Theriologia Ukrainica, **22**: 80–93 (2021)
p-ISSN 2616-7379 • e-ISSN 2617-1120
DOI: 10.15407/TU2209

DISTRIBUTION LIMITS OF FOREST-DWELLING SMALL MAMMALS (EULIPOTYPHLA, RODENTIA) IN THE CRIMEAN MOUNTAINS

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Key words

fauna, small mammals, rodents, shrews, geographic range, Crimea

doi

http://doi.org/10.15407/TU2209

Article info

submitted 07.12.2020
revised 06.11.2021
accepted 23.12.2021

Language

English, Ukrainian summary

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Abstract

Concluding data on distribution limits of small mammals that have isolated geographic ranges in the montane forest zone of the Crimean Peninsula are presented. The analysis is based on data collected for forty years of mammal research in the Crimea, with a total sampling effort of 600 000 trap-nights and more than 63 000 trapped specimens of small mammals. The article considers the geographic range of two insectivore species of the family Soricidae (*Neomys anomalus* and *Sorex pusillus*) and three rodent species that belong to the families Muridae (*Sylvaemus tauricus* and *S. uralensis*) and Cricetidae (*Microtus obscurus*). These are forest-dwelling species that find food, shelter and other favourable conditions necessary for full and permanent existence of their populations in forest communities. This group of Micromammalia is of the greatest interest from the viewpoint of zoogeography and evolution since they have been geographically isolated from their main range for thousands of years. Their gene pool therefore preserved both ancestral genetic material and new alleles that have been amassed during the entire period of isolation and have been filtered by natural selection. Range boundaries of these species have been affected by various environmental components that have been acting as main limiting factors. These are hydroclimatic factors (humidity and moisture that determine meso- and microclimatic parameters of biotopes), floristic factors (dominating flora composition that determine trophic and topic features of local animal populations), and landscape and edaphic factors. *Neomys anomalus* and *Sorex pusillus* are stenotopic and hygrophilous species that inhabit the wettest biotopes of mountain forests of the Crimea thus they have the smallest geographic ranges. The geographic range of *Sylvaemus tauricus* is wider and is related to the distribution of oak-beach forests. The species *Sylvaemus uralensis* and *Microtus obscurus* are the most eurytopic and their geographic range expands even to the Crimean Lowland in a north-eastern direction. Natural and climatic conditions that are present in the montane and piedmont zones are optimal for the species *S. uralensis* and *M. obscurus*, which are thus abundant and dominating here among small mammals.

Cite as

Evstafiev, I. 2021. Distribution limits of forest-dwelling small mammals (Eulipotyphla, Rodentia) in the Crimean Mountains. *Theriologia Ukrainica*, **22**: 80–93. [In English, Ukrainian summary]

Межі поширення гірськолісових видів дрібних ссавців (Eulipotyphla, Rodentia) у Криму

Ігор Євстаф'єв

Резюме. Наведено підсумкові дані по межах географічних ареалів дрібних ссавців, які мають ізольовані ареали в гірськолісовій зоні Кримського півострова. В основі аналізу лежать дані за 40-річний період вивчення фауни ссавців на території Криму. За цей час відпрацьовано більше 600 тис. пастко-ночей і відловлено більше 63 тис. дрібних ссавців. В статті розглянуті ареали двох видів Insectivora, родини Soricidae: *Neomys anomalus* і *Sorex pusillus*, та трьох видів гризунів (ряд *Rodentia*): *Sylvaemus tauricus*, *S. uralensis* (Muridae) та *Microtus obscurus* (Cricetidae). Ці види дрібних ссавців по способу життя є лісовими мешканцями, які в лісових товариствах знаходять собі їжу, укриття та інші сприятливі умови для повноцінного та постійного існування їх популяцій. Ця група Micromammalia представляє найбільший інтерес з точки зору зоогеографії та еволюції, так як саме вони є географічними ізолятами від основного ареалу протягом тисячоліть. Тому в їх популяційному генофонді збереглися як предкові генетичні матеріали, так і з'явилися нові генні характеристики, накопичення яких йшло весь період ізоляції і фільтрувалося природним відбором. На формування меж їхніх географічних ареалів визначальний вплив надають різні компоненти середовища, які виступають в ролі основних лімітуючих факторів. Це, перш за все, — гідрокліматичні фактори (вологість повітря і ґрунту, що визначають мезо- і мікрокліматичні параметри біотопів); флористичні фактори (домінуючий склад флори, що забезпечує основні життєві відправлення мешкаючих в них популяцій тварин, як трофічних, так і топічних); ландшафтні та едафічні фактори. Види *Neomys anomalus* та *Sorex pusillus* — стенобіонтні гігрофіли, які населяють найвологіші біотопи в лісах гірського Криму, тому вони мають найменші географічні ареали. Ареал виду *Sylvaemus tauricus* ширший, і він прив'язаний до розповсюдження дубово-букових лісів. Види *Sylvaemus uralensis* и *Microtus obscurus* — найбільш еврибіонтні види, ареали яких виходять навіть на територію Рівнинного Криму в північно-східному напрямку. Природно-кліматичні умови, які існують як в гірській, так і в передгірній природних зонах, оптимальні для видів *S. uralensis* и *M. obscurus*, тому тут ці види є фоновими домінуючими видами серед дрібних ссавців.

Ключові слова: фауна, дрібні ссавці, гризуни, землерийки, ареали, Крим.

Introduction

Yet in the 19th century, the very first zoologists who had started to study the nature of the Crimea [Pallas 1831; Nordmann 1840; Koeppen 1883] paid attention to the specifics of the local fauna, which had differed in many aspects from faunas of adjacent territories. Primarily it was the sharp heterogeneity between faunas of the Crimean steppe and the Crimean Mountains. In terms of zoogeography, the Crimean steppe represents a slightly impoverished district of the steppe province of the Euro-Siberian region of the Palaearctic, whereas the Crimean Mountains harbour a montane forest fauna, which is close to the fauna of the Mediterranean south such as Transcaucasia, the Balkans, Syria, and the Aegean Islands [Puzanov 1949].

The montane forest zone of the Crimean Peninsula represents a peculiar 'island' harbouring populations of various mammal species that have been existing in isolation for thousands of years and hundreds of kilometres far from the main part of their geographic range [Puzanov 1938]. The role of isolating barriers for populations of Crimean mammals is played by the sea and open steppe and semi-desert areas [Evstafiev 2010]. These sites are characterized by the absence of woody vegetation and arid summer climate.

Due to the centuries of isolation, the gene pool of populations of montane forest species has changed under the influence of evolutionary factors. Since exchange of genetic material with individuals from other, mainland populations did not occur, their gene pool has become particularly unique, which is yet to be studied. The distribution of all montane forest species of small mammals within the zone of mountain forests is mosaic, though continuous in general, and range boundaries are identical from the side of the Crimean southern coast.

In the north, however, from the side of the Crimean steppe, range boundaries of montane forest species vary. They are determined by the heterogeneity of the Crimean foothills, which represent a wide transitional zone between montane meadows and forests and lowland steppe communities, as well as by differences in the level of preference of montane forest species of various habitat types.

But how far north can montane forest species of small mammals disperse to the forest steppe and steppe zones and what factors act as ecological barriers to range expansion beyond the territory of the Crimean Mountains?

Material and Methods

General geographic features of the studied region and the materials and methods used were described earlier [Evstafiev 2015]. The present work is based on materials collected during epizootiological expeditions in the territory of the Crimean Peninsula by zoologists of the Crimean Anti-Plague Station and of the Department of Especially Dangerous Infections of the Crimean Republican Sanitary and Epidemiological Station.

Standard and widely accepted methods of census and trapping of small mammals were used [Kucheruk 1952; Kucheruk & Korenberg 1964; Popov 1967; Karaseva & Telitsyna 1996]. The sampling effort for the entire research period was 600 000 trap-nights and more than 63 000 specimens of small mammals were collected. Primary data have been amassed in electronic spreadsheets using Microsoft Excel [Evstafiev 2017].

Maps of geographic ranges of species were prepared in Quantum GIS v.1.7.4. using spreadsheet data on trappings of small mammals. Each trapping locality of small mammals is a site of around 2 km in diameter with various types of habitats. Within each locality, trapping has been carried out for the past 40 years for 1–3 to 10–15 times in various years and seasons.

Maps presented in this article show the territories through which runs the northern 'forest steppe boundary' of geographic ranges of species considered. In Fig. 1, main trapping localities are shown only within the area of the northern boundary of distribution of the considered forest-dwelling species of insectivores and rodents.

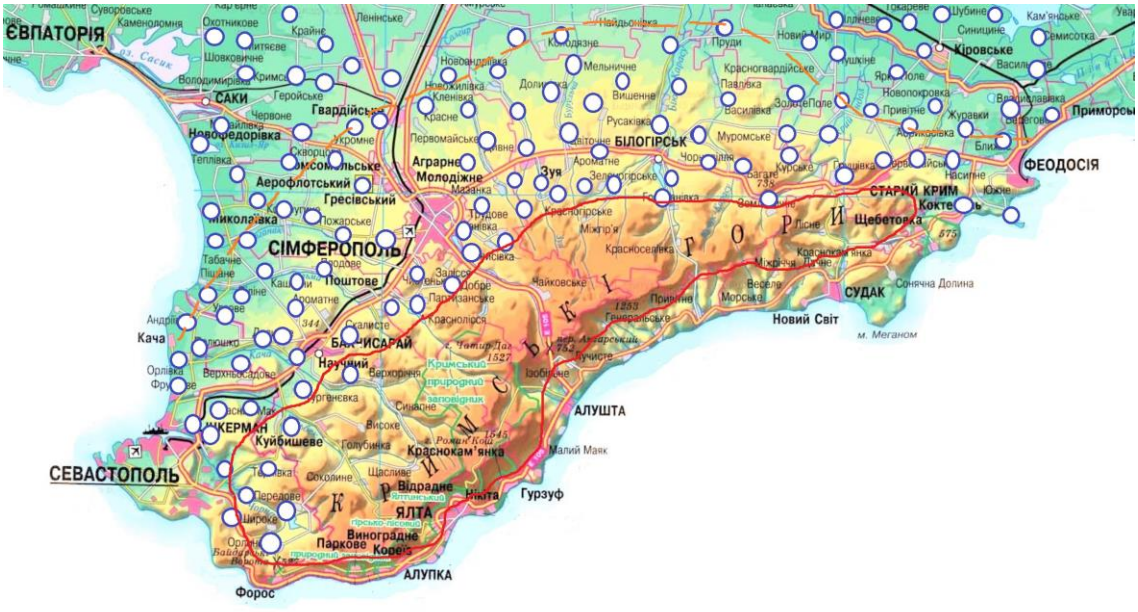

Fig. 1. Trapping localities of small mammals for the last 40 years. The red line outlines the boundaries of the mountain forest zone of the Crimea: the descriptions of species ranges in this article refer to the periphery of this zone.

Рис. 1. Точки відлову дрібних ссавців протягом останніх 40 років. Червона лінія окреслює межі гірськолісової зони Криму: описи видових ареалів у цій статті стосуються периферії цієї зони.

Trapping localities (there are too many of them) related to the montane forest zone of the Crimea (indicated with a red line in Fig. 1), where the species considered have a continuous range, are not shown in Fig. 1. At a first approximation, the boundary of the montane forest zone corresponds to the hypsometric level of 250–300 m a.s.l.

In Fig. 1 and on maps showing range boundaries of montane forest species (Figs 2–6), the boundary between the steppe and piedmont zones is indicated by a thin brown dashed line (after [Andrienko *et al.* 1977]). At a first approximation, this line runs through the settlements Kacha—Viline—Hvardiiske—Annivka—Naidonivka—Prudy—Zolote Pole—Feodosia. Its hypsometric value ranges from around 40 m a.s.l. in coastal areas (Kacha, Feodosia) to almost 140 m in the central part of the piedmont zone (Hvardiiske).

A review of geographic range limits of isolated species

Family Soricidae Fischer, 1817

Both species of the family found in the Crimea—the Caucasian pygmy shrew (*Sorex pusillus*) and the Mediterranean water shrew (*Neomys anomalus*)—are stenotopic and have the most restricted geographic range in the Crimean Mountains.

Mediterranean water shrew (*Neomys anomalus*)

The Mediterranean water shrew is a rare species throuout its range (southern and central West Europe and north-west Ukraine) and it is represented in the Crimea by the subspecies *Neomys anomalus mokrzeckii* Martino, 1917.

In general, the species' biology has been studied insufficiently [Flint *et al*. 1970; Evstafiev 2016]. In the Crimea, the Mediterranean water shrew has been found exclusively in the mountainous part of the peninsula and it does not occur below 400–500 m a.s.l. The abundance of the Mediterranean water shrew in the Crimea has remained low, and a total of 11 specimens have been caught for the entire period of research.

Since the number of record localities of the species is very low, here we present all known localities not only the marginal ones. In particular, the Mediterranean water shrew was caught in the southern, mountainous part of Bilohirsk (Balanov Reservoir), Simferopol, and Bakhchysarai raions, as well as in the territory of Alushta Raion (near the sources of the Kacha and Chorna rivers, which are located on protected areas) at a height of 300 to 600–800 m a.s.l. In addition, the species was recorded (corpses of dead animals) near Velyka Yalta and in Sudak Raion (Fig. 2).

Mediterranean water shrews were caught in the years very unevenly. The first two individuals were trapped in July 1987 on a single trap-line in Bakhchysarai Raion. The next time Mediterranean water shrews were caught was eleven years after the first record: two specimens in 1998 and another two in 1999 in Bakhchysarai and Simferopol raions. The latest known specimen was also trapped in Bakhchysarai Raion in 2008.

The obtained data allows suggesting that the main range of the Mediterranean water shrew is restricted to forested areas of the central and western parts of the Crimean Mountains, which are located in the territory of Bakhchysarai, Simferopol, Bilohirsk, and Alushta raions. It can also be suggested that the species occurs in hardly accessible areas of the eastern Crimean Mountains, from the central part of Bilohirsk Raion to Sudak Raion to the east, which can be confirmed by a record of the species near the village of Shchebetovka.

The analysis of rather scarce data on the abundance and distribution of the Mediterranean water shrew shows that the species' range covers forest habitats with the highest level of moisture along banks of permanent or temporary bodies of water (mainly mountain streams).

Caucasian pygmy shrew (*Sorex pusillus*)

In the Crimea, the Caucasian pygmy shrew forms an isolated population that is clearly separated from the species *Sorex minutus*, which is widely distributed in the Palaearctic [Dolgov 1985].

Fig. 2. The Mediterranean water shrew (*Neomys anomalus*) in the Crimea: circles — all record localities of the species; red bold dashed line — the supposed northern edge of the species' range in the montane forest zone.

Рис. 2. Рясоніжка мала (*Neomys anomalus*) в Криму: точки — всі місця відлову рясоніжок; червона (жирна) пунктирна лінія — імовірна північна межа ареалу виду у гірськолісовій зоні.

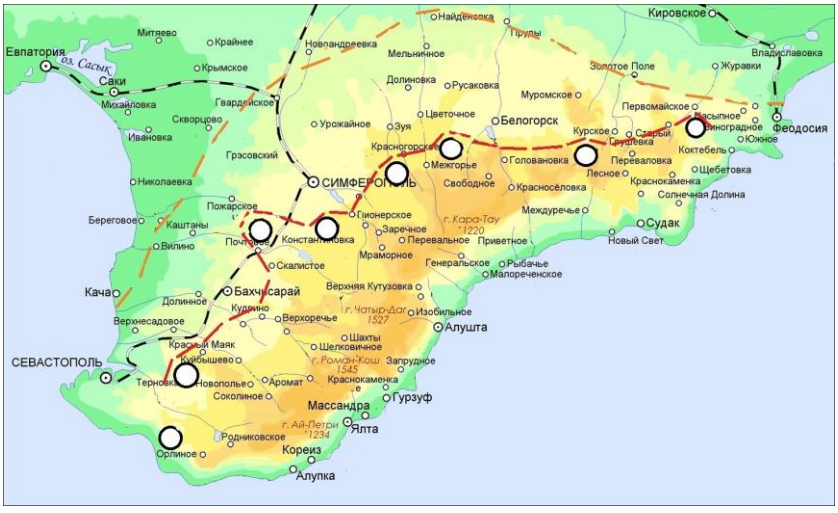

Fig. 3. The Caucasian pygmy shrew (*Sorex pusillus*) in the Crimea: circles — the most northern and northwestern record localities of the species; red dashed line — the supposed northern edge of the species' range in the montane forest zone.

Рис. 3. Мідиця понтична (*Sorex pusillus*) в Криму: точки — найбільш північні та північно-західні місця відлову; червона пунктирна лінія — імовірна північна межа ареалу у гірськолісовій зоні.

Research on shrews of the Crimea allowed S. Dahl [Dahl 1931] to consider them as *Sorex minutus gmelini* Pallas, 1811. However '*Sorex gmelini*' (Pallas, 1811) is identical to *S. pusillus* Gmelin, 1774, not to *S. minutus*, and thus the name '*Sorex (minutus) dahli* Zagorodniuk' [Zagorodniuk 1996] was proposed for the Crimean shrew, which is completely isolated from the continental form. The word 'minutus' here denotes a group of species not a particular species, for which it was proposed to consider the Caucasian *S. pusillus* [Zagorodniuk 1996: 59], also known as '*S. volnuchini* Ognev, 1922.' The latter is also supported by molecular data [Vega *et al.* 2020]. The species has been known in the Crimea since the Pliocene [Dulitsky 2001].

The current distribution of the Caucasian pygmy shrew in the Crimea covers the zone of shibliak and deciduous forests alternating with shrubberies (Fig. 3). The northern range edge of the species in the Crimea practically coincides with the boundary between the forest and piedmont zones, while most records of the species come from below 300 m a.s.l.

A practically isolated micropopulation of the Caucasian pygmy shrew in shibliak near the village of Kazanky of Bakhchysarai Raion should be mentioned separately. This micropopulation has been existing here during the entire period of research. The species' abundance is low everywhere and only in separate years it can slightly increase reaching 3% of catches in 100 trap-nights.

Family Muridae Illiger, 1811

Of the representatives of this family, three species have isolated geographic ranges in the montane forest zone of the Crimea: the yellow-necked wood mouse *Sylvaemus tauricus* s. str. (Pallas, 1811), pygmy wood mouse *Sylvaemus uralensis* (Pallas, 1788) [Heptner, 1940], and black rat *Rattus rattus ruthenus* Ognev et Stroganov, 1936.

Yellow-necked wood mouse (*Sylvaemus tauricus*)

The yellow-necked wood mouse was first described in the Crimea by Pallas based on materials from Chersonesus (now vicinities of Sevastopol) as '*Mus sylvaticus* var. *taurica*' [Pallas 1811: 168], which later was accepted as species name for all European large forms of wood mice—*Sylvaemus tauricus* (= *Apodemus flavicollis* auct.) [Zagorodniuk 1992]. Accordingly, the montane forest population of this species is represented by the nominate subspecies *Sylvaemus tauricus tauricus*.

The yellow-necked wood mouse is a specialized granivore of woody plants (oak, beech, hornbeam and some others), the geographic range of which in the Crimea is thus restricted to forests of the montane forest zone of the peninsula (Fig. 4) [Evstafiev 2003, 2015a].

Fig. 4. Northern range edge of the yellow-necked wood mouse (*Sylvaemus tauricus*) in the Crimea.

Рис. 4. Північна межа ареалу мишака жовтогрудого (*Sylvaemus tauricus*) в Криму.

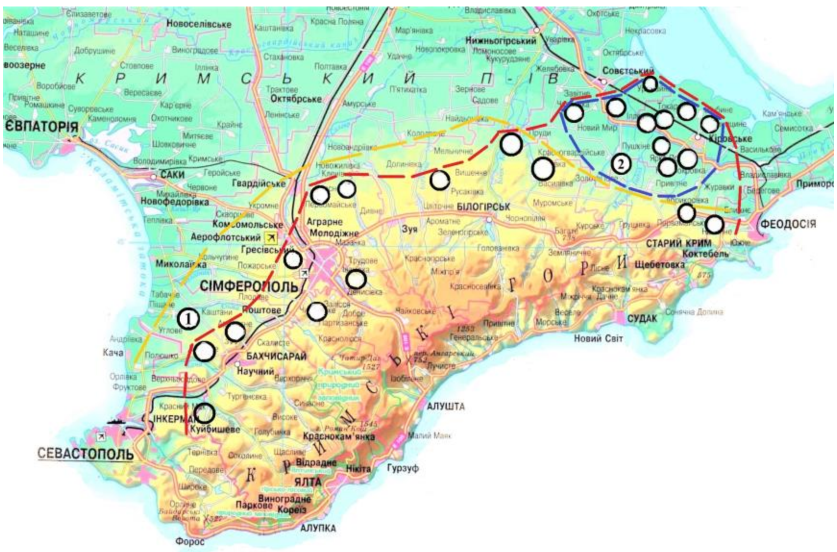

Fig. 5. Northern range boundaries of the pygmy wood mouse (*Sylvaemus uralensis*) in the Crimea with some details on the northern and northwestern directions. Numbers 1 and 2 mark isolates beyond the main range (details in the text).

Рис. 5. Північні межі ареалу миші уральської (*Sylvaemus uralensis*) в Криму з деталізацією у північному та північно-західному напрямках. Цифрами 1 і 2 позначено ізоляти поза основним ареалом (деталі у тексті).

Studies have revealed that the share of yellow-necked wood mice in woody-shrubby biotopes of the forest zone is 35.1% of all small mammals trapped in this zone, whereas 10.3% in the foothills. In natural herbaceous biotopes (glades, forest edge), yellow-necked wood mice made up 19.1% of trapped small mammals in the forest zone and 5.1% in the foothills [Evstafiev 2004].

The yellow-necked wood mouse is widely distributed within its range, which can be confirmed by the share of trap-lines on which the species was recorded. In the montane forest zone, the share of productive trap-lines was 63.3% on woody-shrubby biotopes and 46.9% in herbaceous ones; these numbers in the piedmont zone were 30.7% and 20.1%, respectively.

Pygmy wood mouse (*Sylvaemus uralensis*)

The pygmy wood mouse is represented in the Crimea by the subspecies *Sylvaemus uralensis bessleri* Dahl 1929, which was described as '*Sylvaemus sylvaticus baessleri*' based on materials from the Crimean Mountains ('Crimean State Reserve': Dahl 1929]. Its distinctness has drawn the attention of systematists many times [Heptner 1940; Zagorodniuk 1992], and in the structure of the geographic range of this species the Crimean population clearly has a distinct position as well [Zagorodniuk 2020].

The pygmy wood mouse is one of the most abundant small-mammal species of the montane forest and piedmont zones of the Crimea. Its share is 29.4% of the total number of trapped small mammals in the forest montane zone and 39.1% in the piedmont zone. In biotopes of the steppe zone of the peninsula, the share of the species in samples does not exceed 5.3%.

The geographic range of the pygmy wood mouse covers most parts of the montane forest and piedmont zones of the Crimea; its northern boundaries with some details on the northern and northwestern directions are shown in Fig. 5. The map shows two isolates located beyond the main range: (1) near the villages of Vilino, Otradne, and Kochergino of Bakhchysarai Raion; and (2) record localities in the steppe zone of Kirovske Raion (blue dashed line). This species, similarly to the 'common' vole, enters steppe areas through forest stripes and river valleys, but does not occur north of the valley of the Salgir River.

Black rat (*Rattus rattus ruthenus*)

The black rat is an autochthonous species of the Crimea and currently is the least studied and the rarest species among small mammals of the peninsula. The distribution of the species in the Crimea is restricted to the narrow strip of the southern coast. Single individuals of the black rat were occasionally recorded only in forest and woody-shrubby biotopes, in vicinities of Velyka Yalta.

The origin of these rats is unclear. It is possible that they had arrived to the Yalta Seaport on ships and subsequently dispersed to anthropogenic and natural biotopes of Velyka Yalta. Cases of transportation of black rats to seaports of the Crimea (Kerch, Yalta, and Sevastopol) by merchant ships and the subsequent settlement of animals in the port's territory have been recorded numerous times [Evstafiev, 2015*b*, 2020].

Family Cricetidae Fischer-Waldheim, 1817

Altai vole (*Microtus obscurus*). The vole that inhabits the montane forest south of the Crimean Peninsula had been considered a subspecies of the common vole *M. arvalis iphigeniae* Heptner, 1946 [Heptner 1946; Ognev 1950]. Currently, *M. obscurus* is recognized as separate species, which is represented in the territory of the Crimea by a geographically isolated subspecies *M. o. iphigeniae* Heptner, 1946 [Zagorodniuk 1993].

The Altai vole is the most abundant species in the montane forest zone occurring in yaylas, glades, trails, burnt areas, and on the forest edge. On the other hand, the species avoids continuous deciduous forest with no herbaceous undergrowth, which is related to its feeding specifics. A total of 7870 specimens of *M. obscurus* were collected (64.5% in the mountains, 30.2% in the foothills, and 5.2% in the steppe); their share among all trapped small mammals was 47.2%, 25.6%, and 1.3%, respectively.

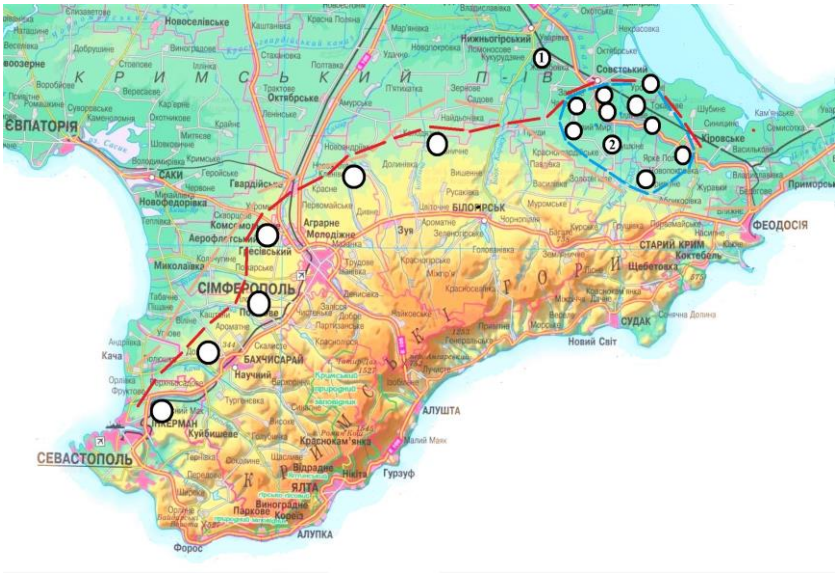

Fig. 6. Northern range boundaries of the Altai vole (*Microtus obscurus*) in the Crimea with some details on the northern and northwestern directions. Numbers 1 and 2 mark isolates beyond the main range (details in the text).

Рис. 6. Північні межі ареалу полівки алтайської (*Microtus obscurus*) в Криму з деталізацією у північному та північно-західному напрямках. Цифрами 1 і 2 позначено ізоляти поза основним ареалом (деталі у тексті).

The species' long-term relative abundance was 5.0, 2.6, and 0.1 individuals per 100 trap-nights. The aggregated distribution of the species in a particular biotope can be suggested by the number of trapped voles on one productive trap-line (100 trap-nights), which was 9.1, 6.6, and 3.9 individuals.

The geographic range of the Altai vole is rather wide and similar to that of the pygmy wood mouse. The northern range boundary of the species in the Crimean Peninsula generally coincides with the boundary of the piedmont zone (Fig. 6). Only in the north-eastern direction beyond the piedmont zone the species has been found in the steppe as relative large isolates, practically in the entire territory of Kirovske Raion and in part of Sovietskyi Raion (see circles No. 2 within the blue dashed line in Fig. 6). The northernmost isolate of *M. obscurus* beyond the main range was found in vicinities of the village of Almazne in Sovietskyi Raion.

The origin of the montane forest mammal assemblage

In order to understand how and when isolated populations of small mammals appeared in the montane forest zone of the Crimea along with their specific complex of ectoparasites we should consider the peninsula's geological history.

Modern lowland and mountain landscapes of the Crimean Peninsula had formed during the Neogene period of the Cenozoic. It was the time when the Crimean Mountains emerged in the south of the peninsula [Puzanov 1938]. In the Pleistocene, the time of large-scale glaciations and alternating periods of glaciations and interglacials, the formation of most of the modern forms of relief, faunas, and floras had completed.

The last glacial maximum in the north of Europe took place in the territory of modern Scandinavia about 100 000 years ago. The ice sheet, which could reach a depth of 2 km, had expanded forcing animals and plants to the south. At that time, sea level had dropped and various kinds of land bridges had appeared allowing many species to spread into new and earlier inaccessible territories, including the area of the Crimean Mountains.

About 7000 years ago, climate had become warmer and continental glaciers had disappeared permanently. The steppe zone of the Crimean Lowland acquired its modern form [Gromov 1961]. Animal species that had colonized mountain forests of the Crimea had lost their connection with their continental populations forming local isolates. The modern fauna of terrestrial mammals of the Crimea has been forming since that very time [Dulitsky 2001].

At present, the group of terrestrial montane forest small mammals in the Crimean Peninsula is represented by two insectivore species (Caucasian pygmy shrew *Sorex pusillus* and Mediterranean water shrew *Neomys anomalus*) and three rodent species (yellow-necked wood mouse *Sylvaemus*

tauricus, pygmy wood mouse *Sylvaemus uralensis*, and Altai vole *Microtus obscurus*). At the same time, the Caucasian pygmy shrew (as '*S. minutus gmelini* Pallas') and the Mediterranean water shrew (as *N. anomalus mokrzeckii* Martino) are considered rare and endangered taxa that require protection [Tovpinets & Evstafiev 2002, 2005].

This group of small mammals represents the greatest interest from the viewpoint of zoogeography and evolution for having been geographically isolated from the main species range for thousands of years. Their gene pool has preserved ancestral genetic materials but also acquired new genetic features that have been amassed during the entire period of isolation and have been filtered by natural selection. Therefore, considering the importance of biodiversity conservation and as detailed as possible account of intraspecific genetic structure of species, the study of isolated population is of great interest on both morphobiological and molecular levels [Evstafiev & Tovpinets 2002].

A brief description of small mammals of the Crimean Mountains

A detailed description of the fauna, ecology, and epizootology of small mammals of the Crimea, including montane forest species, was presented earlier [Evstafiev 2015, 2016, 2017] thus here we only consider some aspects important to the topic of the present study.

The core of the small-mammal assemblage of the montane forest zone includes species that have isolated geographic ranges here. The Altai vole is a clearly dominating species and its share in trappings varies from 35.6% to 71.6% and in average is 46.2%. The pygmy wood mouse is a subdominant (29.4%) followed by the yellow-necked wood mouse (19.2%), while the share of other species is less than 2%.

In the piedmont zone, which is transitional between the montane forest and steppe zones, is a specific ecotone with highly varying abiotic and biotic environmental factors and the highest diversity of biotopes. As a result, species of the montane forest and steppe zones co-exist in this territory.

The fauna of the foothills is quite variable and mosaic, which is related to the ecological preferences of local species and depends on meso- and microclimatic conditions of particular habitats. Wet and shady biotopes with woody-shrubby vegetation are inhabited by species of the montane forest mammal assemblage, whereas light, dry, and steppe-like habitats are occupied by species of the steppe mammal assemblage.

Therefore, the Altai vole in the piedmont zone (25.7%) is dominated by the pygmy wood mouse (39.1%) and is followed by the steppe wood mouse *Sylvaemus witherbyi* (11.7%), house mouse *Mus musculus*, yellow-necked wood mouse *Sylvaemus tauricus*, social vole *Microtus socialis*, and lesser white-toothed shrew *Crocidura suaveolens*.

Factors affecting geographic range limits of isolated species

The formation of range boundaries is affected by a set of biotic and abiotic factors [Lobkov 2004; Lee-Yaw *et al.* 2016]. The southern range edge of all forest-dwelling species practically coincides with the southern coast of the Crimea, where the species considered do not occur below 300–500 m a.s.l. Their range boundaries are determined here by the characteristic southern coastal landscape (rather steep and rocky mountain slopes), quite dry though warm climate, and characteristic xerophytic Mediterranean vegetation [Kochkin 1967; Andrienko *et al.* 1977; Shcherbak 1988].

Contours of geographic ranges are determined by ecological features of species [Lee-Yaw *et al.* 2016]. All of the considered species of small mammals recorded in the piedmont and forest zones are forest-dwelling animals according to their ecological needs and require the presence of woody-shrubby vegetation as source of food and shelter. They react differently to the impact of various abiotic and biotic components of the ecosystem, which defines the main features of their habitats [Slonim 1971]. The habitat of each species is an ecological niche in the structure of a particular natural ecosystem, i.e. a place in the natural environment where individuals of species are able to find food, shelter, protection, and mating partners.

Since individuals of the considered species react differently to the main structural components of the ecosystem, it is important to identify those that are essential for the formation of biotopes and, respectively, range boundaries [Abdurakhmanov *et al.* 2003; Babenko & Markov 2017].

Mediterranean water shrew (Neomys anomalus) and Caucasian pygmy shrew (Sorex pusillus)

The Mediterranean water shrew is a hygrophilous species with low ecological plasticity and thus can be considered as a stenotopic species. Its stenotopic feature is the most evident regarding to the level of moisture of the habitat. The Mediterranean water shrew is adapted to live under conditions of increased moisture and prefers to settle under the canopy of deciduous forest, where it inhabits dense herbaceous and shrubby vegetation in marshy and wet areas, floodplains, banks of streams and other small bodies of water. Such biotopes occur quite rarely in the montane forest zone of the Crimea and thus the geographic range of this species is very restricted (see: Fig. 2). Being stenotopic is what limits widespread distribution and defines local distribution patterns.

The Caucasian pygmy shrew has habitat preferences similar to those of the Mediterranean water shrew thus geographic ranges of the two species in the montane forest zone of the Crimea often overlap (see: Fig. 3). The Caucasian pygmy shrew is also hygrophilous and stenotopic, though has a higher level of ecological plasticity, especially regarding moisture. Respectively, this species inhabits not only banks of waterbodies in moist forest habitats, but also occurs in dense herbaceous and shrubby vegetation under the canopy of deciduous forest, in loose forest floor, and hollows in the soil and rotting wood.

The Caucasian pygmy shrew as a more eurytopic species in comparison with the Mediterranean water shrew is able to spread into the piedmont zone along valleys of permanent rivers, such as Chorna, Kacha, Alma, and others. However, it does not form abundant settlements here either.

The stenotopic nature of both insectivore species limits their ability for widespread distribution under conditions of the arid Crimean climate and determines their mosaic occurrence. These species have all-years-long access to diverse food including insects, terrestrial crustaceans and other small invertebrates only in highly humid microhabitats. Beyond such habitats, especially in ones with low humidity, these animals loose water fast, which leads to their dehydration and death. Therefore, these two species cannot exist in xerophylic and even mesophylic biotopes of the Crimean Mountains for long time. Due to the lack of precipitation in summer months, most small streams and springs dry up and after the vegetation period of spring ephemerals completes the second herbaceous plant cover cannot be formed in forest balkas and valleys. This leads to the lack of diverse invertebrates here, which form the food base for both shrew species.

The dry air and forest floor during the entire summer are limiting factors that affect the formation of highly mosaic geographic ranges of these shrews, mainly in the middle and upper belts of the forest zone.

Yellow-necked wood mouse (Sylvaemus tauricus)

The yellow-necked wood mouse as a specialized granivore is trophically and topically closely related to deciduous trees, such as oak, hornbeam, beech, and others. It can be clearly traced by the boundaries of its range: the species spreads into the piedmont zone only through continuous forests of oak and hornbeam with Oriental hornbeam, European cornel and other shrubs in the understorey (see: Fig. 4). At the same time, the yellow-necked wood mouse avoids light sparse woods with well-developed herbaceous vegetation.

Pygmy wood mouse (Sylvaemus uralensis) and Altai vole (Microtus obscurus)

Geographic ranges of the pygmy wood mouse and the Altai vole (see: Figs 5–6) are similar and the widest. Their northern edge practically coincides with the conditional boundary between the piedmont and steppe zones in Bakhchysarai, Simferepol, and Bilohirsk raions. It runs along the northernmost sites of the downy oak that form isolated shibliak-type woods here alternating with agricultural lands.

In the south-east of the Crimean Lowland, geographic ranges of these two species reach the steppe zone in Kirovske Raion, even up to the bank of Lake Syvash, which practically coincides with the second zone of hydrological zonation that covers the area of river valleys of the eastern slope of the Crimean Mountains [Ovcharuk & Todorova 2016]. This area is crossed by the main streambed of the North Crimean Canal as well as valleys of many rivers that flow from the Crimean Mountains (from Biyuk-Karasu in the north to West Bulganak, Indol, Subash and others in the south-east) and is generally characterized by more hygrophilous conditions that contribute to higher productivity of vegetation during the entire summer. This provides sufficient food base for the herbivorous Altai voles and mainly granivorous pygmy wood mice.

Isolated populations and zoogeographic division. Synperates

Currently two approaches are used to zoogeographic zonation: faunagenetic and landscape-zonal (zonal-climatic). The faunagenetic approach focuses on endemics and relics, the presence of which underlines the uniqueness and ancientry of fauna of a particular region [Menzbir 1934; Semenov-Tyan-Shansky 1935], whereas the landscape-zonal approach is based on the study of animals that are ecologically related to habitats (components of phytocoenoses) and to each other. In the latter case, zoogeographic regions often coincide with landscape zones, which is also observed in the Crimean Peninsula.

Regardless of the approach of zoogeographic division, the establishment of boundaries between different zoogeographic units is of great importance in order to determine the uniqueness of faunal assemblages. In the course of zoogeographic zonation, regional units are formed by superimposition of range boundaries regardless of their coincidence with natural barriers—geographic, climatic, or other. For this purpose, the method of synperates is used [Reshetylo 2012], when range boundaries of various species are superimposed on a map and they coincide or turn out to be closely located to one another (Fig. 7). The revealed stripes of concentration of range boundaries are synperates, which usually coincide with various barriers of species dispersal. At present, however, the exact geographic range is known only for less than 1% of organisms thus the value of synperates as a biological prerequisite of determination of geographic assemblages of the biota has been limited so far.

Analysis of obtained data revealed that geographic ranges of the species considered demonstrate the presence of two synperates. One is formed by ranges of the Mediterranean water shrew, Caucasian pygmy shrew, and yellow-necked wood mouse, and another one is formed by ranges of the pygmy wood mouse and the Altai vole.

The first synperate is clearly associated with the montane forest zone, whereas the second one is not related to any obvious geographic barriers. In the south-western and central parts, range boundaries practically coincide with the boundary between the piedmont and steppe zones, while in the north-western part the synperate expands to the lowland steppe area. At the same time, ranges of West Palaearctic species form the first synperate, whereas the second synperate is related to East-Palaearctic species.

When analysing (visualizing) geographic ranges of the considered species (Fig. 7), it can be seen that they form a specific ‘Russian doll’ when in the row of *Neomys anomalus* → *Sorex pusillus* → *Sylvaemus tauricus* → *Sylvaemus uralensis* → *Microtus obscurus* the range of each subsequent species includes the range of preceding species. At the same time, the relative abundance of each species in this sequence also shows an increasing tendency.

An important prerequisite of formation of geographic assemblages of the biota is the superimposition of area and outlines of geographic ranges of many taxa: small mammals, their arthropod parasites, birds, and others [Mordkovich 2005]. The revealed synperates show that each groups of species is characterized by similar habitat preferences and environmental requirements. The coincidence of range boundaries is not a universal though quite widespread phenomenon largely favoured by coenotic relations of species and especially by the determination of ecological successions [Razumovsky 1999].

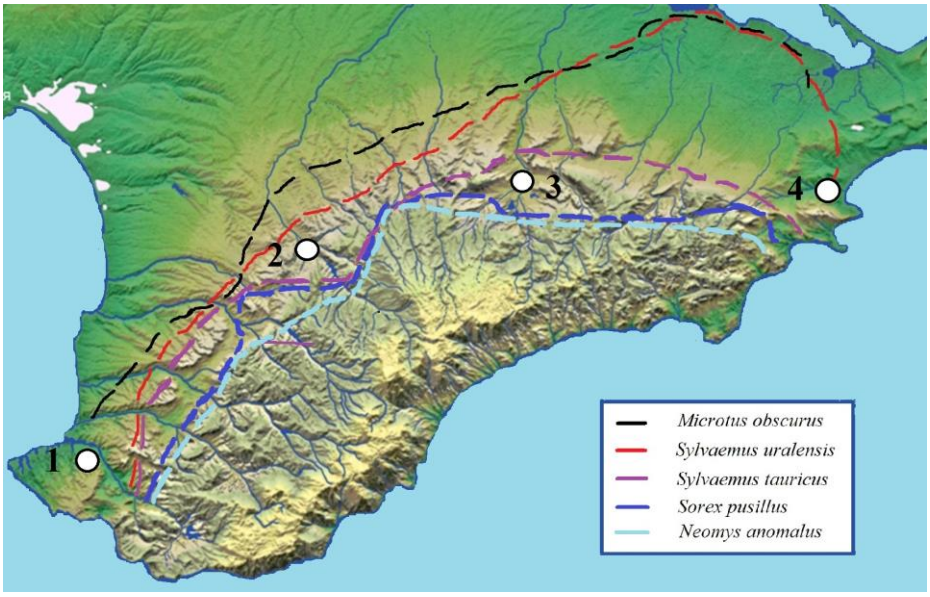

Fig. 7. Northern range boundaries of all of the studied species based on data presented in Figs. 2–6. Numbers indicate landmark cities: 1) Sevastopol, 2) Simferopol, 3) Bilohirsk, 4) Feodosia.

Рис. 7. Північні межі ареалів усіх описаних у цій статті видів за даними, представленими вище на Рис. 2–6. Цифрами позначено міста-орієнтири: 1) Севастополь, 2) Сімферополь, 3) Білогірськ, 4) Феодосія.

Therefore, the Crimean foothills represent an ecotone between the forest and steppe natural zones and a region of concentration and superimposition of range boundaries of various species, including those considered in this study.

Conclusions

1. All of the considered species of insectivores and rodents related to the Crimean Mountains are forest-dwelling species that find food, shelter, and other conditions for full and permanent existence of their populations in woody-shrubby communities. These species form isolates in the Crimea, which are entirely separated from other populations of respective species.

2. Studies revealed that the formation of range boundaries of groups of species and particular species is affected by various components of the environment acting as basic limiting factors. Among them, the most important are (1) hydroclimatic factors: humidity and moisture that define meso- and microclimatic parameters of biotopes; (2) floristic factors: dominating composition of vegetation that supports basic vital functions of animal populations, including trophic and topic requirements; (3) landscape and edaphic factors.

3. The Mediterranean water shrew (*Neomys anomalus*) and Caucasian pygmy shrew (*Sorex pusillus*) are stenotopic hygrophilous species inhabiting the wettest biotopes of montane forests of the Crimea. Due to high aridity and insufficient amount of precipitation (especially in summer), the number of favourable biotopes suitable for all-year-long existence is quite low thus these species have restricted geographic ranges and low population abundance.

4. The geographic range of the yellow-necked wood mouse (*Sylvaemus tauricus*) is wider and associated with the distribution of deciduous oak-beech forests with admixture of hornbeam, Oriental hornbeam, European cornel, and others. The pygmy wood mouse (*Sylvaemus uralensis*) and Altai vole (*Microtus obscurus*) are the most eurytopic species, the geographic ranges of which expand north-east to the territory of the Crimean Lowland up to Lake Syvash. The species *Sylvaemus uralensis* and *Microtus obscurus* are the most abundant among small mammals in the montane and piedmont zones and they dominate in most small-mammal communities.

Acknowledgements

The author would like to thank I. V. Zagorodniuk for the idea of this article and for his valuable comments during its preparation, as well as Z. Barkaszi for the English translation of the manuscript.

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