The Spatiotemporal Structure of Rodent Populations in the Steppe Zone of Western Siberia

M. G. Mal'kova, N. A. Pal'chekh, V. V. Yakimenko, and I. V. Kuz'min

Omsk Research Institute of Natural Foci Infections, Ministry of Health of the Russian Federation,
pr. Mira 7, Omsk, 644080 Russia

Abstract—The spatial structure of populations has been studied in two rodent species inhabiting the subzone of meadow steppes of the steppe zone of Omsk oblast: the narrow-sculled vole (*Microtus gregalis* Pall.) and steppe lemming (*Lagurus lagurus* Pall.). Their populations are represented by combinations of territorial family groups whose structure and spatial distribution vary by season depending on population density, the phase of the population cycle, and the status of their members in the population. In the areas cohabited by *M. gregalis* and *L. lagurus*, the pattern of territory use and the rhythm of animal activity during the day depend primarily on their total density: under conditions of low density, the population groups of both species are spatially separated; at increased density, they are distributed with respect to the pattern of daily activity. Both species jointly use part of the territory but at different times of day: *M. gregalis*, mainly at night and in the morning; *L. lagurus*, in the daytime.

Key words: spatial population structure, *Microtus gregalis* Pall, *Lagurus lagurus* Pall., population groups, daily activity.

One of the urgent tasks of modern population ecology is the study of the spatial structure of animal populations, which is necessary not only for determining the species-specific type of territory use and the pattern of intrapopulation relationships between individuals, but also for estimating the role of a certain species in the formation of the spatiotemporal structure of natural foci of many zoonoses. In this context, it is important to study the principles of functioning of the spatial population structure, which represents both a static system of the ordered distribution of individuals over the territory and a dynamic system of their relations with each other and with their environment (Shilov, 1977).

It is known that the spatial population structure is manifested in the ordered distribution of individuals and their groups with respect to certain landscape elements and to each other (Shilov, 1977, 1991; Smirin, 1991). The pattern of the spatial distribution of individuals and their groups over the territory is highly diverse. Numerous observations on different mammalian species, especially murine rodents, indicate that a more or less uniform animal distribution in space can be observed only as an exception, even under relatively homogeneous habitat conditions. As a rule, the groups of individuals form within a population; these are its structural units that provide a basis for the development of adaptive population responses to changes in external and internal conditions. They are referred to as demes (Gilmur and Heslop-Harrison, 1954), parcels (Naumov, 1971), or simply intrapopulation groups (Shilov, 1977),

and it is their existence that provides for the stability of a population as an integrated system. The rodents leading a group mode of life are characterized by the so-called solitary–family type of species population structure (Bashenina, 1962; Smirin, 1991). The intrapopulation structure of these species is based on social groups that may be represented by extended families (a pair or a female with offspring), extended families and unrelated adults, or only unrelated individuals (McGuire and Getz, 1995). The structural territorial population unit in this case is the area occupied by one family or a mixed group including animals of different sexes and ages. Its size actually corresponds to the total size of family feeding grounds. This area usually includes a group of various shelters (nests, burrows, etc.) interconnected by a network of trodden paths to form a "colony." This term is used here conditionally, according to Bashenina (1962, 1977), because most species of small rodents do not form true colonies.

In studying the population structure of small mammals, much attention is given to the ratio of the resident and migrant parts of the population, which largely determines its ecological stability. The populations always include individuals that have no home ranges at a given moment and travel over large distances in a certain locality (dispersing juveniles or adult intrapopulation migrants). Studies performed as early as the 1940s and 1950s (Rall', 1945; Naumov, 1951) have shown that the rodent fauna of a local area consists of animals belonging to two main groups: permanent dwellers of

this area (currently referred to as settled individuals, or residents) and visitors, which are not connected with this area but periodically travel over it (migrants). Both parts of the population have specific biological features and are qualitatively nonuniform with respect to a variety of characters, due to which the resident animals have certain advantages allowing them to hold a certain rank in the intrapopulation hierarchy and dominate over migrants (Shilov, 1977, 1991; Voopstra and Krebs, 1978; Smirin, 1991).

To date, conflicting opinions concerning the problem of residents and migrants and their role in the population structures have been formed. Some authors believe that long-range migrations away from the home range are not typical of small mammals; the observed animal migrations are regarded as accidental events having a minimal effect on the population dynamics and demographic structure (Lidicker, 1975; Fairbain, 1977). Other authors, conversely, consider that small mammals are characterized by considerable migration activity, which is a mechanism for regulating population density; they have put forward various hypotheses emphasizing the potential role of migrants in this regulation and the existence of linear or nonlinear relationship between migration activity and population density (Tamarin, 1977; Shchipanov *et al.*, 1992; Luk'yanov, 1993; Shchipanov, 1996).

MATERIAL AND METHODS

The spatial structure of rodent populations was studied in the meadow-steppe subzone of the steppe zone of Omsk oblast from 1999 to 2001. Studies were performed in the focus of hantavirus (Tula genotype) circulation in the Steppe Complex Reserve (part of the Kurumbel'skaya Steppe, Okoneshnikovskii and Cherlakskii raions). Animal marking on a permanent plot was performed in spring–early summer (in the second ten-day period of June in 1999 and in the second ten-day period of May in 2000 and 2001) and in autumn, in the first (1999) and the second (2000) ten-day periods of September; each time, the work continued for ten days. In addition, trap-line censuses were taken by the conventional method (Kucheruk, 1952) to estimate the relative abundance of small mammals in 1997–2001. The total amount of work was 19 250 trap-days; data on ten species of small mammals, including seven rodent species, were obtained.

A marking plot 3.3 ha in area was established in a lakeside depression south of Lake Ataich'e. Using the mark–recapture method (Naumov, 1951), we marked by finger clipping a total of 430 animals, including 332 *M. gregalis* and 98 *L. lagurus.* Wire-mesh live traps with standard bait (bread with vegetable oil) had an additional chamber for dry grass and food (oats). They were set in the plot in two ways: (1) in groups of five to ten traps around the inhabited animal colonies (May and June 1999–2000; September 1999), and (2) in an area of 2 ha, where the boundaries between colonies

were undetectable because of high animal density, the traps were arranged in a grid pattern (parallel rows of 11 traps, with the distances between the traps and rows being 10 m); in the remaining part of the plot, the traps were set around the colonies (September 2000). The traps were examined twice a day, in the morning (6:00–9:00 a.m.) and in the evening (7:00–9:00 p.m.). Each newly captured animal was assigned a number, weighed, and analyzed for a combination of external characters to determine its species, sex, and age, distinguishing the groups of young of the year (juv or sad) or adult, overwintered individuals (ad or sen). Its involvement in reproduction was determined from the state of genitals (with sad II and ad regarded as mature, and juv, sad I, and sen, as nonreproductive).

These data were analyzed to calculate the ratio of resident and migrant animals, population density, and sex–age composition. Population density was determined as the number of individuals captured in a 1-ha plot during ten days. The animals that were captured no less than four times and lived in the plot for a long time were assigned to the resident group. The migrant group included the animals that stayed in the plot temporarily and were captured one to three times. Calculating the numbers of residents and migrants and performing subsequent data analysis, we did not take into account the animals that were marked during the last three days of work on the marking plot. The daily pattern of animal activity was estimated from the rates of their capture at different times of day (morning–evening). The proportion of morning captures characterized the relative animal activity at night (from 8:00 p.m. to 8:00 a.m.), and the proportion of evening captures, the relative activity in the daytime (8:00 a.m.–8:00 p.m.). The results were processed statistically using conventional methods. In estimating their statistical significance, the following designations were used: $p < 0.95$, the value or the difference between values is nonsignificant; $p \geq 0.95$, 0.99, or 0.999, the value or the difference between values is significant at the corresponding confidence level.

RESULTS

Relative abundance and population density. The plot for studying the spatial structure of rodent fauna was chosen taking into account the biotopic distribution and relative abundance of animals. Throughout the observation period (1997–2001), *M. gregalis* was dominant among small mammals of the Steppe Reserve: its proportion in captures averaged $76.3 \pm 1.7\%$ ($58.3 \pm 2.6\%$ in spring and $77.7 \pm 2.2\%$ in autumn), and average relative abundance varied by seasons from 1.5 individuals per 100 trap-days in spring to 5.2 individuals per 100 trap-days in autumn. Biotopically, *M. gregalis* prefers lakeside basins of salty lakes, which apparently serve as refuges. The population of these rodents in such biotopes proved to be most stable in all seasons: its proportion in the fauna of small mammals ranged from 62.3 to 100%, and its density was 3.8–5.3 times higher

than in other biotopes, varying from 9.1–11.5 ind./ha in spring to 17.0–52.1 ind./ha in autumn ($p > 0.95$). The proportion of *L. lagurus* in the fauna of small mammals of the Steppe Preserve considerably varied from year to year (from single individuals to 20–27% in captures) and, on average, did not exceed 21% ($20.7 \pm 1.7\%$); the abundance of these animals was low: from 0.4 individuals per 100 trap-days in spring to 1.5 individuals per 100 trap-days in autumn. Biotopically, this species prefers lakeside basins of salty lakes, where it can be a codominant of *M. gregalis* in some years, as well as dry grass–herb and feather grass–sheep's fescue meadow steppes. Its proportion among small mammals in the latter types of habitats averaged approximately 20% (21.4 ± 1.7 and $20.3 \pm 5.2\%$, respectively).

The sex–age population structure. In the early summer and autumn of 1999 and in the autumn of 2000, the proportion of migrants in the *M. gregalis* population was 3.1–3.4 times greater than that of resident animals; in the spring of 2000, these proportions were almost equal. Differences in the sex–age structure of the resident and migrant parts of the population were revealed. In June 1999, the *M. gregalis* population was mainly dominated by reproducing overwintered individuals ($63.2 \pm 7.8\%$), with a significant prevalence of females (the sex ratio was 2 : 1; $p > 0.99$). In May 2000, the proportions of overwintered individuals and young of the year in the population did not differ significantly ($p < 0.95$), but juvenile animals were characterized by early sexual maturation and actively participated in reproduction: individuals weighing 7.0–8.5 in the condition of rut or early pregnancy occurred in catches, and the proportion of mature individuals among young of the year (sad II) comprised $75.0 \pm 9.7\%$). The sex ratio in this period was close to 1 : 1, but females significantly prevailed among resident individuals ($75.0 \pm 12.5\%$, $p > 0.95$), and males prevailed among migrants ($73.3 \pm 11.4\%$, $p > 0.95$). In the spring of 2001, only five *M. gregalis* were captured in the marking plot, including two adult females (lactating and pregnant) and three males (two sad II and one ad).

The bulk of the animal population in autumn (September 1999 and 2000) consisted of young animals of the previous summer generations (sad I): their proportions in the *M. gregalis* population were 98.2 ± 1.8 in 1999 and $97.7 \pm 1.1\%$ in 2000. In 1999, the sex ratio in the population was approximately 1 : 1, with almost 10% of individuals participating in reproduction: the proportion of mature animals was $8.9 \pm 3.8\%$ (among young of the year, $7.3 \pm 3.5\%$). In 2000, the sex ratio remained generally the same, but females significantly prevailed among resident animals ($65.7 \pm 8.0\%$, $p > 0.95$), and males prevailed among migrants, although slightly (58.0 ± 4.5, $p > 0.95$). In addition, none of the examined mature males and females was involved in reproduction at the time (apparently, because field studies in this year began later than in 1999). In *L. lagurus*, the spring population in May 2000 consisted of migrants only; they also prevailed in autumn, comprising $94.5 \pm 3.1\%$ of the population. The sex ratio among migrants was unstable: in spring, it was 1 : 1; in autumn, the proportion of males was 2.5 times greater than that of females ($71.2 \pm 6.3\%$ vs. $28.8 \pm 6.3\%$). The autumn population of *L. lagurus* consisted of immature young of the year (sad I) by 89–100%, and all mature individuals did not reproduce, as in *M. gregalis*.

Spatial distribution of individuals. In June 1999, only *M. gregalis* voles were found in the marking plot. Of 26 recorded settlements (colonies), 14 proved to be inhabited. The greater part of animals ($71.1 \pm 7.4\%$) was captured in the eastern part of the plot, where they formed several territorial groups with an area of 0.01–0.08 ha; one resident colony was in the northern part of the plot (figure). These groups included animals from one colony or from several colonies located at a distance of 20–40 m from each other (Table 1, figure). Each group consisted of three to ten animals; one or two of them were resident females, which were captured four to seven times and always in the same area. The remaining individuals were found in catches once or, less frequently, twice; some of them were incidentally captured beyond the areas occupied by groups. Among them, young of the year and adult individuals occurred at an equal ratio. The distance between the conventional group centers (sites of the greatest animal concentration) varied widely, averaging approximately 80 m (Table 1).

In May 2000, two rodent species, *M. gregalis* and *L. lagurus*, occurred in the plot. Their total density was 16.1 ind./ha. In the plot and at a distance of 40–60 m from its conventional boundaries, we found 42 colonies with traces of rodent life activity (24 in the plot and 18 beyond it). However, the animals were captured in only 23 colonies ($54.8 \pm 7.7\%$) located in the central, western, and northwestern parts of the study area. Narrow-sculled voles used 16 colonies (seven in the plot and nine beyond it) that formed six territorial groups. Steppe lemmings used seven colonies (five in the plot and two beyond it), forming three local groups. Virtually all animal groups were monospecific (five *M. gregalis* and two *L. lagurus*) and spatially separated. No animal movement between them was recorded (figure). In the central part of the plot, individuals from two groups of both species were recorded in the same colony but at different times: initially, two resident *M. gregalis* voles were regularly captured there, and *L. lagurus* appeared in catches only after their death (five animals of this species, all of them being migrant young of the year, were captured 11 times). In the neighboring colony, the catches also included individuals of both species, but mainly of *M. gregalis* (nine captures of four animals, of which one was a resident female); *L. lagurus* occurred singly (two captures of two migrants).

Thus, almost all animal colonies on the plot in this period were monospecific, and single captures of individuals of another species in them were separated in
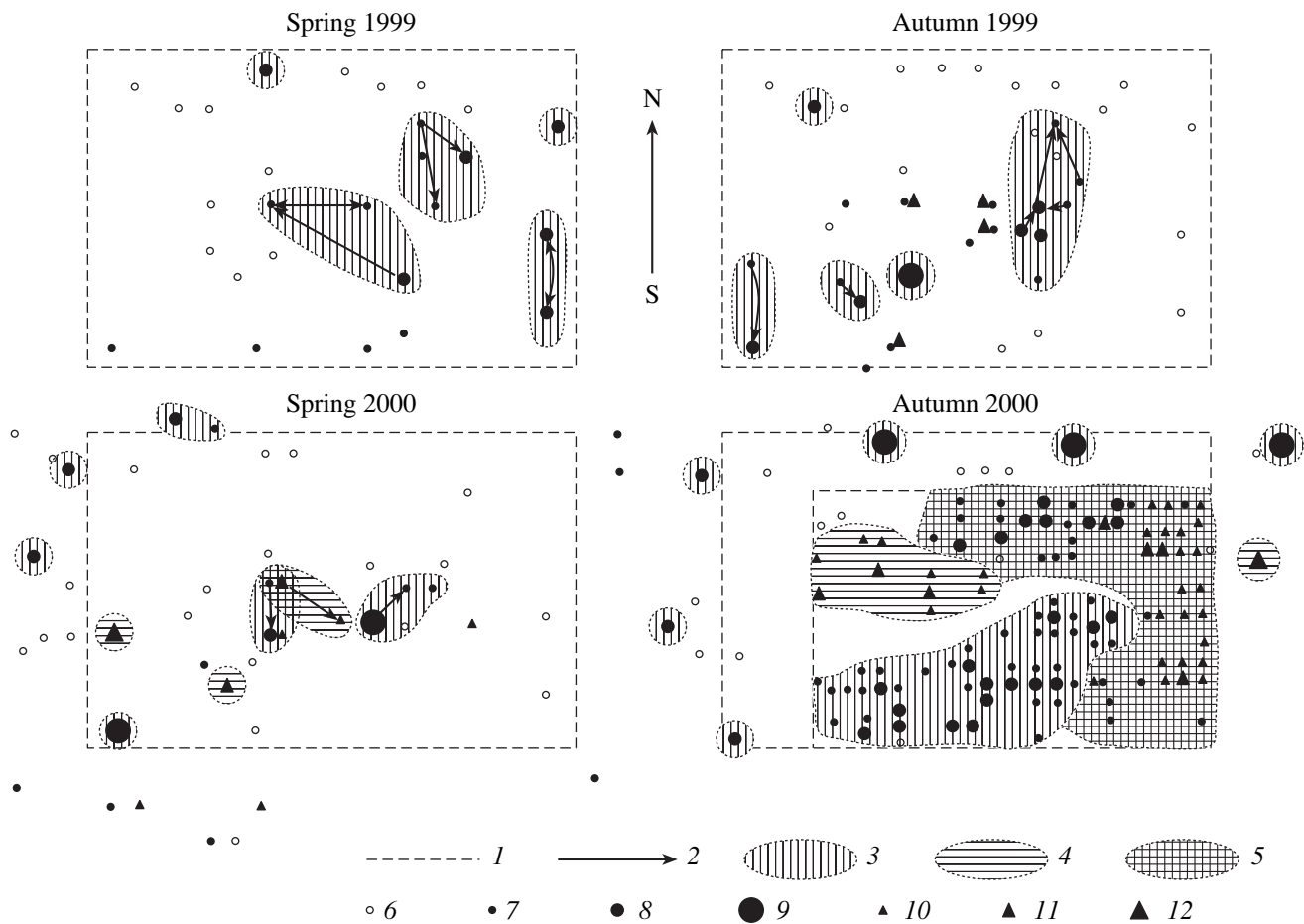
The spatial distribution of *M. gregalis* and *L. lagurus* in the steppe zone of Omsk oblast (according to marking data): (*1*) boundary of the marking plot; (*2*) directions of animal migrations; (*3*) groups of *M. gregalis*; (*4*) groups of *L. lagurus*; (*5*) territory used jointly; (*6*) uninhabited animal colonies; (*7–9*) points of *M. gregalis* captures: (*7*) 1–3 animals, (*8*) 4–6 animals, (*9*) more than 6 animals; (*10–12*) points of *L. lagurus* captures: (*10*) 1–3 animals, (*11*) 4–6 animals, (*12*) more than 6 animals. In the zone jointly used by both species (autumn 2000), symbols indicate the points where the animals of only one species were captured.

time. The average area of *M. gregalis* groups and the number of animals in them did not differ from those in June 1999, but the distance between them was greater by a factor of 1.5 (the difference is significant, $p = 0.95$; Table 1). Among resident members of the groups, $72.7 \pm 13.4\%$ were females (half of them sad II). None of the animals marked in the previous season (September 1999) were found on the plot.

In May 2001, only five resident rodent colonies were recorded on the marking plot and in close proximity to it; four of the five marked *M. gregalis* were captured in the colonies situated in the western part of the plot (one or two times in four colonies each).

The territorial groups of *L. lagurus* in the spring of 2000 included five to seven animals. They had areas of 0.01 to 0.05 ha and, on average, did not differ from the groups of *M. gregalis* in this parameter, but the distance between them was significantly greater ($p > 0.95$). The groups of *L. lagurus* were located 40–120 m (on average, 78.0 ± 16.4 m) away from the groups of *M. gregalis*. As was already mentioned, steppe lem-

mings recorded in this period, according to the number of captures (1–3), were classified as migrants, but they did not occur beyond their own groups (figure).

In September 1999, the population density of *M. gregalis* increased by a factor of 1.5, compared with that in June, and reached 17.0 ind./ha. In addition, four individuals of *L. lagurus* were recorded on the plot in the same period (population density 1.2 ind./ha). Of 35 individuals recorded earlier (in June 1999), only one adult female was captured. Similar to the situation in June, *M. gregalis* used the area of the plot nonuniformly: it was captured in only 19 out of 28 colonies recorded in this period (Table 1). Most *M. gregalis* voles ($42.9 \pm 6.6\%$) concentrated in three groups with an area of 0.01–0.04 ha in the southwestern part of the plot; one-third of them ($32.1 \pm 6.2\%$) formed the largest territorial group with an area of 0.19 ha in the eastern part of the plot, and only $7.1 \pm 3.4\%$ of individuals were captured in a colony located in its northwestern part (figure). Within groups, 4–18 juvenile animals of the same age group were recorded. These were mainly

Table 1. Characteristics of territorial groups in *M. gregalis* and *L. lagurus* according to marking data (1999–2000)

Indices	M. gregalis				L. lagurus	
	June 1999	September 1999	May 2000	September 2000*	May 2000	September 2000*
Population density, ind./ha	11.5	17.0	10.0	74.0	6.1	34.0
Percentage of inhabited colonies, or percentage of territory used by animals	53.8 ± 9.8 –	67.9 ± 9.2 –	38.1 ± 7.5 –	– 55.6 ± 3.5	16.7 ± 5.8 –	– 32.9 ± 3.3
Number of groups	5	5	6	None	3	None
Group area, ha	0.03 ± 0.01 (0.01–0.08)	0.06 ± 0.03 (0.01–0.19)	0.05 ± 0.02 (0.01–0.15)	–	0.02 ± 0.01 (0.01–0.05)	–
Distance between groups, m	79.5 ± 12.2 (30–150)	90.5 ± 11.1 (35–165)	116.0 ± 9.9 (40–160)	–	73.3 ± 11.1 (60–100)	–
Number of individuals in a group	6.6 ± 1.3 (3–10)	9.2 ± 1.7 (4–18)	7.2 ± 1.4 (4–13)		6.0 ± 0.5 (5–7)	
Number of resident individuals in a group	1.2 ± 0.2 (1–2)	1.6 ± 0.7 (0–4)	2.6 ± 0.7 (2–6)	–	– –	–

* Data on the area where the traps were arranged as a 10×10-m grid.

immature young of the year, which included no more than two resident individuals. No captures of animals beyond their own groups were recorded. The distance between the centers of the *M. gregalis* groups averaged approximately 90 m, as in other seasons.

We failed to reveal any trends in the distribution of *L. lagurus* over the marking plot in September 1999, because we recorded only seven captures of four individuals of this species (one to two captures in four colonies each). One male *L. lagurus* marked in this season was captured once in May 2000 beyond the marking plot.

In September 2000, the total population density of rodents of both species throughout the plot increased by a factor of 4.5 and reached 72.7 ind./ha (52.1 ind./ha in *M. gregalis* and 20.6 ind./ha in *L. lagurus*). Of animals marked earlier (May 2000), only four animals were encountered: three *M. gregalis* (one male sen and two female sad II) and one *L. lagurus* (male sad II). In the most densely populated part of the plot, which was completely dug up by animals, the traps were arranged in a 10×10-m grid, as we failed to distinguish the boundaries between individual colonies. Its area was 2 ha, and the total animal density in it reached 108 ind./ha (74.0 ind./ha in *M. gregalis* and 34.0 ind./ha in *L. lagurus*).

The analysis of animal distribution in this area and around it, within the boundaries of the marking plot (3.3 ha), showed that most of the *M. gregalis* population (70.3 ± 3.8% of animals) in the "grid area" concentrated mainly in its southern part; nearly one-third of the *L. lagurus* population (30.9 ± 5.6%) was captured only in the western and northwestern parts; in the northern and northeastern parts, there was a zone jointly used by both species, with *L. lagurus* occurring in almost half of the traps (49.2 ± 6.2%) (figure). The rodents of both species used 88.9 ± 2.2% of the plot, with 32.8 ± 3.3% accounted for by the zone of "overlap. Beyond the "grid area," seven isolated animal colonies were recorded. All of them were monospecific: catches in six colonies located in the northwestern part of the plot included only *M. gregalis* (five to nine animals each); in the colony located on the eastern side, only *L. lagurus* (six animals). No rodents from these colonies occurred in traps arranged in a grid; nor was their movement from one colony to another recorded, although the distance between the neighboring settlements, as well as between them and the extreme trap lines, did not exceed 60 m.

Daily animal activity. In *M. gregalis*, nocturnal activity prevailed throughout the observation period: the proportion of animals captured in the morning varied from 53.1 to 63.6%, averaging 57.2 ± 1.9% ($p > 0.999$; Table 2). This trend was characteristic of both residents and migrants. In the autumn of 2000, however, animals from the "grid area" proved to differ in this parameter: nocturnal activity prevailed only in resident animals but not in migrants. In six isolated colonies, no differences in the daily activity of voles were revealed.

In *L. lagurus*, no differences with respect to the period of animal activity were recorded in the spring of 2000; in autumn, however, diurnal activity significantly prevailed in migrants (the data on residents were insufficient for analysis). In one isolated colony, the animals were captured uniformly in the morning and in the evening. On the whole, the frequency of morning captures of *M. gregalis* in different seasons (on average, 63.1 ± 3.6% in spring and 55.2 ± 2.2% in autumn) was

Table 2. Dynamics of daily activity of narrow-sculled voles (*M. gregalis*) and steppe lemmings *L. lagurus*)

Characteristics of population	M. gregalis				L. lagurus	
	June 1999	May 2000	September 1999	September 2000*	May 2000	September 2000**
Total number of animals	34	27	53	148	19	68
Population density, ind./ha	11.5	10.0	17.0	74.0	6.1	34.0
Total number of captures	77	107	117	363	35	113
Number of morning captures	49	67	73	190	15	47
Proportion of morning captures, %	63.6 ± 5.5	62.6 ± 4.7	62.4 ± 4.5	52.3 ± 2.6	42.8 ± 8.4	41.6 ± 4.6
Number of evening captures	28	40	44	173	20	66
Proportion of evening captures, %	36.4 ± 5.5	37.4 ± 4.7	37.6 ± 4.5	47.7 ± 2.6	57.2 ± 8.4	58.4 ± 4.6
Td* (morning–evening) total	$3.5\,(p > 0.999)$	$3.8\,(p > 0.999)$	$3.9\,(p > 0.999)$	$1.2\,(p < 0.95)$	$1.2\,(p < 0.95)$	$2.6\,(p = 0.99)$
Resident animals						
Number	9	12	13	30	–	3
Number of captures	41	76	53	151	–	13
Number of morning captures	26	46	34	84	–	5
Proportion of morning captures, %	63.4 ± 5.7	60.5 ± 5.8	64.2 ± 6.6	55.6 ± 4.0	–	38.5 ± 13.5
Number of evening captures	15	30	19	67	–	8
Proportion of evening captures, %	36.6 ± 5.7	39.5 ± 5.8	35.8 ± 6.6	44.4 ± 4.0	–	61.5 ± 13.5
Td (morning–evening) for residents	$3.3\,(p > 0.99)$	$2.6\,(p = 0.99)$	$3.1\,(p > 0.99)$	$2.0\,(p > 0.99)$	–	$1.2\,(p < 0.95)$
Migrants						
Number	25	15	40	110	19	52
Number of captures	32	31	60	206	34	88
Number of morning captures	21	21	36	104	14	33
Proportion of morning captures, %	65.6 ± 8.4	67.7 ± 8.4	60.0 ± 6.3	50.2 ± 3.5	41.2 ± 8.4	37.5 ± 5.2
Number of evening captures	11	10	24	102	20	54
Proportion of evening captures, %	34.4 ± 8.4	32.3 ± 8.4	40.0 ± 6.3	49.8 ± 3.5	58.8 ± 8.4	62.5 ± 5.2
Td (morning–evening) for migrants	$2.6\,(p > 0.95)$	$3.7\,(p = 0.999)$	$2.2\,(p > 0.95)$	$0.1\,(p < 0.95)$	$1.5\,(p < 0.95)$	$3.4\,(p > 0.99)$

 * Td, significance of difference between the proportions of captures.
** Data on the area where the traps were arranged as a 10×10-m grid.

1.3–1.5 times higher, and that of evening captures (on average, $36.9 \pm 3.6\%$ in spring and $44.8 \pm 2.2\%$ in autumn) was 1.3–1.6 times lower than the corresponding frequencies of *L. lagurus* captures ($0.95 < p > 0.999$; Table 2).

DISCUSSION

This study provided data for analyzing the spatiotemporal structure of populations of two rodent species belonging to the steppe faunistic complex— *M. gregalis* and *L. lagurus*—in the subzone of meadow steppes of the steppe zone of Omsk oblast.

The *M. gregalis* population in the study area was represented by a combination of territorial groups, which were apparently the family groups. It is known, for instance, that the presence in summer populations of intra- and interfamily animal groups providing a kind of mutual assistance in the period of breeding and rearing the progeny is characteristic of many vole species of the genus *Microtus* (Lambin, 1994). Animals belonging to the same family or kin group can be indirectly estimated from the sex–age composition of these

groups in different seasons of the year: in spring and early summer, each group includes one or two resident adult females and dispersing juveniles (probably, the offspring of these females); in autumn, they comprise young of the year belonging to the same age group (the previous summer generation) dominated by immature individuals, which will apparently remain in the same place for wintering. The formation of wintering rodent communities by individuals of the late-summer and late-autumn generations is an important characteristic of their adaptive behavior (Bashenina, 1977). We revealed no seasonal changes in the area occupied by territorial–family groups: it varied widely (from 0.01 to 0.19 ha) but, on average, did not exceed 0.06 ha. The distance between the conventional centers of these groups also remained virtually unchanged. As to the daily pattern of animal activity, *M. gregalis* voles were significantly more active at night (both residents and migrants). However, at a high population density (autumn 2000), nocturnal activity prevailed only in resident individuals, while the activity of migrants was more or less uniform. This situation apparently reflects a certain adaptive mechanism for relieving tension in the intraspecific relations of voles.

The analogous type of intraspecific relations and the "territorial–family" pattern of spatial distribution was observed in *L. lagurus*. The steppe lemming is a stenotopic species, and its populations, unlike those of *M. gregalis*, have a low ecological flexibility; therefore, it is ecologically more vulnerable to the effects of adverse environmental factors (Gladkina, 1980). At the sites of cohabitation with *M. gregalis* in the study area, the pattern of territory use and the rhythm of diurnal activity of *L. lagurus* changed depending primarily on the level of total animal density. When the density of both species was low (the spring of 2000), the capacity of the territory was sufficient for allowing spatial separation of the population groups of different species. Upon a significant increase in the total population density (the autumn of 2000), we failed to distinguish distinctly isolated family groups of either species; however, some specific features of animal distribution over the marking plot were revealed.

In the "grid area," where the total density of both species reached 108 ind./ha, three zones of animal distribution were formed: the zone inhabited mainly by *M. gregalis* in the southern part of the plot (it accounted for 39.4 ± 3.5 of its total area), the zone where *L. lagurus* prevailed (the western and northwestern parts, $16.7 \pm 2.7\%$), and the zone cohabited by both species (the northern and northeastern parts, $32.8 \pm 3.3\%$). The latter was used by animals nonuniformly: *L. lagurus* was found more frequently in its eastern part, and *M. gregalis*, in the northern part. In addition, under conditions of high animal density, insufficient spatial separation of individuals of these ecologically related species was counterbalanced by their redistribution with respect to the period of activity. Both species used the territory jointly but at different times of day:

M. gregalis was active mainly at night and in the morning, and *L. lagurus*, in the daytime. Apparently, this mechanism is ecologically more important for the steppe lemming, whose population in the corresponding period consists mainly of dispersing juveniles (migrants).

In addition, an interesting feature was noted for both species: in any season, the catches made in the plot had almost no animals marked in the previous season. Such animals occurred singly, and their proportion did not exceed 2%. It appeared as if an almost complete renewal of the population took place in both species. The factors responsible for this phenomenon are as yet unknown. It may well be, however, that parents leave their home range to the growing juveniles, which are the reproductive reserve of the population for the next breeding season. A similar behavioral strategy has been observed, for instance, in the Siberian and collared lemmings: their females disperse at the last stages of pregnancy, and juveniles from the previous litter remain near the maternal burrow (Danilov, 2000).

On the whole, the structure and spatial distribution of *M. gregalis* and *L. lagurus* in the steppe zone of Omsk oblast vary by season depending on the population density, population cycle, and the intrapopulation status of animals. The results of this study provide evidence for species-specific features in the spatial distribution of individuals and seasonal differences in the sex ratio and the structure of different age groups in populations of *M. gregalis* and *L. lagurus*, which reflect the alternation of phases in their population cycles.

REFERENCES

Bashenina, N.V., *Ekologiya obyknovennoi polevki* (Ecology of the Common Vole), Moscow: Mosk. Gos. Univ., 1962.

Bashenina, N.V., *Puti adaptatsii myshevidnykh gryzunov* (Adaptation Pathways in Murid Rodents), Moscow: Nauka, 1977.

Boonstra, R. and Krebs, C.J., Pitfall Trapping of *Microtus townsendii, J. Mammal.*, 1978, no. 59, pp. 136–148.

Danilov, A.N., Dynamics of Abundance and Spatial Distribution of Tundra Rodents in Southern Yamal, *Abstract of Cand. Sci. (Biol.) Dissertation*, Ekaterinburg: Inst. Ekologii Rastenii i Zhivotnykh Ural. Otd. Ross. Akad. Nauk, 2000.

Fairbain, D.J., The Spring Decline on Deer Mice: Death or Dispersal?, *Can. J. Zool.*, 1977, no. 55, pp. 84–92.

Gilmur, J.S. and Heslop-Harrison, J., The Deme Terminology and Units of Micro-Evolutionary Change, *Genetics*, 1954, vol. 27, no. 2, pp. 147–161.

Gladkina, T.S., Specific Features of Adaptive Variations in the Common Vole and Steppe Lemming and Prognosis of Their Distribution, *Gryzuny. Mat–ly V Vsesoyuznogo soveshch.* (Rodents. Proc. 5th All-Union Conference), Moscow, 1980, pp. 172–174.

Lambin, X., Territory Acquisition and Social Facilitation by Litter-Mate Townsend's Voles (*Microtus townsendii*), *Ethol. Ecol. Evol.*, 1994, vol. 6, pp. 213–220.

Lidicker, W.Z., Jr., The Role of Dispersal in the Demography of Small Mammals, in *Small Mammals: Their Production and Population Dynamic*, London, 1975, pp. 103–128.

Luk'yanov, O.A., Investigation of the Density of Resident and the Flow of Migrating Individuals in Populations of Small Mammals, *Ekologiya*, 1991, no. 6, pp. 36–47.

Luk'yanov, O.A., Analysis of Migration Processes in the Populations of Small Mammals, *Ekologiya*, 1993, no. 1, pp. 47–62.

McGuire, B. and Getz, L.L., Communal Nesting in Prairie Voles (*Microtus ochrogaster*): An Evaluation of Costs and Benefits Based in Patterns of Dispersal and Settlement, *Can. J. Zool.*, 1995, vol. 73, no. 2, pp. 383–391.

Naumov, N.P., A New Method for Studying the Ecology of Small Forest Rodents, in *Fauna i ekologiya gryzunov* (Fauna and Ecology of Rodents), Moscow, 1951, vol. 4, pp. 3–21.

Naumov, N.P., Spatial Structure of Mammalian Species, *Zool. Zh.*, 1971, vol. 50, no. 7, pp. 965–979.

Rall', Yu.M., The Dynamic Density of Rodents and Some Methods for Its Study, *Byull. Mosk. O–va Ispyt. Prir., Otd. Biol.*, 1945, vol. 50, nos. 5–6, pp. 62–64.

Shchipanov, N.A., Functional Organization of a Population (An Example of Small Mammals), *Abstract of Doctoral (Biol.) Dissertation*, Moscow, 1996.

Shchipanov, N.A., Oleinichenko, V.Yu., and Kasatkin, M.V., The Functions of Intrapopulation Spatial Structures and Synanthropism of Small Mammals, in *Sinantropiya gryzunov i ogranichenie ikh chislennosti* (Synanthropy of Rodents and Control of Their Populations), Moscow, 1992, pp. 88–110.

Shilov, I.A., *Ekologo-fiziologicheskie osnovy populyatsionnykh otnoshenii u zhivotnykh* (Ecophysiological Principles of Population Relationships in Animals), Moscow: Mosk. Gos. Univ., 1977.

Shilov, I.A., The Principles of Intrapopulation Organization and Biological Importance of Spatial–Ethological Structure, in *Struktura populyatsii u mlekopitayushchikh. Ser. Voprosy teriologii* (Population Structure in Mammals. Problems in Theriology Book Series), Moscow, 1991, pp. 5–20.

Smirin, Yu.M., The Role of Population Structures in Biocenotic Relationships, in *Struktura populyatsii u mlekopitayushchikh. Ser. Voprosy teriologii* (Population Structure in Mammals. Problems in Theriology Book Series), Moscow, 1991, pp. 116–150.

Tamarin, R.H., Dispersal in Island and Mainland Voles, *Ecology*, 1977, vol. 58, pp. 1044–1054.