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MICE OF THE GENUS *MUS* IN THE CRIMEA: SPECIES DIAGNOSTICS, DISTRIBUTION, AND ECOLOGY

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Mice of the genus *Mus* in the Crimea: species diagnostics, distribution, and ecology. — I. Evstafiev. — The paper presents the first detailed summary of the current state of mice of the genus *Mus* in the Crimea, namely of the house mouse (*Mus musculus* Linnaeus, 1758) and steppe mouse (*Mus spicilegus* Petenyi, 1882). Morphological structures of the house mouse and steppe mouse are characterized and external and craniometrical features important for species diagnostics are presented. Most of the morphological characters tend to vary within the entire geographic range of both species. Body length of house mice is significantly greater compared to that of steppe mice. Tail length in house mice is greater than in steppe mice, but the tail index is greater in the latter. Therefore, house mice look more 'short-tailed', and this feature can be used as an additional diagnostic character. In steppe mice, the tail becomes thinner gradually from base to tip and thus it is awl-shaped. The tail of fit house mice, especially of autumn-winter generations, often has a thickened base, which increases the visual effect of a short tail. Among internal characters, the most significant are the differences between testicles size of mature males. For species diagnostics of mice of the genus *Mus*, the size and shape of the following cranial structures can be used: location of the root and frontal wall of the crown of the first upper molar (M1) in relation to the diastema; zygomatic process of the maxilla and zygomatic arch; palatine foramens *foramina palatinum*, and others. These are reliable characters for morphological identification of *M. musculus* and *M. spicilegus* in the territory of the Crimea, in the zone of their sympatry. Reliable diagnostic characters are the dimensions of palatine foramens. In general, the entire complex of characters analysed in this study should be used for correct morphological diagnostics of these species. Features of distribution and population dynamics of the house mouse and steppe mouse in the Crimea are studied. It has been revealed that both the house mouse and the steppe mouse are distributed mainly in the lowland part of the Crimea and the forest-steppe belt of the foothills. Data on the ecology of species are presented, including specifics of reproduction and habitat preferences. The place and role of house mice in small-mammal assemblages of various landscape and ecological zones are estimated.

Key words: house mouse, steppe mouse, *Mus*, diagnostics, distribution, population, Crimea.

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Introduction

Typical mice (genus *Mus*) are the most closely related rodents to humans in both natural and anthropogenic habitats playing a major role in steppe ecosystems and having an important economic and medical relevance (Sokolov *et al.* 1990; Kotenkova 2000). Typical mice are not only pests of agricultural crops and various human food supplies, but also transmitters of pathogens of different natural focal zoonotic infections, as well as important structural parts of small-mammal communities of the Crimea having an important role in natural ecosystems (Evstafiev 2017).

In the Crimea, typical mice were studied by several local authors (Volyanskiy 1929; Khodykina 1964) and other researchers (Lyalyukhina *et al.* 1989; Sokolov *et al.* 1990; Kotenkova *et al.* 1994; Gromov & Erbajeva 1995; Kotenkova 2000), who published rather contradictory results on the bioecology of mice of the genus *Mus* in the peninsula.

According to modern views, two species of typical mice occur in the territory of the Crimea (Mezhzherin & Kotenkova 1989; Korobitsina *et al.* 1990; Zagorodniuk 1996): the house mouse *Mus musculus* L. (s. stricto) and the steppe mouse *Mus spicilegus* Petényi, 1882. The first species is represented by two ecological groups (exanthropic, which occurs only in natural habitats all year long, and synanthropic), whereas the second species inhabits exclusively natural biotopes and agrocoe-

noses avoiding human settlements (Dulitsky & Tovpinets 1997; Dulitsky 2001; Tovpinets & Evstafiev 2005; Tovpinets & Evstafiev 2010).

The present paper aims to generalize the current knowledge on mice of the genus *Mus* in the Crimea, including their diagnostics, distribution, and ecology.

Material and Methods

The study is based on data collected during epizootic field studies carried out in the Crimean Peninsula by zoologists of the Crimean Anti-Plague Station and of the Department of Particularly Dangerous Infections of the Crimean Republican Sanitary-Epidemiological Station.

Census and capture of small mammals were carried out according to standard methods (Kucheruk 1963; Karaseva & Telitsyna 1996). Live-capture traps and spring-loaded bar traps were used. The trapping effort was 648 950 trap-nights. The number of captured small mammals was 66 607, including 13 683 specimens of M. musculus and 637 specimens of M. *spicilegus*.

An important and rich source of field material are pellets of birds of prey, especially of the long-eared owl (Asio otus Linnaeus, 1758) (Tovpinets & Evstafiev 2013). In total, 16 800 pellets were collected, in which remains of more than 38 300 individuals of rodents and shrews were identified, including 7421 specimens (19.4%) of M. musculus and 1344 specimens (3.5%) of M. spicilegus.

In order to study synanthropic populations of rodents and other animals in human settlements, regular trappings were carried out in buildings and open areas of these settlements (Evstafiev 2000). As a result, 2667 specimens of 11 species of small mammals were captured, among which the share of M. musculus was 33.3%. Habitat preference index of mice was calculated according to Pesenko (Pesenko 1982; Zagorodniuk & Naglov 2017).

Various external and cranial characters used to identify both species in different parts of their geographic range were described by many authors of the 20th century (Guliy 1930; Mygulin 1937, 1938; Orsini *et al*. 1983, Mezhzherin & Zagorodniuk 1989, Lyalyukhina *et al*. 1991; Zagorodniuk & Fedorchenko 1993; Zagorodniuk 1996) and in more recent works as well (Zagorodniuk 2002; Polishchuk 2009).

Species diagnostics of mice of the genus *Mus*

Issues of systematics, taxonomy, and diagnostics of typical mice are presented in the literature quite in detail (Argiropulo 1933; Marshall & Sage 1981; Marshall 1986; Korobitsina *et al.* 1990; Kotenkova & Bulatova 1994; Zagorodniuk 1996; 2002; Kotenkova 2000; Cserkész *et al.* 2008 and others). However, discrimination of *M. musculus* and *M. spicilegus* in the field by external characters has certain difficulties, especially in zones of their sympatry. Species diagnostics of these mice can be problematic even by cranial characters, particularly based on bone fragments found in pellets (Polishchuk 2009).

In this study, we aim to estimate which of the main morphological characters are the most effective for species diagnostics in the field, particularly in the territory of the Crimea, since populations of mice of the genus *Mus* have been existing here maximally isolated from the main part of their geographic range for a long period (Evstafiev 2015).

External and internal characters

A number of characters was used to identify species of typical mice during field studies carried out in the territory of the Crimea, which together allowed both species to be distinguished in the field with a high level of confidence. The correctness of such identifications was confirmed (or denied) in the laboratory after skulls of the trapped mice had been examined. We have concluded that, in case of the Crimean populations, body length and hindfoot length can be used to distinguish the two species, especially of adult specimens regardless of sex, as well as the length of testicles in males during the spring–summer breeding season (Table 1).

Table 1. Comparison of the main external and internal characters of the two mice species of the genus *Mus* from the Crimean Peninsula

Таблиця. 1. Порівняння основних екстер'єрних та інтер'єрних ознак двох видів мишей роду *Mus* з території Кримського півострова

Character (measured in mm)	Species		t / p *	Species**	
	M. musculus	*M. spicilegus*		*M. musculus*	*M. spicilegus*
Body length	83.59 (n = 129)	76.79 (n = 121)	**6.61** / 0.000	75–95 mm	60–75 mm
Tail length	64.32 (n = 109)	61.27 (n = 117)	1.58 / 0.12	65–80 mm	55–65 mm
Tail index	0.769 (n = 109)	0.798 (n = 117)	1.34 / 0.18	–	–
Hindfoot length	16.34 (n = 129)	15.55 (n =121)	**2.94** / 0.005	16–18 mm	15–16 mm
Auricle length	12.38 (n = 99)	12.35 (n = 111)	0.13 / 0.899	13–15 mm	12–13 mm
Testicles length	6.23 (n = 52)	9.86 (n = 22)	**20.8** / 0.000	–	–
Testicles width	3.67 (n = 52)	5.59 (n = 22)	**12.4** / 0.000	–	–

Notes: * Values of Student's t-test for characters with significant difference ($p \leq 0.01$) are given in bold; ** Measurements of some external characters in mice of the genus *Mus* from the main part of the geographic range after Zagorodniuk (1996).

Body length of house mice from natural habitats is significantly greater than that of steppe mice. Absolute values of tail length in house mice are slightly greater than in steppe mice, while the tail index, which is calculated as the ratio of tail length to body length, is greater in steppe mice. Despite the statistically insignificant differences between these parameters, the relatively long tail in steppe mice compared to house mice was successfully applied in the field. Because house mice look more 'short-tailed' than steppe mice, the use of this character (as an additional criterion) for visual identification of species requires some experience in visual evaluation of relative tail length against body length.

When examining the tail (either dorsally or ventrally) of the two mouse species it can be observed that the tail of *M. musculus* has a more or less expressed constriction at its base, i.e. the tail is narrower at its base compared to its continuation. This feature is more expressed in well-fed house mice, especially in individuals of autumn–winter generations, which enhances the visual effect of a short tail. In steppe mice, the tail narrows gradually from its base to top thus it has a subulate shape. Therefore, relative tail length and the presence or absence of a constriction at the tail's base could be diagnostic characters to distinguish the house mouse and steppe mouse in the field.

If the specimen that has to be identified is a mature male during breeding season, dimensions of the testicles could be another reliable diagnostic character to identify *M. spicilegus* (Fig. 1). In the steppe mouse, linear dimensions of testicles are 1.5 times greater than in the house mouse despite its relatively smaller body dimensions (see Table 1).

Cranial characters

When analysing cranial material of either trapped animals or skulls extracted from bird pellets or from corpses of dead mice, differences in cranial structures can be applied for species diagnostics.

Fig. 1. The steppe mouse, *M. spicilegus*. Testicles of a mature male during breeding season.

Рис. 1. Курганцева миша *M. spicilegus*. Сім'яники статевозрілого самця в період розмноження.

Mice species of the genus *Mus* can often be discriminated by the dimensions and shape of the following morphological structures: position of the root and anterior wall of the first upper molar's crown (M1) relative to the diastema, zygomatic process of the maxilla and zygomatic arch, etc.

1. Position of the root and anterior wall of the first upper molar's crown (M1) relative to the diastema

When the position of the root and anterior wall of the first upper molar's crown (M1) relative to the diastema is viewed laterally, attention should be paid to the angle formed between the root and crown of the first upper molar (M1) and the diastema (Fig. 2). This angle is right or nearly right in the steppe mouse (Fig. 2 *a*) and clearly obtuse in the house mouse (Fig. 2 *b*). It should be also kept in mind that about every tenth house mouse has an additional cusp on the first upper molar (M1) (Çolak *et al.* 2006; Takada *et al.* 2002) (Fig. 3). The presence of such cusp causes certain visual distortions (at a cursory glance) to the shape and size of the considered angle, although the angle between the root of such molar and the diastema is always obtuse. In the Crimean Peninsula, we have never recorded such additional cusp on the first upper molar (M1) of steppe mice, neither among skulls of trapped animals nor among materials extracted from bird pellets (n = 463) from different parts of the species range.

The character of the angle of the anterior wall and root of the first upper molar (M1) relative to the diastema is considered as one of the main diagnostic characters in most works dealing with the discrimination of the house mouse and steppe mouse (Zagorodniuk, 2002; Takada *et al.* 2002; Çolak *et al.* 2006; Polishchuk 2009).

2. Zygomatic process of the maxilla and the zygomatic arch (zygomatic index)

The relative size (width) of the zygomatic process of the maxilla in its first third and the zygomatic index are reliable characters for diagnostics of *M. spicilegus* and *M. musculus* (Fig. 4). The width of the zygomatic process in its first third is 0.57 ± 0.074 mm in *M. spicilegus* and 0.99 ± 0.017 mm in *M. musculus*.

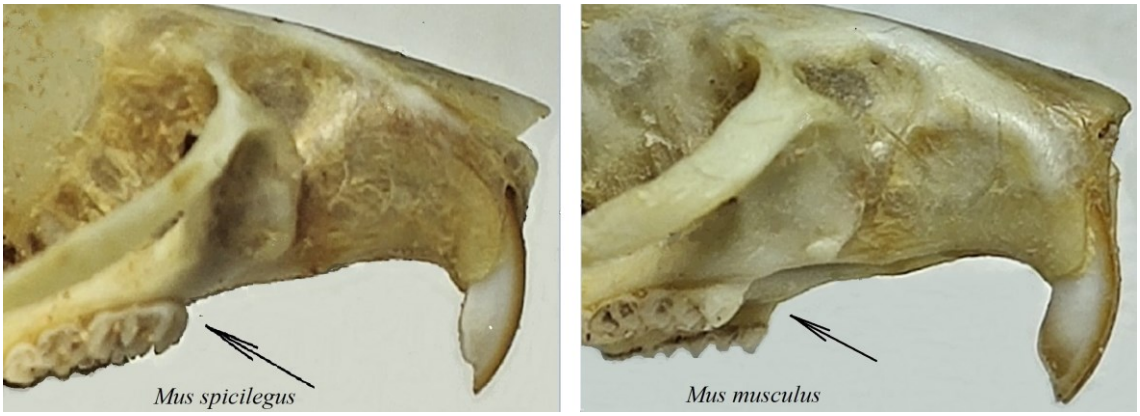

Fig. 2. Position of the root and anterior wall of the first upper molar's crown (M1) relative to the diastema in the house mouse (*M. musculus*) and steppe mouse (*M. spicilegus*).

Рис. 2. Положення передньої стінки коронки і кореня першого верхнього моляра (M1) по відношенню до діастеми у хатньої (*M. musculus*) і курганцевої (*M. spicilegus*) мишей.

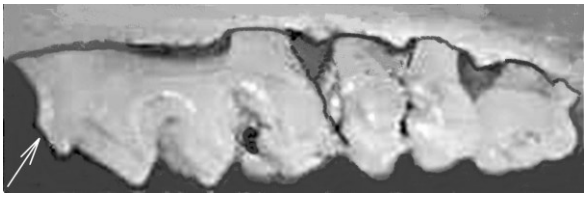

Fig. 3. A variant of the first upper molar (M1) in *Mus musculus* with an additional cusp on the crown (indicated by an arrow).

Рис. 3. Варіант першого моляра (M1) у *Mus musculus* з додатковим зубцем на коронці (зубець вказано стрілкою).

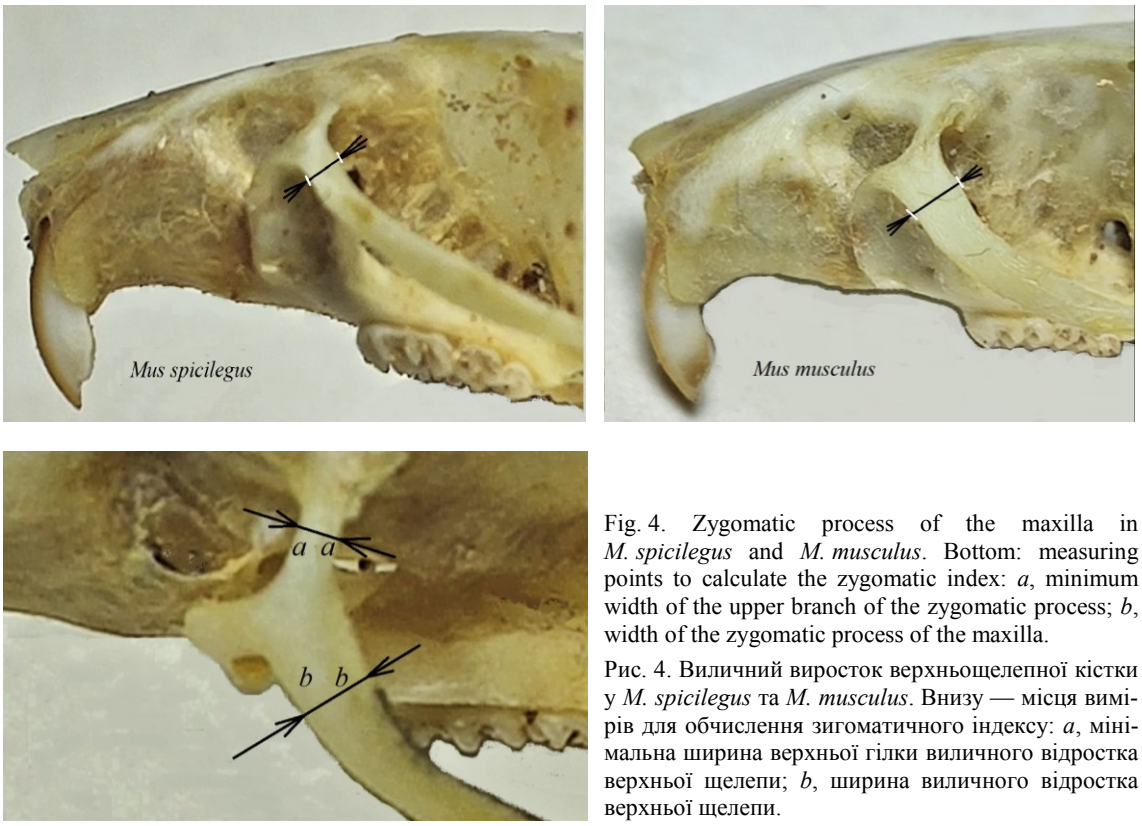

Fig. 4. Zygomatic process of the maxilla in *M. spicilegus* and *M. musculus*. Bottom: measuring points to calculate the zygomatic index: *a*, minimum width of the upper branch of the zygomatic process; *b*, width of the zygomatic process of the maxilla.

Рис. 4. Виличний виросток верхньощелепної кістки у *M. spicilegus* та *M. musculus*. Внизу — місця вимірів для обчислення зигоматичного індексу: *a*, мінімальна ширина верхньої гілки виличного відростка верхньої щелепи; *b*, ширина виличного відростка верхньої щелепи.

Table 2. Comparison of the zygomatic index in *M. spicilegus* and *M. musculus* from western (Greece, Bulgaria, and Austria), Crimean, and East European populations

Таблиця. 2. Порівняння величини зигоматичного індексу у видів *M. spicilegus* і *M. musculus* із західних (Греція, Болгарія і Австрія), кримських і східно-європейських популяцій

Species	Populations		
	western*	Crimean	East European*
M. spicilegus	0.74–0.80	0.93	0.47
M. musculus	0.45–0.48	0.50	0.36

Notes: * Data from Zagorodniuk (2002).

Along with the use of these characters on their own, several authors (Orsini *et al.* 1983; Sokolov *et al.* 1990) also apply the zygomatic index, which is calculated as the ratio of minimal width of the upper branch of the zygomatic process to the width of the zygomatic process Orsini *et al*. 1983; Lyalyukhina *et al*. 1991; Macholán 1996). The value of zygomatic index in *M. spicilegus* from Crimean populations is 0.93 ± 0.195, whereas in *M. musculus* is 0.50 ± 0.093. Comparison of data presented in Table 2 shows that the greatest differences in the value of zygomatic index are observed in the Crimean populations, followed by western populations, whereas minimum differences are noted in East European populations. These data show the reliability of the zygomatic index in species diagnostics of the house mouse and steppe mouse.

3. Palatine foramina

The palatine foramina are not considered as a diagnostic character in most of the published studies. However, the analysis of skulls of *M. musculus* and *M. spicilegus* from the territory of the Crimea revealed that the size of these foramina could serve as an additional diagnostic character. Studies showed that the length of the palatine foramina in *M. musculus* (L_{fp} = 0.43 ± 0.034 mm) is

nearly the same as the coronal length of the third upper molar (M^3) (Fig. 5), whereas in *M. spicilegus* the linear dimensions of these foramina usually do not exceed half of the length of M3 (L_{fp} = 0.31 ± 0.010 mm).

4. Shape of the proximal edge of incisive foramina

According to the literature, the house mouse and steppe mouse also differ by the shape of the proximal edge of incisive foramina (Mygulin 1938): they are narrow and parallel in *M. spicilegus*, whereas wide and rounded in *M. musculus*.

The study of this character in *M. spicilegus* and *M. musculus* showed a wide range of its variation. In *M. musculus*, the proximal edge of incisive foramina has a sharp V-like shape in most skulls (more than 90%), while in *M. spicilegus* it has a more rounded U-like shape (Fig. 6, left top). At the same time, in about the third of skulls of *M. spicilegus* this character is quite similar to that in *M. musculus* (Fig. 6, left bottom).

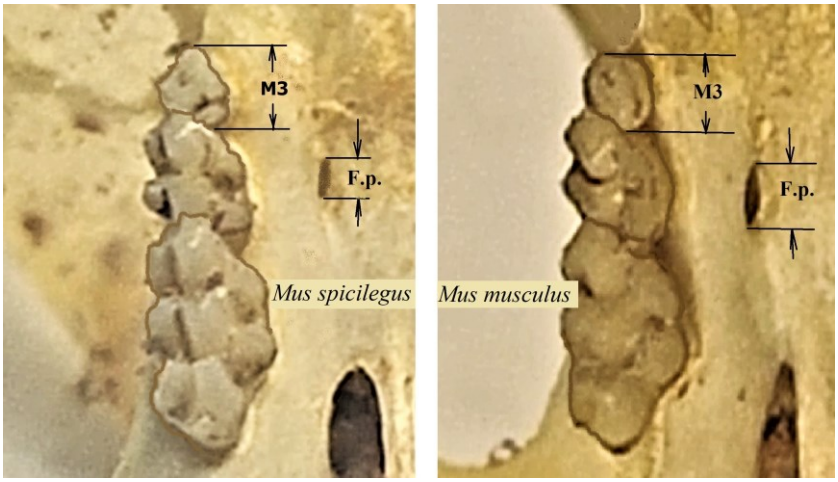

Fig. 5. The hard palate of *M. spicilegus* (left) and *M. musculus* (right). Arrows mark the palatine foramen, the size of which is an additional diagnostic character.

Рис. 5. Кісткове піднебіння *Mus spicilegus* (ліворуч) та *M. musculus* (праворуч). Стрілками позначено піднебінний отвір foramen palatinum, розміри якого служать додатковою діагностичною ознакою.

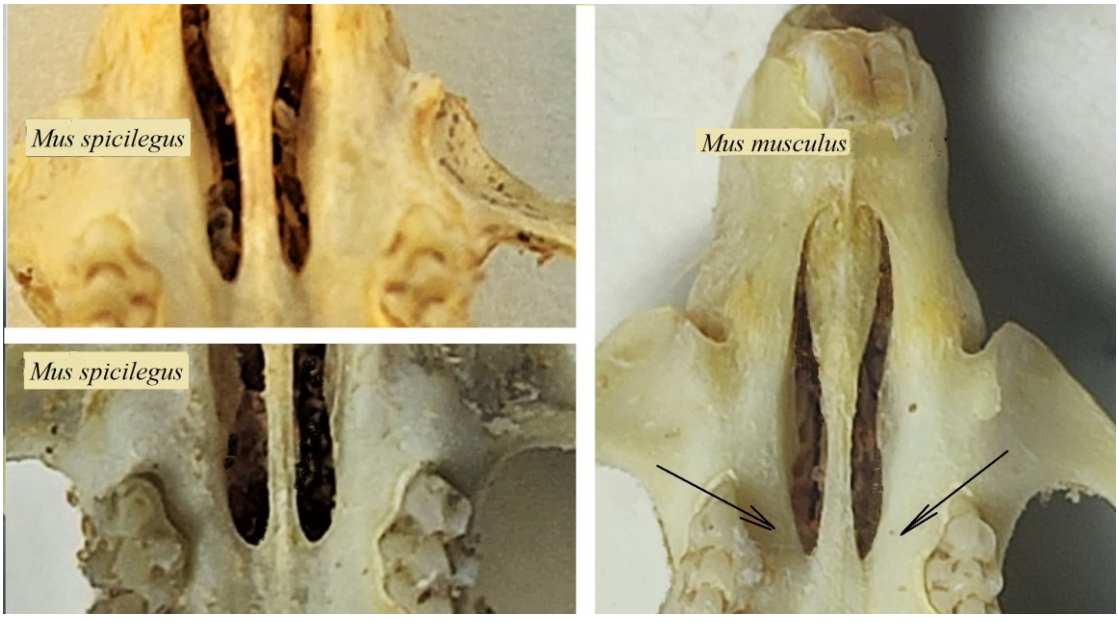

Fig. 6. The proximal edge of the incisive foramina in *M. spicilegus* and *M. musculus*.

Рис. 6. Задній край різцевих отворів у *M. spicilegus* та *M. musculus*.

5. Upper molars length M13 and the M^2/M^3 ratio

The coronal length of upper molars (M13) and the M^2/M^3 ratio are characters also recommended for craniological diagnostics of *M. musculus* and *M. spicilegus* (Mezhzherin & Zagorodniuk 1989; Zagorodniuk 2002). Since the third upper molar M^3 of *M. musculus* is relatively small compared to that of *M. spicilegus*, which has a notably larger M^3, significant differences are observed between the two species by the upper molars length. The M^2/M^3 ratio equals 1.2–1.3 in *M. spicilegus* and 1.6–1.8 in *M. musculus* (Mezhzherin & Zagorodniuk 1989). However, our study has not revealed substantial differences between the two species by the size of M^3: $L_{M3} = 0.64 \pm 0.036$ mm in *M. spicilegus* and $L_{M3} = 0.61 \pm 0.027$ mm in *M. musculus*; the M^2/M^3 ratio in these species was 1.55 ± 0.259 and 1.73 ± 0.310, respectively.

Summing up the section about species diagnostics of mice of the genus *Mus* it should be emphasized that most of the morphological traits, both external and cranial, are characterized by a certain level of variation throughout the geographic ranges of the house mouse and steppe mouse. The exceptions, in our opinion, are the size of testicles, zygomatic process of the maxilla, and the shape of palatine foramina. Therefore, these characters should be treated as the most reliable in morphological discrimination of *M. musculus* and *M. spicilegus*, especially in areas of their sympatry. In general, all of the above characters should be considered together for reliable morphological diagnostics of the two species.

Distribution of mice of the genus *Mus* in the Crimea

The house mouse (*M. musculus*) is a cosmopolitan species. In Eurasia, as a synanthrope species, it expands its range far to the north (occurs in Arctic permafrost regions) and high mountain areas of the Caucasus, Pamir Mountains, and Tian Shan.

The geographic range of the steppe mouse (*M. spicilegus*) is rather restricted (Argiropulo 1940: 89–93; Maltsev *et al*. 2018) stretching from countries of Central of Southern Europe (Austria, Montenegro, Serbia, and Greece), where the subspecies *M. s. adriaticus* is distributed, to the southwestern oblasts (Kursk, Belgorod, and Rostov oblasts) of the Russian Federation.

In Ukraine, the species occurs in several southern oblasts (from Odesa Oblast to Kharkiv, Donetsk, and Luhansk oblasts) (Zagorodniuk 1994; Zagorodniuk *et al*. 1995; Kondratenko 2006). The steppe mouse is a common species in most parts of the Crimean Peninsula (Evstafiev 2004, 2015; Tovpinets & Evstafiev 2010).

The house mouse in the Crimea is one of the most widely distributed and most abundant species of small mammals occurring in various natural and anthropogenic habitats (Fig. 7). Exanthropic populations of the house mouse enter far to the montane zone of the peninsula through agricultural lands and open areas of river valleys of the northern macroslope of the Crimean Mountains. The house mouse avoids continuous forests, both shibliak and high forests, as well as open steppe areas of high-mountain pastures (yaila). In natural habitats of the Southern Shore, the species is non-abundant and rarely occurs in shrubberies and agrocoenoses up to 300 m a.s.l., which are located nearby to human settlements. The house mouse is absent only in areas covered by continuous forests.

The steppe mouse is widely distributed in lowland and piedmont areas of the Crimea in the same habitats as the house mouse (Fig. 8). In the Crimean Mountains and on the Southern Shore, this species does not occur except for a population isolated from the main Crimean range in the far south-west of the Crimean Mountains near Sevastopol. Here the species occurs in open habitats with ruderal vegetation within valley complexes (Tsvelykh 2009; our observations).

In steppe and forest-steppe areas of the peninsula, the two mice species of the genus *Mus* co-occur in most habitats. At the same time, both *M. musculus* and *M. spicilegus* found here the most favourable conditions for themselves, which can be evidenced by periodic population outbreaks of these species. These outbreaks, however, are not synchronous, which can be explained by differences in the biology and ecology of these mice species.

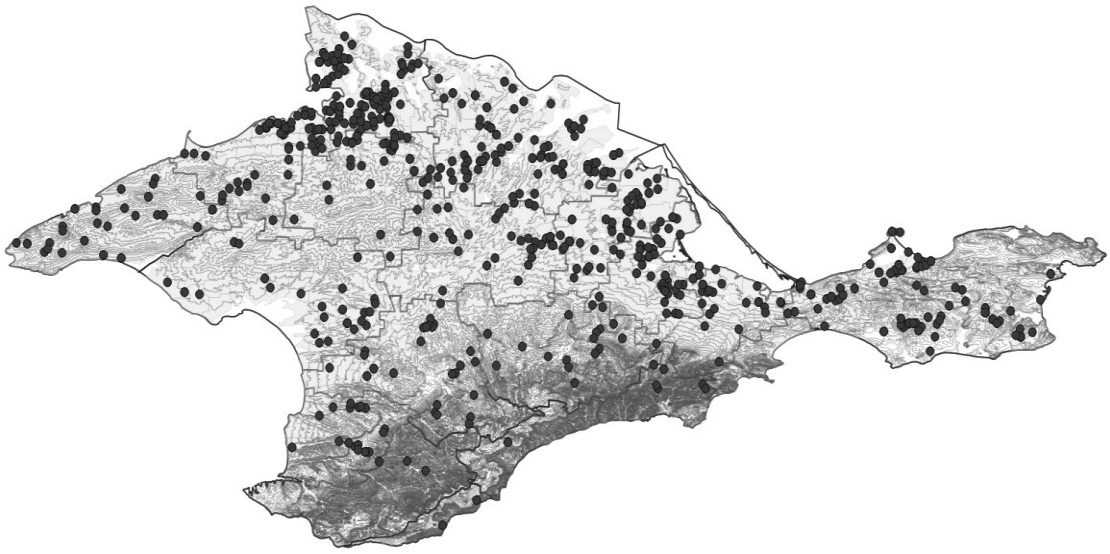

Fig. 7. Distribution of the exanthropic form of the house mouse *musculus* in the Crimea.
Рис. 7. Поширення екзоантропної форми хатньої миші *Mus musculus* в Криму.

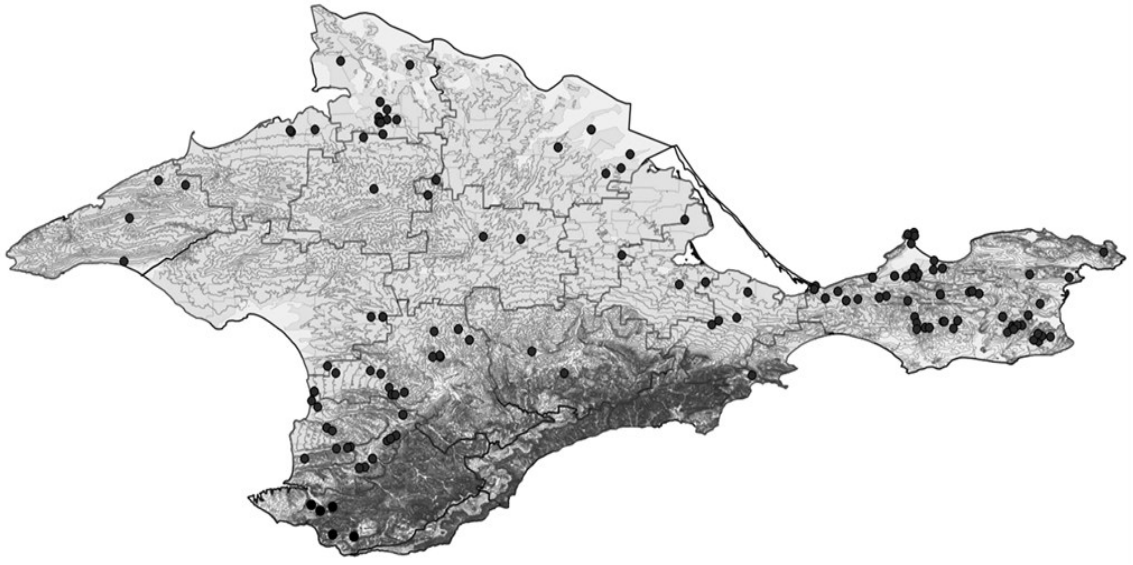

Fig. 8. Distribution of the steppe mouse *Mus spicilegus* in the Crimea.
Рис. 8. Поширення курганцевої миші *Mus spicilegus* в Криму.

Zonal distribution

In the Crimean Peninsula, *M. musculus* is represented by exanthropic and synanthropic populations, whereas *M. spicilegus* only by exanthropic populations. Exanthropic populations of the house mouse occur in all natural zones of the peninsula, although the species' percentage in catches of small mammals differs significantly. The number of trapped mice (specimens and percentage) in a sample of small mammals and relative to the total number of specimens of the species caught in the Crimea is an important parameter of zonal preference (Table 3).

Data presented in (Table 3) show that 90% of specimens of the genus *Mus* are trapped in the lowland steppe zone and in the Kerch Peninsula, and their share in the total sample of small mammals here is 28.2%, of which 27.2% falls on *M. musculus.* In the foothills and Crimean Mountains, the share of typical mice in the total sample of small mammals is only 5.0%.

Table 3. Distribution of the number of captured *M. musculus* and *M. spicilegus* specimens by natural zones of the Crimean Peninsula

Таблиця. 3. Розподіл кількості зловлених особин *M. musculus* і *M. spicilegus* за природними зонами Кримського півострова

Trapping parameters	Natural zone				Total in the Crimea
	Steppe		Foothills	Mountains	
	Crimean Lowland	Kerch Peninsula			
Total number of trapped small mammals	31 389	15 910	8747	10 561	66 607
Sum of *Mus musculus* (*M.m.*)	10 503	2363	634	183	13 683
Share of *M.m.* among all small mammals trapped in the zone (%)	33.46	14.85	7.25	1.73	20.54
Share of *M.m.* caught in the zone among all house mice trapped in the Crimea (%)	76.76	17.27	4.63	1.34	—
Sum of *M. spicilegus* (*M.s.*)	215	265	157	0	637
Share of *M.s.* among all small mammals trapped in the zone (%)	0.68	1.67	1.79	0.00	0.96
Share of *M.s.* caught in the zone among all steppe mice trapped in the Crimea (%)	33.75	41.60	24.65	0.00	—

The role of the house mouse and steppe mouse in small-mammal assemblages is quite variable and depends on many factors, both abiotic and biotic, and their share in mammal complexes may vary to tens of percent. In general, zonal distribution of small mammals of the Crimea was considered earlier (Evstafiev 2004).

House and steppe mice occurring in the same territory and in the same habitat (Figs. 9–10) realize their breeding potential differently in particular years, which reflected in contrasting population abundance. That is, if this year *M. musculus* dominates in a particular habitat, *M. spicilegus* potently can dominate in the following years. The reasons of this pattern is unclear and they obviously depend on various biotic and abiotic factors.

Mus musculus. For many years, the mean relative abundance of *M. musculus* has been 2.7 individuals per 100 trap-days in steppe areas of the Crimean Lowland and 0.9 individuals per 100 trap-days in the Kerch Peninsula. In these regions, climatic and biotopic conditions are the most favourable for this species, especially the food resources. In the Crimean Lowland, the house mouse along with the steppe mouse constitute the dominating core of small-mammal assemblages of the region, where natural steppe habitats (disturbed at various levels) alter with different agrocoenoses and woody plantations (orchards, forest belts, etc.), making up 70% in the composition of fauna. In steppe areas of the Kerch Peninsula, where the share of natural steppe habitats is greater compared to the Crimean Lowland, the steppe field mouse *Sylvaemus witherbyi* (Thomas, 1902) is an absolute dominant (56.6% of abundance), whereas the house mouse is a subdominant together with the social vole *Microtus socialis* Pall., 1773 (10.8%) and lesser white-toothed shrew *Crocidura suaveolens* Pall., 1811 (14.6%).

The piedmont (forest-steppe) zone is a peculiar ecotone between the montane (forest) and steppe zones characterized by maximum gradients of both abiotic and biotic factors. Living conditions for exanthropic populations of *M. musculus* are worse here than in the steppe thus the share of this species in catches is only 7.5% at a relative abundance of 0.5%.

House mice occur in the montane zone even more rarely (1.3 % or 0.1 individuals). At the same time, the species is not part of the group of dominants or subdominants in mammal assemblages of the piedmont and montane zones. While the Ural field mouse *S. uralensis* Pallas, 1811 (31.8%), Altai vole *M. obscurus* Eversmann, 1841 (25.7%), and the steppe field mouse *S. witherbyi* (Thomas, 1902) predominate in the piedmont zone, the dominating species in the montane zone is the yellow-necked field mouse *S. tauricus* Pallas, 1811. The share of these species in catches are as follows: Altai vole—32.9%, Ural field mouse—30.9%, yellow-necked field mouse—28.1%.

Fig. 9. Kerch Peninsula. Fields unploughed for several years and overgrown with ruderal vegetation are habitats of *Mus musculus* and *M. spicilegus*.

Рис. 9. Керченський півострів. Поля, що не орали декілька років, порослі рудеральними рослинністю — місця проживання *Mus musculus* та *M. spicilegus*.

Fig. 10. Typical landscape of the piedmont zone of Crimea, Belogorsk Raion. The alternation of steppe areas with forest belts and tree-shrub communities located along balkas and stream beds is characteristic.

Рис. 10. Типовий ландшафт Предгірного Криму, Білогірський р-н. Характерно чергування степових ділянок із лісосмугами і деревно-чагарниковими угрупованнями, розташованими по балках і руслах струмків.

Therefore, exanthropic populations of the house mouse are the most flourishing in the steppe zone, where living conditions are the most favourable for this species. In the piedmont and montane zones, exanthropic populations are non-abundant and with the increase in elevation and of the area of woody and shrubby vegetation are more related to agrocoenoses and human settlements. In this zone, there is a gradual increase of synanthropic populations and a more intense exchange of individuals between synanthropic and exanthropic populations erasing (blurring) the boundaries between them. The abundance of *M. musculus* is affected by long-term fluctuations that are directly related to the character of realization of their reproductive potential. In average, the abundance of *M. musculus* from spring to autumn increases 2.5–3 times, which is influenced by breeding patterns and mortality during different seasons.

Mus spicilegus. The steppe mouse is more related to the steppe zone, where 75% of its abundance is concentrated (Table 3), whereas only 25% in the piedmont zone (in the montane zone only single settlements were recorded in intrazonal steppe and anthropogenic habitats).

At the same time, its share in catches in the Kerch Peninsula reaches 1.7% at a relative abundance of 0.3 ind. per 100 trap-nights, 0.7% and 0.08 individuals in the Crimean Lowland, and 1.8% and 0.1 individuals in the foothills. The habitat preference index in the Kerch Peninsula also has a high positive value (Fij = +0.60). Regarding the distribution of steppe mice in the Crimea, it is more or less even in the Kerch Peninsula and in the piedmont zone, whereas uneven in the Crimean Lowland. The species is the least abundant in the Tarkhankut Peninsula, in the Syvash area, as well as in areas of rice cultivation and agrocoenoses with intense irrigation.

Features of biotopic distribution

Based on the analysis of long-term data on the abundance of mice of the genus *Mus*, the status of species was determined for mammal complexes of various habitats (Evstafiev 2004). The house mouse is a dominant species (share in catches over 40.1%) only in agrocoenoses of the Kerch Peninsula, where it is abundant (share in catches 24.1–40.0%) in natural herbaceous biotopes. The species has the same status in agrocoenoses of the Crimean Lowland.

The house mouse has a status of common species (share in catches 6.1–24.0%) in biotopes with woody and shrubby vegetation in the Kerch Peninsula, in natural herbaceous biotopes of the Crimean Lowland and of the piedmont zone, as well as in agrocoenoses of the piedmont zone. On the other hand, it is a rare species (share in catches 3.1–6.0%) in woody and shrubby biotopes of the Crimean Lowland, and extremely rare in other types of biotopes (share in catches less than 3.1%).

The status of the steppe mouse in the composition of small-mammal assemblages is lower. In particular, it is a rare species in agrocoenoses of the piedmont zone and in natural herbaceous biotopes of the Crimean Lowland, whereas in other types of biotopes of different natural zones this species is recorded as extremely rare.

The analysis of zonal and biotopic preferences allowed differences in the structure of mammal complexes in various parts of the Crimea to be revealed, in particularly those that affect the ecology and distribution of typical mice in the territory.

It was shown earlier (Tovpinets & Evstafiev 2005; Tovpinets 2012) that mice of the genus *Mus* are take the second place in communities of small mammals and their role changes both within the species range and depending on the type of vegetation. In the Crimean steppe, especially in zones of intense irrigation and rice cultivation, the house mouse had predominated until the mid-2010s. In the past years, however, the absence of irrigation and replacement of rice with perennials (alfalfa) and cereals (wheat, oat) has led to structural changes in small-mammal communities. Now, in such new, more arid biotopes steppe mice began to dominate, while social voles only locally, especially in fields of perennials. The abundance of house mice has declined sharply to minimum values leading to local, mosaic distribution.

Ecology of mice of the genus *Mus*

Reproduction

The reproduction period of exanthropic populations of *M. musculus* is prolonged and it begins in March (Fig. 11). Analysis has revealed that reproduction peaks in June–August, when among mature females more than 40% of specimens are pregnant and near 45% are parous. At the same time, barren females in the middle of summer are practically absent in catches. The average number of embryos reaches its maximum (6.5) in these months. Breeding females of the house mouse are recorded until December. At the same time, the number of embryos decreases to 3.4.

Reproduction in exanthropic populations of the house mouse ceases only in the coldest months of year, i.e. in January and February.

Unlike the house mouse, *M. spicilegus* can engage in two types of building activities. Steppe mice that have wintered in mounds reproduce outside the mounds. To late April, most steppe mice leave their mounds, form pair bonds, and relocate to open habitats for breeding. Here they start to construct burrows, which are structurally similar to those of exanthropic house mice. Summer breeding takes place in these burrows.

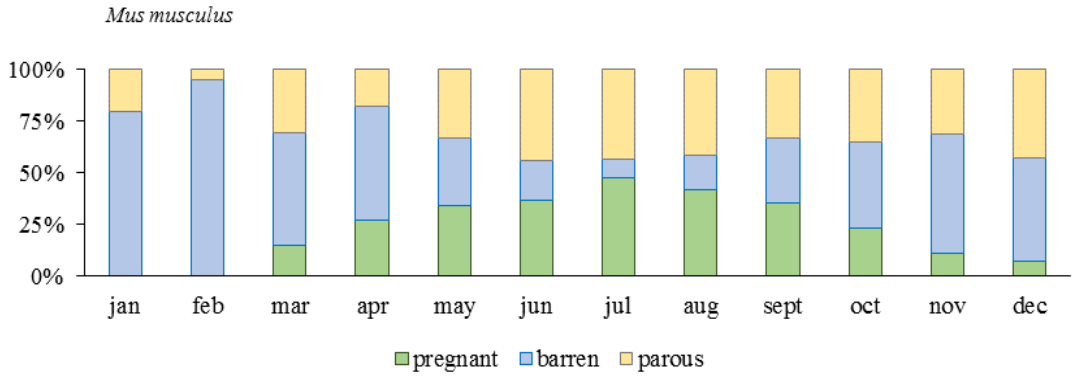

Fig. 11. Seasonal dynamics of reproduction of exantropic house mice *M. musculus* in the Crimea (n = 697 ♀).
Рис. 11. Сезонна динаміка розмноження екзантропних хатніх мишей *M. musculus* в Криму (n = 697 ♀).

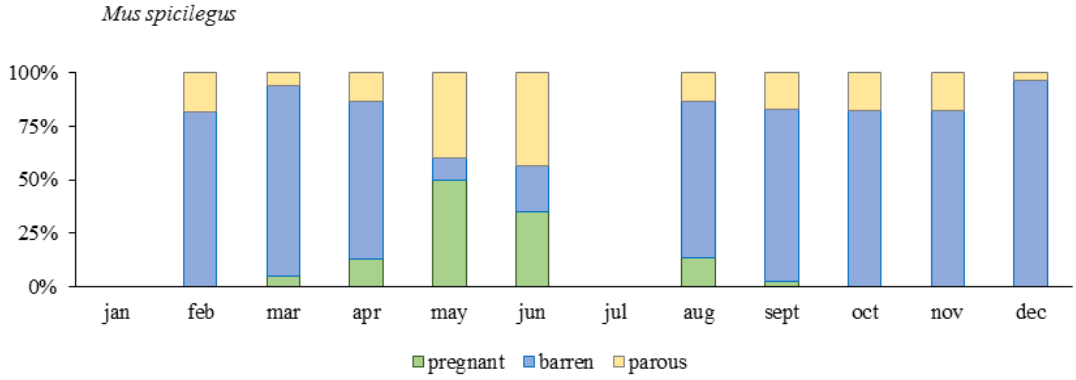

Fig. 12. Seasonal dynamics of reproduction of steppe mice *M. spicilegus* in the Crimea (n = 205 ♀; in January and July this species was not caught).
Рис. 12. Сезонна динаміка розмноження курганцевих мишей *M. spicilegus* у Криму (n = 205 ♀; в січні та липні відловів цього виду не було).

Steppe mice, similarly to house mice, start to reproduce in March (Fig. 12). Copulation, apparently, takes place yet in the mounds and pregnant females can also be trapped at this time beyond the mounds. During March–April, breeding rates remain low and the share of pregnant females does not exceed 10%. A splash is observed only in May, when the share of pregnant females exceeds 60%, and reproduction peaks in June. At this time, practically all trapped females of the steppe mouse are pregnant with embryos at different stages of development.

Hence, the reproduction of steppe mice generally takes place in spring and in the first half of summer, although single pregnant females can be also recorded in early August. Such an early end of reproduction, despite having food in abundance and warm weather, is related to the beginning of mound construction and preparation to unfavourable winter conditions.

At this time, there is a functional change in the activity of the steppe mouse population. In all mature males that participated in breeding, the reproductive organs reduce. Young mature males in autumn–winter period do not breed. At this time, practically the entire population of steppe mice is involved in storing food and building mounds, burrow systems, and wintering nests. In autumn, when night temperature falls up to negative values, a higher moving activity of all individuals is observed with a gradual shift of activity to daytime. Steppe mice collecting food and constructing mounds can observed at this time all day long.

Construction of nests and burrow activity

The two species of typical mice are very similar in their morphology, but differ substantially in their burrow activity, especially in construction of nests. Based on the analysis of burrow activity of *M. musculus*, two specific ecological groups can be identified. The first group comprises house mice of exanthropic populations, which construct both simple burrows with one entrance (particularly common for young individuals) and more complex burrows with several entrances, nesting chamber, storage chamber, and dead ends. Such complex burrows are used for reproduction and wintering.

The second group comprises synanthropic house mice, which live in human settlements in various kinds of buildings. In human settlements, new anthropogenic landscapes emerge along with the destruction of natural habitats, although they cannot be considered as a single ecosystem, but a mosaic of various habitats (Klausnitzer 1990). At the same time, all urban habitats can be divided into two large groups: open areas and constructions considered as habitats created by humans and representing specific ecological niches. These habitats are occupied by house mice due to their high ecological and ethological plasticity (Karaseva *et al.* 1999; Evstafiev 2000).

Synanthropic mice have not entirely lost their connection with natural habitats and a large part of individuals from synanthropic micropopulations are characterized by seasonal migration from human constructions to open natural habitats within the area of human settlements and backwards, which was noted in the Crimea earlier (Khodykina 1964).

The spring migration of house mice to open habitats of human settlements takes place gradually and lasts for several weeks or even months. It is not entirely clarified what triggers such migration, but obviously there could be many reasons, including increasing anthropogenic pressure, depletion of food resources in wintering sites, and appearance of abundant fresh food in neighbouring open habitats sensed due to a variety of olfactory signals. The number of migrating mice depends on particular conditions. If buildings are surrounded by small squares, gardens, weeds, etc. mice actively settle them in spring. In places where herbaceous vegetation (especially ruderal vegetation) is scarce, most mice remain in buildings where they wintered.

Summering burrows of house mice constructed in open habitats are characterized by low protection from unfavourable hydrological and thermal factors. Therefore, from June–August to November–December, waves of migration of house mice take place from open habitats back to buildings. The first waves of migration are triggered by harvesting and subsequent ploughing of fields and gardens, which leads to a substantial change in the structure of these biotopes and to a sharp decline in available food forcing mice to search for new habitats.

The impetus for the completion of autumn migrations is the abrupt deterioration in weather, especially the change of thermal and hydrological conditions. The autumn migration of house mice is usually organized: mice leave open habitats in families and adults with the young of the last generation practically simultaneously settle in new habitats gradually occupying its area. At the same time, house mice continue to reproduce. We have recorded cases of breeding right after settling in buildings. The migration of mice, depending on weather conditions of the particular year, usually completes entirely with the onset of stable frosty weather at night.

Usually, the settlement of buildings by house mice is accompanied with the appearance of characteristic ‘mousy’ (musky) smell. Our long-term observations, however, revealed that this phenomenon is rather ambiguous. In some cases, this characteristic smell in the settled building appears in the first few days, while in other cases it is not found even after a month. The reasons of this lie in the sex-age structure of the population and also depend on the physiologic state of dominants in the given population.

Mounds as a product of building activity of M. spicilegus

Mounds are grand constructions considering the size of their hosts-constructors (Figs. 13–14). Measurements showed that the diameter of mounds in the steppe zone of the Crimea reaches 120–150 cm and more at a height of up to 75 cm. The dimensions of mounds mainly depend on the amount of accumulated resources used for the construction of mound, soil structure, and presence or

absence of herbaceous, woody, or shrubby vegetation. The largest mounds (to 220 cm in diameter and 85 cm in height) were found in the Kerch Peninsula nearby to Shcholkine, on fallow chernozem soils overgrown by ruderal vegetation. In large mounds we have found up to 8–10 kg (2–3 buckets in volume) of stored food such as ears of cultivated and wild cereals, burrs of the rough cocklebur (*Xanthium strumarium*), achenes of the three-lobe beggartick (*Bidens tripartita*) and other plants that are abundant at the site of mound's construction.

Our observations have shown that in various kinds of biotopes of the Crimean Lowland, where steppe field mice (*Sylvaemus witherbyi*) dominate, there is a depressed mound-building activity of steppe mice. In late summer and early autumn, at a high abundance of steppe field mice, the forming heaps of stored seed material are constantly stripped and demolished. At this time, the collected food stocks are not yet covered by soil. Only when the minimum critical mass of storage materials is collected (about 5–8 kg), steppe mice begin to construct the mound. In this period, steppe mice stop collecting food and are fully engaged in covering the accumulated stocks with soil. In several days, the mounds are fully built, when the stocks are covered by about 10–15 cm of soil.

Fig. 13. A mound of the steppe mouse (*Mus spicilegus*) in an artificially planted deciduous forest in Maryivsky forestry, Kerch Peninsula.

Рис. 13. Курганчик миші курганцевої (*Mus spicilegus*) серед штучно посадженого листяного лісу в Мар'ївському лісництві, Керченський півострів.

Fig. 14. A mound from the previous year overgrown with ruderal vegetation with traces of burrow activity of various rodents (social voles, steppe field mice, and house mice).

Рис. 14. Минулорічний курганчик, зарослий рудеральною рослинністю, зі слідами рийної діяльності різних гризунів (полівок гуртових, мишаків степових, мишей хатніх).

Thus, the high abundance of steppe field mice is often a specific obstacle for active building of mounds due to plundering most of the supplies and disturbance of *M. spicilegus* by the more active and more aggressive steppe field mouse. In places where the abundance *S. witherbyi* is low, the building of mounds is more active and completes in shorter terms.

Therefore, the presence or absence of mounds in places of constant occurrence of the steppe mouse in the Crimea depends on various factors, mainly on the abundance of fruits of plants suitable for making food stocks and on the level of disturbance and abundance of other small-mammal species, especially of the steppe field mouse. The presence or absence of fully constructed mounds is an important factor of successful wintering for the steppe mouse, since the role of mounds in the life of *M. spicilegus* is multi-faceted and not restricted only to food storage for winter.

Prolonged rains alternating with frosty snowless weather are usual for the Crimea in the autumn–winter period. Under such conditions, mounds has an important protecting function from low temperatures and precipitation. The excavation of mounds have shown that wintering nests of *M. spicilegus* protected by mounds are always dry and relatively warm, and the ground never freezes there. Such protective features are related to the thickness of both the food stock layer and the covering soil. Besides, a substantial amount of heat is generated by plant materials of the mound (due to 'respiration' of seeds and decomposition of organic matter). In sunny weather, mounds themselves accumulate heat and thus vapour coming from them can be observed even in freezing weather.

Regarding diurnal activity, house mice and steppe mice are the most active at twilight and in the night, although in house mice from synanthropic populations it can change depending on the rhythm of life of people in the building occupied by the species.

Conclusions

Two species of the genus *Mus* occur in the territory of the Crimean Peninsula: the house mouse *M. musculus* and the steppe mouse *M. spicilegus*.

Most morphological characters, both external and craniological, are characterized by a particular variation throughout the geographic range of the house mouse and steppe mouse. For reliable diagnostics of skulls of mice of the genus *Mus*, the dimensions and shape of the following structures can be used: position of the root and anterior wall of the first upper molar's crown (M^1) relative to the diastema; zygomatic process of the maxilla and zygomatic arch; palatine foramina; etc. These characters are reliable in morphological discrimination of *M. musculus* and *M. spicilegus* in areas of their occurrence, especially in zones of their sympatry. In general, all of the considered characters should be used together for reliable morphological diagnostics of these species.

The geographic range of the steppe mouse is restricted to steppe and piedmont areas of the peninsula, whereas in the montane zone only single settlements of the species have been recorded in intrazonal anthropogenic habitats. The abundance of the steppe mouse is about 0.5 ind. per 100 trap-nights, whereas the average relative abundance of house mice is 1.8 ind. per 100 trap-nights.

The house mouse is represented in the Crimea by two ecologically distinct populations: exanthropic, which occur exclusively or mainly in natural habitats, and synanthropic, which inhabit buildings or open areas within human settlements. The geographic range of the house mouse in the Crimea covers the entire area of the peninsula. Exanthropic populations are concentrated mainly in the steppe and piedmont zones and are practically absent in the montane zone, whereas synanthropic populations occur everywhere, in all human settlements of the peninsula.

House mice from synanthropic populations are characterized by seasonal migrations: in spring–summer from closed ecological niches (buildings) to open habitats of human settlements and backwards in autumn. Limited contact between synanthropic and exanthropic populations of house mice (exchange of genetic material) are possible in periods of these migrations.

Mounds build by *M. spicilegus* are an important factor of successful wintering. The role of mounds in the life of steppe mice is multi-faceted, including food storage, protection from carnivores and unfavourable weather conditions.

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