

RANGE DYNAMICS IN SIBLING SPECIES: FACTS AND RECONSTRUCTIONS FOR THE MAMMAL FAUNA OF EASTERN EUROPE

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Range dynamics in sibling species: facts and reconstructions for the mammal fauna of Eastern Europe. — I. Zagorodniuk. — The specifics of distribution and status of local mammal species of sibling complexes demonstrating signs of significant either current or recent range dynamics are considered. These species complexes comprise pairs of sibling and morphologically close species, which until recently have not been unambiguously distinguished, thus it was impossible to analyse their range dynamics. However, range dynamics of this group of species is of great interest since it determines the emergence of high species diversity and realisation of mechanisms of compact organisation of communities that include close species. The amassed by today knowledge on distribution of species and the identification criteria developed for some of those species based on collection specimens allow to analyse changes in their distribution ranges. Such data in most cases allow to perform reconstructions and to develop respective hypotheses on dispersal routes of species in the region. In total, 9 species complexes were considered. Ranges of species that by direct or indirect evidence demonstrate changes in the area of their distribution and in the same time change the system of interspecific spatial relationships within each group are described. These spatial relationships can vary from allopatry to marginal or significant sympatry. Such complexes of “small” species were described in the composition of former “large” polytypic species with signs of invasions or expansions of their components among bats (*Plecotus auritus* + *austriacus*, *Pipistrellus pipistrellus* + *pygmaeus*, *Eptesicus serotinus* + *lobatus*) and rodents (*Spermophilus suslicus* + *odesanus*, *Microtus arvalis* + *obscurus*, *Mus musculus* + *spicilegus*). Similar but less expressed signs can be also traced in some other groups (*Spalax zemni* + *arenarius*, *Sylvaemus sylvaticus* + *whiterbyi*, *Capreolus capreolus* + *pygargus*). Distribution maps for all these species complexes are presented with reconstructions of possible directions of their dispersal through the territory of the region (Ukraine and adjacent countries). Zones of proclisis, where these species most likely were absent in the recent past, are determined and analysed. The time and pace of expansion of “small” species in the region are estimated. The significance of morphological criteria of species and the possibilities of revision of old collection specimens to analyse temporal changes of biota are shown as well as the importance of cartographic data for such analysis. By using data from revisions, it is possible to estimate geographical tendencies and velocity of expansion for many species, including those that represent groups of morphologically close or sibling species.

Key words: sibling species, mammals, range dynamics, biological invasions, biogeography, Ukraine.

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Introduction

The mammal fauna of Ukraine includes 152 species of 87 genera, which for the last three centuries have been known in the wild and being present in natural habitats. Among them are 22 alien species, including 7 domesticated ones, as well as 14 extinct and 5 phantom species (Zagorodniuk, Emelianov, 2012). A significant part of the species list is represented by cryptic species. In fact, the checklist of species largely expands due to the discovery of sibling species, recognition of morphologically close pairs and several allospecies as independent species (Zagorodniuk, 2010).

Data amassment on distribution of “small” species and detection of fine morphological differences between them allowing revision of old collection specimens became one of the next stages of further analysis of the mammal fauna. It enables to clarify their range dynamics, both current and former, as well as to develop several hypotheses on changes of distribution ranges and range interactions of close species. These changes can be explained by species migrations, in particular recent ones, due to which their substantial similarity has remained despite the presence of zones of sympatry. Such processes are largely influenced by anthropogenic environmental changes, creation of zones

of prochoresis and artificial ecological corridors allowing species to disperse into new areas, which is confirmed by several examples of instability of their range boundaries.

The first review of alien species in the mammal fauna of Ukraine was published in 2006 and the data were considered in more detail afterwards (Zagorodniuk, 2010, 2014 etc.). In the present paper, the attention is paid to manifestations of alienness within groups of close mammal species and to the evolution of expansions in space and time. Among the determining factors in evolution of close species are their spatial relationships and we consider distribution range as one of the key characters of species (Zagorodniuk, 2002, 2003, 2004, 2005 etc.). A change in the distribution range means a change in quality of the species and practically means the formation of new specific features, including changes in ecomorphological characters and variation, while the emergence of sympatry becomes not only a test to achieve reproductive isolation but also a factor promoting its escalation. The result of each invasion is that the species new for the community practically becomes “an ecosystem mutation” and its entry into the new community means a transition from the unstable state of “evolutionary species” to the stable state of “ecological species” (Zagorodniuk, 2003).

Data and reconstructions about range dynamics are particularly important for close species, since such species are objects in analysis of three key phenomena related to formation of high biotic diversity (after Zagorodniuk, 2011):

- 1) Hybridization or reproductive isolation as a test for species independence;
- 2) Biotopic, dimensional and other forms of differentiation as bases to avoid competition;
- 3) Sympatry or allopatry as values of the level of evolutionary differentiation of close species.

These three concepts form the basic triad in the study of initial phases of macroevolution and they are fulfilled at the early levels of evolutionary divergence, i.e. at the time of unstable mechanisms of reproductive isolation, ecomorphological differentiation, and niche segregation.

Regarding close species of mammals known in the regional fauna, the proposed biogeographic reconstructions prove their initial allopatry and a subsequent formation of zones of sympatry through dispersal of one species into the range of its sibling species (Zagorodniuk, 2005). Therefore, high cryptic diversity in the region's fauna is not a result of autochthonous development but of significant changes in distribution ranges of close species. This became the main object of analysis and we discovered, amassed, and generalised a number of important facts and hypotheses that allow to reveal the patterns of range dynamics in “small” species.

The aim the present paper is to generalise knowledge on chorology of close species and to analyse the cases that prove current and former dynamics of their distribution ranges, which may significantly affect the system of their ecological and reproductive interactions.

Taxonomic scope and objects of analysis

The objects of the present study are superspecies (groups of siblings and allospecies complexes) that include at least one species demonstrating signs of recent immigration into the region and formation of a contact zone (or sympatry) with its sibling species. Migration routes are similar in different groups which allows to explain the phenomenon of high concentration of sibling pairs in the territory of Eastern Europe (Zagorodniuk, 2005) while maintaining minimum ecomorphological distances between them (Zagorodniuk, 2007 a).

Considering the variety of manifestations of alienness (escape from culture, introduction, expansion, invasion), the main attention is paid to species that have demonstrated natural dispersal and became part of natural or synanthropic communities without maintaining their populations by humans. Besides, the analysis is restricted to species data on range dynamics of which are available for the last two centuries. In a historical aspect, most native species had normally appeared in any region due to expansion from adjacent territories thus they are formally aliens. The time of appearance of each species in a local biota as a criterion of alienness comes from the botanists: they determine this limit as the end of the 15th century and distinguish two groups, such as neophytes and archaeophytes (Kornaś, 1968, 1990; Kucher, 2014). In zoological terms, they are *neozoa* and *archaeozoa*.

All taxonomic details are given according to the checklist of mammals of Ukraine (Zagorodniuk, Emelianov, 2012), which fully covers the list of mammals of Eastern Europe. The checklist includes 23 alien species¹, mainly of superorders Ungulata (8), Glires (7), and Ferae (6) (Table 1).

From the wide variety of types of alien species and depths of their expansions, this analysis deals with species that were either absent earlier in Ukraine and neighbouring countries of Eastern Europe or changed their ranges in this region essentially. The list of alien species was compiled after comparison of the current fauna composition (Zagorodniuk, Emelianov, 2012) with older reviews published in 1840–1960 (e.g., Nordmann, 1840; Kessler, 1851; Charlemagne, 1920; Mygulin, 1938; Serzhanin, 1955, Tatarinov, 1956; Sokur, 1960). Maps of invasion and current distribution were created for species that demonstrated invasion during the last few decades.

Some of the discussed here reconstructions were partly presented in our earlier publications devoted to the revision of separate groups, such as ground squirrels (Zagorodniuk, 2002 b), voles (Zagorodniuk, 2007 b), long-eared bats (Zagorodniuk, Postawa, 2007), serotine bats (Zagorodniuk, 2009 b) and others. Another parts of data were included into recent reviews on bats (Zagorodniuk, 2018) and non-murid rodents (2019).

Table 1. Alien species in different systematic groups of mammals of the region's fauna (after Zagorodniuk, 2014) and species of sibling complexes that demonstrate signs of range dynamics

Таблиця 1. Чужорідні види в різних систематичних групах ссавців у складі фауни регіону (за Zagorodniuk, 2014) та види зі складу двійникових комплексів, що демонструють ознаки динаміки ареалів

Superorder	Orders and alien species in their composition	Species from groups of siblings	Specific of range dynamics
Chiroptera	Vespertilioniformes: <i>Plecotus austriacus</i> , <i>Pipistrellus kuhlii</i> *	<i>Plecotus austriacus</i> (gr. <i>auritus</i>); <i>Pipistrellus pygmaeus</i> (gr. <i>pipistrellus-nathusii</i>); <i>Eptesicus serotinus</i> + <i>lobatus</i> (gr. <i>serotinus</i>)	expansion of <i>austriacus</i> into the range of <i>auritus</i> ; distribution of <i>pygmaeus</i> in mainly synanthropic locations; counter expansion of both forms, <i>serotinus</i> + <i>lobatus</i> towards each other
Glires non-Muroidei	Leporiformes: <i>Oryctolagus cuniculus</i>	none	none
	Muriformes (1): <i>Myocastor coypus</i>	<i>Spermophilus odessanus</i> + <i>suslicus</i> (gr. <i>suslicus</i>); <i>Spalax arenarius</i> (gr. <i>zemni-giganteus</i>)	separation of <i>odessanus</i> from <i>suslicus</i> vs <i>pygmaeus</i> and its westward expansion with introgressive hybridization with <i>citellus</i> ; <i>arenarius</i> as a derivate of <i>giganteus</i> and therefore came from the east
Glires Muroidei	Muriformes (2): <i>Mus musculus</i> , <i>Rattus rattus</i> , <i>Rattus norvegicus</i> , <i>Ondatra zibethicus</i> , <i>Lagurus lagurus</i>	<i>Mus spicilegus</i> (gr. <i>musculus</i>); <i>Sylvaemus witherbyi</i> (gr. <i>sylvaticus</i>), <i>Microtus arvalis</i> + <i>obscurus</i> (gr. <i>arvalis</i>)	<i>spicilegus</i> expanding to the north forming sympatry with <i>musculus</i> ; immigration of <i>witherbyi</i> +? <i>uralensis</i> (gr. <i>sylvaticus</i>) from the east; counter expansion of <i>obscurus</i> + <i>arvalis</i> with formation of their parapatry
Ferae	Caniformes: <i>Felis catus</i> , <i>Nyctereutes procyonoides</i> , <i>Canis familiaris</i> , <i>C. aureus</i> , <i>Neovison vison</i> , <i>Mustela eversmanni</i>	none	<i>eversmanni</i> appeared from the east during first half of 20 century; although it is a well-identified species of the gr. <i>putorius</i> , but errors in identification of polecats in collections occur regularly
Ungulata	Equiformes: <i>Equus caballus</i>	none	none
	Cerviformes: <i>Dama dama</i> , <i>Cervus nippon</i> , <i>Bos taurus</i> , <i>Bubalus bubalis</i> , <i>Capra hircus</i> , <i>Ovis musimon</i> , <i>O. aries</i>	<i>Capreolus pygargus</i> (gr. <i>capreolus</i>)	<i>pygargus</i> is a phantom species in Ukraine, but signs of its presence east of Dnipro to Luhansk allows to suppose its recent expansion in Ukraine
Total	23 species	9 [+1] species*	

¹ Ukrainian populations of *Pipistrellus kuhlii* (s. l.) should be related mainly to *P. lepidus* (see: Mayer et al., 2007), so the expansion of *kuhlii* (s. l.) to the region could developed from two centres, *kuhlii* from SW and *lepidus* from SE.

Superspecies *Plecotus auritus* (sensu lato)

General remarks. Long-eared bats were considered as a monotypic genus *Plecotus* for a long time differentiated on subspecies level, i.e. as vicarious geographical forms including those distributed in Ukraine (Mygulin, 1938; Abelentsev, Popov, 1956). One of those forms, *Plecotus auritus wardi*, known in Ukraine from Transcarpathia, has long been considered a separate form, but only as a subspecies (“*Plecotus auritus austriacus*” in the review Krochko, 1980) despite the substantiated presence of two long-eared bat species in Central Europe (Topal, 1958; Lanza, 1960 etc.). This ignorance lasted for a long time (Korneev, 1965; Kryzhanivsky, Emelyanov, 1985), until the much wider distribution of the south European species *Plecotus austriacus* was shown for much of Europe (review: Mitchell-Jones et al., 1999), including the Black Sea and the Azov Regions in the south of Ukraine (Strelkov, 1988; Zagorodniuk, 2001). In the fauna lists of Ukraine, long-eared bats were listed as two separate species only in 1996 (Zagorodniuk, Tkach, 1996).

Recognition of range dynamics. Despite the mentioned southern records of *P. austriacus* in Ukraine, the predominant attention to its Transcarpathian populations (e.g., Krochko, 1980; Ruprecht, 1998) created the impression of a marginal distribution (within boundaries of Ukraine) of the species, with a rather small abundance in Transcarpathia, Odessa Oblast, and the Crimea (Strelkov, 1988; Zagorodniuk, 1999). By the early 21st century, the situation had changed significantly, not only in population estimates but also in understanding of the limits of species distribution. Earlier, most reconstructions were actually carried out to clarify the boundaries of geographical ranges (e.g., Zagorodniuk, 1999), but the recent revision of old museum collections and the received new data showed the dynamics of ranges and abundance of these bats (Zagorodniuk, 2001). Over the last century, records of *P. austriacus* in many localities have replaced findings of *P. auritus* since the distribution range of the latter increase mainly due to synanthropic locations.

Hypotheses. Three key facts allowed to include this species into the list of likely alien species and to develop a hypothesis on the expansive nature of its distribution in Ukraine: 1) extension in time of the geography of records of *Plecotus austriacus*, 2) increase in the relative frequency of records of this species, and 3) tendency to synanthropy (Zagorodniuk, 2006). It was later confirmed by analysis of collections and earlier reports. In the early and mid-20th century, the species was known only from Transcarpathia and coastal regions of Ukraine (Fig. 1), which viewpoint appeared after the revision of specimens from Transcarpathia, the Black Sea Region, and the Crimea (Strelkov, 1988; Ruprecht, 1998; Zagorodniuk, 2001). Further revision of collections (Zagorodniuk, Postawa, 2007) revealed “new” records of *Plecotus austriacus* from the same parts of western and southern regions of Ukraine (Fig. 1). However, the clear increase in the number of *Plecotus austriacus* specimens in museum collections during the 20th century allows to suggest that this species appeared in Ukraine relatively recently, most likely in the early 20th century (Zagorodniuk, Postawa, 2007).

New key data. Data from the early 21 century show a new wave of expansion. New records beyond the currently recognised species range demonstrate a further expansion to the east and north: the species was found in Smila, Cherkasy Oblast (Bilushenko, 2009) and in vicinities of Kyiv (Godlevskaya, 2012), as well as in several underground localities of Chernivtsi, Khmelnytsky, and Vinnytsia Oblasts (Godlevska et al., 2012). A series of new findings was reported from the territory of Poltava Oblast (Velyki Sorochintsy, 2014; Godlevska et al., 2016 a; Prokhorovka, 2016; Godlevska, Rebrov, 2018), Cherkasy Oblast (Kaniv Reserve, 2017; Zagorodniuk, 2018), Dnipropetrovsk Oblast (Spaske, Novomoskovsky Raion, 2016; Manyuk, Lahuta, 2017). Findings of the species were also reported from the south of Rivne Oblast (Ilyashevka, 2015; Novomalin, 2016; Godlevska et al., 2016 b). However, the species did not appeared in other areas where it could be expected (e.g., in the Chornobyl Zone or in Slobozhanshchyna). Recent records of *P. austriacus* indicate the expansion of its range to the north and east (Fig. 1).

Estimated pace of expansion. Most likely, this species in Ukraine has long existed only in Transcarpathia. In Crimea and adjacent mainland regions, old collected specimens are identified only as *P. auritus* (Zagorodniuk, 2001). The situation with Bessarabia is ambiguous (data from Strelkov, 1988), but probably this species is also a recent invader there. Mapping data with years

indicate that this species has expanded its range to the north and east by 300–400 km over the last 20 years (Fig. 1), where the expansion rate was about 150–200 km in 10 years, or 15–20 km in a year. Estimates for other mammalian groups conducted by us or with our participation are as follows: ca. 5 km per year for *Myodes glareolus* and *Alexandromys oeconomicus* in the east of Ukraine (Zagorodniuk, 2008); 5–10 km per year for *Felis sylvestris* in Podillia (Zagorodniuk et al., 2014); 10 km per year for *Apodemus agrarius* and 15 km per year for *Talpa europaea* in the Donets Basin (Korobchenko, 2008, 2009). Therefore, the rate of expansion in *Plecotus austriacus* is one of the highest among the species considered.

Superspecies *Pipistrellus pipistrellus* (sensu lato)

General remarks. The group is represented in the fauna of Ukraine and neighbouring countries by three species — *P. nathusii*, *P. pipistrellus* (s. str.), and *P. pygmaeus* (Zagorodniuk, 2002 c; Zagorodniuk, Emelianov, 2012), all three being considered as *P. pipistrellus* (s. l.) for a long time. The subspecies status of *P. p. nathusii* was recognised (e.g., Zubko, 1937)² and specialists recognised two species only in 1940–1950: *P. nathusii* and *P. pipistrellus* (Abelentsev, Popov, 1956).

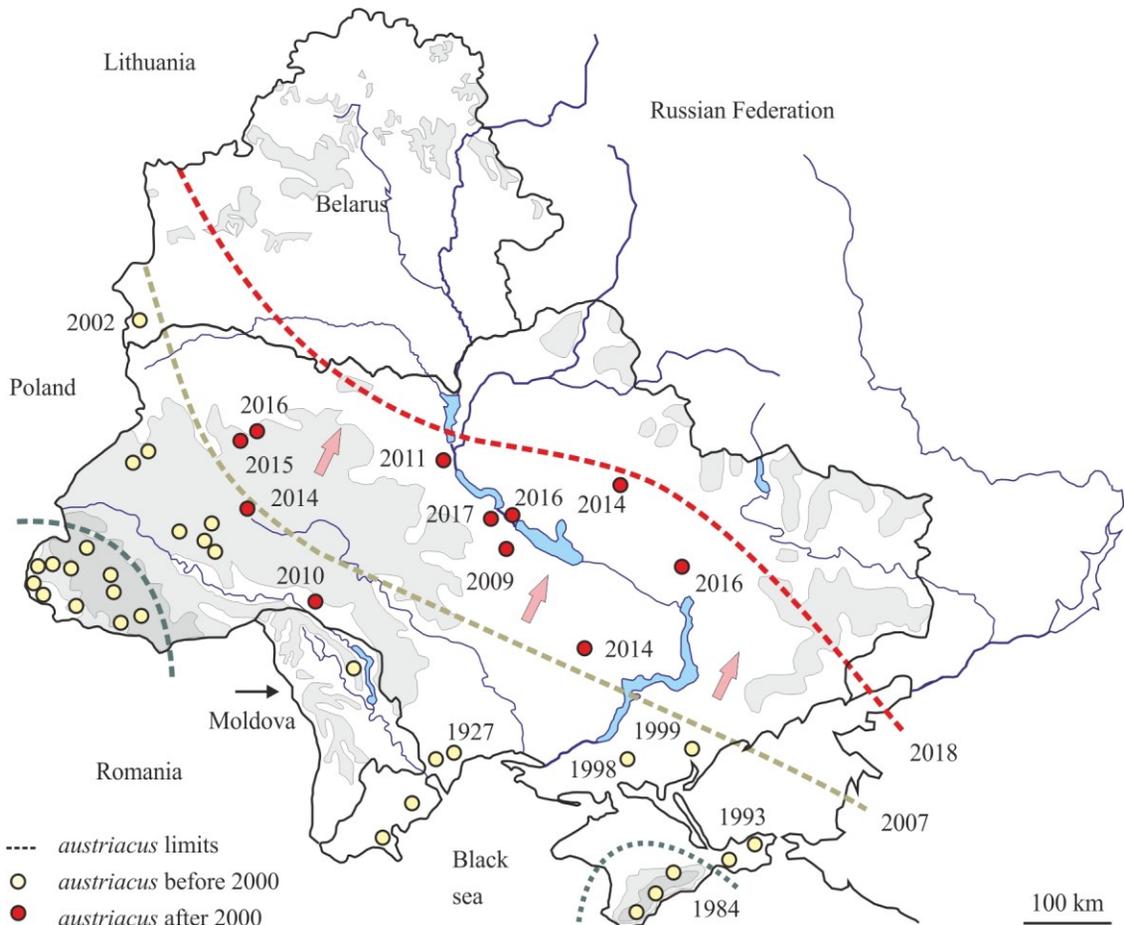


Fig. 1. Distribution and routes of expansion of *Plecotus austriacus* in Eastern Europe (after Zagorodniuk, Postawa, 2007, with additions after Zagorodniuk, 2018). The dotted lines indicate subsequent phases of *Plecotus austriacus* expansion in the region. The latest findings after the review from 2007 are marked by red with the year of record.

Рис. 1. Поширення та шляхи експансії ареалу вуханя *Plecotus austriacus* у Східній Європі (за: Zagorodniuk, Postawa, 2007, з доповн. за: Zagorodniuk, 2018). Пунктирні лінії позначають послідовні фази розселення *P. austriacus* в регіоні. Новіші знахідки після огляду 2007 р. позначено червоним кольором і роком.

² In the article by J. Zubko (1937), two forms of pipistrelles are described as sympatric subspecies.

Analysis of collections showed that these species were often confused, in particular young *P. nathusii* were taken for *P. pipistrellus* (Zagorodniuk, Negoda, 2001). The third species — *P. pygmaeus* — was first identified in the region in 2000 during our detector workshop near Nizhyn (Limpens, 2000). An analysis of geographical ranges of the two species was presented earlier both for Ukraine (Zagorodniuk, 2005, 2018) and the whole of Europe (Mayer, Helversen, 2001 *a–b*; Hulva et al., 2004). Each species of “small” pipistrelles differs by the frequency of ultrasonic signals: 45 kHz in *pipistrellus* (s. str.) and 55 kHz in *pygmaeus* (Jones, Parijs, 1993; Barratt et al., 1997), while morphological differences are less significant. All genetically marked findings from Eastern Europe (Crimea, Dnipro, Bryansk, etc.) belong to *P. pygmaeus* only (Zagorodniuk, 2005). The same is evidenced by mapping of pipistrelle species using ultrasonic detectors (Zagorodniuk, Korobchenko, 2009; Zagorodniuk, 2018; Godlevska, Rebrov, 2018) and signals similar in frequency to *pipistrellus* (s. str.) may refer to the invasive *P. kuhlii*.

Recognition of range dynamics. Revision of old collections shown that only *P. nathusii* occurred in central and northern parts of Ukraine in 1900–1940 and specimens of “*P. pipistrellus*” were re-identified as young *P. nathusii*, which suggests a recent invasion of “small” pipistrelles into the distribution range of *P. nathusii* (Zagorodniuk, Negoda, 2001). In fact, *pipistrellus* (s. str.) was reliably identified in old collections of bats only from the Crimea and Transcarpathia (Zagorodniuk, Negoda, 2001) and all later records of “small” pipistrelles refer only to *P. pygmaeus*, which is confirmed by both detector censuses and morphological analyses (Zagorodniuk, Korobchenko, 2008; Zagorodniuk, 2018; Godlevska, Rebrov, 2018 et al.). Our hypothesis that *P. pygmaeus* is an alien species (Zagorodniuk, 2006) is supported by genogeographic studies of Balkan forms that are basal in the series of races distributed from the south to the north (Hulva et al., 2004).

Hypotheses. The main hypothesis is that the “excessive” species diversity of *Pipistrellus* in the region can be explained by the fact that some species are invasive and have invaded the region due to unnatural habitats. Particularly, it is shown for *P. kuhlii* (Zagorodniuk, Negoda, 2001) and is assumed for *P. pygmaeus* (ibid., Zagorodniuk, 2006; Zagorodniuk, Korobchenko, 2008). The vast majority of soprano pipistrelle finds are related to artificial dwellings. The first clue about its invasive status was the first record of a colony of the species in a village club in Chernihiv Oblast (Limpens, 2000) and all subsequent finds were related to similar habitats such as water towers, cottages, caravans, forestry estates, and churches (Zagorodniuk, Korobchenko, 2008; Zagorodniuk, 2018)³. Recognising the southern roots of the soprano pipistrelle and considering its absence in the steppe zone it can be assumed that the species has settled in the region from two refugia — southern Europe and the Caucasus. The migratory status of *P. pygmaeus* was due to its “cold” synanthropy that sharply distinguishes this species from the other synanthropic bat *P. kuhlii*.

New key data. The new material confirms the three following main facts: 1) the presence of only *P. pygmaeus* among specimens of “small” pipistrelles from most regions, 2) the limitation of most records to synanthropic localities and artificial dwellings, 3) the short-term presence (5 months) of the species in the region during a year. Such data had been accumulated for green areas of Kyiv (Zagorodniuk, Tyschenko-Tyshkovets, 2001; Vlaschenko et al., 2012), for the Chornobyl Zone (Gashchak et al., 2013), Podillia (Kapeliukh, 2018), Cherkassy Oblast (Bilushenko, 2019), forest zone of the Right-bank Dnipro Region (Godlevska et al., 2016 *a–b*), Left-bank Dnipro region (Godlevska, Rebrov, 2018), and for Luhansk Oblast (Petrushenko et al., 2002; Zagorodniuk, Korobchenko, 2008). All the thoroughly researched localities in the Belarusian part of the Central Polissia also showed the presence of only *P. pygmaeus* (Dombrovski, 2013, 2018; Dombrovski et al., 2017). The same concerns the territory of the Russian Federation, in particular the Bryansk Forest, Voronezh and Oka Nature Reserves (Vlaschenko et al., 2016), and Smolensk Oblast (Gukasova et al., 2011). The species is also common in the Baltic states (e.g., Baranauskas, 2010). Contradictory reports include *P. pipistrellus* from the Gomolshansky Forests National Park (Kharkiv Oblast, Ukraine), with remarks that the species has now “moved” to human buildings (Vlaschenko, 2005),

³ Initially, it was supposed that the species is related to large river valleys (Jones, 1999), which was difficult to explain (Zagorodniuk, 2005). However, now it is clear that the species prefers floodplains with villages and cottages.

however, in the following review the name “*pipistrellus*” was replaced with “*pygmaeus*” without any comments (Vlaschenko, 2010). “Common” pipistrelles from Trostianets (Sumy Oblast) stored in the Museum of Nature of Kharkiv University were revised as *P. pygmaeus* and as young *P. nathusii* (Parkhomenko, 2018; own data).

Estimated pace of expansion. Given that most of old findings of pipistrelles were in fact Nathusius' pipistrelles, we can assume that the active formation of populations of the soprano pipistrelle in anthropogenic landscapes of the Forest-Steppe and Polissia was an event of the same period and the time of expansion can be estimated at 80–100 years. We suggest that *P. pygmaeus* formed a migratory population during its active intrusion into the region in summer to form maternal colonies. It is obvious that migration paths should repeat expansion routes. The formation of powerful populations of the soprano pipistrelle could actually occur immediately after its intrusion. Considering the significant number of findings of the species mainly in the east of Ukraine (Zagrodniuk, 2005) and its commonness in adjacent regions of the Russian Federation, we assume that the main expansion route of the species was the Caucasian-Slobozhansky migration corridor, similarly to *P. kuhlii*, another invader (Zagrodniuk, Negoda, 2001).

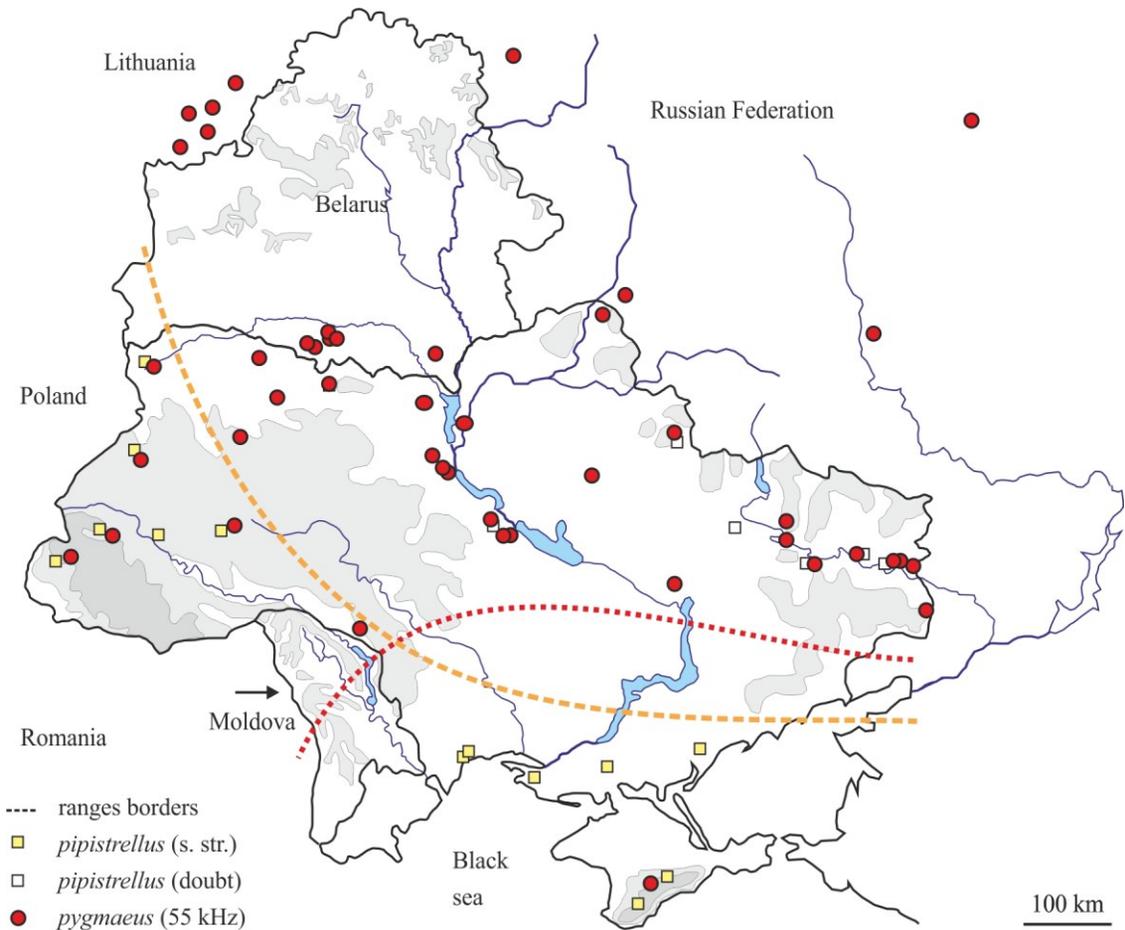


Fig. 2. Distribution of two cryptic species of the “common” pipistrelle according to different sources: *Pipistrellus pygmaeus* (●) and *P. pipistrellus* (■) (after Zagrodniuk, 2018, with additions). The southern border of summer range of *P. pygmaeus* corresponds to the border of the Forest-Steppe zone. The northern border of *P. pipistrellus* coincides with the distribution of *Plecotus austriacus* before its wide expansion in the region (Fig. 1).

Рис. 2. Поширення двох видів «малого» нетопира за сумою даних з різних джерел: *Pipistrellus pygmaeus* (●) та *P. pipistrellus* (■) (за: Загороднюк, 2018, з доповненнями). Південна межа літнього поширення *P. pygmaeus* відповідає межі Лісостепової зони. Північна межа *P. pipistrellus* (s. str.) збігається з межею поширення *Plecotus austriacus* до його широкої експансії в регіоні (рис. 1).

Superspecies *Eptesicus serotinus* (sensu lato)

General remarks. The revision of the east European *E. serotinus* (s. l.), which was considered for a long time an evenly distributed monotypic species, began from the description of *E. lobatus* (Zagorodniuk, 2009 b), the range of which covers the east of Ukraine and adjacent areas of Russia and the North Caucasus. This description provoked interest in the analysis of the heterogeneity of *Eptesicus* using molecular markers. Based on these markers, the eastern *E. serotinus* (s. l.), the range of which overlaps with the range of *E. lobatus*, was assigned to the group “*turcomanus*” (Çoraman et al., 2013; Juste et al., 2013). The morphological differences of the latter (*turcomanus*) confirm the incorrectness of such merge, and the available data suggest that *lobatus* is derived from Caucasian and Transcaucasian forms. In addition, it is similar to samples from Georgia (Zagorodniuk, 2018), which, unlike *turcomanus*, are also characterised by dark fur colouration, small body size, and a well-developed post-calcar lobe. Available information shows the coincidence of morphological and molecular data, which confirms resemblance of *lobatus* to the Caucasian forms (ibid.).

Recognition of range dynamics. The direct and indirect signs of expansion of serotine bats in the territory of Ukraine are as follows: 1) the widespread old vernacular name of the species “mountain bat” (Abelentsev, Popov, 1956), which may indicate its southern origin, 2) prevalence of findings in the southern and central parts of the region (Tyschenko, 1999); 3) the species’ expressive synanthropy and sedentariness throughout Eastern Europe (Godlevska, 2001; Zagorodniuk, 2003); 4) the absence of *serotinus* in the middle of the 20th century in most regions of the north and east of Ukraine, where it is now a common species (Zagorodniuk, 2009 a; 2012)⁴. Findings of serotine bats were unknown in Volyn and Polissia (Tkach et al., 1995; Zenina, 1998). However, new information about this species in the Shatsky National Park (Srebrodolska et al., 2001) and the Polissia Reserve (own data), as well as in northern parts of Ukraine in general (Godlevska et al., 2016; Godlevska, Rebrov, 2018) indicate a further expansion of the species. The range of this species extends to the neighbouring parts of the Russian Federation (Vlasov, 1995) and Belarus (Savarin, 2008). In the east of Ukraine, *E. lobatus* was revealed to be distributed (Zagorodniuk, 2009 b), although previously there were no records of *Eptesicus* in that region at all.

Hypotheses. Our hypothesis is based on the recognition of expansion of serotine bats to the north across Ukraine and adjacent regions of Belarus and Russia (one of the first publications: Vlasov, 1995). This hypothesis was formulated in a 2006 review on alien species, where *E. serotinus* was classified as a “close invader” (Zagorodniuk, 2006). Later, in the review on alien mammal species of the Russian Federation *serotinus* was considered among species that demonstrate expansion, with attention to its range dynamics in regions adjacent to Ukraine (Bobrov et al., 2008). The hypothesis on the expansion of *serotinus* in the territory of Ukraine was detailed after the discovery of two morphologically different allospecies, the south-western *E. serotinus* (s. str.) and south-eastern *E. lobatus* (Zagorodniuk, 2009 b). The latter cannot be inferred by morphology from the more eastern *turcomanus* (small body size and light fur colouration, without post-calcar lobe), but this form shows a clear similarity to the Caucasian *intermedius* (see further). This suggests the expansion of *E. lobatus* from the Caucasus where from it dispersed to the east of Ukraine (Fig. 3).

New key data. The map presented in the description of the *lobatus* form (Zagorodniuk, 2009 b) was supplemented by new data from different regions of Ukraine and neighbouring countries (Fig. 3). Particularly important are materials from the southeast, the Volga region (range of *turcomanus*) and the Caucasus (range of *intermedius*), from which the bat described as *E. lobatus* could disperse to the territory of Eastern Europe. Forms similar to *turcomanus* significantly differ from *lobatus*-like forms, while Caucasian forms are quite similar to them. This conclusion follows from the results of the study of specimens from the Gardabani Forestry (Eastern Georgia; Zagorodniuk, Kandaurov, 2015). In addition, analysis of DNA samples also confirmed the distinctness of the eastern form from European serotine bats (Godlevska et al., 2014). Samples of DNA from the range of *lobatus* form a single group with Caucasian ones (Çoraman et al., 2013; Fig. 3).

⁴ In Luhansk Oblast, serotine bats were not listed in reviews neither in 1956 (Abelentsev, Popov, 1956) nor in 1962 (Sakhno, 1963). In Kharkiv Oblast, this species was first reliably identified only in 1930 (Zubko, 1939).

Estimated pace of expansion. The current distribution of *E. lobatus* in the region covers the area where *Eptesicus* was absent until the mid-20th century at all (see Fig. 3), and the range of serotine probably pulsed repeatedly. The first remarkable “dash” in the species’ distribution was its appearance in the previous phase of global warming in the mid-1930’s in northeast Ukraine (Zubko, 1939), when it expanded its range by 220 km, if measured from the Dnipro River. Later, the species moved 100 km further to the north, reaching in 1988–1993 the Central Black Soil Reserve in Kursk Oblast, Russia (Vlasov, 1995). By the mid-1990s, it had already become known in Luhansk Oblast, Ukraine (Zagorodniuk, 2012), which is about 150 km far from the North Caucasian locations of the species. Thus, the rate of expansion may be about 50 km per decade. Similar processes have taken place in the north, including the first record of the species in the Polissia Reserve in the early 2000s (own data) and in Gomel (Savarin, 2008). In general, the pace of the species’ expansion can be estimated as 100 km over 50 years, which is one of the slowest among the species considered.

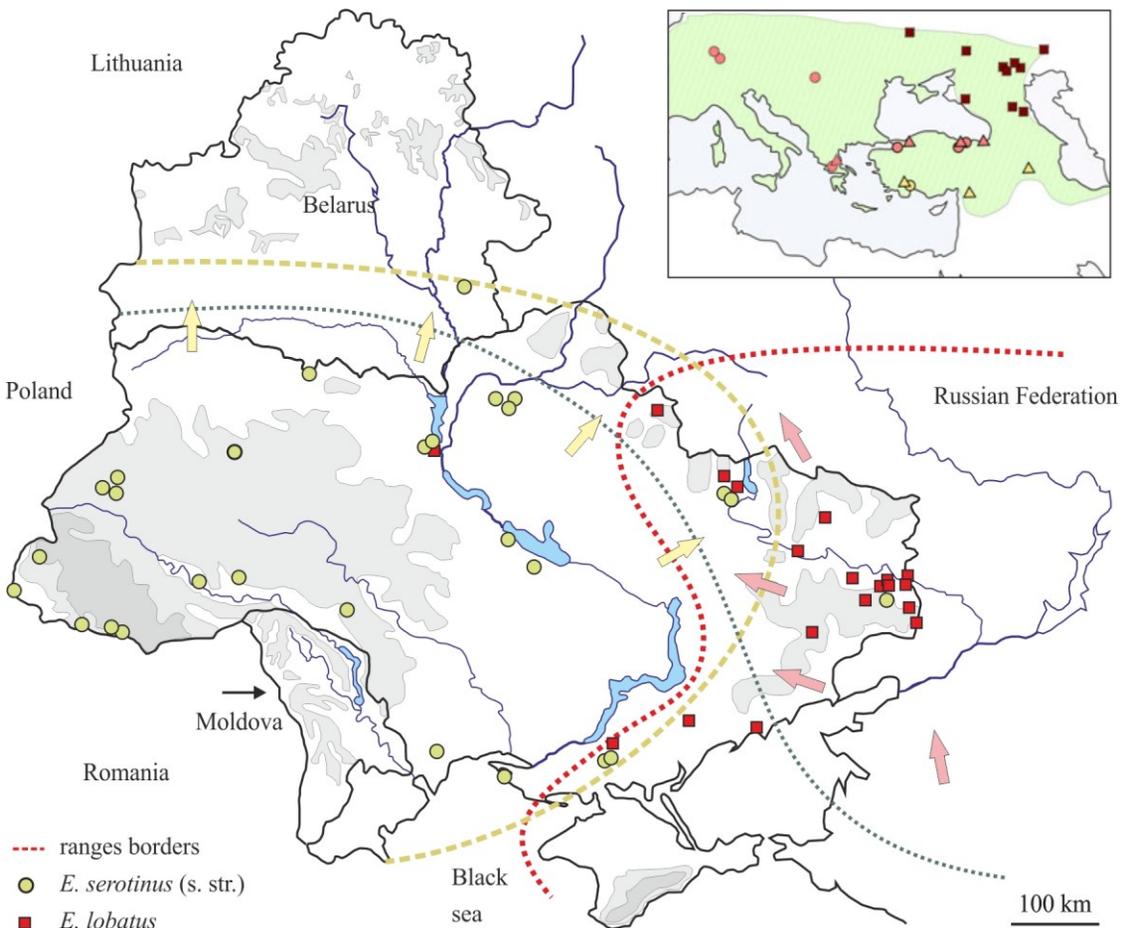


Fig. 3. Distribution of records of *E. serotinus* s. str. and *E. lobatus* in Ukraine based on different morphotypes of the post-calcarial lobe (Zagorodniuk, 2009 b, with additions). The small dotted line indicates the eastern limit of the continuous range of *Eptesicus serotinus* (s. l.) according to the data of the 1950s (Kuziakın, 1950; Abelentsev, Popov, 1956). The filling marks the distribution range of *lobatus* forms. The range of the *lobatus* form is located in the zone of probable prochoresis of the Caucasian *intermedius*. Right above — distribution of different genotypes, one of which (■) should be identified as *lobatus* but it is marked as *turcomanus* (fragment from: Çoraman et al., 2013).

Рис. 3. Розподіл знахідок *E. serotinus* (s. str.) та *E. lobatus* в Україні на підставі виявлення різних морфотипів епіблеми (Zagorodniuk, 2009 b, з доповненнями). Дрібний пунктир — східна межа суцільного ареалу *Eptesicus serotinus* (s. l.) за даними на 1950-ті рр. (Kuziakın, 1950; Abelentsev, Popov, 1956). Заливка — ареал лобатусних форм. Ареал форми *lobatus* розміщений у зоні ймовірного прохорезу кавказьких *intermedius*. Праворуч вгорі — поширення різних генотипів, один з яких (■) має бути ідентифікований як *lobatus*, проте позначений як *turcomanus* (фрагмент, із: Çoraman et al., 2013).

Superspecies *Spermophilus suslicus* (sensu lato)

General remarks. The group *Spermophilus* “*suslicus*” represents a complex of close species (Reshetnyk, 1948 etc.) similar in morphology but highly different in karyotypes (Vorontsov, Liapunova, 1969). The group includes six “small” species of different levels of kinship and their chromosome numbers vary within $2n = 34\text{--}42$ (Zagorodniuk, 2002 *b*). The distribution of species is usually restricted by rivers (Fig. 4), although the hybrid zones are formed on watersheds (Zagorodniuk, 2011). Both forms of speckled ground squirrels ($2n = 34/36$) are allospecies (*S. suslicus* (s. str.) and *S. odessanus*), which may originate either from each other (Zagorodniuk, 2002 *b*) or independently from a third species *S. pygmaeus*. The latter assumption is confirmed by the information on variability and possible evolutionary changes in tooth morphology (Popova, 2007; Popova et al., 2019).

Recognition of range dynamics. The assumption of high mobility of ground squirrel settlements follows from numerous descriptions concerning population outbreaks and dynamics of settlements (Mygulin, 1938; Reshetnyk, 1948; Lobkov, 1999; Zagorodniuk, Kondratenko, 2006). Important facts were obtained by clarification of distribution of hybrids between close ground squirrel species in Podillia: in many places, hybridisation was the result of intrusion of one species into the range of another, which significantly shifted the boundaries of species ranges in the region (Zagorodniuk, 2011). Obviously, similar processes occurred in many places, and the formation of transitive taxonomic systems, clearly existing in the ground squirrels (Zagorodniuk, 2002 *b*), can be explained precisely by population dynamics (Zagorodniuk, 2002 *b*). Important factors in reconstructions are the non-random spatial distribution of chromosomal numbers, the fact that both karyotypes of “speckled” ground squirrels (*odessanus* with $2n = 36$ and *suslicus* with $2n = 34$) are derived from the initial $2n = 36$ known in *pygmaeus*, and the configuration of distribution ranges of these species (Zagorodniuk, 2019) allowing to suggest their dispersal from the Azov Region.

Hypotheses. A key hypothesis is that ranges of all ground squirrel species in the region have undergone substantial changes including reductions and extensions. The greatest changes occurred during the warm climatic phase in the 1910–1940s and were facilitated by large scale land ploughing. There are many reports from the early 20th century on settlements with several millions of specimens within the reconstructed range of *S. odessanus*, in particular in Volyn, Zhytomyr, Kyiv, Poltava, and Kharkiv Oblasts (Mygulin, 1938; Reshetnyk, 1948, etc.), although ground squirrels have recently disappeared in these regions. Ground squirrel populations in Belarus and Poland are close to extinction (Ziółek et al., 2017; Abramchuk et al., 2019). Such significant demographic changes have contributed to the migration of each species into new areas during the period of restoration of abundance and of geographical ranges. These new areas could also include those that were previously inhabited by a neighbouring species. Such range dynamics was clearly facilitated by the significant ecomorphological similarity of all ground squirrel species of this group (Zagorodniuk, 2019) and also intensified by an extremely narrow spatial niche. The latter is determined by the adherence of ground squirrel settlements to slopes of small river valleys (ibid.).

New key data. The accumulation of new data is limited by the widespread decline in the number and distribution of ground squirrels. Even the colonies known in the early 2000s have now disappeared in many places (Zagorodniuk, Kondratenko, 2006). The situation with related species, in particular *S. pygmaeus*, is less stable (Bronskov, Timoshenkov, 2010), however, extinction of populations is widespread, and most species now have conservation status. This is especially evident in both species of speckled ground squirrels that have now disappeared in most parts of their former geographical range, especially in the forest-steppe zone.

Estimated pace of expansion. Unlike the directions of expansion, the rate of expansion of each species is not easy to estimate. Usually resettlement is estimated by the annual dispersion of 4–5 % of young specimens to a distance up to 5 km from the maternal colony (Kalabukhov, Raevskij, 1935). However, it should be considered that each wave of dispersal could occur only after the formation of a stable colony, i.e. not earlier than 5–8 years. Estimates of species expansion in separate parts of the range are similar: about the same rate had the dispersal of *S. odessanus* into the range of *S. citellus* in the Khotyn Upland (Zagorodniuk, 2011).

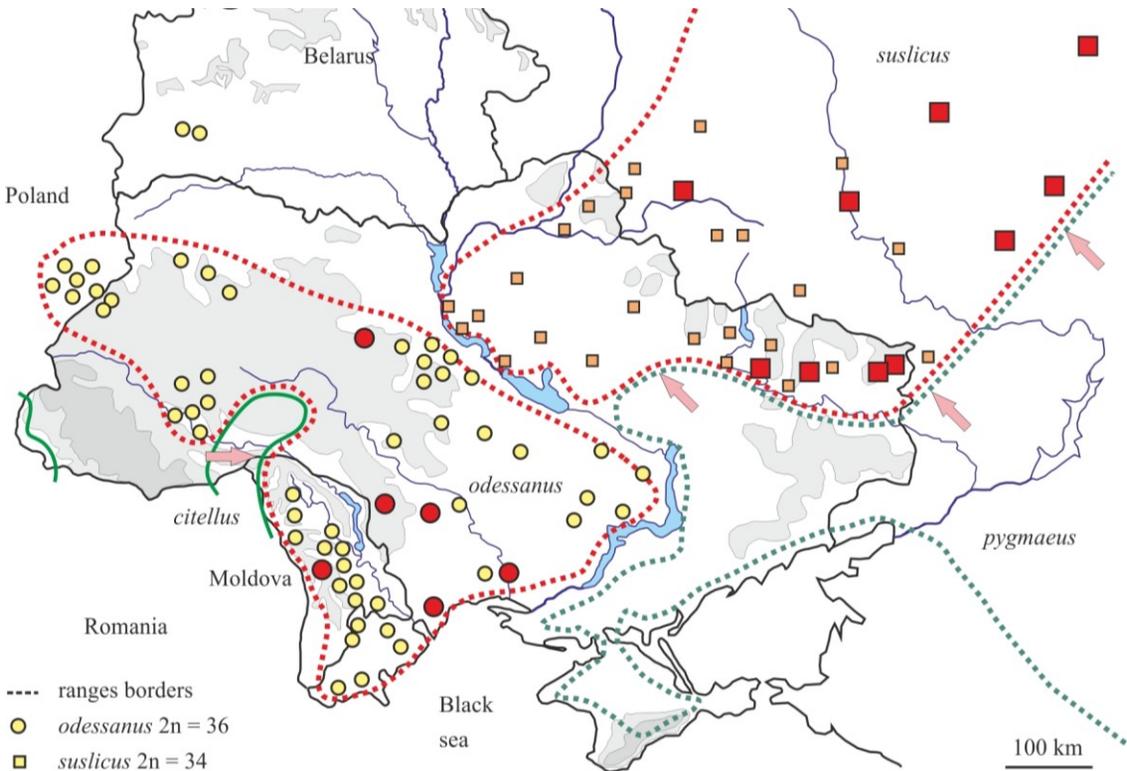


Fig. 4. Distribution range of “small” species of West Palearctic ground squirrels having different chromosome numbers, and the distribution of actual findings of the two forms (species) of speckled ground squirrels (yellow — *S. odessanus*, red — *S. suslicus* s. str., arrows — hybrid zones between these forms and other species). Large marks note places where species status is confirmed by karyotype data (after Zagorodniuk, 2011, with modifications).

Рис. 4. Ареали «малих» видів західнопалеарктичних ховрахів (*Spermophilus* s. str.), відмінних за хромосомними числами, розподіл фактичних знахідок двох форм крапчатих ховрахів (жовті значки — *S. odessanus*, червоні — *S. suslicus* s. str.) та місця гібридизації цих форм з іншими видами ховрахів (стрілки). Великі значки — місця, звідки статус підтверджено даними про каріотиби (за: Загороднюк, 2011, зі змінами).

The wave of expansion of speckled ground squirrels to the west through the north of the forest-steppe (from the Dniro River to Volyn and Roztochia, as well as their appearance in Belarus) took place at a similar pace. However, it should be considered that most rivers are located in this region meridionally, so the expansion rate could be much lower due to flat interfluves and the lack of suitable ecological corridors. Nevertheless, the direction of ground squirrel expansion along the Bug and Dniester Rivers coincided with the existing ecological corridors, particularly with riverine biotopes of the II and III fluvial terraces. Thus, the estimated pace of expansion is ca. 10 km over a decade.

Superspecies *Microtus arvalis* (sensu lato)

General remarks. The wide range of chromosomal races of the “common” vole was initially divided into two groups “*arvalis*” (NF = 80–90) and “*obscurus*” (NF = 66–74) (Malygin, Orlov, 1974), or even into 6 groups (Kral, Liapunova, 1975). Later it was shown that much of this variability is interpretive, and basically there are only two main forms with NF = 72/84 that correspond to the initially established groups *arvalis* + *obscurus* recognised as species (Zagorodniuk, 1991 a). All data, including data on chromosomal forms, indicate that allospecies were formed not by the split of the wide fan of chromosomal races, but by the formation of initiative populations based on founder effects and secondary expansions, which continue today.

In the taxonomic history of 46-chromosomal forms, the most important were the subsequent discoveries of the following facts: 1) *arvalis* + *obscurus* are not only chromosomal races, but independent species with their own patterns of variation (Zagorodniuk, 1991 a); 2) these species have

different centres of their geographical ranges that are located beyond the study area and coincide with those of other species; 3) both species are broadly sympatric with the third species of the group, the 54-chromosomal *M. levis*, and their sympatry extends northward into the area of their possible zone of prochoresis (Zagorodniuk, 2005, 2007). These species have slight differences in habitat preferences and they form mosaic settlements in sites of their coexistence (e.g., Malygin, 1983).

Recognition of range dynamics. The idea of range dynamics in these species is based on three facts. The first is related to the configuration of geographical ranges of 46-chromosomal allopecies (*arvalis* + *obscurus*), which does not coincide with borders of biogeographic regions or natural zones (regions and zones see: Charlemagne, 1937; Mygulin, 1956; Reshetylo, 2012). Therefore, the boundaries of their ranges are unstable and dynamic. The second fact is the dynamics of records of species in areas where they were absent before, in particular in the area between their ranges as of the 1980s-1990s where from only the 54-chromosome species were reported (see: Zagorodniuk, 2007, 2011)⁵. The third fact is that the analysis of biotopic distribution of rodents in the Valdai Hills showed the absence of native habitats of the common vole (Schwartz, Zamolodchikov, 1991), which was also demonstrated for *M. arvalis* (s. str.) in Ukraine (Zagorodniuk, 2005). The scheme of possible ways of formation of sympatry between *M. arvalis* and *M. levis* in Eastern Europe implies an extension of this zone of sympatry to the north (Zagorodniuk, 2005). The relations between *arvalis* + *obscurus* were shown in a series of our publications (Zagorodniuk, 1991 a, 2005, 2007, 2011).

Hypotheses. Several hypotheses were formulated regarding range dynamics of “common” voles. The first is about the configuration of ranges of “small” species around post-glacial zones, which were common in Eastern Europe (Velichko, 1973; Hubberten et al., 2004). Based on this we developed and substantiated a model of formation of an allopatric pair around the area of glacial split of an ancient species into a western and an eastern form, the geographical ranges of which correctly fit into this model (Zagorodniuk, 1991 a, 2005). Such views are expressed in a series of our works with detailed analysis of postglacial expansion scheme and analysis of range convergence in *arvalis* + *obscurus* (Zagorodniuk, 2005, 2011). Based on the available data, we can expect an increase in the *arvalis* + *obscurus* zone of parapatry with further displacement of their niches according to our autogenetic model (Zagorodniuk, 2003 b, 2004). Details of the distribution pattern of these two allopecies allows to analyse two parallel processes (Zagorodniuk, 2007):

1) The increase of the zone of sympatry between *M. arvalis* (s. str.) and *M. levis* in time: with a clear growth its width to the north (Fig. 5), especially in the areas where the sibling species penetrate the former postglacial zone located in the north of the region;

2) Expansion of ranges of *arvalis* + *obscurus* leading to their convergence, which would be a test for their status as independent species, when their interactions will lead to evolutionary differentiation without widespread hybridisation or merging into a single syngameon.

New key data. A review of new facts was presented earlier (Zagorodniuk, 2007, 2011). The most recent data (after 2000, Fig. 5) clearly indicate the convergence of species ranges. Practically the same picture was shown by Russian authors (Malygin et al., 2019), who also interpret the new data as counter-move of species ranges, although not citing articles in which this fact was already described and explained (in particular Zagorodniuk, 2011). Recent data on the distribution of these allopecies in the area of their probable contact (Fig. 5), where from records of only *M. levis* were reported, greatly reduce the spatial gap between the ranges of *arvalis* and *obscurus*.

Marginal records of both allopecies in their contact zone according to various sources regarding Ukraine and the neighbouring regions of the Russian Federation are as follows (Fig. 5):

1) the easternmost records of *M. arvalis* are as follows: Orekhovo, Spassk-Ryazansky, Ryazan Oblast; Michurinsk, Tambov Oblast; Podgornoye, Sindyakino, Lipetsk Oblast; Lopatki, Krasnoye, Kaver'ye, Treshchevka, Voronezh Oblast; Central Black Soil Reserve, Kursk Oblast; Buryn', Sumy Oblast; Ichniya, Chernihiv Oblast; Pishchane, Cherkasy Oblast (and then towards Odesa);

⁵ The very presence of such gap between distribution ranges allows to attribute the form *rossiaemeridionalis* to the 54-chromosomal sibling species (Malygin, Yatsenko, 1986) currently known as *M. levis*, which was confirmed later by analysis of the morphology of type specimens of *rossiaemeridionalis* (Zagorodniuk, 1991 b).

2) the westernmost records of *M. obscurus* are: Arzamas, Nizhny Novgorod Oblast; Zemetchino, Penza Oblast; Morshansk, Izmaylovka, Tambov Oblast; Dvurechki, Izlegoshche, Lipetsk Oblast; Treshchevka, Perlevka, Sevost'yanovka, Voronezh Oblast; Barkalovka, Bol'shiye Butyrki, Kursk Oblast; Novy Oskol, Belgorod Oblast; Svatove, Kryakivka, Provallia, Luhansk Oblast. In several locations, hybrids were found between these species (Baskevich et al., 2012 etc.).

Estimated pace of expansion. The East European ranges of species from the group “*arvalis*” are recent and the centres of these ranges are located beyond the studied region, namely in Asia Minor and the Balkans. The oldest species (*M. levis*) is the most widespread in the region, but the ranges of its 46-chromosomal derivatives *M. arvalis* (s. str.) and *M. obscurus* had been formed as a result of their recent invasion into Eastern Europe and they continue to converge after the split of their ancestor (“pre-*obscurus*”) by the Dnipro glaciation. The existence of an isolated population of *M. obscurus* in the Crimea (Fig. 5) can be explained by its earlier penetration from the north, in which case its modern expansion to the west is a stage of restoration of the species’ range (similar ranges have the Caucasian shrews *Sorex volnuchini* s. l. and barbels *Barbus tauricus* s. l.).

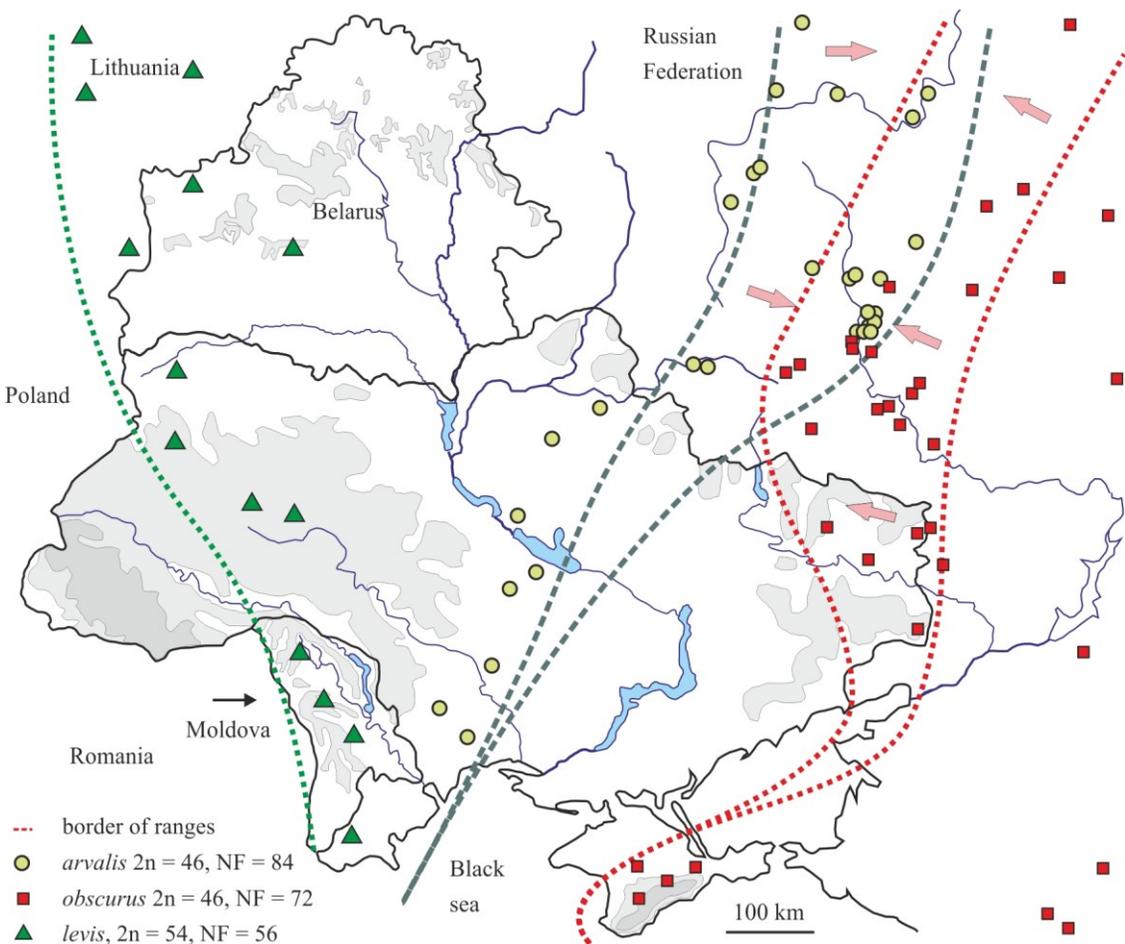


Fig. 5. Borders of distribution of “common voles”: *Microtus arvalis*, *M. obscurus* and *M. levis*. In fact, all records in the contact zone between *M. arvalis* and *M. obscurus* were discovered after 2000, which indicates the convergence of their ranges. The map is an updated version of our previous reconstructions (Zagorodniuk, 1991 a, 2007 b) supplemented by data on range dynamics (Zagorodniuk, 2011) and data from several recent faunal publications.

Рис. 5. Межі поширення «звичайних» полівок: *Microtus arvalis*, *M. obscurus* та *M. levis*. Фактично всі точки з зони контакту *M. arvalis* та *M. obscurus* виявлені після 2000 р., що свідчить про сходження їхніх ареалів. Мапа є обновою попередніх реконструкцій (Zagorodniuk, 1991 a, 2007 b), доповнених даними про динаміку (Zagorodniuk, 2011) та знахідками з низки нових фауністичних публікацій.

Superspecies *Mus musculus* (sensu lato)

General remarks. The species *Mus musculus* has a long history of expansion in Europe, which took place in ancient times (Boursot et al., 1993; Auffray, Britton-Davidian, 2008). In the modern fauna of Ukraine, this species has three types of settlements: stable natural (year-round) in the south, seasonal natural in the Forest-Steppe zone, and strictly synanthropic in the north (Zagorodniuk, 1996 a). In the Steppe and Forest-Steppe zones, it forms a zone of sympatry with the indigenous *Mus spicilegus* considered its sibling species (Mezhzherin, Zagorodniuk, 1989; Kotenkova, Bulatova, 1994; Zagorodniuk, 1996, 2002). The latter became known in the fauna of Eastern Europe under the names *Mus sergii* and “mound mouse” due to the works by B. Valkh (1927) and O. Mygulin (1937). In the studies of the 1940–1980s, this knowledge was forgotten, which was facilitated by the actual mixing of two taxa (the exanthropic *M. musculus* and the typical *M. spicilegus*) under the name “*Mus hurtulanus*” adopted in the monograph by A. Argyropulo (1940): (Zagorodniuk, 1996 a), although the type specimen of *M. hurtulanus* clearly belongs to *M. musculus* (ibid.). The complex taxonomic history of this group ended in recognition of two species in the East European fauna: *M. spicilegus* and *M. musculus* (Sokolov et al., 1998; Zagorodniuk, 2002).

Recognition of range dynamics. The dynamics of the house mouse’s expansion had been studied for a long time repeatedly and in detail (for a review see: Kotenkova, Bulatova, 1994). This alien species forms seasonal exanthropic settlements in the south of the region very similar to the native *M. spicilegus* (Zagorodniuk, 2002). In terms of the region, we can state about an ancient expansion of *M. musculus* and a recent expansion of *Mus spicilegus* having an unstable distribution range. All of the old descriptions of “mounds” refer exclusively to coastal regions of southern Ukraine (Brauner, 1899; Valkh, 1927; Pisareva, 1948). To the north and east, *M. spicilegus* dispersed unevenly with several “tongues” and wide gaps between them into which the species have begun to settle only in the late 20th century, in particular appearing in Podillia (Zagorodniuk, Berezovsky, 1994). A similar process was observed in the east of Ukraine, in particular in Kharkiv Oblast (Zagorodniuk et al., 1995; Tokarsky et al., 2011), Luhansk Oblast (Kondratenko, 1998; Zagorodniuk, Kondratenko, 2001), and later also in adjacent areas of the Russian Federation (see further).

Hypotheses. Signs of the northward expansion of *M. spicilegus* were reported in works of the 1990s. In particular, the species range expanded to Podillia, which was explained by the beginning of a warm period facilitating improved wintering conditions and reduced freezing depth of the soil (Zagorodniuk, Berezovsky, 1994). New records of the species in Slobozhanshchyna and Donbas, including those based on revisions of old collections (Zagorodniuk, 1994; Zagorodniuk et al., 1995), suggested that the species has a much wider distribution covering Sumy and Luhansk Oblasts of Ukraine as well as Belgorod and Rostov Oblasts of Russia. Besides it was revealed that there are “distinct long-term population cycles and at the edges of the species’ range its detection is usually possible only in periods of high population abundance” (Zagorodniuk, Kondratenko, 2001). Further studies confirmed the wider distribution of the species based on the new record from Rostov Oblast (Lipkovich, 2005, etc.) and analysis of old sources concluding that the species was repeatedly noted in the 1920–1930s, in particular by Zverozomb-Zubovsky (1923) and in the manuscripts of Martino (Lipkovich, 2005). Thus, range dynamics is mainly influenced by cyclical climate changes, which, as it was suggested, “in 1940–1950 led to the shift of the eastern boundary of the range of *M. spicilegus* from the western regions of Rostov Oblast, Russia to the steppes of neighbouring Ukraine” (Lipkovich, 2009). The latter is clearly related to the area of Mariupol, where from the species was first described as *Mus sergii* (Valkh, 1927; Zagorodniuk, Parkhomenko, 2018).

New key data. Over the past 20 years, the species has been found in many places where it was absent before. In the west, the species was found in a number of localities of Transcarpathia (Barkaszi, Zagorodniuk, 2018), in the lowland part of Bukovina (Smirnov, 2010), and in 1996–1998 in several localities to the east of the Dnister River, in particular to north to the villages of Torske, Vorulyntsi, and Yuryampil (O. Vikyrchak, pers. comm.). In Vinnytsia Oblast, in addition to the previously published data (Zagorodniuk, Berezovsky, 1994), 5 new locations of occurrence were found, the northernmost of which is Korzhivka, Nemyrivsky Raion (November 2005: Matviychuk et al.,

2015). In Cherkassy Oblast, the species was recorded in the Kaniv Reserve (Ruzhilenko, 2005), near Myronivka (own data, October 2008). In Kyiv Oblast, the species was reported from Deremezna, Obukhov Raion (February 2015, D. Komarovsky, pers. comm.). The species has also become common in Kharkiv Oblast and in the neighbouring areas of Belgorod Oblast, Russia (Tokarsky et al., 2011), as well as in a number of new localities in Luhansk Oblast (Kondratenko, 1998; Zagorodniuk, Kondratenko, 2001). The species has “recovered” in Rostov Oblast, Russia (Lipkovich, 2005; Mal'tsev et al., 2018), including areas east of the Don. The easternmost records were reported from Migulinskaya, Millerovo, Kamensk-Shakhtinsky, Konstantinovsk, Ust-Donetsk, Rostov, Obukhovka (G. Bakhtadze, S. Litvinenko, V. Stakheev, pers. comm.; Lipkovich, 2005). The model covering data up to 2000–2010 (Tytar et al., 2019) explains sufficiently the range boundaries and the appearance of new findings in the north. The new data (Fig. 6) correspond to range expansion and its alignment by the density of records. The species has also re-appeared in the south, where it had not been recorded for a long time (Polishchuk, 2012).

Estimated pace of expansion. The northern boundary of distribution of *M. spicilegus* is clearly biogeographic and it is determined by climatic factors that distinguish this species from a number of other species considered, e.g. common voles or long-eared bats. The shift of this boundary to the north and east takes place evenly around the entire perimeter: Fig. 6 shows how the boundary shifted compared to data for 2002. We suggest that it is a range pulsation and assuming that the last wave of expansion lasted 30 years (1990–2020), the estimated shift of the species' range is 200 km to the east and 100 km to the west. It equals to an expansion rate of 5–7 km per year to the east and 2–3 km per year to the west. These estimates are similar to those for other species discussed in this paper.

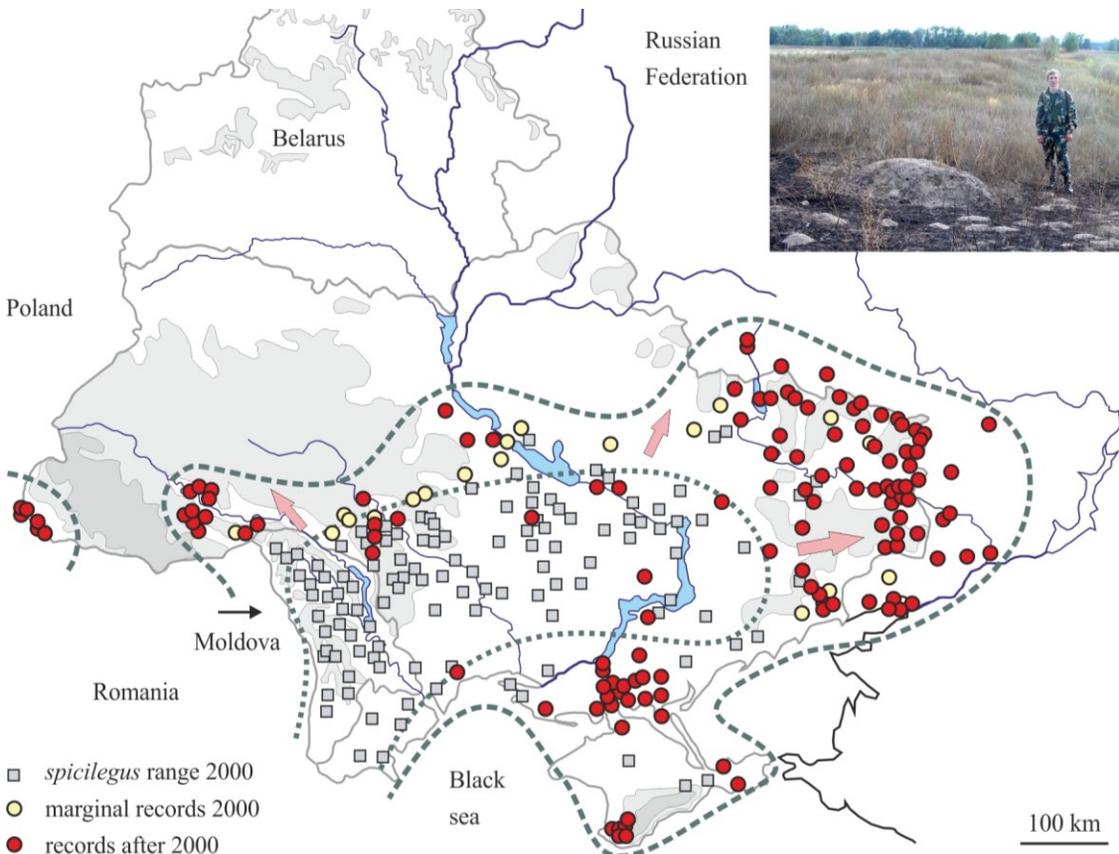


Fig. 6. Distribution of *Mus spicilegus* in Eastern Europe: records before the end of 20th century within the main range (□) and marginal records (○) (Zagorodniuk, 2002); new data after 2000 marked by red circles (●).

Рис. 6. Поширення *Mus spicilegus* у Східній Європі: знахідки до кінця XX ст. в межах основного ареалу (□) та крайові знахідки (○) (Zagorodniuk, 2002); нові дані після 2000 р. позначено червоним (●).

Other species

Three additional polytypic complexes also demonstrate signs of expansions.

Superspecies *Spalax zemni-giganteus* (sensu lato). The key object is *Spalax arenarius* (sandy mole rat) distributed in sand dunes of the Lower Dnipro and which has been considered as a derivate of the Podolian mole rat with recognition of conspecificity of *zemni* = *arenarius* (Reshetnyk, 1939; Tsemsh, 1941; Mezhzherin, Lashkova, 2013). We support a different view, namely a hypothesis on the formation of a steppe faunal core in the Lower Dnipro area as a derivate of eastern steppe complexes, particularly of North Caucasian, Dagestanian, and Trans-Volga steppes (Zagorodniuk, 1999). Such a complex, the core of which was named Dnipro Endemic Group, DEG (Zagorodniuk, 2019), comprises five strictly steppe species of mammals with a distribution restricted in the west by the Dnipro River: *Microtus socialis*, *Sylvaemus witherbyi*, *Spermophilus pygmaeus*, *Scirtopoda telum*, and *Spalax arenarius*. The last species is the only one considered here a distinct species, while the others are subspecies of more eastern species. In case of the sandy mole rat, the eastern species would be *S. giganteus* with which it forms a single group “*giganteus*” (Topachevsky, 1969; Korobchenko, Zagorodniuk, 2009). An important step in proving this hypothesis was the recent identification of a subfossil specimen of *Spalax* from Askania Nova as *S. arenarius* (Zagorodniuk, 2019): this fact is in favour of the secondary nature of the current restricted range of *S. arenarius* and its formerly wider eastward distribution in the Azov Region closer to *S. giganteus*.

Superspecies *Sylvaemus sylvaticus* (sensu lato). The species “*Mus sylvaticus*” (s. l.) had been gradually divided for the past 100 years into four species (regarding the studied region), including three “small” species from the group of small “wood” mice, i.e. *Sylvaemus sylvaticus* (s. str.)⁶, *S. uralensis* (= *microps*), *S. witherbyi* (= *arianus*). The last of them has the most recent (since 1997) and most complicated taxonomic history as well as a unique geographical range restricted by coastal regions and the Lower Dnipro area (Zagorodniuk et al., 1997). Based on chorological data, the species was included into the Steppe Faunal Core (Zagorodniuk, 1999), particularly to its central segment which also includes species of DEG (sensu Zagorodniuk, 2019). The uniqueness of the latter is its most recent appearance in the region from the east. The other two species of “wood” mice, i.e. *Sylvaemus sylvaticus* and *S. uralensis* have clearly unstable geographic ranges: the distribution pattern of *S. uralensis* suggests an origin from two centres — a southwest (Carpathian–Balkan) and an eastern (Caucasian and Trans-Volga). The range of *S. sylvaticus* (s. str.) also has unstable boundaries that do not correspond to limits of biogeographic zones (somewhat similar to that of *Neomys anomalus* and *Terricola subterraneus*). Thus, these two species are currently in the process of dispersal and the zone of their sympatry is expected to increase further. In the same time, *S. witherbyi* is strictly parapatric to *S. sylvaticus* (s. str.), which was noted earlier (Zagorodniuk et al., 1997 and others), i.e. these two species are antagonistic.

Superspecies *Capreolus capreolus* (sensu lato). There are two hypotheses regarding the presence of *Capreolus pygargus* in the fauna of the Middle Dnipro Region: 1) expansion of the Siberian roe deer into the range of the European roe deer from the Don Region, 2) *C. capreolus* s. l. is a transitional species having the ranges of western small forms (field type) and introduced eastern large forms (Siberian roe deer) merged. We argue that the division of roe deer into two species is mostly determined by economic interests, particularly by issues of evaluation of trophy antlers (Zagorodniuk, 2002 d). Even despite their quasi-specific status it is important to notice that the described by A. Brauner (1915) Siberian roe deer specimens from the Samara forest exactly correspond to the Siberian form based on the recognised morphological criteria (Zagorodniuk, 2002 d), which was also confirmed by studies of mitochondrial and nuclear DNA (Danilkin et al., 2017). However, views on such sporadic distribution of the species are incorrect. All of the studied samples of roe deer from Luhansk Oblast and even so from the Donets Ridge (n = 12) turned out to be significantly larger than specimens from the Middle Dnipro Region, Podillia, and western Ukraine and they do not overlap by means of craniometrical characters and dimensions of antlers. Therefore, we suggest the presence of a continuous strip of expansion of *C. pygargus* from the Don to the Dnipro River.

⁶ Due to problems with using the name, a neotype of this form was designated in 1993 (Zagorodniuk, 1993).

Discussion

Several mammal species demonstrate significant range dynamics. These are not only representatives of the macrofauna, which range dynamics can be substantially high (Sokur, 1961; Zagorodniuk, 2014), but also small mammals (Zagorodniuk, 2009 *a*; Barkaszi, 2018), even moles (Korobchenko, 2009). Reconstructions revealed significant changes of geographic ranges in such steppe species as lemmings and ground squirrels. Range dynamics were also revealed in forest-dwelling rodents. Facts of expansion of the golden jackal were reported as well. Such expansions normally concern species that have little common with the indigenous ones.

However, anthropogenic factors had their influence and expansions of numerous species that were normally allopatric have started. Data on close species are often restricted to recent materials and the absence of reliable criteria for their discrimination is a snag in analysis of old facts, specimens, and descriptions. Therefore, every new reconstruction is of high value and can resolve key issues in the triad of evolutionary relationships between close species such as issues of sympatry/allopatry, hybridisation/isolation, ecomorphology/competition (Zagorodniuk, 2011).

The fauna changes and its dynamics is a normal state. The concept of conservation of the past manifested in ideas of the Red Data Book as well as the issues of invasive species manifested in programmes to restrict their part in natural complexes should not be antipodes but supplement each other and form a basis for biota monitoring programmes.

The analysis conducted in the paper showed a significant distribution of the phenomenon of expansion and that such expansions lead or should lead to further ecomorphological or biotopic differentiation of close species. The main directions of expansion range from northeast to northwest, which is determined by the presence of “donor centres” such as the Balkan-Pannonian region and the North Caucasus. The velocity of current expansions of the considered here species vary from 30 to 150 km per decade, while the expansions themselves, obviously, are cyclical and related to climatic events and they have already taken place at least in a part of cases.

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