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The Structure of Narrow-Skulled Vole (*Microtus gregalis* Pall.) Colonies in Western Siberia

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Abstract—The structure of *Microtus gregalis* colonies was studied in different parts of the species range in Western Siberia, both in the south (Omsk oblast) and in the north (Yamalo-Nenets Autonomous Area), in 1999 and 2000. The colonies studied in the steppe zone of Omsk oblast, southern tundras of the Yamal Peninsula, and mountain tundras on the northern slopes of the Polar Urals prove to have some common structural features. In Omsk oblast, seasonal variation in the area of colonies and the number of entrances to the burrows was revealed, although the general structure of colonies (the pattern of tunnels and location of the nest and storage chambers) was largely the same in spring and autumn.

Key words: *Microtus gregalis* Pall., colonies, variability, colony structure.

Narrow-skulled voles (*Microtus gregalis* Pall.) usually live in colonies consisting of individual burrows connected by paths and underground tunnels. As a rule, they contain a nest chamber and a chamber for storing food. The burrows are made in the ground covered with a tough sod formed over many years. Specialists differ in their opinions about the structure of *M. gregalis* burrows in different parts of the species range (Naumov, 1948; Novikov, 1949; Ognev, 1950; Bashenina, 1977; Kucheruk, 1983). A family of rodents occupying a group of shelters (nests, burrows, refuges, etc.) integrated in a single complex forms a colony. The colonies of *M. gregalis* have one or several nest chambers surrounded by smaller burrows with or without storage chambers. The burrows and foraging grounds are usually interconnected by trodden paths with numerous feeding places along them. The openings of burrows bear signs of regular use by the voles (Naumov, 1949). The colony area depends on the distance to which the foraging voles move. Following Bashenina (1962), we apply the term "colony area" to the zone occupied by all burrows of the same family (including the nests, storage chambers, and shelters), irrespective of the number of generations living together, and the network of paths between them (i.e., the feeding grounds). Both the radius of foraging and the entire colony area vary depending on habitat conditions.

Bashenina (1977) has reduced the diversity of burrows to three types: shelters, shelter–storage burrows, and nests. The burrows of *M. gregalis* are of the last type. Gromov and Polyakov (1977) distinguish permanent and temporary burrows, on the one hand, and main and accessory burrows, on the other hand. The permanent burrows have a varying number of entrances to the underground nest; the accessory burrows are connected to them by tunnels or paths; in the aggregate, all burrows form a colony. In addition to the inhabited nest, a colony may also contain abandoned nests. Kucheruk (1983) considers that self-made shelters—burrows—are most widespread in rodents, applying the term "burrow" to any hole (tunnel) dug or gnawed by an animal in the substrate if the hole is at least five times longer than the animal's body. A burrow can have one or several openings on the ground surface; in the latter case, they must be interconnected by a system of underground tunnels. Several burrows lacking underground connections but interlinked by paths on the ground surface are defined as a system of burrows, or a settlement. This author distinguishes several structural types of burrows in voles: the burrows without chambers, the burrows with chambers but without the nest, the nest burrows without storage chambers, the nest burrows with storage chambers, and the nest burrows with a system of branching tunnels in the upper ground layer that usually have no openings on the surface. The rodents that remain active in winter, including *M. gregalis*, have complex burrows with the nests, storage chambers, and a number of openings on the ground surface. According to Kucheruk (1983), there is no apparent seasonal variation in the structure of burrows, but an increase in animal density leads to the enhancement of burrowing activity in general.

Microtus gregalis voles inhabit open landscapes in different zones, from desert steppes to the flatland and mountain tundras and Alpine meadows. Western Siberia is inhabited by two subspecies of these voles: *Microtus gregalis gregalis* Pall. (the Western Siberian narrow-skulled vole), whose range extends from the

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Table 1. Basic parameters of *Microtus gregalis* colonies in the steppe zone of Omsk oblast (1999–2000)

Parameter	Spring (May–June)	*n*	Autumn (September)	*n*
Average area of a colony, m^2	29.5 ± 4.3	5	3.4 ± 0.8	11
Average depth of underground tunnels, cm	8.4 ± 0.6	100	9.4 ± 0.6	220
Average number of entrances per colony	57.8 ± 18.7	289	19.1 ± 2.7	205
Size of new nest, cm	16.5 × 16.5–25 × 30	3	11 × 12–19 × 22	12
Size of old nest, cm	10 × 14–16 × 20	7	12 × 15–18 × 21	8
Depth of location of new nest, cm	16.6 ± 3.1	3	21.7 ± 3.6	12
Depth of location of old nest, cm	11.6 ± 1.2	7	18.0 ± 3.6	8

middle and southern Ural region eastward throughout the Western Siberian Plain and southward to Karaganda, and *Microtus gregalis major* Ognev (the large narrow-skulled vole), which inhabits the Yamal Peninsula and the Northern Urals (Ognev, 1950; Gromov and Polyakov, 1977; Balakhonov, 1978; Lobanova and Balakhonov, 1981; Balakhonov and Shtro, 1995). The narrow-skulled vole living in the tundra retains some ecological features indicative of its steppe origin. In particular, the animals build deep burrows, which drastically restrict the range of biotopes suitable for this species and, therefore, its spread in the tundra (Kucheruk, 1959). In general, the number of natural shelters for *M. gregalis* voles in the steppe and tundra zones is limited, and their distribution largely depends on the presence of tough sod formed over many years.

MATERIAL AND METHODS

The structure of *M. g. gregalis* and *M. g. major* colonies was studied in different parts of the species range, both in the south (Omsk oblast) and in the north of Western Siberia, in the Yamalo-Nenets Autonomous Area (YNAE). In Omsk oblast, studies were performed in the steppe zone, in the State Steppe Wildlife Sanctuary (Okoneshnikovskii and Cherlakskii raions), both in spring (May–June 1999–2000) and autumn (September 2000). Sixteen colonies excavated in this region were located in depressions near salt lakes and in the meadow steppe. In the YNAE, studies were performed in the tundra zone—in southern tundras of the Yamal Peninsula (Yamal’skii raion) and mountain tundras on the northern slopes of the Polar Urals (Nyavape Ridge, Priural’skii raion)—in August and September 2000. Thirteen colonies were excavated: five in the southern Yamal Peninsula (meadows in the Khatyda-Yakha River floodplain) and eight in the Polar Urals (dwarf-birch hummocky tundras). On the whole, 29 colonies were studied.

The colonies were excavated by the method described by Novikov (1949), taking into account that the colonies of murine rodents consist of both underground components (entrances, burrows proper, nests, and storage chambers) and surface components (feeding places, paths, and nests made under the snow). The area of a colony was measured as the area of a polygon formed by the lines connecting the entrances located farthest away from its center. For each colony, we determined the number of entrances, the type of the nest and the depth of its location, and the depth, length, and pattern of underground tunnels. Attention was also paid to the availability of natural shelters and the surface components of the colony (paths and feeding places).

RESULTS AND DISCUSSION

The steppe zone of Omsk oblast. The area of excavated *M. g. gregalis* colonies varied from 20.2 to 41.6 m^2 in spring and from 0.4 to 8.6 m^2 in autumn; i.e., the average colony area was 8.7 times greater in spring than in autumn ($p > 0.999$) (Table 1). The peripheral tunnels were relatively close to the surface (at a depth of 5–7 cm), whereas the central tunnels sometimes descended near the nest to a depth of 12–17 cm. Bashenina (1962) described such descents in *Microtus arvalis* burrows. The average depth of tunnels in spring and autumn was the same (Table 1). The number of entrances varied widely but was significantly greater in spring: 25–126 (on average, 57.8), compared to 7–32 (on average, 19.1) in autumn ($p > 0.95$). Each colony excavated in spring or autumn had two or three peripheral storage chambers 85.9 to 376 cm^2 in volume (Fig. 1). They contained the leaves or thin stems of grasses or, less frequently, dicots that were accurately cut into equal fragments (approximately 10 cm long) and arranged in neat stacks. There were no seeds. The feeding places were located at sites with a dense grass stand, either in the colony or near it (1–2 m away from the peripheral entrances), and were connected to the burrows through a network of trodden paths.

Yamalo-Nenets autonomous area. The areas of the colonies excavated in the southern Yamal Peninsula and the Polar Urals did not differ statistically ($p < 0.95$): 0.7–11.8 and 0.7–7.8 m^2, respectively. Underground tunnels of the colonies were deeper in the dwarf-birch hummocky tundras of the Polar Urals than in the floodplain meadows of southern Yamal ($p > 0.95$). The numbers of entrances to the burrows excavated in autumn were similar ($p < 0.95$): 6–24 in the floodplain mead-

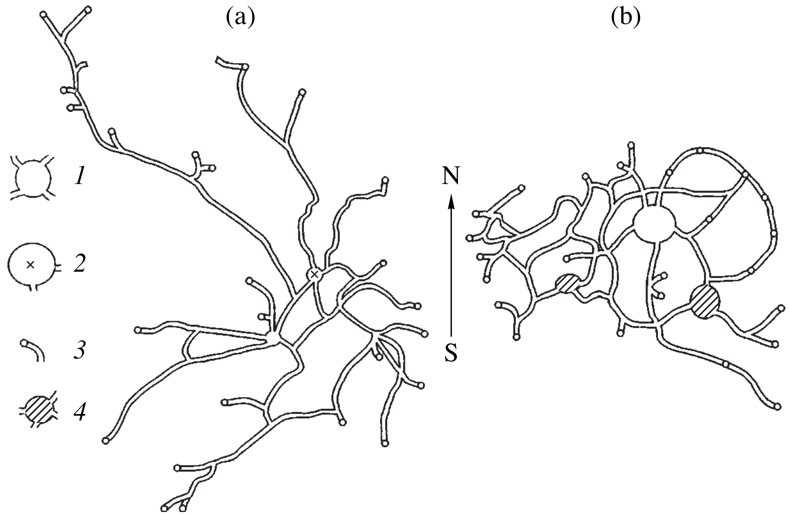

Fig. 1. Colonies of *Microtus gregalis* voles in the steppe zone of Omsk oblast (a) in spring (scale 1 : 60) and (b) in autumn (scale 1 : 30): (*1*) new nest, (*2*) old nest, (*3*) tunnels with entrances, (*4*) storage chamber.

ows of Yamal and 8–29 in the lowland and mountain tundras of the Polar Urals, averaging about 17 in both cases. Storage chambers (one to three per colony) were found only in the dwarf-birch hummocky tundras. They had a very large size (675–18088 cm^3) and were located either at the periphery of the colony or closer to its center (Fig. 2b). Some chambers were new and empty, and some were full of plant roots and rhizomes.

Both in the steppes of Omsk oblast and in the YNAO, the nest chamber in the excavated colonies was usually in the center and had a simple structure (Figs. 1, 2). A freshly made burrow had one nest chamber; the burrows used for a long time additionally had one or two old (abandoned) nest chambers. The density of tunnels increased in the vicinity of the nest, which was shaped like a sphere flattened on the top. In the steppe zone, the size and depth of new and old nests recorded in different seasons were similar (Table 1). In dwarf-birch hummocky tundras of the Polar Urals, new nests ($p > 0.95$) were located deeper than in the floodplain meadows of Southern Yamal, whereas the depth of old nests was almost the same (Table 2). The average sizes of new and old nests and the location of new nests in southern Yamal were similar to those in the steppe zone; in the Polar Urals, new nests were located significantly deeper than in the steppe zone ($p > 0.95$).

Analyzing the structure of *M. gregalis* colonies in the south (the steppe zone) and the north (the tundra zone) of Western Siberia, we revealed the following features.

In Omsk oblast, *M. g. gregalis* voles established mostly compact colonies at meadow-steppe sites near the lakes. Their general structure (the pattern of tunnels, location of the nest and storage chamber, etc.) was largely the same in spring and autumn, but the area of colonies and the number of entrances obviously varies from season to season (Table 1). The average area of colonies was smaller in autumn than in spring. This could be attributed to the dispersal of young animals and the formation of new colonies. Thus, young of the year were absolutely dominant (97.7 ± 1%) among the animals captured near new nest burrows in the autumn of 2000.

In the YNAE, the colonies of *M. g. major* colonies in the floodplain meadows near the Khadyta River were

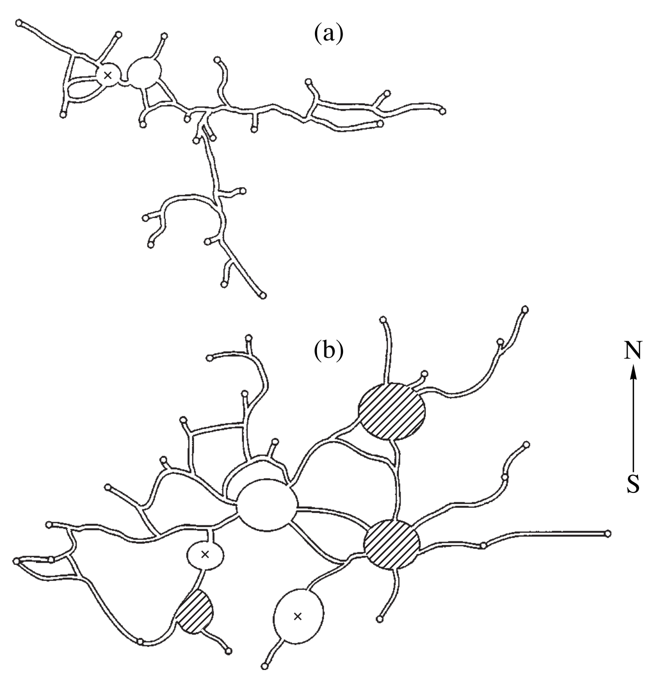

Fig. 2. Colonies of *Microtus gregalis* voles in the YNAE: (a) meadow in the Khadyta River floodplain, southern Yamal (scale 1 : 30); (b) dwarf-birch hummocky tundra, the Polar Urals (scale 1 : 30). For other designations, see Fig. 1.

Table 2. Basic parameters of *Microtus gregalis* colonies in the southern Yamal Peninsula and the Polar Urals (YNAE, August–September 2000)

Parameter	Yamal Peninsula (August)	*n*	Polar Urals (September)	*n*
Average area of a colony, m^2	3.6 ± 2.0	5	3.3 ± 0.9	8
Average depth of underground tunnels, cm	6.7 ± 0.9	100	9.1 ± 0.7	800
Average number of entrances per colony	17.4 ± 3.1	87	17.1 ± 2.3	137
Size of new nest, cm	11 × 14–20 × 21	5	15 × 19–28 × 33	8
Size of old nest, cm	12 × 14–15 × 28	2	12 × 14–26 × 30	6
Depth of location of new nest, cm	22.2 ± 2.3	5	30.7 ± 1.8	8
Depth of location of old nest, cm	19.0 ± 2.3	2	19.5 ± 2.9	6

located at the periphery of brushwood and along the riverbank. Most colonies were compact: their area did not exceed 12 m^2, and they had no more than 24 entrances. Note that, according to Lobanova and Balakhonov (1981), such colonies may occupy up to 1000 m^2 and have 100–120 entrances. In the Polar Urals, the colonies of narrow-skulled voles concentrated on well-warmed elevations in the dwarf-birch hummocky tundra and were also compact: no more than 8 m^2 and 29 entrances. The figures reported by Lobanova and Balakhonov (1981) for *M. g. major* colonies in these habitats—400–600 m^2 and 10–15 entrances—appear unlikely.

Comparing the structure of colonies in different parts of the species range (the steppe and southern tundras of Western Siberia, autumn 2000), we revealed no significant differences in the colony area and location of tunnels and nest chambers. Similarity with respect to the colony area in autumn could be explained by the seasonal dispersal of young animals (as in the steppe zone, immature young of the year prevailed in the Khadyta floodplain meadows: their proportion in catches reached 55.2 ± 9.2%). The nest chamber in the colonies studied in the Polar Urals and underground tunnels in the colonies studied in the Khadyta floodplain were located significantly deeper than in the steppe colonies, which could be due to differences in the degree of sod development.

The voles build nests of grass stems and leaves split into strips, which ensures effective thermal insulation. The paths connecting feeding places and entrances to the burrows are well-trodden and smooth, allowing the voles to move swiftly through the herbaceous cover. Naumov (1948) described such paths in *M. arvalis* burrows. In the areas with a thick herbaceous cover, the voles gnaw through the vegetation to form a kind of hidden aboveground tunnels.

In the YNAE, storage chambers were found only in the Polar Urals (Fig. 2). It is unclear why they were absent from the burrows in the Khatyda floodplain: published data (Ognev, 1950) provide evidence for the presence of storage chambers in the colonies located in a variety of habitats in different regions, including the Yamal Peninsula. Probably, our studies (performed in August) were finished before the voles began to store food.

In the areas with a thin herbaceous cover, the voles moving on the surface are more visible to predators and, therefore, more vulnerable. To protect themselves, the voles build burrows with a more complex structure, which are larger and have more entrances. Extensive steppe fires in the study region (Omsk oblast) in the early spring of 2000 deprived the voles of natural shelters in the thick grass stand. In this period, we recorded the greatest number of entrances to the peripheral burrows (up to 126 per colony), with the vole population density in the depressions near lakes being 17.0 ind./ha. By autumn, this density increased by a factor of 3.1, and the voles pitted the ground throughout their vast steppe habitats, so that it was impossible to separate one colony from another.

On the whole, the results of this study show that *M. gregalis* colonies in different parts of the species range inhabited by different subspecies—in the south of Omsk oblast and in the YNAE—have generally the same structure, with seasonal variation in some parameters. This fact confirms the well-known thesis (Kucheruk, 1959) that *M gregalis* voles living in the tundra retain the basic ecological features of this species in the optimum of its range (i.e., in the steppe zone), providing additional evidence that *M. gregalis* is originally a steppe species.

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