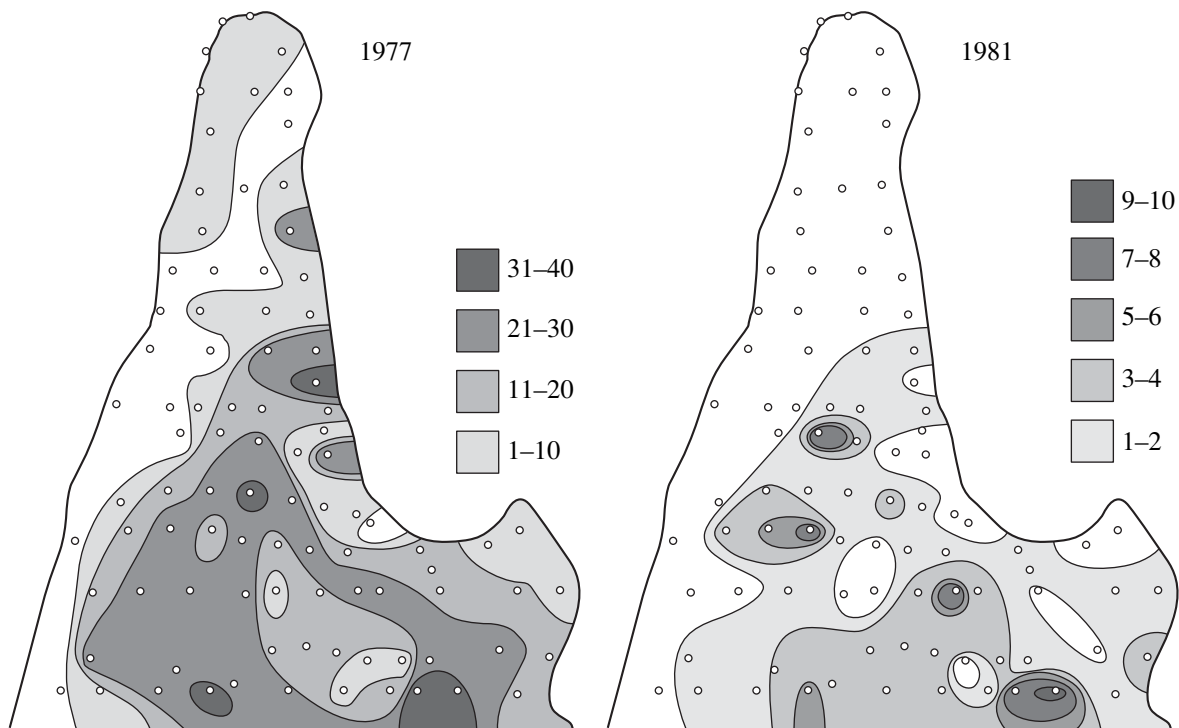* Differences are significant at $p \leq 0.05$.

Fig. 7. Intensity of area use by bank voles in 1977 and in 1981. Gradient shading indicates the number of repeated captures.

CONCLUSIONS

(1) The home range size of bank voles depends on the functional status of individuals, which is determined by their development along one of the two alternative ontogenetic pathways.

(2) The home range size of adult overwintered individuals (PFG1) is the most stable and depend the least on climatic conditions and population density in different years. Home ranges of nonreproductive young of the year (PFG2) are always smaller than those of individuals belonging to other groups. Home ranges of overwintered individuals (PFG1) and reproductive young of the year (PFG3) are similar in size. As overwintered individuals die, reproductive young of the year occupy the places that became vacant.

(3) In autumn, as reproductive individuals (PFG1 and PFG3) disappear, an increase in the home range size of the animals belonging to PFG2 is recorded, which is indicative of their increasing mobility. The sites vacated by the end of the breeding season can be occupied by both juvenile individuals of the dominant species and individuals of other species. This is evidence for both intraspecific and interspecific competition for the habitat area.

(4) Average home range size of males is generally considerably larger than that of females in the groups involved in reproduction (PFG1 and PFG3), whereas no such difference is observed in the group of nonreproductive animals (PFG2).

ACKNOWLEDGMENTS

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