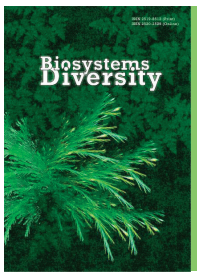

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Steppe rodents at the edge of their range: A case study of *Spalax microphthalmus* in the north of Ukraine

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Based on results obtained during 2000–2018 by field research, polls of colleagues, and OSINT analysis, features of distribution of the greater mole rat *Spalax microphthalmus* in the eastern forest steppe of Ukraine were considered. The studied part of the species' range is unique and represents the northern range edge of the entire Spalacidae family and of European steppe faunal assemblages in general. In total, data on 146 record localities were amassed, including 13 localities in the fragmented and 133 in the continuous part of the range. The offshoots of the Central Russian Upland in the valley of the Psel river (east of Sumy Oblast) are the sites with the highest density of settlements, while the species' type biotopes are steppe balka slopes. The abundance of the greater mole rat decreased from the east to the west, and its colonies are the most fragmented along the Dnipro River. The species occurs in steppe and meadow habitats of an area of at least 20–50 ha. Analysis of the current and former distribution of the greater mole rat revealed that the species range contracts from the west; earlier it was a common species in different regions of the Middle Dnipro Area (including Kyiv city), but the current range edge runs along the line connecting Buryn – Nedryhailiv – Lokhvytsia – Myrhorod – Hadiach – Zinkiv – Zaliznychne. Isolated settlements exist in adjacent territories, particularly in Ichnia Raion of Chernihiv Oblast, and Lubny, Khorol, and Kobeliaky Raions of Poltava Oblast. The study showed that the species' range contracted by two times to 35,000 km^2 for the last 100 years, which includes only 430,000 ha of suitable habitats (15% of the range), allowing the existence here of 86,000–215,000 individuals. In fact, the species remained only in habitats that have been minimally affected by arable farming and other forms of active agricultural use. Besides, the species shows a clear confinement to habitats located near human settlements such as untilled lands, pastures with moderate grazing, waste and neglected lands, which constitute a separate group of transformed and semi-natural habitats. Formally, this allows the greater mole rat to be considered as a synanthropic species, because its inhabited biotopes, beside the zone of offshoots of the Central Russian Upland, have remained only near villages and along roads. The species also has an important biocoenotic role due to its burrowing activity and as prey of predatory birds (e.g., of the long-legged buzzard and Eurasian eagle owl) and mammals. The feeding period of the offspring of these predators generally coincides with the aboveground activity of mole rats, which lasts during May–July with a peak in June. Aboveground activity is mainly related to the resettlement of mole rats to new sites and dispersal of the young, due to which they became victims of predators.

Keywords: Spalacidae; geographical distribution; fauna dynamics; steppe biocoenosis; Eastern Europe.

Introduction

Mole rats (*Spalax*) are highly specialized subterranean mammals and a part of steppe faunal assemblages (Zagorodniuk, 1999). These animals are clearly related to steppe communities and are not only their indicator species, but also ecosystem engineers mainly due to their burrowing and foraging activities (Andersen, 1987; Hagenah & Bennett, 2013). Recent reduction of natural habitats is especially serious in the case of steppe and steppe-like grasslands, including those in Eastern Europe (Cremene et al., 2005; Habel et al., 2013).

The distribution of spalacids is restricted mainly to the southern regions of Eastern Europe (Reshetnyk, 1941), but also reaching northern areas up to the northern parts of the forest steppe zone, where they inhabit slopes of uplands, where, due to exposure, aridity and other features, generally southern-type communities are formed. In the research area (to the east of the Dnipro river) only a single mole rat species occurs – the greater mole rat *Spalax microphthalmus* Guldenstaedt, 1770 – which significantly simplifies the taxonomic attribution of collected faunal data (Korobchenko & Zagorodniuk, 2009).

Research into the distribution of mole rats in northeast Ukraine can give answers on where steppe complexes can be preserved and what role mole rats play in such communities. Under the influence of total transformation and fragmentation of natural habitats, many species, and especially steppe ones, have significantly contracted their former distribution range and disappeared from many localities. However, data on distribution of the greater mole rat in the region have been rather ambiguous from the very beginning. In particular, as stated in V. Averin's review (Averin, 1915: p. 32), the greater mole rat is "quite common in our governorate … especially in its eastern part, where it substitutes the European mole. To clarify the borders of its distribution to the north and west might be an interesting issue." Later, in O. Migulin's review (Migulin, 1928: p. 175) it was stated: "The mole rat is widely distributed in the former Kharkiv Governorate, although in its northwest part it less abundant than in the southeast, where some fields are densely burrowed by mole rats." The situation has not changed since. The last reviews indicating the disappearance of the greater mole rat in the western parts of Poltava Oblast were published by B. Golov (1975). Later data are unknown. The aim of the present paper is to study the current distribution of the greater mole rat within the forest-steppe zone in the northeast of Ukraine based on records dated 2000–2018. Additionally, we aim to determine the regions with the highest density of settlements, to describe the species' typical habitats, clarify the borders of its range, the rate of range contraction and the level of range fragmentation.

Material and methods

In terms of biogeographic division, the research area covers regions of the East European deciduous forest and forest steppe zone (1.2.b) to

the east of the Dnipro river (subarea 1.2.bb after Szczerbak, 1988). In general, the research area lies between the Desna, Dnipro, Orel, and Siverskyi Donets rivers within Ukraine, and it borders with the Central Russian Upland in the northeast.

Field diagnostics based on molehills. Only two species of subterranean burrowing mammals occur in the studied area, namely the greater mole rat and the European mole. The molehills of these species essentially differ by the size and volume of excavated soil. Besides, molehills also differ by patterns of location and biotope types where they can be found. Molehills of *S. microphthalmus* are usually located in a line of 20–30 hills with a distance of 2–3 m between them, while molehills of the European mole are located chaotically in compact groups. The diameter and volume of molehills also vary from 50–90 cm and 5–20 l in the greater mole rat, and 25–40 cm and 2.5–3.2 l in the European mole (own data; Kutseryb, 2011). Although, molehills of the mole rat were similar to that of the European mole in several cases (Fig. 1*a*), the latter excavates fine-grained soil, while the greater mole rat excavates soil clouts of 3–5 cm (Fig. 1*c*), which are especially visible at the top of the molehills (own data). Moreover, these two species also differ by the type of habitat they occupy: the European mole occurs in forests and floodplain meadows, while the greater mole rat prefers balkas with steppe and meadow communities (interfluves between large rivers) (Fig. 1*a*). In several cases, the diameter of the burrow is also informative, which is about 5–8 cm in the mole rat (Fig. 1*b*) and 3.5–4.5 cm in the mole. However, the European mole occasionally may build molehills similar to that of mole rats (V. Khodzynskyi, pers. comm. and own unpublished data). This is a seasonal phenomenon related to the cleaning of burrows before wintering and breeding. These molehills occur simultaneously with typical small ones, they are still fine-grained with a spiral tunnel inside. Soil clouts may occur on the top of such molehills as well, but their size is less than 2–3 cm in diameter.

Distribution and biotope analyses. Field research was carried out in 2000–2018 in the territory of Sumy, Chernihiv, Poltava, and in the northwest of Kharkiv Oblasts, mainly in natural habitats. Data available from literature sources were also analysed, among which it is worth mentioning reviews by E. Reshetnyk (1941) and B. Golov (1975). Additionally, polls of colleagues working in the region (Poltava, Hadiach, Sumy, Nizhyn, Konotop, Kobeliaky, and Krasnokutsk cities and more than 30 villages) were also conducted. Data were collected not only concerning record localities, but also specifics of biotopic distribution of mole rats and their sightings on the surface and in leavings of predators.

In different periods and seasons, together with our local colleagues we conducted six route censuses by vehicle in general direction of the transect Kyiv – Pyriatyn – Poltava – Kharkiv, during which localities with dense settlement or their absence were recorded. These data were used for the zones of sporadic and continuous distribution, and in some cases for creation of an inventory as well. Additionally, OSINT analysis was conducted, based on which two records of mole rats were obtained. Finally, all available museum collections of Ukraine were revised.

Records were mapped by GIS tools using the QGis application. All records were described according to a similar scheme including the names of administrative units, closest human settlements or nature conservation areas, date of observation, biotope, and the observed object (usually molehills), as well as data sources (names of colleagues who reported the record). The main record localities were wide dry steppe valleys without watercourses, which are common in the studied region, and are called "balka." This term is used here according to geographical sources (Sycheva et al., 2003; Kotlyakov & Komarova, 2007). The following abbreviations were used in descriptions of record localities: SBS, steppe balka slopes; NMNHU, National Museum of Natural History, Ukraine.

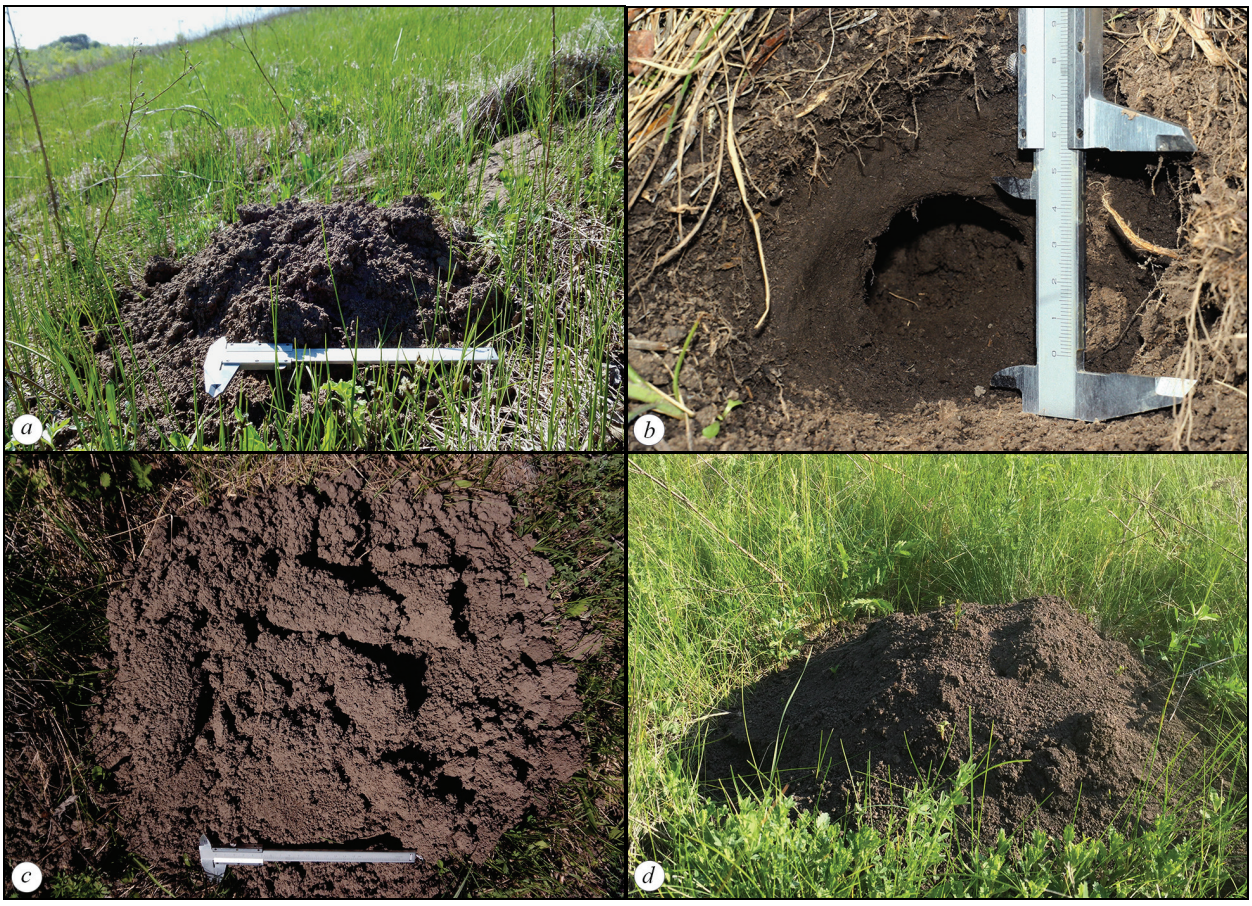

Fig. 1. The general view and patterns of molehills of mole rats: *a* – a fresh molehill in a steppe plot of a balka; *b* – measuring the diameter of the burrow hole (6 cm, which is clearly larger than that of the European mole); *c* – view of the top of the molehill with clearly visible clouts of excavated soil; photos *a*–*c* were taken near Vakalivshchyna on 3 May 2018 by V. Parkhomenko); *d* – typical *Spalax microphthalmus* molehill in a steppe plot near the Donets river (diameter ca. 80–90 cm, 24 May 2017; photo by I. Zagorodniuk)

General description of the species' status in the region. The greater mole rat *S. microphthalmus* is the only mole rat species in the north of Ukraine. This part of the genus's range clearly belongs to this species, although morphological materials from the region have not yet been analysed properly. The colouration pattern of the greater mole rat is generally grey fur and a dark rhinarium, the latter occasionally with small grey spots on the sides. A common character of adult and old individuals collected in the Left Bank Ukraine is the greyed front of the head, when almost the entire forehead becomes white (Reshetnyk, 1941).

The four specimens we analysed by (Fig. 2*a–f*) are characterized by evenly dark rhinarium, without grey or pink spots. Large dark grey spots of irregular shape (Fig. 2*d–f*) are well visible on the feet (clearly on the forelegs and ambiguously on the hind legs). By this particular character, the greater mole rats of north-eastern Ukraine (Sumy and Kharkiv Oblasts) clearly differ from mole rats of eastern Ukraine (Luhansk Oblast), because the latter have a long and narrow grey stripe on the outer side of the feet (of both forelegs and hind legs).

The oldest and most complete description of the species' distribution in the region is given by Reshetnyk (1941). She wrote that in Poltava Oblast, based on research results for 1937–1938, the greater mole rat was a widely distributed and abundant species, particularly in Reshetylivka, Shyshaky, Kobeliaky, Myrhorod and other raions (districts). However, in 1996–1997 (our data) the species was not sighted in the territory of these raions. The contraction of the species' range occurred in the second half of the 20th century. Most of the settlements described for Poltava Oblast by Golov (1975) have recently disappeared. He also noticed the clear tendency of the species' extinction in the west of Poltava Oblast.

Fig. 2. Aboveground records of mole rats: *a*, *b* – a mole rat from the vicinity of Velyka Pysarivka, 13 June 2012 (a young specimen (< 20 cm, white incisors) showing typical aggressive behaviour, photo by V. Parkhomenko); *c* – a mole rat walking along a kerb, near Kotliary, June 2013 (photo by S. Dubynskyi); *d* – colouration of the rhinarium and foreleg of a mole rat from Chernetchyna (the same specimen as on Fig. 1*a–b*); *e–f* – colouration of the foreleg and hind leg of a mole rat from the vicinity of Synivka, 25 May 2018 (photo by A. Statyva)

From this part of species' range, there are only four old specimens in zoological collections of the National Museum of Natural History (NMNHUZ). They were obtained from two localities of the same region that is considered in the present paper, both in Kharkiv Oblast: 1) Ogultsi, Valky Raion, 1917, n = 1 (leg. Bogdanov); 2) Duvanka, Zolochiv Raion, 1925, n = 1; 1929, n = 2 (leg. O. Migulin). More recent materials are absent in the collections.

Results

Review of records. In total, data on 146 record localities of the species in the region were collected, including 13 records in the fragmented and 133 in the continuous part of the range.

Information on the species' distribution is presented further in the list of records. Record localities are shown on a map of the region (Fig. 3). In Sumy Oblast, the greater mole rat was recorded in most of the southern raions to the east of the line Buryn – Nedryhailiv. These are mainly not numerous records. However, the species has a high abundance in two other regions. In Poltava Oblast, current records are confined mainly to the northern (bordering with Sumy Oblast) and eastern raions. In Kharkiv Oblast, the species is common everywhere. In Chernihiv and Sumy Oblasts as well as in the west of Poltava Oblast, records of the species are isolated from other finding localities, and are, practically, the relicts of the former wider range of the species.

Zone of fragmented distribution. The entire northwestern (including the Dnipro region) part of the species' range is the zone of sporadic distribution. Range fragmentation occurred apparently in the middle of the 20th century, but it has become more intense in the last 2–3 decades. Obviously, not all range fragments can be detected within a single study, but the fact of both their small number and area is unambiguous. Comments on locations where the current distribution of the greater mole rat has not been confirmed are given in the first part of the discussion.

Chernihiv Oblast. This spatial segment includes the westernmost records of the species in the studied region and in Ukraine in general. ● Nizhyn Raion, near Nizhyn, railway crossing at the exit from the city towards Kruty, 09.2010, roadside virgin land, morning observation of a mole rat (O. Voblenko, pers. comm., according to information from O. Ohienko, a game-keeping expert); ● Ichnia Raion, near Leonidivka (between Losyniwka and Halytsya), 1998–1999, large molehills on old fallows (S. Gladkevich, pers. comm.); ● Ichnia Raion, near Parafiivka, 2016, finding of a dead mole rat (A. Mokhir, pers. comm.).

Poltava Oblast (west and south). Since the long-standing descriptions by Golov (1975), no new data have been reported. The author even then already noticed the population decrease and the process of the species' extinction. This part of the range is probably represented by fragmented populations of the greater mole rat.

Lubny fragment. ● Lubny Raion, near Pyshne, molehills along a road, 27.04.2018 (N. Brusentsova, pers. comm.).

Khorol fragment. ● Khorol Raion, near Khorov, molehills on a field, 27.04.2018 (N. Brusentsova, pers. comm.); ● Khorol Raion, near Lobkova Balka, a row of molehills along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Khorol Raion, near Khorol city, regular observations of molehills in roadside virgin land stripes, 2005–2017 (S. Shevchenko, pers. comm.).

Bahachka fragment. ● Velyka Bahachka Raion, near Bilotserkivka, regular observations of molehills in roadside virgin land strips, 2005–2017 (S. Shevchenko, pers. comm.); ● Reshetylivka Raion, near Reshetylivka city, regular observations of molehills in roadside virgin land strips, 2005–2017 (S. Shevchenko, pers. comm.).

Poltava fragment. ● Poltava Raion, near Abazivka, molehills on a field along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Poltava Raion, near Zhuky, holiday village, regular observations of molehills in virgin and fallow lands, 2000–2007 (S. Shevchenko, pers. comm.).

Kobeliaky fragment. ● Kobeliaky Raion, near Kobeliaky city, regular observations of molehills in roadside virgin land stripes and balks running towards the Vorskla River, until the early 2000s, no later observations (S. Shevchenko, pers. comm.); ● Kobeliaky Raion, near Luchky (biostation of the Poltava Pedagogical Institute), regular observations of molehills and burrows on virgin plots (on field practice with students), until the early 2000s, no later observations (S. Shevchenko, pers. comm.).

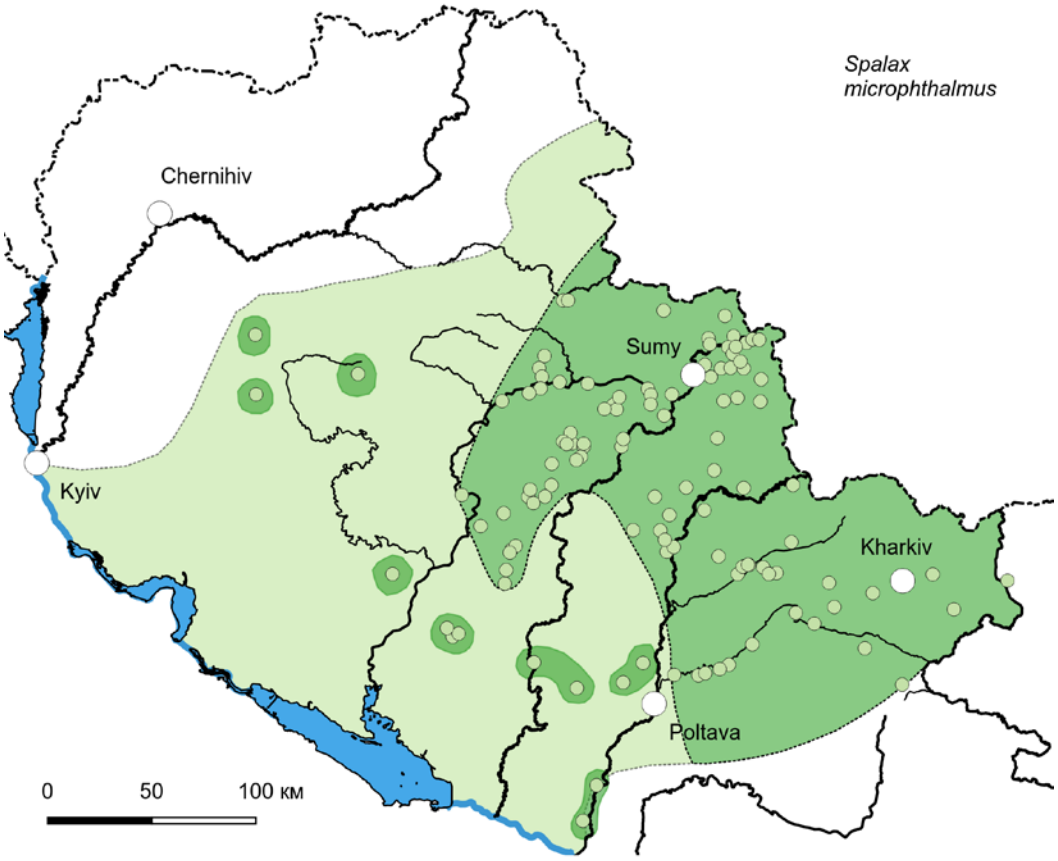

Fig. 3. The distribution range of the greater mole rat in the north of Ukraine based on all records since 2000: circles designate the exact record localities, and the dark green filling indicates the current range

Zone of continuous range. This part of the species range is relatively solid. Obviously, it is fragmented naturally (rivers, forests) and by artificial obstacles (roads, farmland, forest strips). In this part of the range, most of the stable populations are concentrated on offshoots of the Central Russian Upland (the so called Voronezh Massif) that extend from the territory of Belgorod and Kursk Oblasts in a southwestern direction, towards both the Dnipro and Donets rivers. Analysis of habitats, or territories available for mole rats, and the evaluation of the mole rat population in this part of the range are presented in the second part of the Discussion.

Sumy Oblast 1 (central west and southwest). The western part of the forest steppe zone within Sumy Oblast, only with a few findings. The species' abundance varies spatially: the greater mole rat is not numerous in Nedryhailiv Raion, while the species is quite abundant in Lypova Dolyna Raion. ● Buryn Raion, near Diakivka and Klepaly (left bank of the Seym River), SBS, 20.05.2009 (recorded by V. Parkhomenko); ● Sumy Raion, near Yastrubyne, until 2000 (recorded by V. Parkhomenko); ● Nedryhailiv Raion, near Khoruzhivka, Kulishivka, Komyshanka, Lavrove, Golubivka and Korovyntsi, 19.06.2009, 12.09.2010, and 19.06.2018; SBS (recorded by V. Parkhomenko); ● Nedryhailiv Raion, near Tsybulenky, 13.05.2018, in the village and its vicinities, regular observations in 2007–2018 (O. Soloviov, pers. comm.); ● Romenskyi Raion, vicinity of vil. Pustoviitivka, SSA, 19.06.2018 (recorded by V. Parkhomenko); ● Lypova Dolyna Raion, near Koliadynets, remains in leavings of the long-legged buzzard (Stativa & Knysh, 2010); ibidem, 2015–2016, molehills on balkas with steppe or meadow biocoenosis (recorded by V. Parkhomenko); ● Lypova Dolyna Raion, near Oleschenkove, Beyevo-Komuna (= Melnykove), Kolisnyky, Kolomiytseva Dolyna, and Synivka, 2015–2016, molehills on balkas with steppe and meadow biocoenosis (recorded by V. Parkhomenko); a high abundance of mole rats in balkas was recorded in this area of the Khorol river basin (M. Knysh, pers. comm., 2010); ● Lypova Dolyna Raion, near Pidstavky, remains in leavings of the long-legged buzzard (Stativa & Knysh, 2010); ● Lypova Dolyna Raion, near Greky, remains of one specimen in leavings of the long-legged buzzard; ● Lypova Dolyna Raion, near Synivka, a roadkill, 25.05.2018 (A. Statyva, pers. comm.).

Sumy Oblast 2 (southeast). In the southeast of Sumy Oblast, the greater mole rat occurs more frequently than in other territories, although the density of settlements here is rather low. The relief in this region is largely represented by gullies and balkas, i.e. the proportion of tilled lands is low. Therefore, favourable conditions exist here for the conservation of steppe areas as mole rat habitats. ● Sumy Raion, near Mohrytsia, SBS, 2001–2017, high abundance (recorded by V. Parkhomenko); high abundance of the mole rat in a balka near Mohrytsia was also indicated by other investigators (records in 2009, M. Knysh, pers. comm.); ● Sumy Raion, near Vilshanka, Vakalivshchyna, Bytytsia, Bezdryk, Junakivka, Sadky, Tokari, Zatsarne, and Shpylivka villages, 2001–2017, SBS; the settlement in Vilshanka disappeared by 2018 (in 2000–2009 the mole rat was rare in this locality, occurred on balka slopes but later completely vanished due to considerable growth of the blackthorn (recorded by V. Parkhomenko); high abundance of mole rats on balkas near Vakalivshchyna was also reported by colleagues in 1962–2017 (M. Knysh, pers. comm.); ● Krasnopillia Raion, near Velyka Rybytsia, Zapsillia, Barylivka, Sinne, Grunivka, and Marchenky, 2001–2017, meadow and steppe plots on balkas (the picture of the habitat in Fig. 4); this is the locality with the highest abundance of mole rats, up to 70 molehills per ha. Additionally, some molehills usually are registered in roadside meadows (e.g., along the Sumy–Myropillia road), in vicinities of villages listed above, commonly near balkas (recorded by V. Parkhomenko); ● Krasnopillia Raion, near Velykyi Bobryk and Dumivka, 2009–2017, SBS, low abundance compared to the previous locations (recorded by V. Parkhomenko); ● Krasnopillia Raion, near Krasnopillia, Ugroidy, Osoivka, and Gnylytsia, 2001–2009, SBS, regular observations of molehills (recorded by V. Parkhomenko).

Sumy Oblast 3 (south). The species is relatively common here; regular records are reported from the south of Sumy Oblast, as well as from adjacent parts of Poltava Oblast (see below). ● Lebedyn Raion, near Katerynivka, Pidoprygory, and Grytsyny, 2003–2006, SBS (recorded by V. Parkhomenko); ● Lebedyn Raion, near Shtepivka and Sula (2003–2012); SBS (recorded by V. Parkhomenko); ● Lebedyn Raion, near Zelena Roshcha, Lyfyne, and Vorozhba, 2004–2010, SBS (recorded by V. Parkhomenko); high abundance of the mole rat on a balka near Zelena Roshcha was also indicated by other investigators (observations in 1993–2005, M. Knysh, pers. comm.); ● Lebedyn Raion, near Chervlene and Kurhan, balka with steppe biocoenosis, 18.07.2005 (recorded by M. Knysh and V. Parkhomenko); ● Okhtyrka Raion, near Chupakhivka, 2009–2012, SBS (recorded by V. Parkhomenko); ● Okhtyrka Raion, near Kuzemyn, Skelka, Hrun, Hnylytsia, and Viazove; balkas with steppe and meadow biocoenosis, 12–13.05.2012 (recorded by V. Parkhomenko); ● Okhtyrka Raion, western vicinity of Okhtyrka, 2009–2012, SBS (recorded by V. Parkhomenko); ● Trostianets Raion, near Boromlia and Trostianets, 2006–2012, balkas with steppe and meadow biocoenosis (recorded by V. Parkhomenko); locals from Trostianets reported (2011) that "moles" were stealing potatoes from kitchen gardens (M. Knysh, pers. comm.); ● Velyka Pysarivka Raion, near Velyka Pysarivka, roadside virgin land, 13.06.2012, a young specimen was observed on the surface (Fig. 2); ● Velyka Pysarivka Raion, near Katanske, 14.05.2012, burrows on SBS (recorded by V. Parkhomenko).

Poltava Oblast (north and centre). The most stable part of mole rat populations in Poltava Oblast with regular records of both animals and molehills. The new findings were recorded from the Sula, Khorol, and Psel river valleys. ● Hadiach Raion, near Hrechanivka; mole rats were reported by a forester; regular records are known at local plots, including 2015–2016 (S. Lytvynenko, pers. comm.); ● Hadiach Raion, near Petrivka-Romenska, in vicinities and to the north (towards Serhiivka), left bank of the Khorol river, 2014–2017, observations of molehills, the locals passed killed animals (S. Lytvynenko, pers. comm.); ● Hadiach Raion, Baliasne, private estate, autumn 2017, killed as a pest in the garden (S. Lytvynenko, pers. comm. based on reports of locals); ● Hadiach Raion, near Bukhalove, kitchen gardens, 06.2017, trapped by locals (S. Lytvynenko, pers. comm.); ● Hadiach Raion, near Osniahy, 8–15 molehills near a highway, between a steppe plot and a cornfield, 2017–2018 (O. Baryshnikov, pers. comm.); ● Lokhvytsia Raion, near Lokhvytsia, separate molehills on SBS, 19.06.2018 (recorded by V. Parkhomenko); ● Lokhvytsia Raion, near Saranchyne (uninhabited), 01.05.2017, about a dozen of large molehills on a slope of southeastern exposition near the village cemetery (A. Podobailo, pers. comm.); ● Lokhvytsia Raion, hamlet west of Nyzhnia Budakivka village (along the Bodakva river, the left tributary of the Sula river), private plots; autumn 2017, when manoeuvering in the garden, a car fell into a cavity, which turned out to be a mole rat hoarding chamber containing about one bag of potatoes [One bag according to gardening standards can hold more than 5 (five) 10-liter buckets of potato, which equals 37.5 kg; at the rate of 7–8 potatoes per 1 kg it will be about 280 potatoes, and such a stock allows the mole rat to consume 1–2 potatoes per day] (S. Lytvynenko, pers. comm.); ● Myrhorod Raion, near Velyka Hremiacha, 8–15 molehills on the slope of a dry balka with steppe vegetation, 2017–2018 (O. Baryshnikov, pers. comm.); ● Myrhorod Raion, near Komyshnia, Verkhovyna, and Stupky, 5 15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.); ● near Myrhorod city, 10–15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.); ● Zinkiv Raion, near Severynivka, 10–15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.).

Poltava eastern fragment. ● Poltava Raion, near Zaliznychne, more than 5–6 molehills on a meadow slope near a forest belt (embankment along a railroad), 2017–2018 (O. Baryshnikov, pers. comm.); ● Poltava Raion, near Male Ladyhyne, molehills along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Vasylivka, a row of molehills in a field, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Zelenkivka, numerous molehills in a meadow between two villages along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Voinivka, numerous molehills in a roadside meadow, 27.04.2018 (N. Brusentsova, pers. comm.).

Kharkiv Oblast. The least studied region in terms of the greater mole rat's distribution. Data are available only from 2007, 2012, and due to recent inquiry of colleagues in 2018, mainly from the northern districts, where the mole rat was recorded in several localities. Nevertheless, according to our colleagues from Kharkiv (H. Tkach, pers. comm.), the greater mole rat is usually common across the northwestern part of the oblast.

Zone of continuous range. This part of the species range is relatively solid. Obviously, it is fragmented naturally (rivers, forests) and by artificial obstacles (roads, farmland, forest strips). In this part of the range, most of the stable populations are concentrated on offshoots of the Central Russian Upland (the so called Voronezh Massif) that extend from the territory of Belgorod and Kursk Oblasts in a southwestern direction, towards both the Dnipro and Donets rivers. Analysis of habitats, or territories available for mole rats, and the evaluation of the mole rat population in this part of the range are presented in the second part of the Discussion.

Sumy Oblast 1 (central west and southwest). The western part of the forest steppe zone within Sumy Oblast, only with a few findings. The species' abundance varies spatially: the greater mole rat is not numerous in Nedryhailiv Raion, while the species is quite abundant in Lypova Dolyna Raion. ● Buryn Raion, near Diakivka and Klepaly (left bank of the Seym River), SBS, 20.05.2009 (recorded by V. Parkhomenko); ● Sumy Raion, near Yastrubyne, until 2000 (recorded by V. Parkhomenko); ● Nedryhailiv Raion, near Khoruzhivka, Kulishivka, Komyshanka, Lavrove, Golubivka and Korovyntsi, 19.06.2009, 12.09.2010, and 19.06.2018; SBS (recorded by V. Parkhomenko); ● Nedryhailiv Raion, near Tsybulenky, 13.05.2018, in the village and its vicinities, regular observations in 2007–2018 (O. Soloviov, pers. comm.); ● Romenskyi Raion, vicinity of vil. Pustoviitivka, SSA, 19.06.2018 (recorded by V. Parkhomenko); ● Lypova Dolyna Raion, near Koliadynets, remains in leavings of the long-legged buzzard (Stativa & Knysh, 2010); ibidem, 2015–2016, molehills on balkas with steppe or meadow biocoenosis (recorded by V. Parkhomenko); ● Lypova Dolyna Raion, near Oleschenkove, Beyevo-Komuna (= Melnykove), Kolisnyky, Kolomiytseva Dolyna, and Synivka, 2015–2016, molehills on balkas with steppe and meadow biocoenosis (recorded by V. Parkhomenko); a high abundance of mole rats in balkas was recorded in this area of the Khorol river basin (M. Knysh, pers. comm., 2010); ● Lypova Dolyna Raion, near Pidstavky, remains in leavings of the long-legged buzzard (Stativa & Knysh, 2010); ● Lypova Dolyna Raion, near Greky, remains of one specimen in leavings of the long-legged buzzard; ● Lypova Dolyna Raion, near Synivka, a roadkill, 25.05.2018 (A. Statyva, pers. comm.).

Sumy Oblast 2 (southeast). In the southeast of Sumy Oblast, the greater mole rat occurs more frequently than in other territories, although the density of settlements here is rather low. The relief in this region is largely represented by gullies and balkas, i.e. the proportion of tilled lands is low. Therefore, favourable conditions exist here for the conservation of steppe areas as mole rat habitats. ● Sumy Raion, near Mohrytsia, SBS, 2001–2017, high abundance (recorded by V. Parkhomenko); high abundance of the mole rat in a balka near Mohrytsia was also indicated by other investigators (records in 2009, M. Knysh, pers. comm.); ● Sumy Raion, near Vilshanka, Vakalivshchyna, Bytytsia, Bezdryk, Junakivka, Sadky, Tokari, Zatsarne, and Shpylivka villages, 2001–2017, SBS; the settlement in Vilshanka disappeared by 2018 (in 2000–2009 the mole rat was rare in this locality, occurred on balka slopes but later completely vanished due to considerable growth of the blackthorn (recorded by V. Parkhomenko); high abundance of mole rats on balkas near Vakalivshchyna was also reported by colleagues in 1962–2017 (M. Knysh, pers. comm.); ● Krasnopillia Raion, near Velyka Rybytsia, Zapsillia, Barylivka, Sinne, Grunivka, and Marchenky, 2001–2017, meadow and steppe plots on balkas (the picture of the habitat in Fig. 4); this is the locality with the highest abundance of mole rats, up to 70 molehills per ha. Additionally, some molehills usually are registered in roadside meadows (e.g., along the Sumy–Myropillia road), in vicinities of villages listed above, commonly near balkas (recorded by V. Parkhomenko); ● Krasnopillia Raion, near Velykyi Bobryk and Dumivka, 2009–2017, SBS, low abundance compared to the previous locations (recorded by V. Parkhomenko); ● Krasnopillia Raion, near Krasnopillia, Ugroidy, Osoivka, and Gnylytsia, 2001–2009, SBS, regular observations of molehills (recorded by V. Parkhomenko).

Sumy Oblast 3 (south). The species is relatively common here; regular records are reported from the south of Sumy Oblast, as well as from adjacent parts of Poltava Oblast (see below). ● Lebedyn Raion, near Katerynivka, Pidoprygory, and Grytsyny, 2003–2006, SBS (recorded by V. Parkhomenko); ● Lebedyn Raion, near Shtepivka and Sula (2003–2012); SBS (recorded by V. Parkhomenko); ● Lebedyn Raion, near Zelena Roshcha, Lyfyne, and Vorozhba, 2004–2010, SBS (recorded by V. Parkhomenko); high abundance of the mole rat on a balka near Zelena Roshcha was also indicated by other investigators (observations in 1993–2005, M. Knysh, pers. comm.); ● Lebedyn Raion, near Chervlene and Kurhan, balka with steppe biocoenosis, 18.07.2005 (recorded by M. Knysh and V. Parkhomenko); ● Okhtyrka Raion, near Chupakhivka, 2009–2012, SBS (recorded by V. Parkhomenko); ● Okhtyrka Raion, near Kuzemyn, Skelka, Hrun, Hnylytsia, and Viazove; balkas with steppe and meadow biocoenosis, 12–13.05.2012 (recorded by V. Parkhomenko); ● Okhtyrka Raion, western vicinity of Okhtyrka, 2009–2012, SBS (recorded by V. Parkhomenko); ● Trostianets Raion, near Boromlia and Trostianets, 2006–2012, balkas with steppe and meadow biocoenosis (recorded by V. Parkhomenko); locals from Trostianets reported (2011) that "moles" were stealing potatoes from kitchen gardens (M. Knysh, pers. comm.); ● Velyka Pysarivka Raion, near Velyka Pysarivka, roadside virgin land, 13.06.2012, a young specimen was observed on the surface (Fig. 2); ● Velyka Pysarivka Raion, near Katanske, 14.05.2012, burrows on SBS (recorded by V. Parkhomenko).

Poltava Oblast (north and centre). The most stable part of mole rat populations in Poltava Oblast with regular records of both animals and molehills. The new findings were recorded from the Sula, Khorol, and Psel river valleys. ● Hadiach Raion, near Hrechanivka; mole rats were reported by a forester; regular records are known at local plots, including 2015–2016 (S. Lytvynenko, pers. comm.); ● Hadiach Raion, near Petrivka-Romenska, in vicinities and to the north (towards Serhiivka), left bank of the Khorol river, 2014–2017, observations of molehills, the locals passed killed animals (S. Lytvynenko, pers. comm.); ● Hadiach Raion, Baliasne, private estate, autumn 2017, killed as a pest in the garden (S. Lytvynenko, pers. comm. based on reports of locals); ● Hadiach Raion, near Bukhalove, kitchen gardens, 06.2017, trapped by locals (S. Lytvynenko, pers. comm.); ● Hadiach Raion, near Osniahy, 8–15 molehills near a highway, between a steppe plot and a cornfield, 2017–2018 (O. Baryshnikov, pers. comm.); ● Lokhvytsia Raion, near Lokhvytsia, separate molehills on SBS, 19.06.2018 (recorded by V. Parkhomenko); ● Lokhvytsia Raion, near Saranchyne (uninhabited), 01.05.2017, about a dozen of large molehills on a slope of southeastern exposition near the village cemetery (A. Podobailo, pers. comm.); ● Lokhvytsia Raion, hamlet west of Nyzhnia Budakivka village (along the Bodakva river, the left tributary of the Sula river), private plots; autumn 2017, when manoeuvering in the garden, a car fell into a cavity, which turned out to be a mole rat hoarding chamber containing about one bag of potatoes [One bag according to gardening standards can hold more than 5 (five) 10-liter buckets of potato, which equals 37.5 kg; at the rate of 7–8 potatoes per 1 kg it will be about 280 potatoes, and such a stock allows the mole rat to consume 1–2 potatoes per day] (S. Lytvynenko, pers. comm.); ● Myrhorod Raion, near Velyka Hremiacha, 8–15 molehills on the slope of a dry balka with steppe vegetation, 2017–2018 (O. Baryshnikov, pers. comm.); ● Myrhorod Raion, near Komyshnia, Verkhovyna, and Stupky, 5 15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.); ● near Myrhorod city, 10–15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.); ● Zinkiv Raion, near Severynivka, 10–15 molehills near agricultural lands, 2017–2018 (O. Baryshnikov, pers. comm.).

Poltava eastern fragment. ● Poltava Raion, near Zaliznychne, more than 5–6 molehills on a meadow slope near a forest belt (embankment along a railroad), 2017–2018 (O. Baryshnikov, pers. comm.); ● Poltava Raion, near Male Ladyhyne, molehills along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Vasylivka, a row of molehills in a field, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Zelenkivka, numerous molehills in a meadow between two villages along a road, 27.04.2018 (N. Brusentsova, pers. comm.); ● Chutove Raion, near Voinivka, numerous molehills in a roadside meadow, 27.04.2018 (N. Brusentsova, pers. comm.).

Kharkiv Oblast. The least studied region in terms of the greater mole rat's distribution. Data are available only from 2007, 2012, and due to recent inquiry of colleagues in 2018, mainly from the northern districts, where the mole rat was recorded in several localities. Nevertheless, according to our colleagues from Kharkiv (H. Tkach, pers. comm.), the greater mole rat is usually common across the northwestern part of the oblast.

Kharkiv Oblast (southwestern fragment). ● Kolomak Raion, near Kalenykove, roadside forest belt, molehills, 27.04.2018 (N. Brusentsova, pers. comm.); ● Bogodukhiv Raion, near Sharivka, a row of molehills in a roadside meadow, 27.04.2018 (N. Brusentsova, pers. comm.); ● Valky Raion, near Perekip, autumn 2016, numerous molehills on a fallow; autumn 2017, molehills on the same field with harvested corn (H. Tkach, pers. comm.); spring 2018, burrows (N. Brusentsova, pers. comm.); ● Valky Raion, near Valky, spring 2018, burrows (N. Brusentsova, pers. comm.); ● Kharkiv Raion, near Kotliary, at the branching of roads P-51 and E-105, observation of a mole rat on the road moving along the kerb, June 2013 (S. Dubynsky, pers. comm.); ● Nova Vodolaha Raion, near homesteads in Nova Merefa, a mole rat feeding on potatoes and flower bulbs; molehills were also found in the vicinity of the village (O. Bezrodnova, pers. comm.).

Kharkiv Oblast (western fragment). ● Bohodukhiv Raion, vicinity of Bohodukhiv, SBS, 2007, typical molehills (recorded by V. Parkhomenko); we found a high abundance of the mole rat in 1984–1988 in this area; ● Bohodukhiv Raion, between Pryvokzalne and Skosohorivka villages, molehills in a steppe balka between fields (O. Bezrodnova, pers. comm.); ● Krasnokutsk Raion, near Parkhomivka, Murafa, and Krasnokutsk, steppe and meadow slopes of balkas, 13.05.2012 (recorded by V. Parkhomenko); ● Krasnokutsk Raion, Parkhomivka Sector of Slobozhansky National Park (quarters 33 and 35) and near Osnovyntsi (near quarter 35), typical molehills, 2015–2017 (recorded by N. Brusentsova); ● Krasnokutsk Raion, near Murafa, private estate, 2008, mole rat hoarding chamber containing three bags of potatoes, one bag of carrots, and 0.5 bag of beetroots discovered during excavation of an old cellar (N. Brusentsova, pers. comm., according to residents; locals understand the volume of one bag as the volume of 3 buckets); ● Krasnokutsk Raion, near Volodymyrivka (near Slobozhansky NP), virgin plot near a forest, typical molehills, recent years (H. Tkach, pers. comm.); ● Krasnokutsk Raion, near Cherneshchyna (between two sectors of Slobozhansky National Park), private estate, 2003 ("about 15 years ago"), hoarding chamber containing 4 boxes of potatoes and discovered during tillage, when the tractor fell into it (N. Brusentsova, pers. comm., according to locals); ● Zmiiv Raion, near Pasiky, tops of open steppe balkas near a forest in the Homilshansky Lisy National Park, 2015–2016 (V. Timoshenkov, pers. comm.).

Analysis of biotopes and abundance. The analysis is based on the whole dataset, although most of the records were reported from the south-east of Sumy Oblast, which is due to the significant share of natural habitats in this region. Large territories of steppe sites on the slopes of balkas have remained here and optimum conditions for the mole rat exist, the area has a high abundance of grassland and steppe communities in the branched gully–balka system. Generally, the population density is low in these locations, although the total abundance is significant due to the large number of suitable habitats. The type habitats of the greater mole rat are sites with clearly expressed rolling relief, often with marlstone outcrops, such as the offshoots of the Central Russian Upland in the valley of the Psel river. Some data refer to records in roadside virgin strips (e.g., a young animal was spotted in 2012 in a similar location in Velyka Pysarivka Raion, Fig. 2). Almost all marginal records (Fig. 3) are related to balka slopes (rolling relief), especially in systems of wide balkas.

Fig. 4. The offshoots of the Central Russian Upland are the type habitat of mole rats with the highest abundance in the studied area: near Mohrytsia, Sumy Raion; the density of burrows is 10–50 molehills per hectare. Photo by V. Parkhomenko, 12 June 2010

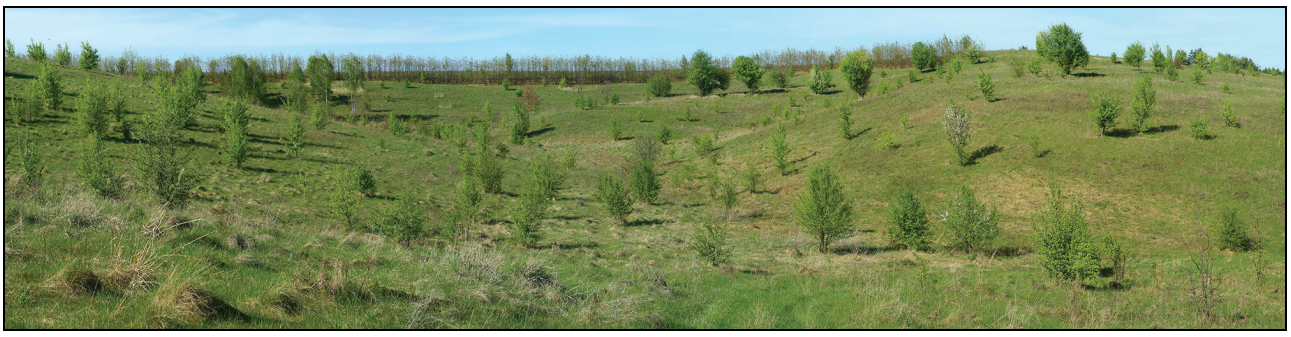

Fig. 5. Succession of the steppe balka slope (common pear and European crab apple): near Vakalivshchyna, 3 May 2018. Photo by V. Parkhomenko

Flat interfluves are unavailable for the species, because they are tilled almost everywhere (only a small patch in Mykhailivska Tsilyna Reserve remains untilled). The species can occur on tilled lands only temporarily, during the dispersal. The mole rat usually only passes through tilled lands often crossing long distances when it can became an easy prey of predators (Korobchenko, 2009). The death of mole rats during passage through unsuitable habitats is the price for the possibility to migrate into safer and more productive ecosystems.

The geography of abundance. Generally, some changes in the level of abundance occur through the entire range. The "landscape of abundance" significantly repeats the natural landscape: mole rats have low abundance or became extinct in the lowland part of the range and in interfluves, although they have remained on slopes running towards river valleys and are especially abundant in areas having gully-balka relief. This pattern is clearly visible on transects along rivers running from the Central Russian Upland towards the Dnipro, including the

Sula, Khorol, Psel, and Vorskla rivers (to the south, in the valley of the Orel river it is not clearly expressed). Wide gully-balka systems (Fig. 4–5) exist in the upper reaches of these rivers, where mole rats can find suitable conditions for existence and form stable populations with an abundance of ca. 2–5 animals per 10 ha (it corresponds to 5–10 fresh molehills per 1 ha; in separate sites the number of molehills reaches 10–30). See further for detailed comparisons with levels of abundance in other times and other regions.

On the contrary, the abundance of the species notably decreases to the west. Beyond the zone of continuous range, particularly in lower reaches of tributaries of the Dnipro river, only isolated settlements exist, restricted to the remains of steppe coenoses in small patches (usually of several dozen hectares), unsuitable for agriculture or other forms of economic use. In such places either roadside strip populations often remain (practically, remains of former populations) with a density of 1–2 individuals per 10 km, or local residual micropopulations with a density of 0.1–0.2 individuals per 1 ha on an area less than 10 ha (Table 1). Practically, the mole rat remains on these sites only due to constant migration from other sites thus they do not belong to stable settlements.

Estimation of settlement density. The species' abundance can be estimated if we accept that one series of molehills belongs to a single individual and that mole rats are solitary animals (Zuri & Terkel, 1998; Korobchenko et al., 2010). Respectively, we can estimate the number of individuals on a hectare by the number of molehill groups. However, such estimation significantly depends on the development of vegetation cover and relief. For instance, we can observe the whole slope of the balka and conduct an accurate census near Koliadynets village (the same can be done, for example, in case of route censuses on roadside virgin land strips). However, on sites with well-developed vegetation, molehills are less visible, resulting in lowered estimations (e.g., near Mohrytsia). According to our data, the average distance between molehill groups in relatively open sites (e.g., near Koliadynets) is ca. 120–150 m. Besides, estimations are low in the spring until the time of dispersal of the young and when old molehills are blurred by melting snow, and the abundance of animals after wintering is low. The density of molehills significantly grows in the autumn. When individuals are evenly distanced in the census site, their abundance can be calculated using the area of the site (S) and the average distance between individuals, i.e. between groups of molehills (L) according to the formula $n = S/L^2$. At a distance between the groups of molehills of 150 m on 10 ha (100,000 m^2) we have an abundance of 4.4 individuals. In different sites, according to our estimations, the abundance of mole rats is ca. 2–5 individuals per 10 ha.

Distribution by the main types of habitats. Based on the totality of observations, we can conclude the following distribution of the greater mole rat by the main types of habitats:

a) Steppe balka slopes. These particular habitats represent the largest area of remaining steppe and meadow coenoses. The density of molehills notably differs in different balkas, even a little distance apart, which is 10–70 molehills per hectare (one individual per 1–5 ha). Since these sites are used as cattle pastures (especially near villages), the abundance of mole rats can significantly vary at different distances from the villages. At high rates of grazing, the abundance of the species notably decreases (to one individual per 10 ha), although at low grazing rates, the abundance remains the same as in sites where grazing is completely absent.

b) Virgin lands on flat interfluves. These habitats have remained only in the Mykhailivska Tsilyna Reserve. The abundance of the species here is low, up to 8 molehill groups per hectare, often 1–4 molehill groups (individuals) per 10 hectares.

c) Roadside virgin land strips. Only 5 records with low abundance but regular presence, usually up to 3–5 mole-hill groups per 1 km of route. However, these locations neighbour either balkas or pastures where the larger mole rat populations exist.

d) Fallows and wastelands. Single records of mole rats. As in the case of fields, irregular presence of the species, only in close proximity to steppe balka slopes.

e) Fields. Sporadically, irregularly. The species is present only when it exists on neighbouring virgin areas of steppe and meadows. Recorded near Koliadynets in Lypova Dolyna Raion (2015–2016), Mohrytsia in Sumy Raion, and Zapsillia in Krasnopillia Raion (2001–2017).

Observations of aboveground activity. The mole rat actively moves above the ground during resettlement in order to pass through unsuitable habitats more quickly. Usually the route of such movement is 50–100 m. Direct observations of aboveground moving of mole rats are rather rare, thus each record of such activity is of high value. The sum of data on aboveground activity allows us to draw some conclusions about the features of ecology and behaviour of the species (Korobchenko, 2009). Seven records were obtained, including two by OSINT analysis, of aboveground movement of the greater mole rat in the following locations: ● Nizhyn, eastern vicinity, virgin roadside strip near the railway crossing, 09.2010, morning observation (O. Voblenko, pers. comm.); ● Sumy Raion, Vakalivshchyna, upper course of the Bytytsia River, forest-meadow edge, 06.1972, recorded by a forester (leg. V. Kravchenko; M. Knysh, pers. comm.); ● Sumy Oblast, near Velyka Pysarivka, virgin roadside strip, 13.06.2012, at 6 pm, an actively moving young specimen (Fig. 2) (recorded by V. Parkhomenko); ● Lypova Dolyna Raion, near Synivka, roadkill of a young specimen, 25.05.2018 (reported by A. Stativa); ● Kharkiv Raion, near Kotliary, roadway part, 06.2013; at noon at the junction of the roads P-51 and E-105), the animal was moving along the kerb (photo and report from S. Dubynskyi); ● Ichnia Raion, near Parafiivka, roadside meadow, 07.2016, a dead mole rat was found (A. Mokhir, pers. comm.); ● Russia, Kursk Oblast, near Gubkin city, Yamsky Steppe (from 1999 as part of Belogorie Nature Reserve), morning observation of an animal in a steppe plot during an excursion, 06.1973 (V. Grama, pers. comm.).

Table 1

The main types of habitats inhabited by the greater mole rat and estimated population abundance based on the collected data

Habitat type	Common examples	Portion of habitat type *	Estimated abundance
1. Steppe balka slopes	northeast and east of Sumy Oblast, partly also in other districts and oblasts	ca. 90% of records and ca. 15% of total area	2–10 ind./10 ha, 20–70 molehills/ha
2. Virgin lands on flat interfluves	almost destroyed type of habitat, partly remaining either as protected areas (only one example) or roadside virgin land strips (type 3) in the entire region	ca. 1% of records and ca. 1% of total area	1–4 ind./10 ha
3. Roadside virgin land strips	in the whole region, although mole rats practically inhabit only in the southeastern raions of Sumy Oblast, northeastern raions of Poltava Oblast, and most of Kharkiv Oblast	ca. 5% of records and 5–10% of total area	up to 1 ind. (3–5 molehill groups) per 10 km
4. Fallows and wastelands	single records, practically as in case of habitat type 3	ca. 5% of records and ca. 10% of total area	–
5. Fields	temporary visits to fields in areas where large settlements exist on neighbouring virgin lands (types 1–2)	sporadically (no records because all cases are visits from neighbouring virgin lands), ca. 60% of total area	–

Note: * – the portion of different habitat types is agreed with estimations published in the review on natural complexes of Sumy Oblast (Karpenko & Kovtun, 1996), with some modifications in order to expand the data to the entire region.

All records were obtained in the summer (one in May, four in June, one in July, and one in August) on sunny days. Such aboveground activity pattern is in accordance with results published earlier (Korobchenko, 2009): based on the sum of all data, the peak of mole rats' aboveground activity is in daytime in the warm period of the year, especially at noon in early summer. New data completely support the results obtained earlier. The period of aboveground activity coincides with the period of nourishing of the young of several predators (see further). Aboveground

activity is clearly related to the resettlement of mole rats into new plots and dispersal of the young beyond the breeding site.

Discussion

Absence as a fact. When gathering data on the species' distribution, the authors collected quite a few records of locations, where the mole rat is absent and the locals have no knowledge about them. In particular, there were already no records of the greater mole rat in the mid-1990s, when one of the authors worked at the Public Health and Epidemiology Service of Velyka Bahachka Raion, Poltava Oblast as well as during working in the adjacent Myrhorod Raion (M. Korobchenko, 1995–1996). In over 20 years of observation, the species was not recorded in Shyshaky and its vicinities (O. Zhuk, pers. comm.). There are no records of mole rats from many locations of Poltava Oblast as well, particularly from the region to the east of the Psel river; here the boundary of the continuous range is sharply shifted to the north and corresponds to the line of Myrhorod – Hadiach – Zinkiv – Dykanka – Poltava (S. Lytvynenko, pers. comm.). There are also no records of the species in the Pyriatynskyi National Park and its surroundings (A. Podobailo, pers. comm.), as well as in vicinities of Kremenchuk (A. Makohon, pers. comm.) and Hlobyne (S. Goryslavets, pers. comm.).

The greater mole rat was also not recorded in several locations in the north of the region including the vicinities of Konotop (A. Mokhir, pers. comm.), Ivot, Shostka Raion (after photo by M. Knysh) [The only claim of a molehill of a mole rat was reported on 01.04.2001 from the vicinities of Ivot village, "on a dryish meadow on the floodplain along the Ivotka river (tributary of the Desna river)"; we reidentified it as a record of European mole], Shevchenkove (former Zavody), Konotop Raion, and Shapovalivka (26–27.04.2018, M. Knysh, pers. comm.). The species is also absent in the Desniansko-Starohutskyi National Park. In the review on the fauna of the park (Gavrys et al., 2007), only an old and unconfirmed record of the greater mole rat is mentioned. For some reason, it is usually cited by another source as "Burrows and mole-hills of the mole rat were recorded in the 1980s on floodplain meadows along the Ulychka river (Karpenko et al., 1999), but we did not find the species" (Gavrys et al., 2007). According to the description of the biotope, the abovementioned record obviously should be of the European mole.

The mole rat is also absent in the Baturin Military Training Area (near Baturyn city, Bakhmach Raion, Chernihiv Oblast; O. Voblenko, pers. comm.). At least for the last 10 years, mole rats and other steppe rodent species have been absent in Mezyn National Nature Park and its surroundings (N. Nasarov, pers. comm.). Thus, many locations in Chernihiv Oblast and the west of Poltava oblast, which 50–100 years before were part of the greater mole rat's range, are currently not inhabited by this rodent.

False records. False records of mole rats are related exclusively to sightings of large sized molehills (an example is mentioned in the Methods section and illustrated on Fig. 6). We have received several records of settlements of greater mole rat, in some cases also supported by photographs, although they were reidentified as settlements of the European mole. Some pictures of molehills could not be identified more certainly. Usually these are records in floodplain habitats or other places with plain relief, or on overgrazed meadows with chaotic (non-linear) placement of molehills often not quite large in size. These records are considered as clearly the southernmost findings of the European mole in the region: ● Lubny Raion, near Tyshky, left bank of the Sula river, "molehills of the mole rat", 2000–2017 (recorded by Y. Semenov; the author of the record himself doubts that it was a mole rat); ● Sumy Oblast, Trostianets Raion, Trostianets city, floodplain along the Boromlia river, 05.12.2011, photo of molehills (received from M. Knysh); ● Sumy Oblast, Shostka Raion, near Ivot, meadows, 01.04.2001, photo of molehills (received from M. Knysh); ● Cherkasy Oblast (left bank of the Dnipro), Chornobai Raion, Sula bay, near Liashchivka, numerous molehills in virgin plots on the banks of the bay, 16.12.2006, 06.2017, series of photo, one of them is presented on Fig. 6 (M. Gavryliuk, S. Domashevsky, pers. comm.).

Colleagues have different views on these records [The authors of the record (in particular M. Gavryliuk) insist that it is the mole rat, although M. Klestov, a local zoologist, reports that mole rats are absent there, but that moles have been caught on large molehills; V. Khodzynsky, an acclaimed specialist on moles, suggests that, according to the state of the soil (narrow "sausages") and to the season (moles often clean out their galleries in autumn resulting in large molehills), it is the European mole; in other parts of the surroundings of Liaschivka, locals trapped only moles but not mole rats from similar large mole-hills].

Fig. 6. Unusually large molehills and typical molehill rows of the European mole in lower humid part of a balka: *a* – a large molehill of European mole near Liaschivka at the mouth of the Sula River, Cherkasy Oblast (photo by M. Gavryliuk, 17 June 2017); *b* – typical molehills of *Talpa europaea* near Mohrytsia in Sumy Raion (21 November 2009, photo by M. Knysh)

We also experienced difficulties regarding the identification of molehills when we started to pay special attention to mole rats. Particularly, there are several pictures of molehills (from 8 locations) in the photo

archive of our expeditions, which were initially identified as mole rat's molehills, although further analysis (of the structure, size, and character of placement of molehills, biotopes) revealed the misidentification of these records. Among them, there were, in particular, records from vicinities of Velykyi Bobryk and Velyka Chernechchyna, Sumy Raion (2001–2012) and Mykolaivka, Buryn Raion (2004). In some of these records were, of course, unambiguous records of mole rats (see above), but from other plots.

Current range boundaries and its analogues. The northwestern range edge of the greater mole rat runs through the studied region and it can be out-lined by the following geographical objects (villages, rivers, drainage divides, forests, uplands); to the Seim river on the north, and, generally, along the valleys of the Sula and Vorskla rivers through such towns as Nedryhailiv, Lokhvytsia, Myrhorod, Hadiach, Zinkiv, and Poltava in the west. The range boundary can be described in detail as a line running through the following settlements (Fig. 3): Buryn (Klepaly and Diakivka in Buryn Raion) → Nedryhailiv (Lavrove, Khoruzhivka and Korovyntsi in Nedryhailiv Raion) → Romny (Pustoviitivka in Romny Raion) → Lokhvytsia (Lokhvytsia Raion) → Myrhorod (Myrhorod and Verkhovyna in Myrhorod Raion) → Hadiach (Baliasne and Osniahy in Hadiach Raion) → Zinkiv (Syverynivka in Zinkiv Raion) → to the southwest from Okhtyrka (Gryn, Viazove and Kuzemyn in Okhtyrka Raion) and Zaliznychne (Poltava Raion).

Contraction of the western fragment of the species' range is especially visible when we compare current and former data. In particular, Charlemagne (1915) in his review on mammals of Kyiv city and its surroundings mentioned the mole rat for the "holiday village Darnytsia [20 versts from Kyiv], Oster Powiat of Chernihiv Governorate" (female, 07.1910, leg. Zvierozomb-Zubovsky). In the present time, these localities are 200–225 km far from the closest current localities of occurrence of the mole rat such as Khorol, Nedryhailiv, etc. Actually, the process of range contraction was already noticed by B. Golov more than 40 years ago (Golov, 1975), who wrote about the significant decrease of mole rat populations in the west of Poltava Oblast (not to mention Kyiv and Chernihiv Oblasts). Eventually, the total area of the range in the studied region of northern Ukraine (to the east from the Dnipro, to the west from the Donets and to the north from the Vorskla and Merla rivers) contracted at least twice. However, if we consider not the total area but only the area of suitable biotopes, the species range contracted by more than 10 times.

Therefore, the distribution range of the greater mole rat became fragmented and a significant number of current record localities are probably isolated fragments of the species' former wider range. Range fragmentation also takes places in other typical subterranean species (Patton & Yang, 1977; Petrova et al., 2014; Visser et al., 2018) In particular, insular type settlements of the mole rat exist as local populations at the lower course of the Sula (Liashivka, Orjitsia) and Vorskla rivers (Luchky, Kobeliaky). Isolated are also the records from Ichnia Raion (Leonidivka, Parafiivka) and Nizhyn Raion (eastern vicinities of Nizhyn city) in Chernihiv Oblast. Presumably, there are some more similar isolated settlements, although they can be revealed only by further research. Mole rat settlements along large roads and railways also seem to be isolated, in particular to the west of Poltava on the section Poltava – Reshetylivka – Khorol.

Range contraction due to habitat loss. The former wider distributeon of the mole rat in northeast Ukraine (so-called "Sloboda Ukraine") described in works of Reshetnyk (1941) and Golov (1975) has long been a fact of the past. Population decrease in steppe burrowing animals is the result of contraction of steppe ecosystems, although the opposite side of the problem, i.e. contraction of steppe biotopes due to decrease of burrowing species, is also fair since underground animals are of key importance in steppe communities (Davidson et al., 2012). In the past decades, the decrease of many local mole rat populations has occurred resulting in range contraction and fragmentation. The modern range of the greater mole rat in the northern edge of its distribution is considered as a remnant of the former wider range, which reached the territories of Hlukhiv Raion, Ukraine (Pidoplichka, 1929), Bryansk (Tyutkova, 1991) and Tula Oblasts, Russia (Topachevsky, 1969) in the north. Range contraction occurred mainly due to habitat loss and incapability of mole rats to survive in microsettlements.

According to our estimations, stable and sustainable settlements of the greater mole rat exist on plots of an area ca. 50 ha. At a "typical" for the region density of settlements of 0.2–0.5 individuals per hectare (see above for more details about the density), a local population consists of 10–25 individuals. In practice, we have the following examples and estimations:

1) areal settlements: a) a plot of virgin steppe in the Mykhailivska Tsilyna Reserve, where an isolated mole rat colony remained surrounded by fields (150 ha, of 880 ha of total area); according to average estimations (without special census) about 30–75 individuals can exist here; b) steppe balka slopes near Vakalivshchyna and Bytytsia villages, a plot with an area of virgin sites of about 100–150 ha, practically isolated from other localities by a zone of tilled lands, the population size can be estimated as 20–75 individuals;

2) linear settlements: a standard plot of roadside virgin land strip of 10 m of width on each 1 km section has an area of ca. 100 ha, on a 5 km section (which corresponds to the distance between two large villages) an area of ca. 500 ha, i.e. a site of about 100–250 individuals. However, in fact, localities are more dispersed: route census in April 2018 (data obtained from N. Brusentsova) showed that on the road section Kharkiv – Poltava – Pyriatyn of a length of 325 km only 10 mole rat settlements were recorded (map of Fig. 3).

This attempt of a general estimation of population size is based on available space, although trophic and protective conditions are diverse and often insufficient for establishing sustainable colonies. Therefore, such estimations of population abundance are rather approximate and concern exclusively separate and the most suitable sites. Obviously, there are not only less suitable sites with smaller carrying capacity, but also suitable sites yet uninhabited by mole rats due to several reasons. A key limitation is that the species remains in the region only in untilled zones. Accordingly, three groups of localities can be highlighted based on abovementioned five habitat types potentially available for mole rats:

1) natural complexes that have remained due to difficulties in their agricultural development, in particular the extensive gully – balka system of the southern offshoots of the Central Russian Upland. Practically, the main group of settlements of the greater mole rat have remained precisely here and the species' range has contracted mainly to this zone. Virgin land on flat interfluves, which has almost totally disappeared (an example of such virgin lands is the Mykhailivska Tsilyna Reserve), can be also included to this group of localities;

2) sites with mild anthropogenic pressure around human settlements, including pastures, virgin strips between fields, fallows, cemeteries, abandoned gardens and estates, etc. The total area of these sites is sufficient, yet such ecosystems are not natural and have an excessive number of alien species. In several cases, mole rats form "pulsing" populations, which occur only seasonally in these seminatural communities (Korobchenko, 2012);

3) roadside virgin land strips, which are exclusively belt-like biotopes unsuitable for long-term existence of a sufficient number of animals (because mole rats are mostly solitary animals, i.e. they behave aggressively towards other individuals beyond the breeding season); the density of settlements in these localities is about one individual per 10 km of route, which is not enough to form a sustainable local population.

One of the factors influencing the species' extinction, in addition to tillage which directly destroys virgin biotopes, is the anthropogenic transformation of biotopes. The range contraction in the greater mole rat occurred due to the overgrowth of gullies and balkas, which earlier were suitable for this steppe species, by weeds and bushes. The significant decline in the area of steppe plots was also affected by the decrease or total lack of grazing pressure and hay mowing (particularly due to decrease of the number of cattle in nearby villages). As stated earlier, the decline of cattle breeding (and, consequently, of grazing pressure) in the east of Ukraine during 1980–2005 was catastrophic and reached 45–94% in different animal groups (Zagorodniuk, 2006). Earlier, in the middle of the 20th century, a directive was issued on planting trees in each gully, including those where steppe communities existed, which was the beginning of the "second turn" of destruction of steppe complexes that remained in gully–balka systems.

The phenomena of facultative and forced synanthropization. A number of our observations showed that the greater mole rat tends to live in

surroundings of villages demonstrating conditional synanthropy. This trend is especially visible from vehicles (cars, trains) during route censuses, when observing settlements on long transects, e.g., during mapping of mole rat settlements on the route Kharkiv – Poltava – Pyriatyn (data by N. Brusentsova).

Synanthropic trends can be explained by the noncasual coincidence of the most preserved type biotopes of the mole rat with human settlements. Steppe or steppe-like ruderal plots usually remained precisely near villages, but are absent at far distances because they were tilled and transformed into fields. Another explanation of synathropy in the mole rat might be that the vegetation on slopes is usually mowed near villages, which prevents the overgrowth of weeds, bushes, and trees. On the other hand, steppe balka slopes located more distantly from villages quickly overgrow due to succession.

Roadside meadows as type habitats for modern mole rat settlements practically are also anthropogenic habitats. Non-synanthropy in the case of mole rats is observed only in zones of balkas, where natural vegetation and a mild grazing pressure have remained.

Hence, the greater mole rat, as with the entire steppe assemblage, is now restricted to marginal localities similar by the character of vegetation to steppe tracts that were formerly distributed over large areas of drainage divides. Such sites are largely managed by humans as economically important (pastures), or valuable for the community (recreation zones, cemeteries, exclusion zones around economic objects), or nonvaluable hence little occupied localities (balka slopes, wastelands and landfills around villages, etc.). Actually, the portion of all these sites is the highest in the zones of rolling relief.

Estimated range area and absolute abundance. Thanks to available Google Maps™ instruments, we could estimate the area of the distribution range. The whole part of the former most complete range of the greater mole rat within the left-bank part of the Forest Steppe District ("East European Deciduous Forests and Forest Steppe"), which can be equated to the area of this biogeographic unit (after Szczerbak, 1988), covers an area of 73,800 km^2. However, the current continuous part of the species' range has an area of 29,400 km^2, while the total area of 7 additional range fragments can be conditionally accepted as 6,000 km^2, meaning that the entire species range in the region is 35,000 km^2, which is 47.4% of the area of the former range. Thus, the distribution range of the greater mole rat in the region has contracted in two times over the past hundred years (since the descriptions by M. Charlemagne and E. Reshetnyk).

This is a general area estimation, based on range contours without consideration of the area of different biotopes. However, the area of biotopes actually available for the mole rat is far less, which is due to the limited distribution (preservation) of biotopes suitable for the species. Since natural and seminatural ecosystems make up of about 15% of the territory (Table 1), we should consider the same proportion: 15% of 35,000 km^2 is only 4,300 km^2 or 430,000 ha. This is the highest possible estimation, which is yet might be at least two times lower in reality, because the species is not necessarily present in each patch of potentially suitable habitat. Although, considering these estimations and the density of settlements in suitable habitats as 2–5 individuals per 10 ha, we can also calculate the population abundance as 86,000–215,000 individuals. Considering that steppe covered more than 70% of the region's territory in the past, the mole rat's absolute abundance decreased by at least 5 times.

The density of settlements in suitable habitats, as estimated in this paper, generally corresponds to the calculations for former periods of research and for adjacent regions as well. As O. Migulin stated, the burrow system of a single mole rat can cover an area of 3–6 ha (Migulin, 1928) or 3–5 ha (Migulin, 1938). The density of molehills in the steppe can reach 156 molehills per hectare during a season (Puzachenko & Vlasov, 1993). Usually, researchers indicate data closer to the latter estimation.

In particular, the average settlement density in the Streletskaya Steppe Reserve (Kursk Oblast, Russia) is about 3.7–3.8 individuals per ha (Puzachenko & Vlasov, 1993; A. Puzachenko, pers. com.). In Kharkiv Oblast, the density of mole rat settlements in the early 20th century was 10 ind./ha on balkas, 5–7 ind./ha on hayfields, and 2 ind./ha on fields (Reshetnyk, 1941). In Luhansk Oblast, the density of settlements after WWII was estimated as 1 ind./ha on steppe drainage divides and 4–11 ind./ha on different lower plots and northern slopes of balkas (Gulyaevskaya, 1954). Our estimations (see above) are notably lower, because they concern the range periphery and zone of range contraction: the density of mole rat settlements in suitable habitats, particularly on steppe balkas, is up to 0.2–0.5 ind./ha.

Aboveground activity and its role in dispersal and death. Migration of mole rats into new sites and the exchange of individuals between different settlements take place on the surface, i.e. beyond the species' basic ecotope. Aboveground relocation also occurs when the vegetation on a site is not able anymore to provide required feeding conditions. In such case, it is energetically more advantageous to move to new sites on the surface than dig unproductive burrows that might not provide food and would serve only as migratory corridors.

Due to this mechanism, mole rats appear on different isolated sites where their former and lasting existence is hard to imagine. Apparently, these sites are inhabited only by migrants. Moving on the surface, mole rats can occupy potential sites, where the species was absent before. Aboveground migration also provides the opportunity of genetic exchange between different population groups. It means that the metapopulational organization of mole rat settlements is due not only to gradual and slow dispersal during development of underground feeding burrow systems, but also to aboveground migratory activity. Since mole rats are regularly active above the ground (we have about 230 records in our database on aboveground activity of mole rats from different regions of Ukraine), it seems that the risk of being caught by a predator is smaller than the risk of settling down in a foodless site. The indirect evidence for this is that in newly colonized sites molehills are located in small groups with large distances between the groups (particularly in fields and roadside strips, Table 2). Nonetheless, during such migrations mole rats often fall prey to predatory birds and mammals, as well as victims of traffic (Korobchenko, 2009).

Table 2
Cases of discovery of mole rat remains left by some predators in Ukraine in the last 20 years

Predator species	Number of mole rat scraps	Share of mole rat remains and additional data	Sources*
Buteo rufinus (long-legged buzzard)	several mole rats identified as "*Spalax microphthalmus*" (should be *zemni*)	44.4 % of the all food samples, Oleksandria, Kirovohrad Oblast	Shevtsov, 2001
Buteo rufinus (long-legged buzzard)	pellets containing remains of 2 mole rats	ca. 20 pellets collected under the nest, south of Sumy Oblast	Stativa & Knysh, 2010
Buteo buteo (common buzzard)	twice in one period, among scraps in the nest	remains in the nest (3 heads) and under the nest (1 body) in the south of Sumy Oblast	A. Stativa, pers. comm. (Fig. 7)
Buteo rufinus (long-legged buzzard)	36 individuals of *Spalax zemni*	17.1% of remains in pellets from Mykolaiv Oblast	Redinov, 2010
Buteo rufinus (long-legged buzzard)	(no data, small sample)	the share of mole rats in the diet is 41–49% based in investigation of three nests	Kravchenko, 2008
Aquila heliaca (imperial eagle)	7 mole rats	scraps under the nest	D. Pylypenko, pers. comm.
Larus cachinnans (Caspian gull)	9 individuals of *Spalax microphthalmus*	9 mole rats among 25 victims in pellets, 34.6% of all mammals, Stanytsia-Luhanska Fish Farm, Luhansk Oblast	Atamas, Tovpinets, 2006
Bubo bubo (eagle owl)	17 mole rats in pellets and 6 remains near the nest	3.66% in pellets; 4.14% near the nests	Vetrov, Kondratenko, 2002
Vulpes vulpes (red fox)	9 mole rats	different parts of Luhansk Oblast, including Svatove and Striltsivka	S. Zaika & G. Guz, pers. comm. 2008–2009

Note: * – all presented data clarified by the authors of records.

Mole rats are not only available but also beneficial and favourable victims for many predators – it is an herbivorous species weighting about 200 to 300 g. The most intense aboveground activity of mole rats takes place in summer (Korobchenko, 2009), when the young disperse

from maternal colonies (Rado et al., 1992). It coincides with the period of nourishing of the young of many predators, i.e. there is a need for large amount of prey. The mole rat actually plays the role of such prey.

In the region of research, mole rat remains were discovered in leavings of the long-legged buzzard (*Buteo rufinus*) in the south of Sumy Oblast (Stativa & Knysh, 2010). In particular, two mole rats were found in the composition of ca. 20 pellets and leftovers (the number of animals is clarified after A. Stativa, pers. comm.). Three heads of mole rats were also found in the nest of the common buzzard (*Buteo buteo*), and remains of another mole rat were found under the nest (A. Stativa, pers. comm.). All animals, as far as visible on the pictures, were young; their remains were found on 10.07.2011 in the nest and on 20.07.2011 under the nest (Fig. 7). Similar cases were discovered during the investigation of feeding of the long-legged buzzard in other parts of the species range, including Kirovohrad (A. Shevtsov, pers. comm.), Dnipro (Kravchenko, 2008), Mykolaiv (Redinov, 2010), and Donetsk Oblasts (D. Pylypenko, pers. comm.). Mole rat remains were also discovered in pellets of the Caspian gull (*Larus cachinnans*) in Luhansk Oblast (N. Atamas, pers. comm.) and of the eagle owl (*Bubo bubo*), also in Luhansk Oblast (V. Vetrov, pers. comm.). The greater mole rat was also reported as prey of the steppe polecat, red fox, domestic cats and dogs, as well as a number of predatory birds, although without details (Reshetnyk, 1941). Mole rats are prey of owls in other regions as well (Charter et al., 2009). For comparison, data suggest that about 26 species of predatory birds and mammals prey on blind mole rats (*Nannospalax leucodon*) either regularly or occasionally (Németh et al., 2016).

Fig. 7. Mole rats as prey of the common buzzard near Koliadynets, Sumy Oblast, 10 November 2011 (in the nest) and 20 November 2011 (under the nest): courtesy of A. Stativa

Such a high significance of mole rats in the diet of predators suggests the not coincidental co-occurrence of localities of stable mole rat populations and of breeding sites of predators, in particular of the long-legged buzzard. Mole rat settlements could be important indicators of long-legged buzzard nesting sites. Although mole rats are not mentioned in the list of typical prey of this bird species (Strigunov, 2009), it is obvious that by its share of total weight the greater mole rat is an important food source for many steppe species. Regarding the long-legged buzzard, K. Redinov describing the ecology of this species discovered that "contours of the distribution range of hamsters, mole rats, and ground squirrels in Ukraine are similar to each other (…) and to the contours of the range of the long-legged buzzard" (Redinov, 2010: p. 130).

Therefore, the breeding range of typical steppe predators largely depends on the distribution of settlements and abundance of mole rats. The latter is an important factor at least for the existence of predatory birds, but also mammals. Among mammals, according to our data, the marbled polecat *Vormela peregusna* seems to be a specialized predator of mole rats. Practically, the range and state of population of the mole rat currently are the most notable indicators of the state of steppe faunal and also partly of floristic assemblages.

Prospects of further range and population dynamics. Range periphery is always characterized by fragmented distribution of zonal communities, including steppe plots in the edge of the steppe biome. Predicting the effects of fragmentation effects on species requires a good understanding of their biology and habitat use (Wiegand et al., 2005).

The influence of habitat fragmentation on range dynamics is a topical issue in ecological and conservation research (Andrén, 1994; Fahrig, 1997, 2002; Bender et al., 1998; Wiegand et al., 2005). Large-scale transformation of the steppe as a biome became especially relevant in case of steppe species, including fossorial rodents. Mole rats suffer largely from habitat loss and, therefore, as key species of steppe assemblages, are a suitable model not only for analysis of related range dynamics of steppe species, but also for understanding the further history of the steppe due to their ecology (burrowing activity, impact on vegetation, creation of underground ecotopes, etc.).

After the actual disappearance of the steppe as a zonal complex and its remaining steppe sites on flat interfluves, an expressive decrease of steppe plots on balkas occurred in the entire region over the last 2–3 decades. This was due to their natural forestation (intensive growth of the blackthorn, common pear and European crab apple (Fig. 5), also of the silverberry and caragana in the south), plantation of the black locust by foresters, overgrowth of weeds because of the lack of hay mowing and cattle grazing. Despite unsuitability for arable farming, the tillage of steppe sites for gardens and terraced agricultural lands have also taken place (e.g., two such sites were created in Krasnopil Raion in 2009 and 2011). All these processes are irreversible and steppe plots that remained practically only in gully–balka systems continue to decrease.

The distribution range of the greater mole rat is expected to contract further to the main population core located in the region of the Central Russian Upland. The species might disappear quite soon in locations where it was recently recorded, e.g. in Sumy Oblast (central and southern raions). Hence, we observe the "melting" of the species' range leading to gradual disappearance of isolated populations and to appearance of new range fragments on the edge of conditionally continuous range, i.e. fragmentation of the range periphery occurs simultaneously with disappearance of remote settlements.

The western part of the range contracts more than the northern one (Fig. 3). Considering global warming and the fact that burrowing activity is realized within a narrow temperature niche (Nikolskii, 2007), we suppose that the main factors affecting range dynamics are mainly of anthropogenic but not natural origin. Nevertheless, global climate change may also have a great impact on the species range, considering that, due to the narrow ecological niche, the response of their populations to large scale changes are rather limited. Among possible responses of the species to global changes (Dawson et al., 2011), the greater mole rat can respond by toleration (in the range centre), habitat shift (in transformed

landscapes), migration (in the range periphery) and extinction (in remote isolated settlements). Thus, the impact of global climate change along with anthropogenic influence cannot be neglected.

The range dynamic can result in formation of new isolated settlements. When the density of local suitable patches is much higher than the mean, it allows local persistence of the species and, therefore, a postponement of extinction (Dytham, 1995). Moreover, such isolated settlements could be characterized by their own evolutionary history and isolation can lead to new stages of microevolutionary changes, which in the case of mole rats often lead to speciation (Nevo et al., 1995; Hadid et al., 2013; Lövy et al., 2015). The high level of sedentariness and restricted possibilities of dispersion along with high instability of the karyotype determine the extremely high potential for evolutionary changes and explain the large number of described chromosomal races (Arslan & Zima, 2014; Arslan et al., 2016). Eastern Europe is a zone of intense speciation in mole rats and range dynamics is one of the factors that contribute to this process.

Conclusions

The greater mole rat as a species of the steppe assemblage demonstrates a significant range contraction and general population decrease. It is due to habitat loss as a result of anthropogenic landscape transformation. The current distribution of the species is restricted to three types of biotopes in which steppe and meadow type vegetation have remainned, namely to the slopes of gully – balka systems, fragments of steppe on flat interfluves, and fallows and virgin sites along roads and near human settlements. Data allow us to suggest that further range contraction of the mole rat will take place in the region.

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