

# Coat Color Polymorphism in Populations of the Northern Mole Vole in the Ural Region

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**Abstract**—Collections made in the course of long-term field studies on ecology of the northern mole vole *Ellobius talpinus* Pall, in the Ural Region and neighboring areas (more than 2000 individuals from 24 points of the species range) were used to analyze geographic variation in its coat color (color morphs). On the basis of long-term observations (1985-1999) on marked animals from a polymorphic population (Kurtamyshskii raion, Kurgan oblast), the life spans of males and females and the dependence of life span on population density and structure were estimated in animals of different color morphs. Each color morph of *E. talpinus* was shown to have specific features of the seasonal dynamics of age structure and migrations.

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**Key words:** northern mole vole, color polymorphism, geographic variation, age structure, life span, migration, adaptation.

The ratio of color morphs in populations of *E. talpinus* is determined genetically. Analysis of coat color in parents and their offspring has shown that segregation into black and differently colored individuals in the progeny from different crossing variants does not contradict the hypothesis of monogenic inheritance of these color variations. For instance, black *E. talpinus* are recessive homozygotes (genotype *aa*), dominant homozygotes (*AA*) have brown coat color, and heterozygotes (*Aa*) may be brown or of an intermediate color (Cheprakov et al., 2005).

In the Russian fauna, *E. talpinus* is one of a few mammal species with a high level of variation in this character, including geographic variation. In particular, distinct population variation in coat color, from light brown to coal black, is observed in the Ural Region and neighboring areas (Evdokimov and Pozmogova, 1992; Evdokimov, 2001). Earlier data on this phenomenon in the region concern only the frequency of black (melanist) forms in the common hamster (Gershenson, 1946) and northern mole vole (Kirikov, 1952). The purpose of this study was to estimate the frequencies of different color morphs in *E. talpinus* and the role of color polymorphism in mechanisms of population adaptation and regulation.

## MATERIAL AND METHODS

Studies were performed from 1974 to 1976, 1980 to 1999, and 2001 to 2004 in the mountain and lowland parts of the Southern Urals and lowland parts of the

Transural Region and Western Siberia. Animal samples were taken from 21 geographic points spaced apart both latitudinally and longitudinally, which allowed us to regard them as individual populations. They were divided into four groups according to the geographic location of the sampling sites (Fig. 1).

The first group represented the mountain part of the Southern Urals (from south to north) and consisted of seven populations. Two of them were from Orenburg oblast—(1) Khmelevka (near the village of the same name in Gaiskii raion) and (2) Kuvandyk (near the village of Kashkuk, Kuvandykskii raion)—and six from Bashkortan: (3) Yuldybaevo (near the village of the same name in Zilairskii raion); (4) Bairamgulovo (near the village of the same name in Uiskii raion); (5) Baimakskaya (near the village of Saksei, Baimakskii raion); (6) Uchalinskaya (near the village of Poljakovka, Uchalinskii raion); and (7) Burangulovskaya (near the village of the same name in Uchalinskii raion).

The second group represented the lowland part of the Southern Urals (from the south to north of Chelyabinsk oblast) and consisted of five populations: (8) Troitsk (Troitskii raion), (9) Plastovo (near the village of Radiomaika, Plastovskii raion), (10) Krasnoarmeisk (Krasnoarmeiskii raion), (11) Kunashak (near Shugunyak Lake, Kunashakskii raion); and Kyshtym (near the village of Metlino, Kyshtymskii raion).

The third group represented the lowland part of the Southern Transural Region and consisted of five populations from Kurgan oblast: (13) Zverinogolovskaya

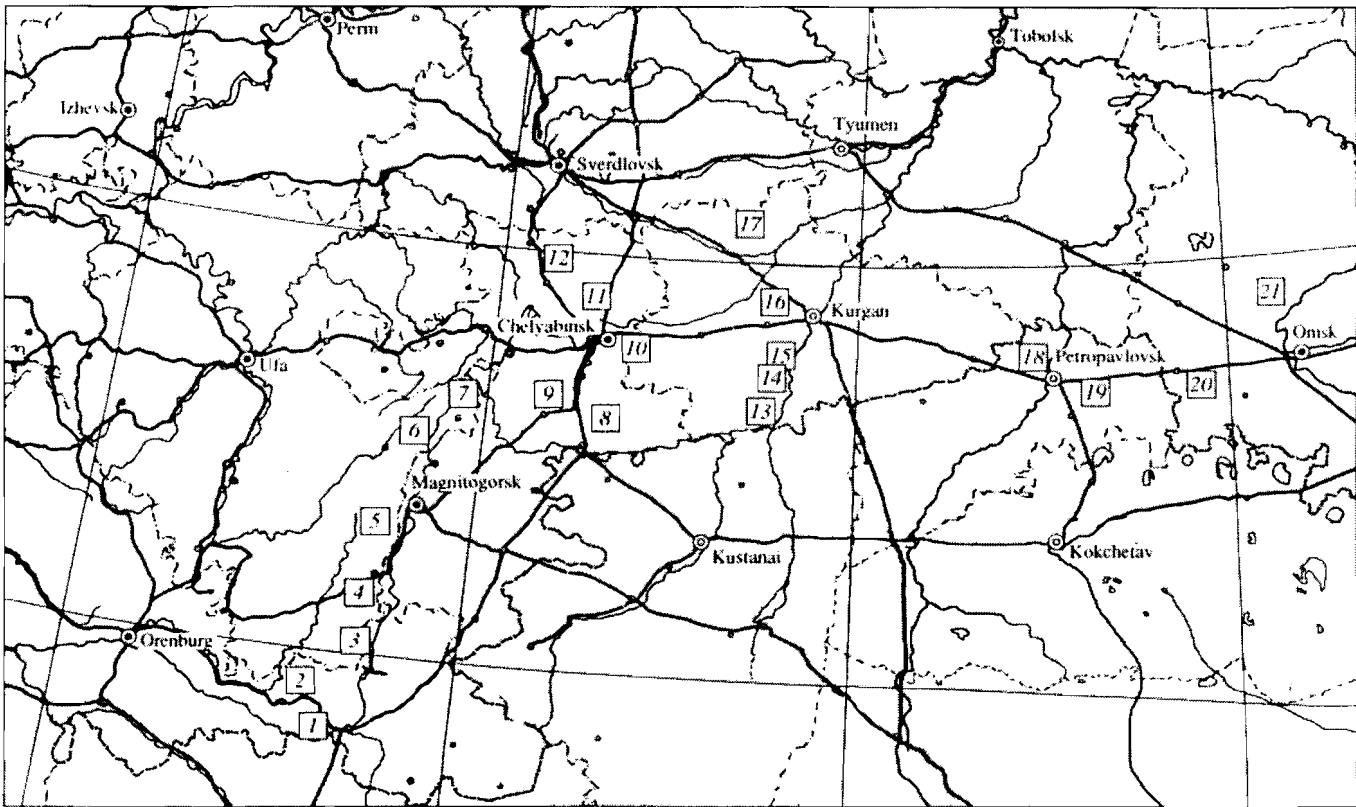


Fig. 1. Map of the study region and locations of *E. talpinus* populations studied (boxed figures): (1) Khmelevka, (2) Kuvandyk, (3) Yuldybaevo, (4) Bairamgulovo, (5) Baimak, (6) Uchaly, (7) Burangulovo, (8) Troitsk, (9) Plastovo, (10) Krasnoarmeisk, (11) Kunashak, (12) Kyshtym, (13) Zverinogolovskaya, (14) Kurtamysh, (15) Galaevo, (16) Kargapol'e, (17) Shadrinsk, (18) Sokolovo, (19) Bishkul', (20) Moskalensk, and (21) Sargat populations.

(near the village of the same name in Pritobol'nyi raion), (14) Kurtamysh (Kurtamyshskii raion), (15) Galaevo (near the village of the same name in Ketovskii raion), (16) Kargapol'e (near the village of the same name in Kargapol'skii raion); and (17) Shadrinsk (near the villages of Sibirki and Yuldus, Shadrinskii raion).

The fourth group represented the lowland part of Western Siberia and consisted of four populations: (20) Moskalensk, (21) Sargat (from similarly named raions of Omsk oblast), (18) Sokolovo, and (19) Bishkul' (from similarly named raions of North Kazakhstan oblast, Kazakhstan).

Until 1981, all animals were caught by hand, according to Novikov (1953); later, Golov's (1954) live traps were used. The total catch reached 3000 ind. The animals were marked by the traditional method of finger/toe clipping, which allowed permanent observations on each marked individual throughout its presence in the marking plot without disturbing the normal life of a family (colony).

In the Kurtamysh population (Kurgan oblast), *E. talpinus* were caught and marked twice a year, in spring and autumn, over 15 years: from 1985 to 1999; 24 families were kept under observation, and 745 animals were recorded, with the number of recaptures ranging

from 2 to 13. The Kurtamysh population is polymorphic and comprises animals of three color morphs: black, brown, and transitional.

Long-term observations on marked animals in Kurtamyshskii raion showed that *E. talpinus* in nature can live to an age of five-six years or even older, depending on the year of its birth (Evdokimov, 1997). The first age group (young of the year) after wintering (in spring) passes into the second group (yearlings); after the second wintering, to the third group (two-year-olds); after the third wintering, to the fourth group (three-year-olds); after the fourth wintering, to the fifth group (four-year-olds); after the fifth wintering, to the sixth group (five-year-olds); and after the sixth wintering, to the last, seventh group (six-year-olds). Beginning from the second age group, animals are considered adult. Migrant *E. talpinus* include animals of the first three age groups (Evdokimov, 1999).

Trapping and marking were performed in spring and autumn. Accounts of migrants and mortality of older individuals were taken on the following principle: marked animals of the first, second, and third groups that were absent in spring catches were classified as migrants; when animals of the fourth, fifth, sixth, and seventh groups were absent in spring catches, it was considered that they died in autumn of the preceding

year; and when these animals were absent from autumn catches, it was considered that they had migrated or died in spring of the same year. The life span of an individual was counted from the year of its birth to the time of its last catch, regardless of its movements from one family to another.

Figure 2 shows the maximum life span of resident northern mole voles and the dynamics of their total population numbers, including not only resident adults and young of the year but also different groups of migrants and deceased individuals.

The collection material was processed using conventional zoological methods. The life spans of males and females of different color morphs were compared using the Quattro PRO 5.0 program, and correlation analysis was performed with the Statistica 5.5 program package.

## RESULTS AND DISCUSSION

The frequencies of different color morphs in the populations arranged in a series from southern steppes of Orenburg oblast and Kazakhstan to forest-steppes of the Southern Urals and Transural Region show no definite trend. From south to north, the frequency (proportion) of the black morph in mountain populations increases from 0 to 67.3%, whereas that of the brown morph decreases from 100 to 4.1% (Table 1). The proportion of the transitional morph is characterized by saltatory changes. On average, animals of the brown morph dominate by numbers in the mountain group of populations (71.6%), with the proportions of black and transitional animals being almost equal.

In populations of the Southern Ural lowland group (Chelyabinsk oblast, from Troitskii raion in the south to Kunashakskii and Kyshtymskii raions in the north), the proportion of melanists increases from 13.0% in the Plastovo population to 100.0% in the Kunashak and Kyshtym populations. Correspondingly, animals of the brown and transitional morphs disappear in the northern part of the oblast. On average, the black morph dominates in this group (51.1%), and the proportions of brown and transitional morphs are almost equal.

In the third group of lowland Transural populations (from the south to the north of Kurgan oblast), animals of all three color morphs occur in the south, but the transitional morph completely disappears in the north, while the proportion of melanists slightly decreases. Animals of the brown and black morphs dominate in this group, with their proportions averaging 51.5 and 41.7%, respectively.

In the fourth group of lowland Western Siberian populations (east of Kustanai to Omsk oblast), no northern mole voles of the transitional and black morphs were recorded. The coat color in animals is closer to that in the brown morph from the Shadrinsk and Kargopol'e populations.

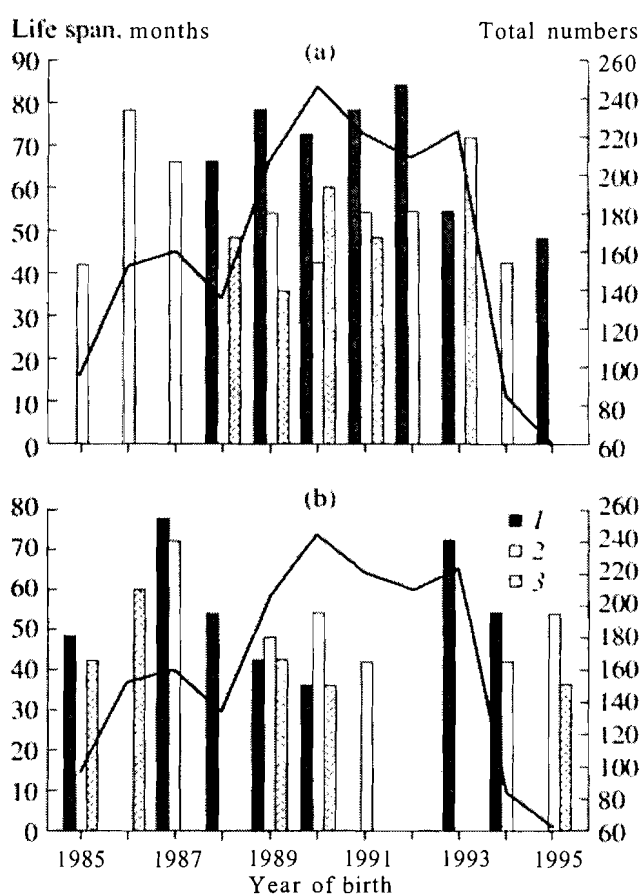


Fig. 2. Maximum life spans of resident (a) male and (b) female *E. talpinus* of (1) black, (2) brown, and (3) transitional coat color morphs born between 1985 and 1995 (according to marking data on the Kurtamysh population).

Thus, when moving from south to north over and along the Ural Ridge, the proportion of melanists in *E. talpinus* populations increases, reaching 100% in the north of Chelyabinsk oblast. When moving from the Transural Region in the west to northern Kazakhstan and Omsk oblast (at the latitude of Chelyabinsk and Kurgan) in the east, the proportions of the black and transitional morphs decrease while that of the brown morph increases, with catches from Omsk oblast consisting only of brown animals.

In polymorphic *E. talpinus* populations, the frequencies of different color morphs may differ within the same population from year to year and in different populations in the same year (Table 1). For instance, during 15 years of observations on the polymorphic Kurtamysh population, the proportion of the black morph in it varied from 37.5 to 62.1%; of the brown morph, from 18.5 to 44.8%; and of the transitional morph, from 13.4 to 28.0% (Evdokimov, 2005). These variations may well be of adaptive significance, since different color morphs of *E. talpinus* are known to have specific physiological features (Bol'shakov et al., 1982,

**Table 1.** Frequencies of (Bl) black, (Br) brown, and (Tr) transitional coat color morphs in *E. talpinus* populations, %

Popu- lation no.	Sampling year	Morph			<i>n</i>	Popu- lation no.	Sampling year	Morph			<i>n</i>
		Bl	Br	Tr				Bl	Br	Tr	
Group I						Group II					
1	2004	0	100.0	0	26	8	1983	50.0	19.2	30.8	52
2	1974-1976	0	100.0	0	276	8	1987	27.5	23.5	49.0	51
2	2001	2.9	77.1	20.0	35	8	1989	13.1	23.9	63.0	48
3	1985	0	100.0	0	48	9	1976	13.0	76.2	10.8	46
4	1985	3.7	77.8	18.5	54	9	1989	13.1	23.9	63.0	48
5	1980	12.8	84.0	3.2	125	10	1983	72.0	0	28.0	25
6	1985	<b>14.0</b>	29.7	56.3	64	11	1975-1987	100.0	0	0	850
7	2001	67.3	4.1	28.6	49	12	2001	100.0	0	0	55
<i>M±m</i>		12.6 ± 9.3	71.6 ± 5.6	15.8 ± 7.3	677	<i>M ± m</i>		51.1 ± 6.2	26.2 ± 8.8	22.7 ± 8.4	1154
Popu- lation no.	Sampling year	Morph			<i>n</i>	Popu- lation no.	Sampling year	Morph			<i>n</i>
		Bl	Br	Tr				Bl	Br	Tr	
Group III						Group IV					
13	1983	0	88.2	11.8	51	18	1984	0	100.0	0	36
13	2001	24.0	76.0	0	25	18	1985	0	100.0	0	21
14	1983	54.0	30.0	16.0	50	19	1984	0	100.0	0	39
14	1985-1999	51.0	32.9	16.1	745	20	1984	0	100.0	0	38
14	1989-1991	85.0	11.7	3.3	60	20	2004	0	100.0	0	38
15	1984	31.3	55.2	13.4	67	21	2004	0	100.0	0	34
15	1986	2.5	89.9	7.6	79	<i>M±m</i>		0	100.0	0	206
16	1981-1983	83.8	16.2	0	74						
17	1982	12.8	87.2	0	39						
17	1983	72.3	27.7	0	47						
<i>M ± m</i>		41.7 ± 5.5	51.5 ± 5.0	6.8 ± 4.2	1237						

1989; Moshkin et al., 1991) as well as genetic features (Cheprakov et al., 2005; Gileva et al., 2006).

Analysis of the age structure of several *E. talpinus* populations from different parts of the range showed that the life span of certain color morphs is related to their dominant or subdominant position in the population with respect to abundance (Sineva, 2004).

As an illustration, let us consider the age structure of the Kurtamysh population of *E. talpinus* in spring and autumn, before and after the breeding season (Table 2). During almost the entire period of observations on marked animals, the black morph dominated (except between 1985 and 1987, when a slight prevalence of the brown morph was recorded); the brown and transitional morphs ranked second and third.

The proportions of young of the year (the first age group) in spring and autumn were almost equal in the black and brown morphs, slightly exceeding that in the transitional morph (especially in autumn). Equal proportions of yearlings (the second group) were recorded

in the black and transitional morphs in spring and in the black and brown morphs in autumn; in the transitional morph, this proportion was slightly higher. Two-year-olds (the third group) were more abundant in the transitional and brown morphs than in the black morph both in spring and autumn, and the same (but to a slightly smaller degree) was also observed in the fourth group (three-year-olds). In the fifth group, conversely, the proportions of four-year-olds of the brown and transitional morphs decreased slightly, compared to the black morph. In the sixth group, their proportions decreased further. All animals living up to the age of six years or older (the seventh group in autumn) were black; a few brown six-year-olds occurred only in spring, and all animals of the transitional morph had died before this age.

Consider the life span of marked males and females of the three color morphs depending on the year of birth (from 1985 to 1995) and the total population numbers (Fig. 2). The maximum life span (84 months) was

Table 2. Seasonal dynamics of age structure in a polymorphic population of *E. talpinus* (the Kurtamysh colony, 1988-1999)

Age group	Morph												Total	
	black				brown				transitional					
	spring		autumn		spring		autumn		spring		autumn		spring	autumn
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%		
1	81	19.8	254	52.9	49	19.8	139	53.9	27	17.4	70	46.0	19.4	52.0
2	165	40.3	96	20.0	107	43.3	51	19.8	63	40.6	35	23.0	41.3	20.4
3	62	15.2	47	9.8	43	17.4	33	12.8	31	20.0	24	15.8	16.8	11.7
4	41	10.0	34	7.1	27	10.9	20	7.7	18	11.6	14	9.2	10.6	7.6
5	29	7.1	26	5.4	12	4.8	11	4.3	10	6.5	7	4.6	6.3	4.9
6	20	4.9	15	3.1	7	2.8	4	1.5	6	3.9	2	1.3	4.1	2.4
7	11	2.7	8	1.7	2	0.8	-	-	-	-	-	-	1.6	0.9
Total	409	100	480	100	247	100	258	100	155	100	152	100	811	890

recorded in male *E. talpinus* of the black morph (four animals), compared to 78 months in the brown morph (two individuals) and 72 months in the transitional morph (two individuals). The same was true of females: 78 months in the black morph (one individual) compared to 54 months in the brown morph (one individual) and 60 months in the transitional morph (one individual).

The life span of northern mole voles born in 1985 was relatively short, 42-48 months; these were only males of the brown morph and females of the black and transitional morphs (Fig. 2). The fact that males of the black and transitional morphs born in 1985 were absent in the marking site indicated that these individuals had migrated from it between 1985 and 1987; the same concerned females of the brown morph. Subsequently, the animals born in the period of a small population rise (1986-1987) actively migrated from the marking site, except for males of the brown morph. Among the animals born in 1988 (the year of a small decrease in population numbers), males of the black and transitional morphs and females of only the black morph remained in the families in subsequent years. Between 1985 to 1988, the families consisting of brown males and females of the black and transitional morphs formed the reproductive potential of the population for subsequent years. Females of the aforementioned morphs are known for their major contribution to the total *E. talpinus* population growth (Evdokimov, 2005).

In the years of active population growth (1989-1990), males and females of all three color morphs remained in the families; however, the life span of females was considerably lower than in males. In the years of population peak (1989-1990) and stabilization (1991-1993), the longest life span was recorded in males of the black morph that were born in this period. At the same time (in the presence of males of older age groups), males of the transitional and brown morphs

born in 1992 and 1993 had to migrate from the colony. None of the five males of the transitional morph born in 1992 and 28 males of the brown morph born in 1993 remained in the colony two years later.

Even more conspicuous was the absence of resident females born between 1991 and 1993, namely, of black and brown females in 1991, females of all three morphs in 1992, and of brown and transitional morphs in 1993. Thus, although the population appeared to be in a good state (with respect to abundance), the absence of young individuals (mainly among females) and the increasing proportion of old animals (especially males) were alarming symptoms. Such a situation naturally leads to a decrease in fecundity and, when aggravated by increased migration and mortality (Evdokimov, 2003), to an abrupt population decline, which was indeed observed in 1994 and 1995. Among northern mole voles born in these years, the group of emigrants included mainly males of all three color morphs and females of black and transitional morphs; on the other hand, males and females of all three color morphs remained in the families, along with animals of different ages.

These results were fairly unusual and could not be interpreted unambiguously. To understand them better, a correlation analysis was performed. Its results showed that the life span of black males strongly correlated with the total numbers of black animals ( $r = 0.673$ ,  $p < 0.05$ ) and also with the life span of males of the transitional morph ( $r = 0.637$ ,  $p < 0.05$ ). The life span of brown males negatively correlated with the life span of males of the transitional morph ( $r = -0.644$ ,  $p < 0.05$ ). The life span of females of any color morph showed no significant correlation either with the total animal numbers or the life span of males and females of other color morphs. Thus, the dependence of life span on animal numbers was revealed only in males of the dominant black morph.

Table 3. Parameters of seasonal migration in *E. talpinus* of different color morphs by age groups (based on data shown in Table 2)

Age group	Morph											
	black				brown				transitional			
	from spring to autumn		from autumn to spring		from spring to autumn		from autumn to spring		from spring to autumn		from autumn to spring	
	%	n	%	n	%	n	%	n	%	n	%	n
1			35.0	89			23.0	32			10.0	7
2	27.1	69	13.4	34	40.3	56	5.8	8	40.0	28	5.7	4
3	5.9	15	2.4	6	7.2	10	4.3	6	10.0	7	8.6	6
Total	33.0	84	50.8	129	47.5	66	33.1	46	50.0	35	24.3	17

Such a variation in the life span of male and female *E. talpinus* of different color morphs creates conditions for diverse age and coat color combinations in crosses. It is quite probable that coat color plays a certain role in the formation of family pairs. In certain cross combinations, females of each color morph supplement the population with individuals of not only their own but also of two other morphs (Evdokimov, 2005). Therefore, the maintenance of certain balance between color morphs in the population is not accidental but plays a certain role in the dynamics of its size and structure.

Seasonal migrations (dispersal) are also highly important for population regulation and maintenance of homeostasis. The dynamics of migration process in different *E. talpinus* color morphs may be traced with reference to the Kurtamysh population (Table 3). The proportion of migrants among black animals reached 83.8% of their initial number (254 ind., Table 2); among brown animals, 80.6% (139 ind.); and among animals of the transitional morph, 74.3% (70 ind.). Most individuals of the black morph (50.8% of the initial number) migrated before or after wintering (in late autumn or early spring), i.e., in colder periods of the season of *E. talpinus* activity; the proportion of black animals that migrated in the warmer period (from spring to autumn) was considerably lower, 33.0%. Conversely, most animals of the brown and transitional morphs migrated in the warmer rather than in the colder period (47.5 and 50.0% vs. 33.1 and 24.3%, respectively). According to the study on the energetics of tissue (mitochondrial) oxidative metabolism in *E. talpinus* of the black and brown morphs (Bol'shakov et al., 1982), animals of the black morph (melanists) are better adapted to cold owing to their ability to use the energy resources of the liver tissue more efficiently, which is an important prerequisite for colonization of areas near the northern boundary of the species range.

Thus, the results of this study show that the color polymorphism of *E. talpinus* plays a major role both in the population dynamics of the species and in the maintenance of population structure and homeostasis. It provides for a high adaptation potential of local popula-

tions, which enables the species to exist in several geographic zones, from desert to forest-steppe.

#### ACKNOWLEDGMENTS

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#### REFERENCES

- Bol'shakov, V.N., Mazina, N.K., and Evdokimov, N.G., Specific Features of Interior Characters and Energetics of Tissue Oxidative Metabolism in the Black and Brown Color Morphs of the Northern Mole Vole, *Dokl Akad. Nauk SSSR*, 1982, vol. 263, no. 1, pp. 244-246.
- Bol'shakov, V.N., Evdokimov, N.G., Moshkin, M.P., and Pozmogova, V.P., Color Polymorphism and Its Relation to Stress Reactivity in the Northern Mole Vole (*Ellobius talpinus* Pallas), *Dokl Akad. Nauk*, 1989, vol. 263, no. 2, pp. 500-502.
- Cheprakov, M.I., Evdokimov, N.G., and Glotov, N.V., Inheritance of Coat Color in the Northern Mole Vole (*Ellobius talpinus* Pallas), *Genetika*, 2005, vol. 41, no. 11, pp. 1552-1558.
- Evdokimov, N.G., The Dynamics of Population Structure in the Northern Mole Vole (*Ellobius talpinus* Pall.), *Ekologiya*, 1997, no. 2, pp. 108-114.
- Evdokimov, N.G., Analysis of Dispersal in Populations of Northern Mole Voles, *Ekologiya*, 1999, no. 5, pp. 352-357.
- Evdokimov, N.G., *Populyatsionnaya ekologiya obyknovennoi slepushonki* (Population Ecology of the Northern Mole Vole), Yekaterinburg: Yekaterinburg, 2001.
- Evdokimov, N.G., Fluctuations of Population Size and Structure in the Northern Mole Vole: Preliminary Analysis, *Ekologiya*, 2003, no. 3, pp. 234-242.
- Evdokimov, N.G., Comparative Analysis of Coat Color Morphs in a Polymorphic Population of the Northern Mole Vole, *Ekologiya*, 2005, no. 6, pp. 438-445.
- Evdokimov, N.G. and Pozmogova, V.P., Mountain and Plain Populations of the Northern Mole Vole (Southern Urals and Transural Region), in *Ekologiya mlekopitayushchikh Ural'skikh gor: Sb. nauch. trudov* (Ecology of Mammals in the Ural Moun-

- tains: Collected Scientific Works), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 1992, pp. 100-119.
- Gershenzon, S.M., Role of Natural Selection in the Spread and Dynamics of Melanism in Hamsters (*Cricetus cricetus*), *Zh. Obshch. Biol.*, 1946, vol. 7, no. 2, pp. 97-130.
- Gileva, E.A., Bol'shakov, V.N., Yalkovskaya, L.E., and Sineva, N.V., Chromosomal Instability and Cranial Asymmetry in the Mole Vole *Ellobius talpinus* Pallas, 1770 Polymorphic for Coat Coloration, *Dokl. Akad. Nauk*, 2006, vol. 410, no. 5, pp. 705-708.
- Golov, B.A., A Live Trap for Mole Voles, *Byull. Mosk. O-va Ispyt. Prir. Otd. Biol.*, 1954, vol. 59, no. 5, pp. 95-96.
- Kirikov, S.V., *Ptitsy i mlekopitayushchie v usloviyakh landshaftov yuzhnoi okonechnosti Urala* (Birds and Mammals in Landscapes of the Southernmost Urals), Moscow: Akad. Nauk SSSR, 1952.
- Moshkin, M.P., Evdokimov, N.G., Miroshnichenko, V.N., and Pozmogova, V.P., Variation of the Corticosteroid Function in Populations of Northern Mole Voles (*Ellobius talpinus* Pall.), *Usp. Sovrem. Biol.*, 1991, vol. 111, no. 1, pp. 95-100.
- Novikov, G.A., *Polevye issledavaniya po ekologii nazemnykh pozvonochnykh* (Field Studies on the Ecology of Terrestrial Vertebrates), Moscow: Sovetskaya Nauka, 1953.
- Sineva, N.V., Experience in Reconstructing the Population Structure of Northern Mole Vole (*Ellobius talpinus* Pall.), in *Ekologicheskie mekhanizmy dinamiki i ustoichivosti bioty: Materialy konf. molodykh uchenykh* (Proc. Young Sci. Conf. "Ecological Mechanisms of Biota Dynamics and Stability"), Yekaterinburg: Akademkniga, 2004, pp. 233-241.