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ECOLOGY OF THE NORTHERN MOLE VOLE (*ELLOBIUS TALPINUS*) IN THE CENTRAL REGIONS OF ITS RANGE: CHARACTERISTICS OF HABITATS IN AREAS OF THE SPECIES' OCCURENCE

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Key words

northern mole vole, burrowing animals, fauna, biotope, soil, landscape, steppe, Middle Volga region

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Abstract

Burrowers are the main creators, converters, and keepers of landscapes and soils of steppe ecosystems. The northern mole vole *Ellobius talpinus* (Pallas, 1770) is a rather widespread species of burrowing animals, an indicator species of various types of steppes, with a pronounced environment-forming activity. Fourteen large colonies of *E. talpinus* were studied in the Middle Volga region during the field seasons of 2006–2021. The agrochemical indicators of the soil characterise the possibility of developing certain steppe microstations, in which specific plant associations are formed. The parameters of soil samples and their combinations show the suitability of the formation of those plant associations that will correspond to the conditions of existence, reproduction, and feeding of burrowing rodents, in this case, the northern mole vole. The agrochemical features of steppe landscapes and habitats of the northern mole vole *E. talpinus* in the Middle Volga region are considered as stable trends in the formation of steppe communities. The northern mole vole *E. talpinus* prefers soils with a neutral or slightly alkaline pH, moderate phosphorus and calcium content, high copper and manganese content, moderate zinc content, uncontaminated by heavy metals (sometimes with an excess of cadmium content in the ancient layers of the parent rock) and rather loose (from loose sand and sandy loam to light and medium loam), which is easily carried out when digging the burrow, easily digs and deepens, for arranging chambers and passages, when extracting rhizomes, tubers, and bulbs of fodder plants. In the studied region, the steppe mole vole is generally attached to steppe and steppe landscapes, forb-feather grass-fescue steppes on parent sand and sandstone, chalk rocks; it chooses burrowing sites with steppe vegetation of various options, preferring calciphilic and psammophilic associations. The mole vole, as well as other burrowing rodents, are indicators of steppe landscapes and the preservation of soil in their biotopes, which, in turn, are indicators of the preservation of steppe habitats. The type of soil, its main features, as well as landscape characteristics of the habitat are important regional diagnostic characters of *E. talpinus* colonies.

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Екологія сліпачка степового (*Ellobius talpinus*) у центральних областях ареалу: характеристика біотопів у місцях поселення виду

Єлєна Артем'єва

Резюме. Землерої-норники — головні творці, перетворювачі та зберігачі ландшафтів і ґрунтів степових екосистем. Сліпачок *Ellobius talpinus* (Pallas, 1770) — досить поширений вид землероїв-норників, індикаторний вид ссавців для різних типів степів, з виразною середовищетвірною активністю. Досліджено 14 великих колоній *E. talpinus* у Середньому Поволжі протягом польових сезонів 2006–2021. Агрохімічні показники ґрунту характеризують можливість розвитку окремих степових мікростацій, на яких сформовані специфічні рослинні асоціації. Показники зразків ґрунту та їх комбінації свідчать про придатність утворення тих рослинних асоціацій, які відповідатимуть умовам проживання та розмноження, живлення норників — у даному випадку сліпачка. Сталими тенденціями у формуванні степових угруповань є агрохімічні особливості степових ландшафтів і біотопів сліпачка *E. talpinus* у Середньому Поволжі. Сліпачок *E. talpinus* віддає перевагу облаштуванню нір у ґрунтах з нейтральним або слаболужним pH, помірним вмістом фосфору та кальцію, високим вмістом міді та марганцю, помірним вмістом цинку, незабрудненому важкими металами (іноді з надлишком кадмію в давніх шарах материнської породи) і досить пухких (від пухких пісків і супісків до легких і середніх суглинків), які легкі для риття підземних ходів, довгих тунелей та облаштування камер, викопування кореневищ, бульб і цибулин кормових рослин. У досліджуваному регіоні сліпачок в основному приурочений до степових і степових ландшафтів, різнотравно-ковилових і злаково-типчакових степів на материнських пісках і пісковиках, крейдяних породах, обираючи місця для норіння зі степовою рослинністю різних варіантів і віддаючи перевагу кальцифільним та псамофільним асоціаціям. Сліпачок, як і інші підземні гризуни, є індикатором степових ландшафтів і збереженості корінних ґрунтів, які у свою чергу є показниками збереженості степових біотопів. Тип ґрунту, його основні характеристики та ландшафтні характеристики біотопу є важливими регіональними діагностичними особливостями поселень *E. talpinus*.

Ключові слова: сліпачок, землерої-норники, фауна, біотоп, ґрунт, ландшафт, степ, Середнє Поволжя.

Introduction

The northern mole vole *Ellobius talpinus* (Pallas, 1770) (Rodentia, Cricetidae) is a widespread species, typical for the steppes, which are now being aggressively developed by humans. The northern mole vole through most of its range is represented by the nominative subspecies *Ellobius talpinus talpinus* (Pallas, 1770) [Zubko 1940; Pavlinov *et al.* 2002; Pavlinov & Lisovsky 2012].

The species is widely variable with different forms of fur colouration (from light beige to black). The species has different body measurements. Individuals of both small and large sizes are found throughout the range. The species is represented by two geographical forms corresponding to two subspecies inhabiting the western and central parts of the range. In the western parts of the range (east and south of Ukraine, including Donets basin, Lower Dnipro region, Azov Region and Steppe Crimea), it is represented by the subspecies *Ellobius talpinus tanaiticus* Zubko, 1940.

It is an indicator species in ecological studies of the steppes [Zagorodniuk 1999; Kondratenko & Zagorodniuk 2006; Korobchenko *et al*. 2010] and a model object of palaeontological studies of the fauna of the Quaternary period [Topachevsky & Rekovets; Vinogradov & Gromov 1952]. It is easily vulnerable species living in virgin steppes. With fresh ploughing of steppes, the species can live only one to two seasons. The species is very sensitive to habitat changes. It requires obligatory living conditions: maintenance of food supply [Sakhno 1971, 1978; Korobchenko 2008] and uncontaminated soils. It does not settle in areas that have been cultivated for a long time [Tovpinets 1993].

The species shows little terrestrial activity. As a rule, the animals spend most of the time underground in their burrows. The key features of the biology and ecology of the species are associated with the choice of certain habitats. In a wide range, habitat preferences of the species change; it leaves its usual habitats. In the central areas of the range, the choice of habitats is stable.

In the Middle Volga region, the northern mole vole lives only in the Right Bank, on virgin lands [Abrakhina *et al.* 1993]. The main diet of mole voles is the underground parts of plants: bulbs, rhizomes, and tubers. It prefers irises, garlic, onions and tulips [Elina *et al.* 2016], gladioli, rhizomes of cereals, aerial parts of herbaceous plants. The range of fodder plants is wide and includes most plant species that occur in burrow-suitable habitats [Sakhno 1971, 1978].

The aim of the article is to study the ecology of the northern mole vole *E. talpinus* in the central region of its geographic range.

Materials and Methods

During the field seasons of 2006–2021, mapping and survey of *E. talpinus* settlements, collection and laboratory analysis of soil samples were carried out in the following areas of the Ulyanovsk region, Russia: Arbuginska Steppe, Vyrystaykinska Steppe, and Shilovska Forest-steppe in the Sengileevskie Mountains National Park of the Sengileevsky district); Marievska Steppe, Vasilevska Steppe, and Surulovska Forest-steppe in the Novospassky district; Akulovska Steppe and Varvarovska Steppe in the Nikolaevsky district; Oktyabrska Steppe and Bogdanovsky Reserve in the Radishchevsky district; Bakhteevsky Ridges Reserve in the Starokulatkinsky district; Shikovska Steppe and Andreevska Steppe in the Pavlovsky district.

The number of individuals in *E. talpinus* settlements was estimated according to previously developed methods, as for the western parts of the species range [Korobchenko 2008; Korobchenko & Zagorodniuk 2008; Zagorodniuk & Korobchenko 2008*a–b*] and for the eastern parts of the range [Chernogaev 1981; Evdokimov & Pozmogova 1998]. For the eastern parts of the range, a method for counting colonies of the species was developed [Evdokimov 1997, 2001].

Route survey was carried out on a 367.2 km long distance by walking and on a 2478.5 km route by car. The choice of routes was dictated by the study of the preservation of the habitats of the species, that is, the search for primary indigenous steppe sites that have been preserved in the studied region. The author understands a colony as a group of settlements of a species. Large colonies mark 6 populations of the studied region. A total of 6 populations, 13 colonies, and 102 settlements of this species were studied on a total area of 3.927 km^2 (steppes make up 1862.5 km^2 or 5% of the total area of the study region). Eleven soil samples were analysed; one from each colony marking the population (Table 1). The identification of plants was carried out according to Maevsky [2006] and Blagoveshchensky [1984]. A list of 17 reference points (coordinates) of the studied territories of the Middle Volga region is presented in Table 1.

The collection and analysis of photographs of mole voles living in different types of soils was carried out. According to the photographs of the colour phenotypes of *E. talpinus*, the correspondence of the colour phenotype to a certain type of soil was revealed. Photos were taken from publica domain sources (OSINT): 250 photos.

Study of the soil cover of *E. talpinus* colonies. Soil types, its main characteristics, and assessment of the condition of *E. talpinus* colonies in the Middle Volga region were determined. Soil samples were taken from the sites of population groups of the species according to the standard method, the mechanical composition of the soil and the content of heavy metals, micro- and macroelements were determined from the soil dumps of the mole vole in the sites of its settlements in burrow-suitable habitats [Artemieva 2022*a*].

Mapping of animal habitats. Field observations and mapping of habitats with mole vole settlements were carried out using GIS-technologies. Thus, to identify colonies of *E. talpinus* in the Middle Volga region, a general map of animal habitats was developed based on special maps and atlases: general geographic and topographic maps of the Ulyanovsk region, soil, geological, landscape maps, etc. (see below) [Artemieva *et al.* 2018]. Further, in accordance with the topic of this study, private maps were prepared: maps of specific settlements of the species with the indicated points of their locations. Light green colour shows areas of preserved native steppes under typical steppe vegetation. All other types of animal habitats have been removed from the map to avoid excessive visual variegation, distracting attention.

Table 1. Results of the analysis of soil samples and the degree of availability (total content of mobile forms of mineral substances) in the habitats of *E. talpinus* colonies in the Middle Volga region

Таблиця 1. Результати аналізу ґрунтових проб та ступінь забезпеченості (валовий вміст рухомих форм мінеральних речовин) у біотопах з розташуванням колоній *E. talpinus* у Середньому Поволжі

No. of samples, date	Location, coordinates	Habitats, station	Soil type	No. in Tables 3–4
1. 3.05.2009	near the village of Vyrystaikino, Sengileevsky district; 53.823083 N, 48.930972 E	feather grass-tyrsa-fescue steppe	sandy loam	–
2. 6.05.2009	near the village of Bakhteevka, Starokulatkinsky district; 52.755083 N, 47.761722 E	petrophytic steppe, the foot of the chalk hills	carbonate chernozem	–
3. 9.05.2009	near the village of Shikovka, Pavlovsky district; 52.630028 N, 47.41175 E	petrophytic steppe	carbonate chernozem	–
4. 10.05.2009	near the village of Nova Andreevka, Pavlovsky district; 52.647250 N, 47.408028 E	petrophytic steppe	carbonate chernozem	–
5. 4.05.2010	near the village of Marevka, Novospassky district; 53.131306 N, 48.125889 E	sandy steppe	sands, sandy loam	–
6. 5.05.2010	near the village of Vasilevka, Novospassky district; 53.059611 N, 48.044194 E	sandy steppe	sands, sandy loam	–
7. 28.07.2016	near the village of Varvarovka, Nikolaevsky district; 53.105722 N, 47.480528 E	sandy steppe	sands, sandy loam	–
8. 24.08.2017	near the village of Staroe Zelenoe, Starokulatkinsky district; 52.801083 N, 47.815694 E	petrophytic steppe, the foot of the chalk hills	humus-calcareous soils	9
9. 20.05.2018	near the village of Surulovka, Novospassky district; 53.058917 N, 47.741306 E	petrophytic steppe, the foot of the chalk hills	carbonate chernozem	–
10. 20.05.2018	near the village of Solovchikha, Radishchevsky district; 52.968322 N, 47.801761 E	petrophytic steppe, the foot of the chalk hills	carbonate chernozem	6
11. 5.05.2019	near the village of Shilovka, Sengileevsky district; 50.0081667 N, 48.6724444 E	feather grass-tyrsa-fescue steppe	sandy loam	–
12. 27.06.2019	near the village of Solovchikha, Radishchevsky district; 52.968322 N, 47.801761 E	petrophytic steppe, the foot of the chalk hills	chalky chernozem soils	7
13. 28.06.2019	near the village of Sytinka, Pletma, Pavlovsky district; 52.618211 N, 46.824172 E	valley of the Kasley-Kadada river, floodplain meadow	chalky chernozem soils, sandy outcrops, sandstones	11
14. 29.06.2019	Akulovska Steppe SPNA, Nikolaevsky district; 53.081478 N, 47.385078 E	stone chalk steppe, chalk outcrops, old chalk quarry	chalky chernozem soils	3
15. 29.06.2019	Akulovska Steppe, Nikolaevsky district; 53.101194 N, 47.365972 E	sandy steppe, outcrops of brown sands and drain sandstones	sandy soils	4
16. 29.06.2019	Akulovska Steppe, Nikolaevsky district; 53.101194 N, 47.365972 E	sandy steppe, outcrops of pink ferruginous sands	sandy soils	5
17. 9.09.2019	Arbuginska Steppe, Sengileevsky district; 54.1122222 N, 48.5734722 E	feather grass-tyrsa-fescue steppe	sandy loam	1
18. 11.06.2020	near the village of Staroe Zelenoe, Starokulatkinsky district; 52.801083 N, 47.815694 E	petrophytic steppe, the foot of the chalk hills	carbonate chernozem	10

No. of samples, date	Location, coordinates	Habitats, station	Soil type	No. in Tables 3–4
19. 14.06.2020 13.07.2021	near the village of Oktyabrsky, Radishchevsky district; 53.017569 N, 47.926746 E	Oktyabrsky pond, halophyte meadow	chernozem	8
20. 1.08.2021	near the village of Mordovo, Sengileevsky district; 54.344475 N, 49.4851139 E	Mordovian Bay, halophytic meadow	chernozem	2

The map scale of 1 : 500 000 makes it possible to simultaneously reflect the existing patterns in the distribution of animals and the most fully characterise their living conditions. Visual interpretation of natural differences (a special term for visual spatial differences in the surfaces of photographs of biotopes, adopted in GIS-technologies) was carried out according to their structure, geometry, and colour based on Landsat multispectral images (Landsat 4.5 TM, Landsat 7 ETM+, Landsat 8 OLI/TIRS); medium and high resolution program Google Earth 6.1. The georeferencing of the points was made with the help of satellite GPS navigators. For all natural types of landscapes, the level of their anthropogenic transformation was necessarily taken into account.

The basis for creating a map of the natural landscape complexes of the region under study are satellite images of the Landsat program, up-to-date satellite imagery data from the USGS (Science for a changing world) website, U.S. Department of the Interior (http://www.usgs.gov/); website of GloVis, U.S. Department of the Interior (http://glovis.usgs.gov/), and Earth Explorer (http://earthexplorer.usgs.gov/). The collected material was processed and analysed using the Google Earth and SAS programs Planet. As a topographic basis for field work and subsequent processing of the material, atlas maps at a scale of 1 : 200 000 and 1 : 100 000, a forest map of the Ulyanovsk region at a scale of 1 : 200 000 and 1 : 100 000, and Landsat/ETM+2000 satellite images were used.

Point descriptions are the information base of the database created in Google Earth 6.1. The number of described points is 308; they cover almost all areas of the studied region. In general, 858 images of the study area were analysed. Skectch maps were compiled using ArcGIS 10.2 and Google Earth Pro 7.3.3.7786 software and graphic editors.

Results

Colonies of the northern mole vole

The section presents data on the spatial position of *E. talpinus* colonies in the studied territory of the Middle Volga region, landscape and soil features of the areas where they are located. The data is given in chronological order. Steppe maps of the studied region show areas of colonies and individual settlements of *Ellobius talpinus* (Fig. 1).

The studied region is located between the forest and the steppe zones and is part of the forest-steppe zone. In the territory of the Ulyanovsk region, two provinces of the forest-steppe landscape zone can be distinguished: the Volga Upland (Right Bank) and the forest-steppe of the Lower Volga region (Left Bank), as well as a transitional territory between the Lower and Upper Volga regions—the area of the Kondurcha River (Left Bank). In the territory of the Ulyanovsk region, two natural regions have been identified: Predvolzhsky and Zavolzhsky. Predvolzhsky lies entirely within the central part of the Volga Upland, whereas Zavolzhsky in the low valley of the Volga River [Artemieva *et al*. 2018].

The structure of the Predvolzhsky natural complex includes various forest-steppe and steppe ecosystems of the Right Bank: upland cretaceous pine and pine-broad-leaved, broad-leaved-pine and broad-leaved forests, steppes. The Zasyzran steppe ecosystems include shrub, stony chalk, sandy, clay, saline steppes and their mixed variants. The Zavolzhsky natural complex includes flat forest and steppe ecosystems of the Left Bank: floodplain pine and broad-leaved, mixed forests, floodplain meadows, and preserved areas of primary feather-grass-fescue steppes [Artemieva *et al.* 2018]. The mole voles live only in the steppes of the Right Bank, but not of the Left Bank.

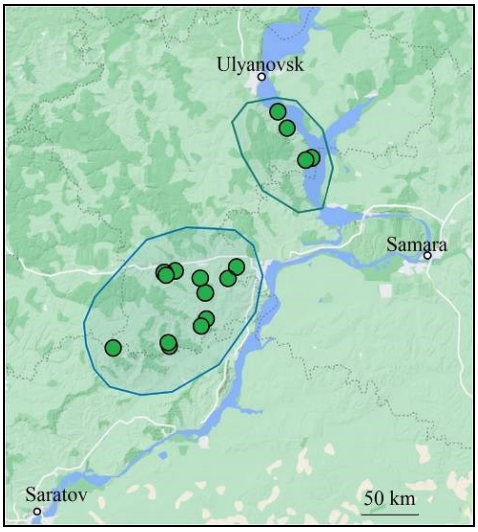

Fig. 1. Map of the study areas of *E. talpinus* in the Middle Volga region (GIS resources of Google were used: https://bit.ly/3HK7em9).

Рис. 1. Карта-схема районів дослідження *Ellobius talpinus* у Середньому Поволжі (використано ГІС-ресурси Google: https://bit.ly/3HK7em9).

The area of preserved primary steppes in the studied region is 1862.5 km^2 or 5 % of the total area of the region. The terrain in the habitats of the mole vole is steppe areas under typical vegetation, sometimes in combination with forest pegs, as well as hayfields and pastures on steppe lands. At present, a significant area of the indigenous steppes has been ploughed up and turned into agricultural landscapes. They were preserved mainly in places not suitable for farming: along the slopes of gullies and ravines, forest edges, roadsides, and small watersheds. The type of steppe vegetation depends mainly on edaphic (soil-ground) conditions.

Sandy and stone chalk steppes occupy the poorest soils and ground substrates. Psammophyte steppe areas are formed on sandy soils, as a rule, on the site of flattened pine forests. Petrophytic steppes are distributed only in the Predvolzhsky region and cover the southern areas of the Middle Volga under study. They are usually located on strongly gravelly, even skeletal soils on chalk slopes of the southern exposure and petrophytic areas of vegetation along the slopes of river valleys (Sura and Inza rivers). Shrub steppes are rarely located on the slopes of the northern exposure. The steppe areas occupy the largest area in Sengileevsky, Novospassky, Nikolaevsky, Radishchevsky, Starokulatkinsky, and Pavlovsky districts.

Sengiley population

The Sengiley population unites four large colonies of the species (Fig. 2).

Vyrystaikino colony of *E. talpinus*. Located near the village of Vyrystaikino of the Sengileevsky district, Tubaik ravine (Vyrystaykinska Steppe SPNA, cluster of the Sengileevsky Mountains National Park).

> Landscape areas in the locations of the settlements: rocky chalk steppe on hills, feather grass-fescue, feather-grass and fescue steppes with tyrsa, feather-grass-fescue-crinitaria steppes with pinnate feather grass *Stipa pennata* L. Background vegetation includes bulbous and rhizomatous ephemeroids; prostrate twig *Kochia prostrata* (L.) Schrad., spring adonis *Adonis vernalis* L. [Artemieva *et al*. 2017].

Shilovka colony of *E. talpinus*. Located in the territory of the Shilovska Forest-steppe SPNA of the Sengileevsky district (a cluster of the Sengileevsky Mountains National Park).

> Landscape areas in the locations of the settlements: tyrs and tyrs-fescue steppes with tyrsa *Stipa capillata* and fescue *Festuca valesiaca*, with pinnate feather grass *Stipa pennata* L. [Artemieva *et al.* 2017]. Background vegetation: hill violet, dwarf iris, *Potentilla vernalis*, *Scorzonera austriaca*, *Astragalus testiculatus*, *Ephedra dystachya*, russian hazel-grouse, *Alyssum lenense*, etc.

Arbuga colony of *E. talpinus*. Located in the territory of the Arbuginskaya Steppe protected area of the Sengileevsky district (a cluster of the Sengileevsky Mountains National Park).

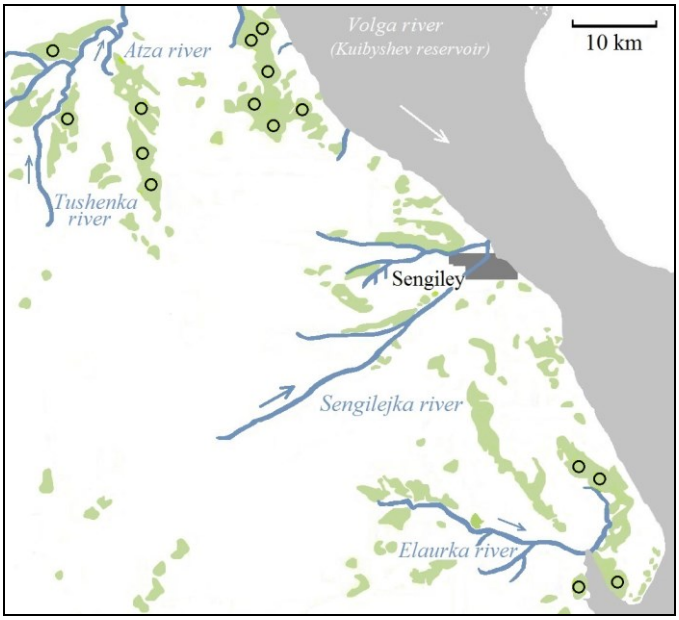

Fig. 2. Sketch-map map of *E. talpinus* settlements in the Sengileevsky district: Shilovska, Tushninska colonies; Vyrystaykinska, Mordovian colonies. The circles show the settlements in the steppe areas.

Рис. 2. Карта-схема поселень *Ellobius talpinus* у Сенгілеївському районі: Шиловська, Тушнінська колонії; Виристайкінська, Мордовська колонії. Кружками показано поселення на степових ділянках.

Landscape areas in the locations of the settlements: tyrsa and tyrsa-forb steppes with *Stipa capillata*, pinnate feather grass steppes with *Stipa pennata*, shrub steppes with *Spiraea crenata*, tyrsa-rump and meadow brome-forb steppes with coastal rump *Bromopsis riparia*. Background vegetation includes *Fritillaria ruthenica*, *Goniolimon elatum*, *Hedysarum grandiflorum*, *Scabiosa isetensis*, *Iris pumila*, *Pimpinella titanophila*, *Onosma simplicissima*, *Gypsophyla altissima*, and *Ephedra distachya* [Artemieva *et al.* 2017].

Mordovo colony of *E. talpinus*. Located on the shore of the Mordovian bay near the village of Mordovo of the Sengilevsky district.

Landscape plots in the locations of the settlements: a halophyte meadow along the shore of the Mordovia bay of the Kuibyshev Reservoir. Background vegetation includes yellow iris, *Lythrum salicaria*, riparian and meadow rhizomatous plant species.

Novospassky population

The Novospassky population includes three colonies of the mole vole (Fig. 3).

Surulovka colony of *E. talpinus*. Located in the territory of the Surulovskaya Forest-steppe protected area of the Novospassky district.

Landscape areas in the settlements: sandy steppe with *Cleistogenes squarrosa*, *Helichrysum arenarium*, *Sedum acre*; relic steppes with sheep *Helictotrichon* associations on the cretaceous eluvium. Background vegetation includes *Hedysarum grandiflorum*, *Scabiosa isetensis*, *Onobrychis arenaria*, etc.

Marevka colony of *E. talpinus*. Located in the territory of the Maryevska Steppe protected area of the Novospassky district.

Landscape areas in the locations of settlements: steppe petrophytic communities of clay and carbonate substrates, solonets and solonchak communities; fescue, fescue-forb, feather grass and feather-grass-forb steppes, with *Festuca valesiaca* and *Stipa capillata*, and *Stipa pennata* [Artemieva *et al.* 2017]. Background vegetation includes *Goniolimon elatum*, *Artemisia sanionica*, *Kochia prostrata*, *Limonium gmelinii*, *Salicornia europaea*, *Suaeda prostrata*, *Bassia sedoides*, *Amygdalus nana*, *Fritillaria ruthenica*, and *Tulipa biebersteiniana*.

Vasilevka colony of *E. talpinus*. Located in the territory of the Vasilevska Steppe SPNT of the Novospassky district.

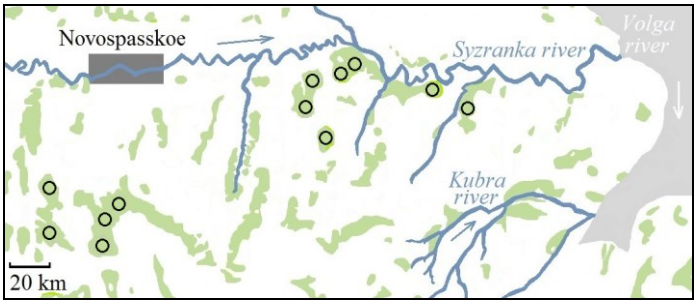

Fig. 3. Sketch-map of *E. talpinus* settlements in the Novospassky region: Maryevska and Vasilyevska colonies. The circles show the settlements in the steppe areas.

Рис. 3. Карта-схема поселень *Ellobius talpinus* у Новоспаському районі: Мар'ївська та Василівська колонії. Кружками показано поселення на степових ділянках.

Landscape areas in the locations of settlements: steppe petrophytic communities of clay and carbonate substrates, solonets and solonchak communities; fescue, fescue-forb, feather grass and feather-grass-forb steppes with *Festuca valesiaca*, *Stipa lessingiana*, and *Stipa capillata* [Artemieva *et al.* 2017]. Background vegetation includes *Palimbia salsa*, *Astragalus ucrainicus*, *Ferula caspica*, *Atraphaxis frutescens*, *Dianthus leptopetalus*, *Astragalus macropus*, *Jurinea multiflora*, *Kochia prostrata*, *Artemisia sanionica*, *Hedysarum grandiflorum*, *Iris pumila*, *Salvia nutans*, *Valeriana tuberosa*, and *Tulipa biebersteiniana*.

Nikolaevka populaition

This population includes two large colonies of the species (Fig. 4).

Akulovka colony of *E. talpinus*. Located in the territory of the Akulovska Steppe protected area of the Nikolaevsky district, which is situated on the watershed of the right bank of the Ardovat River (right tributary of the Kanadei River), 8 km south of the village of Praskovyino and 4 km west of the village of Kuroedovo of the Nikolaevsky district. The settlement Akulovka and the chalk factory do not currently exist, only the old chalk quarry has survived.

Landscape areas in the locations of the settlements: indigenous tyrso-fescue and tyrs steppes, slightly disturbed stony steppes on chalk substrates, feather-grass-fescue, brome, tyrs, pinnate-feather grass, oats, stony forb steppe communities; sandy steppes with *Festuca polesica*, *Stipa pennata*, *Cleistogenes squarrosa*, steppes dominated by *Bromopsis riparia* and *Phleum phleoides*, sheep and sheep-forb steppes with *Helictotrichon desertorum* [Artemieva *et al.* 2017]. Background vegetation includes endemic *Linaria volgensis, Alyssum gmelinii, Scorzonera ensifolia*, endemic *Dianthus volgicus*, *Matthiola fragrans*, *Allium tulipifolium*, *Oxytropis hippolyti*, *Clausia aprica*, etc.

Varvarovka colony of *E. talpinus*. Located in the territory of the Varvarovska Steppe protected area of the Nikolaevsky district, 4 km north-east of the village of Kuroedovo of the Nikolaevsky district.

Landscape plots in the locations of the settlements: feather grass-fescue and sandy steppes, feather-grass-fescue, brome, tyrs, pinnate-feather grass, ovsets, communities; sandy steppes with *Festuca polesica*, *Stipa pennata*, *Cleistogenes squarrosa*, *Bromopsis riparia*, sheep-forb steppes with *Helictotrichon desertorum* [Artemieva *et al*. 2017]. Background vegetation includes endemic *Linaria volgensis*, *Alyssum gmelinii*, *Scorzonera ensifolia*, endemic *Dianthus volgicus*, *Matthiola fragrans*, *Hedysarum grandiflorum*, *Nepeta ucranica*, *Campanula sibirica*, *Thalictrum minus*, *Syrenia cana*, *Scabiosa isetensis*, *Salvia stepposa*, *Adonis rosverna*, and *Phlomis rosverna*, *Phlomis pungens*, *Veronica spicata*, *Euphorbia seguieriana*, *Gypsophyla altissima,* and *Onosma simplicissima*, *Clausia aprica*, etc.

Radishchevo population

The Solovchikhinska and Oktyabrska colonies are the largest in this population (Fig. 5).

Solovchikha colony of *E. talpinus*. Located in the territory of the Bogdanovsky Reserve, near the village of Solovchikha of the Radishchevsky district.

Landscape areas in the locations of the settlements: rocky chalk forb steppes with *Stipa pennata*, *Cleistogenes squarrosa*, tyrsa steppes. Background vegetation includes calciphils: *Adonis vernalis*, *Polygala. sibirica*, *Scabiosa isetensis*, *Globularia punctata*, *Thymus cimicinus*, *Salvia nutans*, *Centaurea ruthenica*, *Artemisia armeniaca*, *Artemisia sericea*, *Iris pumila*, and *Iris aphylla*.

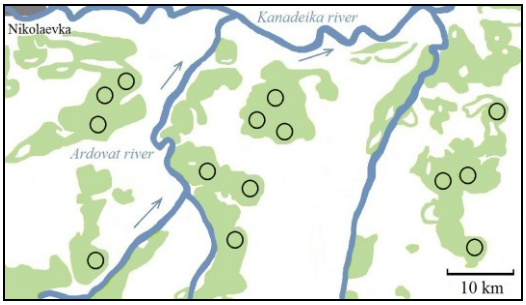

Fig. 4. Sketch-map of *E. talpinus* settlements in the Nikolaevsky region: Akulovska and Varvarovska colonies. The circles show the settlements in the steppe areas.

Рис. 4. Карта-схема поселень *Ellobius talpinus* у Миколаївському районі: Акулівська, Варварівська колонії. Кружками показано поселення на степових ділянках.

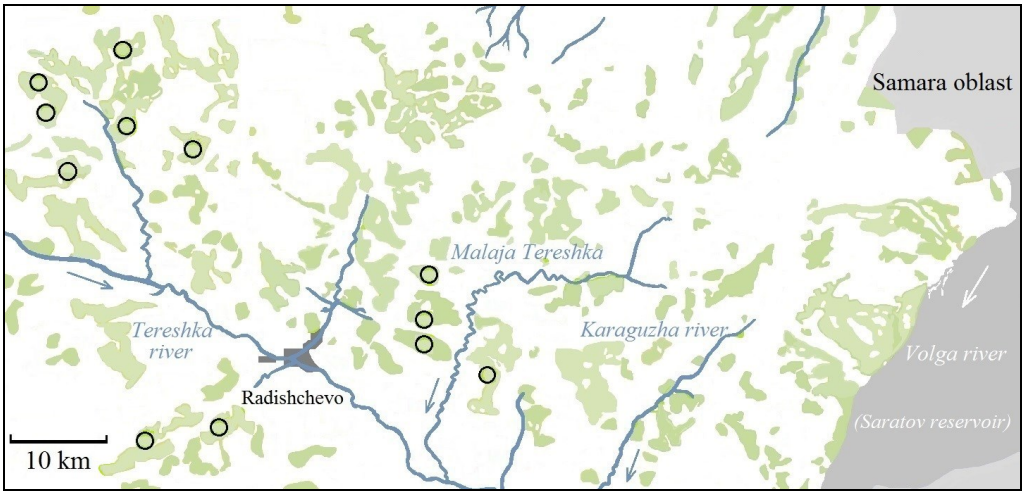

Fig. 5. Sketch-map of *E. talpinus* settlements in the Radishevsky district. The circles show the settlements in the steppe areas.

Рис. 5. Карта-схема поселень *Ellobius talpinus* у Радищевському районі. Кружками показано поселення на степових ділянках.

Oktyabrvsky colony of *E. talpinus*. It is located on the coast of the Oktyabrsky pond of the Radishchevsky district.

Landscape plots in the locations of settlements: forb-feather grass-fescue steppe with *Stipa pennata*, *Festuca polesica*. Background vegetation: *Lathyrus tuberosus*, *Astragalus austriacus*, *Astragalus onobrychis*, *Melilotus officinalis*, *Melilotus albus*, *Melilotus volgicus*, *Verbascum orientale*, *Verbascum lychnitis*, *Savia tesquicola*, *Salvia stepposa*, *Inula helenium*, *Senecio schvetzovii*, etc.

Stara Kulatka population

The largest colony of this population is the Bakhteevka colony (Fig. 6).

Bakhteevka colony of *E. talpinus*. Located in the territory of the Bachteevsky Ridges Reserve protected natural area of the Starokulatkinsky district.

Landscape areas in the locations of the settlements: feather-grass-forb steppes with *Stipa pennata*, forb stony steppes with *Globularia punctata*, *Koeleria sclerophylla*. Background vegetation includes *Paeonia tenuifolia*, *Viola tanaitica*, *Crambe tataria*, *Hedysarum grandiflorum*, *Astragalus cornutus*, *Astragalus henningii*, *Linum ucranicum*, *Cephalaria uralensis*, *Veronica jacquinii*, *Salvia nutans*, *Iris aphylla*, etc.

Pavlovka population

The Shikovska colony is the most significant in the Pavlovka population (Fig. 7).

Shikovka colony of *E. talpinus*. Located in the Shikovska Steppe and Andreevska Steppe protected areas near the villages of Shikovka and Nova Andreevka of the Pavlovsky district.

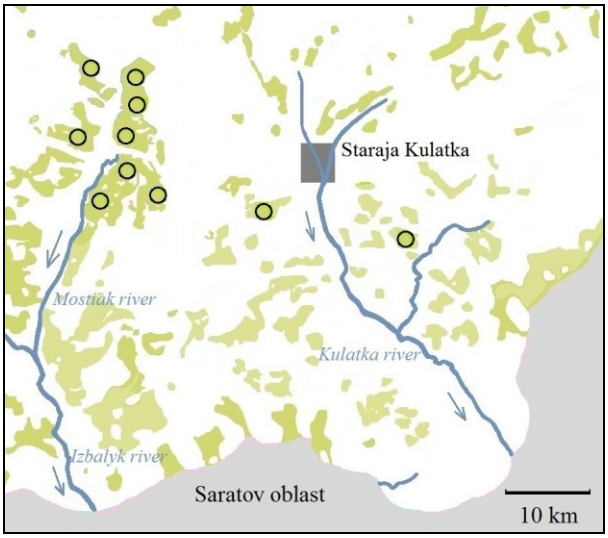

Fig. 6. Sketch-map of *E. talpinus* settlements in the Starokulatkinsky district. The circles show the settlements in the steppe areas.

Рис. 6. Карта-схема поселень *Ellobius talpinus* у Старокулаткінському районі. Кружками показано поселення на степових ділянках.

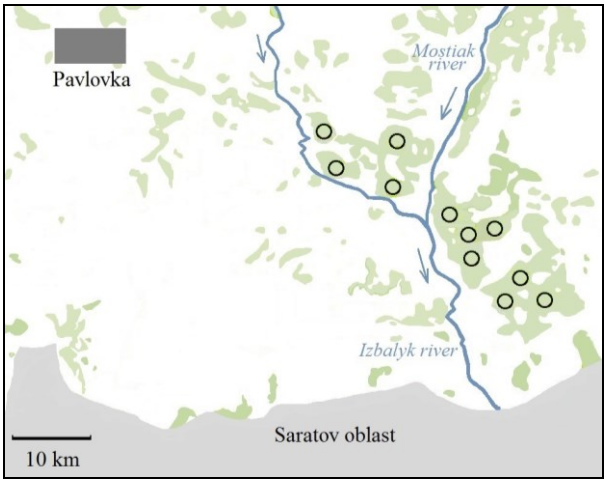

Fig. 7. Sketch-map of *E. talpinus* settlements in the Pavlovsky region. The circles show the settlements in the steppe areas

Рис. 7. Карта-схема поселень *Ellobius talpinus* у Павлівському районі. Кружками показано поселення на степових ділянках

Landscape areas in the locations of the settlements: stony, feather grass-forb, feather-grass-rump and shrub steppes, feather-grass-fescue-forb steppes with *Stipa pennata*, steppe solonetsous meadows [Artemieva *et al*. 2017]. Background vegetation includes *Iris pumila*, *Tulipa biebersteiniana*, etc.

Summary data

The data on the mole vole colonies are summarised in Table. 2.

The number of a completely developed family of *E. talpinus*, on average, is 15–20 individuals. The method for determining the abundance of *E. talpinus* is based on the fact that, on average, a young family comprises 3 to 6 individuals [Evdokimov 2001]. Therefore, the estimate of the total abundance of the species in the settlements is from 3 to 240 individuals, on average 121.5 individuals (1.215 ind./100 ha), 0.122 individuals per 1 ha (0.00122 ind./100 ha). The abundance of the species in the studied area is 0.031 ind./ha (0.00031 ind./100 ha) and in the area of preserved habitats of primary steppes (3.927 km^2).

The abundance of the species in the sandy steppes is 391 individuals per ha, or 0.329 individuals per ha (0.00329 ind./100 ha) on an area of 1187 m^2 (1.187 km^2). The abundance of the species in the stony cretaceous steppes is 701.5 ind./ha, or 0.288 ind./ha (0.00288 ind./100 ha) on an area of 2438 m^2 (2.438 km^2). The abundance of the species in halophyte meadows is 79 ind./ha, or 0.245 ind./ha (0.00245 ind./100 ha) on an area of 302 m^2 or 0.302 km^2. In the sandy steppes, 34 settlements were found on a total area of plots of 1187 m^2 (1.187 km^2). In the petrophytic steppes, 61 settlements

were noted on a total area of 2438 m^2 (2.438 km^2). On halophytic meadows, 7 settlements were recorded on an area of 302 m^2 (0.302 km^2). A total of 102 colonies of this species were identified on a total area of 3927 m^2 (3.927 km^2). Percentage of the number of settlements in different types of habitats is as follows: 59.80% of settlements were found in petrophytic steppes; 33.33% are located in sandy steppes; 6.87 % were recorded on halophytic meadows.

Table 2. Characteristics of *E. talpinus* colonies in the Middle Volga region

Таблиця 2. Характеристики колоній *E. talpinus* в Середньому Поволзі

No. of colony, habitat, soil type	Date of observation	Number of settlements / ha	Number of soil emissions	Settlement area square, m^2	Average number of individuals in the settlement	Average relative density, ind./km^2	Average relative density, ind./100 ha
1. Vyrystaikino colony, petrophytic steppe, carbonate chernozem	30.04.–3.05.2009	3	82	129	13	0.035	3.5
2. Shilovka colony, petrophytic steppe, carbonate chernozem	5.05.2019	6	210	276	11.7	0.104	10.4
	9.09.2019	2	39	126			
	8.05.2021	2	19	40			
				Σ 442			
3. Arbuga colony, feather petrophytic steppe, carbonate chernozem	9.09.2019	5	22	46	13.1	0.012	1.2
	8.05.2021	2	25	50			
				Σ 96			
4. Mordovo colony, halophytic meadow, chernozem	1.08.–2.09.2021	6	160	282	11.5	0.069	6.9
5. Surulovka colony, petrophytic steppe, carbonate chernozem	13–15.05.2017	5	165	363	16.4	0.035	3.5
	18–20.05.2018	3	102	250			
				Σ 613			
6. Marevka colony, sandy steppe, sands, sandy loam	2.05.2009	7	210	357	15.5	0.104	10.3
	1–4.05.2010	2	45	120			
				Σ 477			
7. Vasilevka colony, sandy steppe, sandy loam	1–4.05.2010	2	48	160	11.5	0.023	2.3
8. Akulovska colony, sandy steppe, pink ferruginous sands, sandy soils	8–13.06.2010	11	385	489	13.2	0.138	13.8
	27.07.2016	2	21	36			
				Σ 525			
9. Varvarovka colony, sandy steppe on brown sands, sands, sandy loam	8–13.06.2010	6	180	249	10.9	0.115	11.5
	28.07.2016	4	76	117			
				Σ 366			
10. Solovchikha colony, chalky steppe, carbonate chernozem	11–17.07.2006	2	25	37	14	0.092	9.2
	2.07.2010	2	23	34			
	13–15.05.2017	5	98	163			
	10–14.06.2020	2	26	32			
				Σ 266			
11. Oktyabrsky colony, halophytic meadow, chernozem	14.06.2020 13.06.2021	1	18	20	10	0.112	11.2
12. Bakhteevka colony, chalky steppe, carbonate chernozem	18–24.05.2009	10	285	337	14	0.138	13.8
	29.06.–5.07.09	1	49	164			
				Σ 501			
13. Shikovka colony, steppe, carbonate chernozem, sandy soils	5–10.05.2009	11	275	407	13.4	0.127	12.7
Total	25 observations	102	2588	4284	168.2	1.104	110.3
Average		7.85	199.1	329.5	12.94	0.085	8.485

Soil characteristics of habitats of *E. talpinus* colonies

The analysis of the composition of soil emissions at plots in the habitats of *E. talpinus* colonies in the study region was performed (Table 3–4). The primary analysis of the soils was carried out earlier [Artemieva 2022*a*], here is presented an update of the extended and more detailed analysis for the development of the study. This allows to show new provisions that have not previously been received and published.

In Table 3, the given K_2O values are not per 1 kg of native soil or per 1 kg of dry soil, but the total content of mobile forms of mineral substances (similarly for other characteristics). The indicators of potassium and phosphorus in the soil are quite high, which is associated with the presence in this area of remains of a farmer large village where cattle were bred, and an old chalk factory and a quarry, which are no longer functioning, as well as the close proximity of modern settlements with cattle farms. Phosphorus, potassium, trace elements are given in mg/kg, and calcium and magnesium are given in μmol/100 g, which is required by the method of chemical analysis (State standard).

The manganese levels are also quite high, which is associated with the features of rocks that underlie the soil in this area. The uniqueness of the Akulovska Steppe and the Varvarovska Steppe lies in the fact that the fault of the Zhiguli dislocation passes through this territory, which formed a characteristic chalk landscape with chalk and sand outcrops on the surface. Manganese compounds are part of fluorite veins, which are located near the fault of the Zhiguli dislocation, as well as in the composition of silicified flasks. Geomorphologically, the middle plateau (in the southern part) of the Volga Upland is developed here with absolute elevations of 200–225 m a.s.l, composed of chalks and marls of Upper Cretaceous age. In the northern part, on the surface, there are remains of the Paleogene cover, composed of confluent ferruginous sandstones and sands with a high content of iron, which gives the sands a characteristic pink-crimson hue, as well as silicified flasks, which also include manganese compounds.

This section of the middle plateau was formed in the Miocene. Therefore, the Paleogene sandy-stony deposits here have already been destroyed by denudation. To the west and south, the remains of Paleogene deposits are still preserved. Agricultural crops are cultivated on the plakor, under which complex mineral additives with microelements, including manganese, are applied. Rain streams wash the remains of the compounds down the chalk and sandy slopes and soak into the chalk rocks and linger there, and are quickly washed out of the sandy rocks by rainfall.

The range of soil characteristics of colony habitats is quite wide and includes characteristic features of both sandy and carbonate chernozem soil types, which indicates the presence of two types of settlements of the species. This is important for the understanding of habitat choice by the species.

The species *E. talpinus* shows plasticity in the choice of soil with a wide variation in chemical parameters. This allows the species to live not only in steppe communities, but also in anthropogenically modified ones: on fresh arable lands, in secondary and upland meadows, etc. The mole vole avoids monodominant reed grass wastelands (with *Calamagrostis epigeios*) due to the dense, difficult-to-pass sods of the reed grass and the absence of forbs as the basis of the food supply. The sites of each group of *E. talpinus* settlements are characterised by their own unique set of soil characteristics of the station, which determines the features of the landscape, vegetation and food supply, as well as the size and density of the colony. The species is extremely dependent on the quality of the soil environment. Under conditions of severe soil contamination, in particular heavy metals, the existence of the mole voles is impossible. Therefore, when assessing the state of the populations of the species, it is necessary to identify the level of heavy metal compounds in the soil (Table 4).

In the studed areas of *E. talpinus* settlements, the content of heavy metals does not exceed the permissible norms (the landscape and habitats are not contaminated with heavy metals). In two sites of settlements (Akulovka colony and Solovchikha colony), an excess of cadmium content was noted, which may be due to the presence of Jurassic and Triassic deposits of cretaceous rocks, Paleogene drain sandstones, and oil deposits.

In comparison with the central areas of the range, *E. talpinus* also prefers well-preserved habitats to settle in the conditions of the Southern Urals: sandy steppes on sandy loams, stony steppes.

Table 3. Results of the analysis of soil samples and the degree of availability (total content of mobile forms of mine?-al substances) in the habitats of *E. talpinus* colonies in the Middle Volga region

Таблиця 3. Результати аналізу ґрунтових проб та ступінь забезпеченості (валовий вміст рухомих форм мінеральних речовин) у біотопах колоній *Ellobius talpinus* у Середньому Поволзі

No. of soil samples, habitat, soil type	pH*	Organic matter %	P_2O_5 mg/kg, mobile	K_2O mg/kg, mobile	Ca μmol/ 100 g, ex-change	Mg μmol/ 100 g, ex-change	S mg/kg, mobile	Cu mg/kg	Zn mg/kg	Mn mg/kg	Mechanical composi-tion***, fraction <0.01 mm, %
1. Arbuga colony, feather petrophytic steppe, carbonate chernozem	7.5	6.0	40	>1000	24.7	1.9	4.0	2.9	3.2	22.0	33.6 medi-um loam
2. Mordovo colony, halophytic meadow, chernozem	6.4	10.6	80	310 >180	14.3	3.8	15.0 >12.0	6.6 >3.3	0.9 <2.0	38.2	35.5 medi-um loam
3. Akulovska colony, petrophytic steppe, carbonate chernozem	7.3	3.9	118	490	10.6	0.6	2.0	1.8	5.3	52.0	32.5 medium loam
4. Akulovska colony, sandy steppe, brown sands, sandy soils	7.3	0.6	50	8	3.7	0.4	1.0	0.8	1.2	6.7	3.2 loose sand
5. Akulovska colony, sandy steppe, pink ferruginous sands, sandy soils	6.1	0.0	15	15	9	0.5	7.5	0.2	0.5	1.5	1.0 loose sand
6. Solovchikha co-lony, chalky steppe, carbonate chernozem	7.3	8.8	80.0	450.0	17.0	1.5	9.0	2.8	9.00	51.0	35.4 medium loam
7. Solovchikha co-lony, chalky steppe, carbonate chernozem	6.5	21.8	220	330	16.1	1.4	6.0	5.2	16.2	118.0	28.9 light loam
8. Oktyabrsky co-lony, halophytic meadow, chernozem	7.4	6.1	20	780	24.6	2.4	7.0	4.7	4.4	34.1	55.0 heavy loam
9. Bakhteevka co-lony, chalky steppe, carbonate chernozem	7.1	15.9	78.0	430.0	32.1	1.5	4.0	1.6	5.3	31.3	23.1 light loam
10. Bakhteevka co-lony, chalky steppe, carbonate chernozem	7.6	6.0	55	180	16.3	0.9	3.0	1.9	4.9	39.8	36.4 medi-um loam
11. Shikovka colony, steppe, carbonate chernozem, sandy soils	5.7	1.6	140	255	10.2	2.2	4.0	2.5	1.23	7.8	13.9 sandy loam
Total: 11 samples; Lim	5.7–7.6	0.6–21.8	15–220	15–>1000	3.7–32.1	0.4–3.8	1.0–15.0	0.2–6.6	0.46–16.2	1.5–118.0	1.0–55.0
probability, p	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
State standard**	[1]	[2]	[3]	[4]	[5]		[6]	[7]	[8]	[8]	

Note: * For pH ≤ 7.0, determination of phosphorus content (P_2O_5) and potassium content (K_2O) was carried out according to the Chirikov method; for pH>7.0, the values are determined by the Machigin method; ** [1] State standard 26483-85; [2] State standard 26213-91; [3] State standard 26204-26205; [4] State standard 26204-91; [5] State standard 26487-85; [6] State standard 26490-85; [7] State standard 50684-94; [8] State standard 50686-94; [9] State standard 50685-94. *** Gradation of soil fractions of the mechanical composition: 5 to 10—connected sand; 10 to 20—sandy loam; physical clay particles <0.01 mm.

Table 4. Content of heavy metals (HM) in the analysed soil samples (total content of mobile forms of mineral substances) from the habitats of *E. talpinus* colonies in the Middle Volga region

Таблиця 4. Зміст важких металів (ТМ) у ґрунтових пробах (валовий вміст рухомих форм мінеральних речовин) у біотопах колоній *E. talpinus* у Середньому Поволзі

No. of soil samples, habitat, soil type	Cu, mg/kg	Zn, mg/kg	Pb, mg/kg	Cd, mg/kg	Ni, mg/kg
1. Arbuga colony, feather petrophytic steppe, carbonate chernozem	17.7	74.5	5.4	0.3	51.5
2. Mordovo colony, halophytic meadow, chernozem	17.1	30.3	10.9	0.5	55.5
3. Akulovska colony, petrophytic steppe, carbonate chernozem	9.2	85.6	24.7	5.6	31.6
4. Akulovska colony, sandy steppe, brown sands, sandy soils	2.0	8.9	2.8	0.4	13.7
5. Akulovska colony, sandy steppe, pink ferruginous sands, sandy soils	0.9	3.8	1.2	0.3	3.1
6. Solovchikha colony, chalky steppe, carbonate chernozem	12.8	33.8	31.0	3.9	53.5
7. Solovchikha colony, chalky steppe, carbonate chernozem	18.5	69.0	26.5	3.2	36.5
8. Oktyabrsky colony, halophytic meadow, chernozem	32.2	86.9	17.9	0.5	62.0
9. Bakhteevka colony, chalky steppe, carbonate chernozem	11.7	49.6	11.5	0.3	19.8
10. Bakhteevka colony, chalky steppe, carbonate chernozem	15.3	57.6	5.4	0.9	53.7
11. Shikovka colony, steppe, carbonate chernozem, sandy soils	6.4	16.2	5.7	0.8	10.7
Lim	0.87–32.2	3.8–86.9	1.2–31.0	0.285–5.6	3.1–62.0
Maximum allowable concentrations	55.0–132.0	100.0–220.0	32.0–130.0	2.0–3.0	80.0–85.0

The main characteristics of the soil of the settlement sites are neutral or slightly alkaline pH, high copper content, high manganese content, and the mechanical composition of the soil is from sandy loam to light loam. In the most extreme cases, the species may use a denser soil in the absence of a more suitable one: medium and even heavy loam. In the Orenburg region, the mole voles are also tied to steppe and steppe landscapes, forb-feather grass-fescue steppes on parent sandy and sandstone, chalk and red-coloured rocks. It chooses burrowing sites with steppe vegetation of various variants, preferring calciphilic and psammophilic associations.

The following plant species are characteristic for the mole vole station: *Salvia tesquicola*, *Taraxacum serotinum*, *Crinitaria villosa*, *Ceratoides papposa*, *Aster tripolium*, *Salicornia europaea*, *Tulipa scythica*, *Tulipa gesneriana*, *Gagea* sp., *Tanacetum millefolium*, *Tanacetum kittaryanum*, *Nedysarum grandiflorum*, *Hedysarum argyrophyllum*, *Nepeta ucranica*, *Onosma simplicissima*, etc. [Artemieva 2022*b*]. The station in the eastern regions of the range is shown in Fig. 8*e–f*.

Discussion

Number of colonies and edaphic factor

The species was first described from the Middle Volga region (Samara region) by P. S. Pallas in 1769. At present, *E. talpinus* is a rare endangered species everywhere. Over the past 20 years, the number of the mole vole throughout its range has significantly decreased, which is associated with the disappearance of suitable habitats. The species disappears as a result of the reduction of indigenous steppes. *E. talpinus* is a Neogene relic; colonies of this species mark refugia of ancient Neogene fauna and flora in the region [Beliakov 1976].

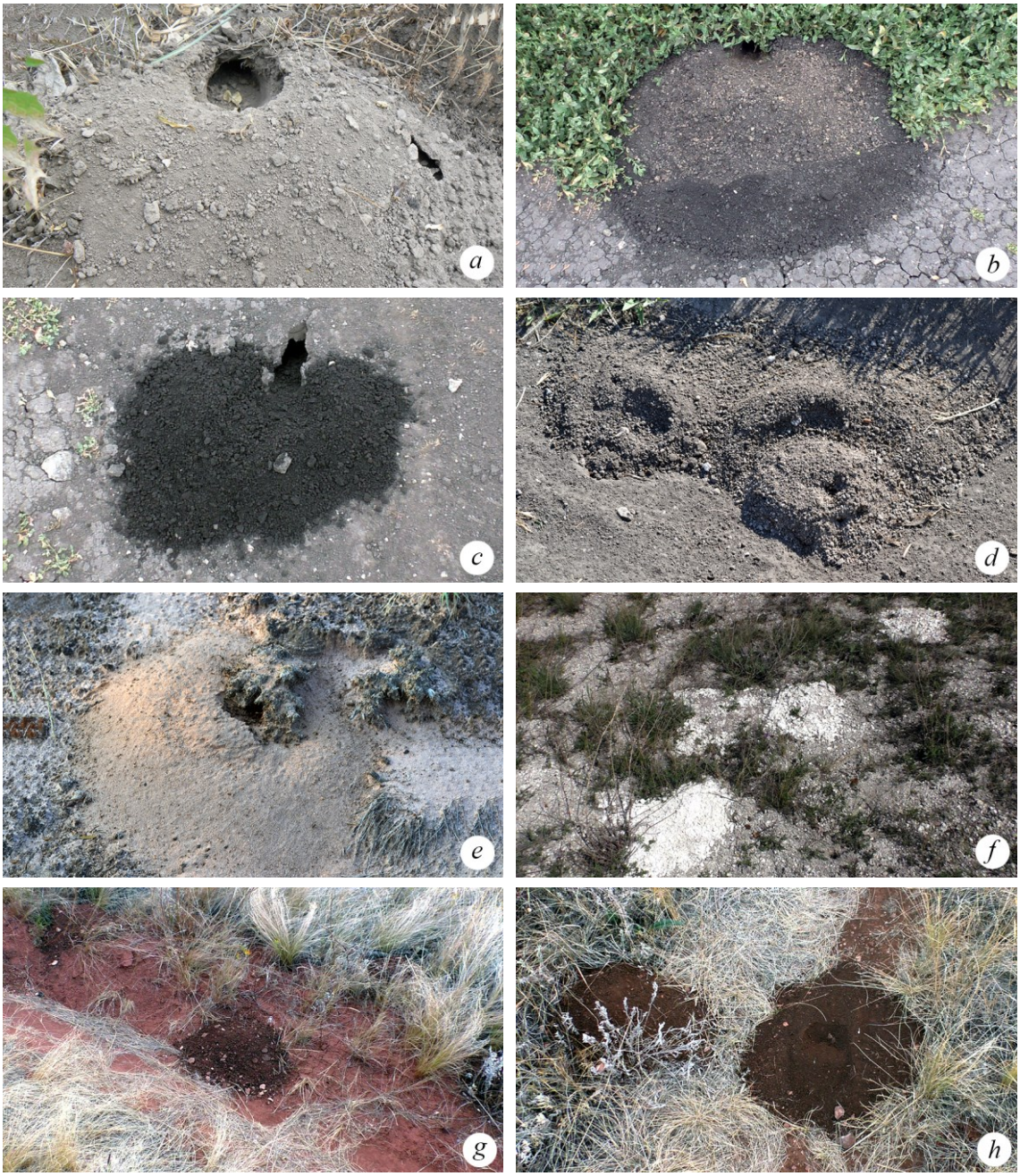

Fig. 8. Soil emissions and burrows of *E. talpinus*: *a*—Bogdanovsky Reserve SPNA, stony chalk steppe, carbonate chernozem, 02.07.2010; *b*—Oktiabrsky lake, halophytic meadow, clay loam, 13.07.2021; *c*—Oktyabrsky lake, stony chalk steppe, carbonate chernozem, 13.07.2021; *d*—Bachteevsky Ridges SPNA, stony chalk steppe, carbonate chernozem, 12.07.2021; *e*—Akulovska Steppe SPNA, sandy steppe, ferruginous sands, 27.07.2016; *f*—Surulovska Forest-steppe SPNA, cretaceous steppe, 20.05.2018; *g*—Orenburg region (Southern Urals), 14.09.2018; *h*—fescue-forb steppe with tulips, thin chernozems on Triassic redstones, 14.09.2018. Photo by the author.

Рис. 8. Викиди землі та нірки *Ellobius talpinus*: *a* — ООПТ «Богданівський заказник», кам'янистий крейдяний степ, карбонатний чорнозем, 02.07.2010; *b* — Октябрьський ставок, галофітний луг, суглинок, 13.07.2021; *c* — Октябрьський ставок, кам'янистий крейдяний степ, карбонатний чорнозем, 13.07.2021; *d* — ООПТ «Бахтеевские увалы», кам’янистий крейдяний степ, карбонатний чорнозем, 12.07.2021; *e* — ООПТ «Акулівський степ», піщаний степ, залізні піски, 27.07.2016; *f* — ООПТ «Сурулівський лісостеп», крейдяний степ, 20.05.2018; *g* — Оренбурзька область (Південний Урал), 14.09.2018; *h* — типчаково-різнотравний степ з тюльпанниками, малопотужні чорноземи на тріасових червоноцвітах, 14.09.2018. Фото автора.

The species was known to palaeontologists in Central Europe as widespread, but in recent decades it has literally 'melted' in nature. This is due to the catastrophic reduction of virgin steppes, the deterioration of soil quality, an increase in the degree of their pollution, a sharp reduction in the indigenous steppe vegetation and ploughing of the steppes. *E. talpinus* is a species hostage to the specifics of its ecology. The study of the key characteristics of its habitats (landscape, soil, vegetation, and food base) is the basis for monitoring and protecting its populations.

The species' abundance in the past was high, but it had begun to decline sharply by the middle of the last century. The species has become rare in the western and central regions of its range [Bazhanov 1930; Erofeev 1930; Stroganova 1954; Davidovich 1964]. The abundance of the species remains low [Oparin *et al*. 2010; Beliakov 1976; Vinogradov 1995]. In Ukraine, *E. talpinus* was a widespread species in the past [Charlemagne 1920; Pidoplichko 1930; Kryzhov 1936; Zubko & Ostriakov 1961], but is currently endangered [Tovpinets 1993; Zagorodniuk & Korobchenko 2008*a–b*; Korobchenko *et al*. 2010]. The prospects for the survival of a species are determined by its key needs: environment quality (soil, landscape) and food supply (vegetation). Respectively, its existence in nature will be possible only if there are preserved sections of the primary indigenous steppes.

Previously, it was shown that the populations of the mole vole on sandy arenas have a lower abundance, but a higher density compared to the settlements on chalk arenas, which is probably due to the lower density of the sandy substrate compared to the chalk soil [Artemieva 2022*a*].

The most important factor in the habitat for *E. talpinus* is the mechanical and chemical composition of the soil. The animals, of course, do not have special organs that analyse chemicals and trace elements. However, they practically unmistakably choose steppe areas suitable for their habitation, focusing on the vegetation (food base) suitable for them, which is formed on certain types of soils with a certain chemical composition.

The species *E. talpinus* prefers soils that are not contaminated with heavy metals (sometimes with an excess of cadmium content in ancient soil layers) and rather loose (as a rule, loose sand, sandy loam, light loam, medium loam). Such soils are easily excavated and brought to the surface when digging burrows and constructing underground passages and chambers. Similar results were obtained earlier for ground-nesting birds (Middle Volga region) [Artemieva & Kalinina 2018, 2019; Artemieva *et al*. 2020; Artemieva & Grudinin 2021].

Soil-ground substrates are important for the formation of the specificity of the mole vole settlements, tied to a certain composition of the soil. The edaphic factor also influences the choice of food objects of the species, as it is decisive in the formation of certain plant associations of the steppes. Two ecological groups of the mole vole live in the Middle Volga region, which are associated with sandy arenas (sandy steppes) and with chalk arenas (stone chalk steppes). In settlements on sandy arenas, the fur colouration of the animals has reddish-sandy tones. In settlements on chalk arenas (stone chalk steppes), the fur colouration has a dark grey tone or it is melanistic (black).

The edaphic factor on a wide geographical scale varies across landscape zones in accordance with the general law of zonation [Isachenko 1991]. The edaphic factor influences steppe communities, vegetation, and burrowers through the plant components of the biocoenosis. Specific plant associations are formed due to the diversity of habitat conditions, including soil, due to the selectivity of plants in a certain landscape-geographical zone towards them [Glazovskaya 2002]. In the same landscape zone, unequal soil conditions are created, which are reflected in the type of vegetation. This determines the spatial distribution of plants and burrowing animals [Sochava 1978; Milkov 1986].

Steppe Eurasia is a transcontinental megaregion stretching almost 9000 km across the entire continent with a heterogeneous strip up to 600 km wide in the latitudinal direction between 41°N and 56°N. This belt is united by modern and palaeohistorical exogenous processes, which determined the formation of loess and loess-like deposits, as well as erosional landscape genesis characteristic of arid and semi-arid climates [Chibilyov 2017]. The range of forest-steppe, steppe and desert-steppe landscapes forms an almost continuous mega-region of Inner Eurasia, which, in terms of natural history, is divided into three main sectors: western, central, and eastern. The western sector of Steppe Eurasia (East European steppe region) covers the forest-steppe, steppe, and desert steppe

of Eastern Europe (from the Carpathians to the Southern Trans-Urals, 3000 km long). The steppe zone of Eastern Europe covers the entire Black Sea region, Azov Sea, the southern outskirts of the Central Russian, Kalach, and Volga uplands, the Common Syrt and the South Urals with Mugodzhary. This territory is characterised by the development of powerful and high-humus chernozems (up to 2 m thick and 15%), which contribute to the formation of rich forb-grass steppes [Chibilyov 2017]. Representatives of the genus *Ellobius*, including *E. talpinus*, are distributed almost throughout the entire length of this megaregion.

The species *Ellobius talpinus* plays an environmental role in steppe communities. An example of a similar impact is the burrowing activity of the little ground squirrel *Spermophilus pygmaeus* (Pallas, 1778) in the Caspian Sea, which determines the structure of biogeocoenoses of semi-desert and arid steppes. In the same way, the steppe lemming *Lagurus lagurus* (Pallas, 1773) affects the levelling of vegetation in arid steppes [Zaletaev 1976; Mordkovich 1982]. The result of zoogenic environment formation can be considered as a new stage in the development of the zonal landscape [Zaletaev 1976]. The environmental activity of animals is the most important in open landscapes, primarily of desert and semi-desert [Zaletaev 1976], and steppe and forest-steppe [Pakhomov 1998; Bulachov & Pakhomov 2006; Pakhomov & Micheev 2007].

Ellobius talpinus as an index species and transformer of steppe landscapes

The area of *E. talpinus* settlements vary from 10–20 to 100 m^2 and up to several hectares. The height of soil emissions can reach 35 cm [Beliakov 1976; Vinogradov 1995]. The area of the steppe inhabited by mole voles is full of mounds. These mounds are traces of the underground activity of the animals. Lateral burrows and entrances to burrows are clogged with ground plugs. From the burrow of the mole voles, one can see a small earthen fountain. The animal quickly works with its hind legs. Dry earth is crushed by teeth into small lumps. Heaps of earth thrown out by mole voles look like a dune or a miniature volcano. The mole vole pushes the ground with its paws, destroying the hard soil with large, forward-facing incisors. The length of the underground passage is 1.5 m. The animals dig daily and in the surface layers of the soil, make long passages into the depths of the subsoil, transfer and crush huge masses of ground. A small family of mole voles covers more than 25 m^2 of the surface with heaps of soil over the summer [Formozov 2006].

Colonies of *E. talpinus* are confined to the forest-steppe and steppe landscapes of the Right Bank of the Middle Volga region (Fig. 9*a*). The lower plateau of the Middle Volga region is mainly composed of chalk deposits, where ploughed open spaces predominate on chernozem and humus-calcareous soils. The area of development of ancient accumulative Volga terraces is composed of sandy and loamy deposits. Chernozem soils formed under the steppe vegetation [Natural… 1978; Mil'kov 1986; Artemieva *et al.* 2017].

Settlements of *E. talpinus* are confined to ancient territories that were under the influence of geological processes during the Paleocene period, parent rocks (rocks underlying soil horizons). Relic settlements of the mole vole exist on ancient sands, sandstones, and components of the cretaceous system (chalk, marl) (Fig. 9*b*). The mole vole settlements in areas of indigenous steppes are of ancient origin and of relic nature. The surviving fragments of the indigenous steppes are refugia of the core of calciphilic and psammophilic communities in the region. Settlements of *E. talpinus* are associated with certain types of soil: typical chernozems, especially calcareous ones (Fig. 8*a–d*), which were formed under the long-term influence of steppe vegetation, less often solonetzes and solods (Fig. 9*c*), calcareous soils (in areas with outcrops of cretaceous rocks).

The settlement areas of *E. talpinus* are quite conservative in time, confined not only to the currently preserved areas of steppe vegetation, but also to those that are located on former steppes, which indicates the presence of some kind of ‘ecological memory’ of the species. The surviving areas of primary steppes and meadows include forb meadow steppes, saline meadow steppes, moderately arid forb-fescue-feather grass steppes, steppe meadows, and halophytic meadows in the floodplains of steppe water bodies (Fig. 9*d*).

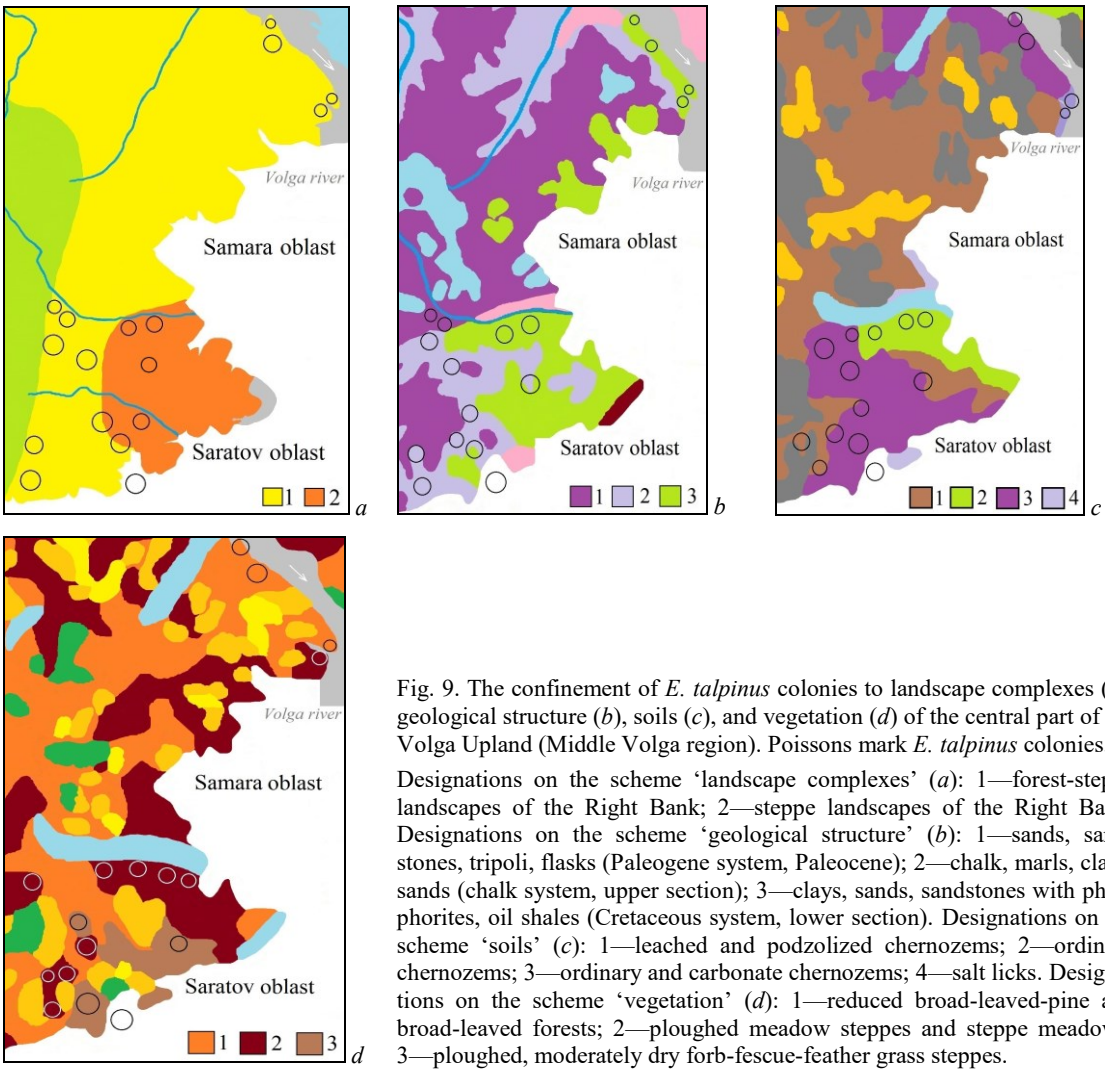

Fig. 9. The confinement of *E. talpinus* colonies to landscape complexes (*a*), geological structure (*b*), soils (*c*), and vegetation (*d*) of the central part of the Volga Upland (Middle Volga region). Poissons mark *E. talpinus* colonies.

Designations on the scheme 'landscape complexes' (*a*): 1—forest-steppe landscapes of the Right Bank; 2—steppe landscapes of the Right Bank. Designations on the scheme 'geological structure' (*b*): 1—sands, sandstones, tripoli, flasks (Paleogene system, Paleocene); 2—chalk, marls, clays, sands (chalk system, upper section); 3—clays, sands, sandstones with phosphorites, oil shales (Cretaceous system, lower section). Designations on the scheme 'soils' (*c*): 1—leached and podzolized chernozems; 2—ordinary chernozems; 3—ordinary and carbonate chernozems; 4—salt licks. Designations on the scheme 'vegetation' (*d*): 1—reduced broad-leaved-pine and broad-leaved forests; 2—ploughed meadow steppes and steppe meadows; 3—ploughed, moderately dry forb-fescue-feather grass steppes.

Рис. 9. Приуроченість колоній *Ellobius talpinus* до ландшафтних комплексів (*a*), геологічної будови (*b*), ґрунтів (*c*) та рослинності (*d*) центральної частини Приволзького височини (Середнє Поволжя). Пуасонами показані колонії *Ellobius talpinus*.

Позначення на схемі «Ландшафтні комплекси» (*a*): 1 — лісостепові ландшафти Правобережжя; 2 — степові ландшафти Правобережжя. Позначення на схемі «Геологічна будова» (*b*): 1 — піски, пісковики, трепели, опоки (палеогенова система, палеоцен); 2 — крейда, мергелі, глини, піски (крейдова система, верхній відділ); 3 — глини, піски, пісковики з фосфоритами, горючі сланці (крейдова система, нижній відділ). Позначення на схемі «ґрунти» (*c*): 1 — чорноземи лужні та опідзолені; 2 — чорноземи прості; 3 — чорноземи звичайні та карбонатні; 4 — солонці. Позначення на схемі «рослинність» (*d*): 1 — зведені широколистяно-соснові та широколистяні ліси; 2 — розорані лучні степи і остепенені луки; 3 — розорані помірно-посушливі різнотравно-типчаково-ковилові степи.

Ellobius talpinus in the central regions of its range (Middle Volga region) prefers habitats with the following landscape and community characteristics: sandy steppes (sandy and sandy soils, sand and sandy loam), stony chalk steppes (carbonate chernozems, light and medium loams), and ancient sandstone deposits (with good preservation of habitats). Soil parameters characterise the possibility of development of certain microstations and plant associations that form them. The indicators of soil samples and their combinations indicate the suitability of the formation of those plant associations that will correspond to the living conditions and reproduction of burrowing rodents (*E. talpinus*), as well as the living conditions of other animal species that form this zoocoenosis.

The species *E. talpinus* in the Middle Volga region shows a clear dependence in the choice of habitats with certain soil characteristics (light sandy and carbonate-chernozem soils), confined to a certain type of landscape (steppe landscapes): sandy and chalk steppes, which is associated with living in the forest-steppe zone. *E. talpinus* exhibits plasticity in the choice of soil with a wide variation of parameters, which allows it to live not only in steppe communities, but also in anthropogenically modified areas: old fallows, fresh arable lands, secondary and upland meadows, even at the border of forest belts, etc. In this case, *E. talpinus* does not avoid monodominant reed heaths as a component of upland meadows. Other representatives of small mammals are often unable to master the dense, impenetrable sods of the ground reed grass due to the lack of herbs.

Compared to the central areas of the range, *E. talpinus* in the eastern regions (Southern Urals) shows a greater dependence on the choice of habitats with certain characteristics of the soil and landscape, which is associated with living in the zone of true steppes. Whereas the Volga popul-?tions are located in the forest-steppe zone. For the same reason, populations of the mole vole in the eastern regions of its range (Southern Urals) are more specialised than in the central regions (Middle Volga) [Artemieva 2022*b*].

Criptic role of colouration

The influence of the edaphic factor on the variability of fur colouration and of the size of *E. talpinus* was established earlier [Artemieva 2022*c*]. The species is characterised by a wide variability in fur colouration, which marks groups of populations from different areas of the range.

An analysis of photographs of the colour phenotypes of *E. talpinus* showed that the black-and-brown, brown-red colour phenotypes are characteristic of the species' populations in the Orenburg region (Southern Urals); clay and red-colored soils are developed here. For carbonate chernozems, phenotypes of individuals of grey and greyish colour are characteristic. Melanistic individuals are characteristic in areas of true chernozems. In general, the colour of the fur of the dorsal part of the body varies from light grey and sandy-buffy-reddish to brownish, black-brown, and black. The colouration of the ventral part of the body is also brown or with a brownish tint [Pavlinov *et al*. 2002].

The conformity of the fur colouration in *E. talpinus* to the soil substrate of the settlements is as follows: reddish-sand-beige shades of individuals from settlements on sands and sandy loams (81 individuals; 32.4%). They are characteristic of the western parts of the range. Brownish and brown shades of individuals are typical for settlements on light and medium loams (55 individuals; 22%), which is characteristic of the central part of the range. Greyish and grey shades of individuals are characteristic of settlements on carbonate chernozems (47 individuals; 18.8%). They are noted in the Middle Volga region. Blackish and black (melanistic) individuals are found in settlements on ordinary, as well as leached and podzolized chernozems (33 individuals; 13.2%). Greyish-brown phenotypes are characteristic of settlements on gravelly soils (19 individuals; 7.6%). They are marked in the Crimea. More exotic variants of phenotypes are black-backed and reddish, which correspond to settlements on redstones (15 individuals; 6%) and are typical for the Southern Urals.

The colour of the top of the head is of particular importance in the life of the mole voles, since the predators first notice the head of the animal. The mole vole is often active during the daytime. It quickly digs a burrow and yet is forced to stick its head out for a while. Therefore, the colour of the head is always cryptic and corresponds to the colour of the soil in which the animal lives. In the territory of the Middle Volga region and the Southern Urals, partial and complete melanists were also noted (Fig. 10).

Habitat preferences of Ellobius talpinus

Soil as an edaphic factor determines the main characteristics of settlements, colonies, and populations, regional groups of populations of *E. talpinus*. The soil determines the spatial frames of the ecological option of the species in different areas of the range based on the soil substrate and the development of vegetation (food base) on these substrates. Therefore, soil characteristics are an important diagnostic parameter. This character determines the ecomorphology of the species: the type of fur colouration and the main morphometric parameters of individuals [Artemieva 2022*c*].

Fig. 10. Melanistic *E. talpinus* from the colonies in the Middle Volga region: *a*—partial melanist on loamy light calcareous soils (02.06.2020), photo by state inspectors of the Sengileevskiye Gory National Park; *b*—complete melanist on carbonate chernozems (summer 2021), photo by state inspectors of the Sengileevskiye Gory National Park (https://ulpressa.ru; https://ulpressa.ru/tag/).

Рис. 10. Меланісти *E. talpinus* із колоній Середнього Поволжя: *a* — неповний меланіст на суглинних легких карбонатних ґрунтах (2.06.2020), фото держінспекторів нацпарку «Сенгілеївські гори»; *b* — повний меланіст на карбонатних чорноземах (літо 2021 р.), фото держінспекторів Національного парку «Сенгілеївські гори» (https://ulpressa.ru; https://ulpressa.ru/tag/).

The species *E. talpinus* prefers for its colonies soils with neutral pH, with a moderate content of P_2O_5 and Ca, high content of Cu and Mn, moderate content of Zn, uncontaminated by heavy metals and rather loose (from loose sand and sandy loam to light and medium loam), which is easily taken out when digging a burrow, extracting rhizomes, tubers, and bulbs of fodder plants. In the Middle Volga region, colonies of *E. talpinus* are associated with steppe and steppe landscapes, forb-feather grass-fescue steppes on parent sandy, sandstone, and chalk rocks. It chooses burrowing sites with steppe vegetation of various variants, preferring calciphilic and psammophilic associations. Colonies of *E. talpinus* mark psammophilous communities of psammophyton refugia on ancient deposits of parent sandy rocks, calciphilic complex of vegetation on ancient cretaceous rocks too.

Thus, the mole vole marks two types of steppe communities:

1) Sand steppes (arenas). In fescue steppes, the phytocoenosis includes dominant species of the psammophilic complex. The species is also capable of inhabiting secondary steppes and upland meadows.

2) Stony chalk steppes. In petrophytic steppes, the phytocoenosis includes dominant species of the calciphilous complex (Fig. 11).

Fig. 11. *Ellobius talpinus* habitat: stony chalk steppe (Middle Volga region), 20.05.2018. Photo by the author.

Рис. 11. Біотоп *Ellobius talpinus*: кам'янистий крейдяний степ (Середнє Поволжя), 20.05.2018. Фото автора.

Conclusions

As a result of studying the ecology of *E. talpinus* in the central area of its range, the following has been revealed.

1. The species *E. talpinus* plays an important environmental role, supporting the very existence of the steppes. Eurasian steppes (including anthropogenically transformed ones) can be considered typical habitats not only of the mole vole, but also of animals of other groups living next to it.

2. Soil type, its main characteristics as an edaphic factor, vegetation and landscape characteristics of the habitat are important regional diagnostic parameters of *E. talpinus* populations.

3. The mole vole is a key species of modern sandy and petrophytic (stony chalk) steppes preserved in its range. The mole vole is an index species of psammophilous and calciphilous communities. At present, many steppe burrowers are in a depressed state or have already disappeared on the remaining fragments of sandy and stony steppes, or they prefer other types of soils. This species is an indicator of the state and preservation of steppes and agricultural lands within Northern Eurasia.

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