

Variability of the Ecological and Morphological Characteristics of Field Vole (*Microtus agrestis*) in the Southern and Middle Urals

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Abstract—The variability of the ecological and morphological characteristics of the field vole was studied on samples collected in its two localities of the Southern Urals and three localities of the Middle Urals. Voles were caught in similar biotopes; namely, in berry pine forests. The field vole is a common species in these habitats. The voles of the studied regions are characterized by a large body and skull size and a high frequency of occurrence of the additional internal loop on the first (M^1) molar. The results are consistent with the hypothesis that the ancestors of contemporary field vole of the eastern subline of cytochrome b survived the coldest period of the Late Pleistocene in the Ural Refugium.

Keywords: field vole, biotopic distribution and abundance, occurrence of M^1 morphotypes, body and skull size, Southern and Middle Urals

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Over the past years, the study of the phylogeographic structure of the field vole (*Microtus agrestis*), which was carried out by a number of researchers using the mitochondrial (cytochrome b) and nuclear loci, has revealed the existence of three highly genetically differentiated lines of this species: Portuguese, southern, and northern lines [1, 2]. The range of representatives of the northern line covers Great Britain, France (except its southern part), Denmark, Germany, Poland, the Czech Republic, Romania, Scandinavian countries, and Russia [1, 2]. There are six sublines within the northern line: North British, Western, French, Central European, Scandinavian, and Eastern. The representatives of the Eastern subline occur in Russia, Finland, northern Sweden, and northern Norway [3]. According to the demographic model based on the Bayesian method, the population began to grow in the northern line of the species from the early Holocene and continues to the present day [2].

In Fennoscandia, the spatial distribution of individuals of the eastern subline of cytochrome b corresponds to the distribution of the northern subspecies *M. a. agrestis*: they occur in Finland, northern Sweden, and northern Norway [4]. This subspecies is characterized by certain ecological and morphological features: large body and skull size and additional internal loop on M^1 [5]. It has been hypothesized [1] that the Southern Urals could probably serve as a refugium for the ancestors of the Eastern subline during the Last Glacial maximum.

The fauna of the first half of the Late Pleistocene in the Southern and Middle Urals is characterized by a relatively high proportion of field vole. During the

Late (Glacial) Valdai, field vole was a very rare representative in the fauna of these regions. It was an ordinary species throughout the Holocene period [6–8]. At the end of the Late Pleistocene, the field vole spread in the Southern and Middle Urals to the north (up to 58° N). This species gradually spread to the Northern Urals (up to 62° N) in the Late Glacial Period (about 12 thousand years BP) and to the Polar Urals (up to 67° N) about 11 thousand years BP [9]. These data suggest that the Ural refugium, in which the ancestors of the contemporary field vole of the Eastern subline of cytochrome b survived the coldest period of the Late Pleistocene [1], included not only the Southern but also the Middle Urals. In the Late Glacial Period, representatives of this line began to expand their range and currently advance to the north.

Comparison of the morphological features of field vole samples from the Southern and Middle Urals may confirm the hypothesis of the origin of the Eastern subline of cytochrome b from the Ural refugium.

The purpose of this research was to study the variability of the ecological and morphological characteristics of field vole in the Southern and Middle Urals. For this purpose, we characterized the biotopic distribution and abundance of voles and studied the variability in their body and skull size with respect to their reproductive-age status and sex. We studied the morphotypic variability of M^1 in Ural field vole populations with respect to the reproductive-age status, sex, year, and habitat area. To estimate the individual variability of the M^1 occlusal surface, we compared the occurrence of different morphotypes of the left and

Table 1. Reproductive-age and sex structure of field vole samples from the Southern and Middle Urals (above the line—number of individuals, under the line—%)

Group	Sample				
	SU	DSD1	DSD2	SW	NE
Young immature individuals	7/18	22/37	88/58	11/26	13/30
Young mature individuals	3/8	13/22	28/19	9/22	13/30
Overwintered individuals	28/74	24/41	34/23	22/52	17/40
Males	20/53	23/39	77/51	15/36	17/40
Females	18/47	36/61	73/49	27/64	26/60

right molars. The studied morphological parameters were compared with those from other regions where individuals of the Eastern subline of cytochrome b are recorded, which allowed us to test the consistency of our data with the hypothesis of the origin of the Eastern subline of cytochrome b from the Ural refugium.

MATERIAL AND METHODS

In the Southern Urals (SU), the small mammals were caught in forest habitats: in the surroundings of the town of Karabash (SK, 55.51° N, 60.10° E, 1983–1987) and in the Ilmen Nature Reserve (IR, 55.01° N., 60.16° E, 1986). In the Middle Urals (MU), they were caught in a natural forest stand located 50 km southeast of Yekaterinburg (the surroundings of the village of Dvurechensk, SD, 56.60° N, 61.04° E: SD1 in 1983–1987 and SD2 in 1991–2016) and in two forest parks in Yekaterinburg: Southwestern Park (SW, 56.80° N, 60.53° E, 1990–2012) and Kalinovsky Park (in the northeast of the city: NE, 56.92° N, 60.64° E, 1990–2016). A total of 27550 trap-nights were analyzed. Catches were performed in summer by the trap-line method (using live traps in 1983–1987 and small traps from 1990 to 2016) with a one-time inspection per day. Bread fried in sunflower oil was used as bait. The total number of captured voles was 445 individuals; 332 skulls and 664 M¹ teeth (right and left) were studied. We differentiated three reproductive-age groups: young immature, young mature, and overwintered individuals. Young individuals were classified into the immature and mature groups by the state of their generative system. The body mass and size and craniometrical and odontological features were used as age criteria: body mass (BM), length of body (LB), length of tail (LT), condylobasal length of skull (CBL), and length of maxillary row of teeth (LMT) [10, 11].

As in other rodents of the boreal forest zone, the field vole has a regular change in its reproductive-age structure during summer. In particular, the proportion of overwintered individuals decreases and that of new ones increases by the end of summer [10]. SD1, SW, and NE samples consist mainly of individuals captured in mid-summer and have a similar proportion of overwintered individuals (Table 1). Vole samples from the Southern Urals were combined, since they have a similar reproductive-age structure. The SU sample is

dominated by overwintered individuals captured in early summer and their proportion is the highest in this sample. The SD² sample is represented mainly by late-summer new individuals. The reproductive-age groups do not differ in the male/female ratio in any of the samples. The samples themselves also do not differ in sex ratio.

The collected vole skulls are stored in the Museum of the Institute of Plant and Animal Ecology, Russian Academy of Sciences, Yekaterinburg.

We used the StatSoft STATISTICA for Windows 6.0 software package to analyze the variability in the body and skull size (analysis of variance and *t* statistics) and morphotypic variability of M¹ (loglinear analysis and χ^2 statistics).

RESULTS AND DISCUSSION

Biotope distribution and abundance of the field vole in the Southern and Middle Urals. There are several altitudinal vegetation belts in the middle mountains of the Southern Urals: from the mountain–steppe to mountain–tundra belt. The mountain–forest belt occupies the largest area [6].

According to the published data [6, 12], the abundance of the field vole differs in different biotopes. Within the mountain–steppe belt, the field vole is common in floodplain meadow associations and in thickets of large-fruited trees and shrubs, growing on stream and river floodplains. It rarely occurs in shrub rocky steppes and in forest outliers and rocky placers of the mountain forest–steppe belt and is abundant in the dense floodplain birch forests of the mountain forest–steppe belt [6, 12]. In the mountain forest belt, the field vole is abundant in mixed pine–birch forests and recently felled forests. It is a common species in lower and upper taiga and a rare species in the rocky placers of this belt.

The field vole is rare in spruce low forests and birch crooked forests of the subalpine belt and in the rocky placers of the mountain–tundra belt, while it is common in the grass–moss tundra of the mountain–tundra belt [6, 12].

In the low mountains of the Middle Urals, field vole is common in horsetail–hedge–sphagnum spruce forests, sedge–sphagnum pine forests, sphagnum–horsetail spruce–cedar forests, and sedge–grass birch forests and on forest glades [1315] and rare in

horsetail–fern spruce and green-moss–short-grass forests, tall-grass fir–spruce forests, and reedgrass–short-grass birch forests [14, 15].

The biotopes in which we caught the animals in the Southern and Middle Urals are comparable and belong to the same type of forest; namely, berry pine forests: green-moss berry forests (IR, SK, and SD) and berry forests (SW and NE) [16–19]. The significant development of herbaceous vegetation is a necessary condition for the habitation of field vole in forest areas [20]. It is known that the green parts of herbaceous plants and dwarf shrubs prevail in the diet of this species all year round: their occurrence in its diet varies from 83 to 92% by season [10].

Comparison of the estimates of the abundance (ind./100 trap-nights) of field vole between the regions in synchronous periods (for 1983–1987) revealed a similarity of their mean values: 2.59 ± 0.31 (SD1, $n = 70$) and 2.96 ± 0.47 (SU, $n = 40$). The annual abundance values varied within similar ranges: from 0.4 to 5.5 (SD1) and from 0 to 6.7 (SU).

In 1991–1995, the abundance of the field vole in the Middle Urals was 5.49 ± 0.49 , $n = 128$ for SD2, 2.87 ± 0.44 , $n = 43$ for SW, and 1.60 ± 0.33 , $n = 24$ for NE. It became lower after 1995: 1.07 ± 0.12 , $n = 78$ for SD2, 0.63 ± 0.11 , $n = 32$ for SW, and 0.52 ± 0.09 , $n = 30$ for NE ($p < 0.01$). We associate this decrease with an increase in the recreational load after 1995. From 2010 to 2012, the projective cover of cereals was still 10–14% in the SD, SW, and NE localities [19].

Despite abundance fluctuations, the field vole is common in berry pine forests both in the Southern and Middle Urals.

The variability in the body and skull size of field vole with respect to the reproductive-age status (three gradations) and sex was studied using an analysis of variance on a combined sample. No gender differences were found for the body mass (BM), body length (LB), and length of maxillary row of teeth (LMT) in field vole ($F_{1,326} < 1.1$, $p > 0.29$). The average condylobasal length (CBL) of the skull for the reproductive-age groups was higher in females (25.15 ± 0.08) than in males (24.81 ± 0.08 , $F_{1,255} = 8.6$, $p < 0.01$), while the tail length (LT) was higher in males (30.2 ± 0.3) than in females (29.4 ± 0.3 , $F_{1,326} = 5.0$, $p < 0.03$). There are clear differences between all reproductive-age groups with respect to all features ($F_{2,326} > 180$, $p < 0.001$).

Overwintered field vole individuals from our combined sample (Table 2) are similar ($t < 1.5$, $p > 0.15$) to those from the north of the European part of Russia (Vologda oblast, $n = 63$) in their body weight (41.3 ± 0.8 g), body length (118.7 ± 1.0 mm), and tail length (33.7 ± 1.0 mm) [21]; in addition, their limits also coincide: 21–61 for BM, 102–145 for LB, and 26–42 for LT [21]. Similar limits of the body and tail length variability are characteristic of voles from the north of Siberia (101–138 for LB and 30–42 for LT, $n = 78$); from the Altai and Sayan mountains (110–134 for LB and 29–41 for LT, $n = 84$) [22]. The limits of variabil-

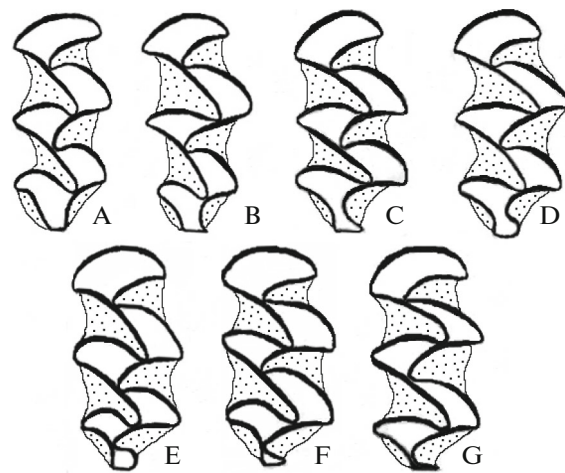


Fig. 1. M^1 molar morphotypes differentiated by the features of the additional internal loop.

ity in the condylobasal skull length and length of maxillary row of teeth coincide in voles from our combined sample (see Table 2) and voles from the European north of Russia (26.0–28.2 for CBL and 6.2–7.0 for LMT, $n = 78$), from the north of Siberia (26.2–28.3 for CBL and 6.3–6.9 for LMT, $n = 118$), and from the Altai and Sayans (26.4–29.0 for CBL and 6.0–6.7 for LMT, $n = 84$) [22]. Consequently, the large body and skull size of the northern subspecies *M. a. agrestis* are characteristic of both voles from the European north of Russia and north of Siberia and voles from the Southern and Middle Urals, Altai, and Sayans.

Variability of the occlusal surface of the M^1 molar.

The main component of the variability of the occlusal surface of this molar in field vole is an additional internal loop. We differentiated seven morphotypes with respect to the features of the additional internal loop on this molar (Fig. 1) and grouped them into three categories: (1) lack of the additional internal loop ((A) and (B)), (2) open loop ((C) and (D)), and (3) closed loop ((E), (F), and (G)).

The reproductive-age state ($\chi^2 = 6.2$, $df = 4$, $p = 0.19$), sex ($\chi^2 = 4.3$, $df = 2$, $p = 0.12$), and left- and right-side tooth position in the jaw ($\chi^2 = 0.3$, $df = 2$, $p = 0.86$) do not influence the distribution of the M^1 molar with respect to the morphotype categories. Samples from the Southern Urals are homogeneous in the frequencies of the morphotype categories when compared by year and locality ($\chi^2 = 8.0$, $df = 4$, $p = 0.09$); samples from the forest parks of Yekaterinburg are also homogeneous when compared by year and locality ($\chi^2 = 9.3$, $df = 8$, $p = 0.32$; Fig. 2). The SD locality was heterogeneous in the frequencies of morphotype categories. Thus, the proportion of closed loops is 78% in the 1991 sample ($n = 78$), while it is 38% in the 1994 sample ($n = 32$, $\chi^2 = 15.9$, $df = 1$, $p < 0.0001$). The proportion of closed loops is 87% ($n = 30$) in the early-summer sample of 2006, while it

Table 2. Variability in the average body and skull size of field vole from the Southern and Middle Urals with respect to its reproductive-age state (above the line— $M \pm SE$, under the line—limits, in brackets— n).

Attributes	Reproductive-age groups		
	Young immature individuals	Young mature individuals	Overwintered individuals
Body mass, g	18.7 ± 0.5 10–24 (141)	31.8 ± 0.7 25–52 (66)	40.8 ± 0.5 25–61 (125)
Length of body, mm	90.6 ± 0.6 75–100 (141)	106.8 ± 0.9 97–121 (66)	118.1 ± 0.6 100–140 (125)
Length of tail, mm	25.8 ± 0.3 18–34 (141)	29.9 ± 0.4 24–37 (66)	33.7 ± 0.3 25–41 (125)
Condylbasal length of skull, mm	23.25 ± 0.09 20.5–25.4 (93)	24.93 ± 0.12 24.2–25.6 (59)	26.76 ± 0.09 25.6–28.8 (109)
Lengths of maxillary row of teeth, mm	5.86 ± 0.02 5.5–6.3 (141)	6.17 ± 0.02 6.0–6.3 (66)	6.53 ± 0.02 6.3–7.0 (125)

is 37% ($n = 60$, $\chi^2 = 20.4$, $df = 1$, $p < 0.0001$) in the late summer sample. Consequently, significant inter-annual and seasonal differences in the frequency of the

morphotype categories of the M^1 molar can be observed in a separate locality.

The total samples from the SD locality ($n = 418$) and Yekaterinburg forest parks ($n = 170$) are similar in the frequencies of the morphotype categories ($\chi^2 = 0.83$, $df = 2$, $p = 0.67$), while the total samples from the Southern ($n = 76$) and Middle ($n = 588$) Urals are statistically different both in the frequency of the first category of morphotypes (7.9% for SU, 2.7% for MU, $\chi^2 = 5.6$, $df = 1$, $p < 0.02$) and in the frequency of the third category (45% for SU, 59% for MU, $\chi^2 = 5.5$, $df = 1$, $p < 0.02$). However, the frequency of the additional internal loop on the first (M^1) molar in samples from both studied regions shows a significant dominance (92–97%), which is characteristic of the Northern subspecies of *M. a. agrestis* [5].

We compared our data on the frequency of the additional internal loop on the M^1 molar with the data for overwintered field vole from the Lower Ob region ($87.7 \pm 3.8\%$, $n = 81$) and Polar Urals ($93.0 \pm 2.3\%$, $n = 129$). They have a high frequency of the additional internal loop of this molar; at the same time, it proved to be somewhat lower for young voles ($77.3 \pm 3.3\%$, $n = 163$) [23]. This frequency is $98 \pm 1.6\%$, $n = 78$ in the north of the European part of Russia [22], $68 \pm 9.9\%$, $n = 22$ in Finland and northern Scandinavia [24], and $51 \pm 5.5\%$, $n = 84$ in Altai and Sayans [22]. A similar frequency distribution of this feature, which can serve as a certain marker of the eastern subline of cytochrome b [4, 5], may indicate that field vole expanded from the southern Middle Ural refugium not only to the west but also to the east.

As a result, our data show that field vole is a common species in the berry pine forests of the Southern and Middle Urals. We revealed a high level of similarity of the morphological characteristics of the field vole from the Southern and Middle Urals with samples from other regions in which individuals of the

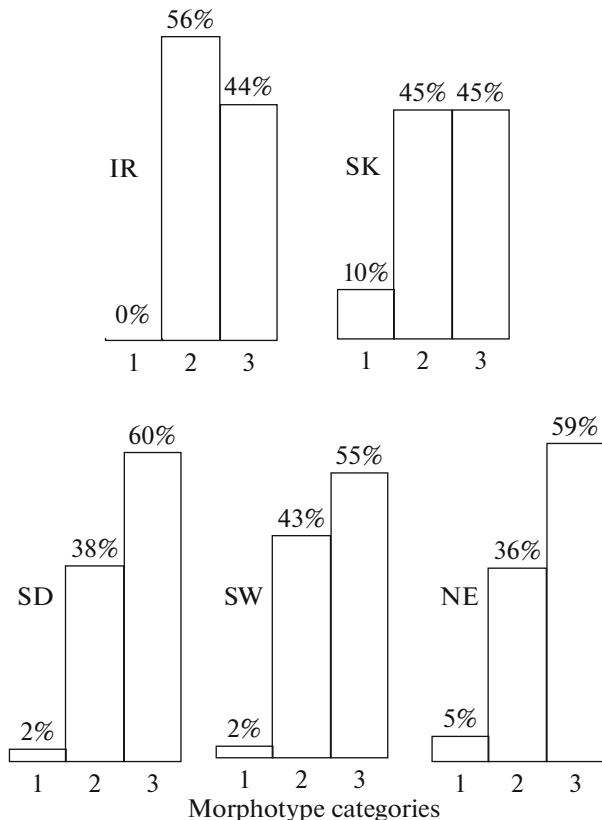


Fig. 2. Distribution of field vole by M^1 molar morphotypes in the localities of the Southern and Middle Urals. Southern Urals: IR, Ilmen Reserve, SK, surroundings of the town of Karabash; Middle Urals: SD, surroundings of the village of Dvurechensk, SW, Southwestern Forest Park, NE, Kalinovsky Forest Park.

Eastern subline of cytochrome b are recorded. The results are consistent with the hypothesis of the origin of the Eastern subline of cytochrome b from the Southern and Middle Ural refugium, where the ancestors of this subline survived the Last Glacial Maximum; the results also suggest that field vole expanded from this refugium not only to the west but also to the east.

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