European Journal of Ecology, 9.1, 2023, pp. 70-85

LEAPING ON URBAN ISLANDS: FURTHER SUMMER AND WINTER RANGE EXPANSION OF EUROPEAN BAT SPECIES IN UKRAINE

Anton Vlaschenko[1,2,3,6*], Vitalii Hukov[1,2,3], Olha Timofieieva[1,4], Marharyta Moiseienko[1,4,7], Anastasia Domanska[1,5], Oleksandr Zinenko[3], Alona Prylutska[1,2]

1- Bat Rehabilitation Center of Feldman Ecopark, 62340 Lesnoye, Kharkiv Region, Ukraine
2- Ukrainian Independent Ecology Institute, Plekhanov st. 40 61001 Kharkiv, Ukraine
3- The Museum of Nature, School of Biology, V.N. Karazin Kharkiv National University, Svobody sq. 4, 61077 Kharkiv, Ukraine
4- Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 7, 30-387, Kraków, Poland
5- Center of Clinical Veterinary, Alchevskih st. 38, Kharkiv, Ukraine
6- H.S. Skovoroda Kharkiv National Pedagogical University, Institute of Natural Sciences, Valentynivska St. 2, Kharkiv, 61168, Ukraine
7 - Institute of Botany, Jagiellonian University, Kraków, Poland, Gronostajowa 3, 30-387 Kraków, Poland
** Corresponding author: anton.vlaschenko@gmail.com Tel.: +380-678031533*

Abstract.
Urban areas are the new types of landscapes that have rapidly developed in the Anthropocene and generally mimic mountains and rock habitats. Such areas attract different vertebrate species that naturally prefer rocky habitats, for example, bats, which are common animal inhabitants of the cities in the Northern Hemisphere. Here we review records of four bat species (Hypsugo savii, Plecotus austriacus, Pipistrellus nathusii *and* P. pygmaeus) *inhabiting human settlements in Ukraine, encompassing the period from 2011 to 2022. Over the last 20 to 30 years, the winter range of* P. nathusii *has shifted 200-300 km north, and now covers all Black Sea coast steppe regions of continental Ukraine. The* Pl. austiacus *range most likely covers the whole territory of Ukraine. We documented the first factual records of* H. savii *in continental Ukraine and the first winter records of* P. pygmaeus *for the country. Our observations clearly demonstrate colonization of newly formed urban landscapes by bats species from different ecological groups. Along with the increase in the number of bat records in urban areas. Therefore, bats, same as some other mammalian species, can be considered beneficiaries of urbanization and urban heat islands.*

Key words: bats, *Hypsugo savii, Plecotus austriacus, Pipistrellus nathusii, Pipistrellus pygmaeus*, *urbanization, range expansion*

Introduction

Urbanization as a shift towards a growing proportion of the human population living in cities (United Nation 2014) forms a unique and new type of landscape called urban areas or city areas. Generally, urban landscapes are the total antagonists to natural (primeval) landscapes. Core urban areas are characterized by dense built-up areas, limited vegetation coverage, specific microclimate and different types of pollutions. On the one hand, urban landscapes are not vast terrains and they cover less than 3% of the terrestrial surface of the Earth (Schneider et al. 2010). On the other hand, urban areas become the centres of significant energy consumption resulting in a warm microclimate; additionally, they form a specific environment mimicking mountain and rocky areas. Urban landscapes contribute to a great loss of biodiversity (McKinney 2008; Grimm et al. 2008) due to fundamental modifications of the land surface and, consequently, loss of naturalness. However, modern urban landscapes also represent novel ecosystems that create opportunities for their repopulation (by native species) or invasion (mainly by cosmopolitan ones). Among the differences between urban and natural landscapes there are three key factors that provide novel opportunities for animal species. These include increased warmth (urban heat islands) (Grimm et al. 2008), plethora of potential shelters and dwelling sites (Sumasgutner et al. 2014; Russo &Ancillotto 2015), and abundance of

food sources for generalists and granivores (Clergeau et al. 1998; Evans et al. 2011). These factors enable changes in the migratory status of animal species or lead to shifts in breeding seasons and numbers of breeding cycles. As a result, species can repopulate urban landscapes and adjust for the new harsh conditions of the Anthropocene to become less sensitive in terms of the sixth mass species extinction.

Bats are one of the vertebrates' groups that might tolerate or even benefit from living in urban conditions (Ancillotto et al. 2015; Russo & Ancillotto 2015; Maksinova et al. 2016). Usually they represent a more diverse group in cities in the Northern Hemisphere compared to other vertebrates (e.g. Jung & Threlfall 2016; Russo & Ancillotto 2015). This is due to several reasons. First, urban landscapes provide multiple opportunities for roosting, which is an important factor in bat life-history. Further, urban heat islands and house heating provide better environmental conditions for bats during hibernation period, namely: presence of unfrozen water-bodies (Zahn & Kriner, 2014; Mass et al. 2022) and stable above-zero temperatures in the hibernacula (Russo & Ancillotto, 2015; Vlaschenko et al. 2019). However, many other environmental features of urban landscapes, such as light, air, and water pollution, as well as loss of natural vegetation provide an undoubtedly negative impact on bats (Russo & Ancillotto, 2015; Krauel & LeBuhn, 2016). Actually, bats considered to be one of the best bio-indicators, as they are sensitive to human environmental transformations and are more diverse and abundant in natural, primeval habitats (Jones et al. 2009; Russo & Ancillotto, 2015; Russo et al. 2021). Therefore, it is unclear how European bats actually make use of newly created urban landscapes. Do they benefit from these or are urban habitats act as environmental/ecological traps (Russo & Ancillotto, 2015; Vlaschenko et al. 2019; Zuñiga-Palacios et al. 2021)? In addition, the existing data on urbanization of European bats does not equally cover the continent: information from the Eastern Europe is lacking or difficult to reach. And finally, more detailed information on the status, presence and first records of bats in cities' areas is strongly needed for better understanding of their capacity for adjustment to urban areas, as well as for conservation priorities.

Here, we review new records of four bat species inhabiting urban landscapes of Ukraine. This terrain has seen remarkable changes in bats' migratory status and range expansion over the last several decades or even a half century. For example, *Nyctalus noctula,* which used to be a typical long-distance migrant bat species, has now formed numerous winter aggregations in most cities and towns of Eastern Europe (e.g. Strelkov 2002; Rodenko et al. 2014; Godlevska 2015; Kravchenko et al. 2017; Shpak 2018) and has become partly sedentary (Vlaschenko et al. 2020; Kravchenko et al. 2020). Another example is a rapid range expansion of *Pipistrellus kuhlii* s.l., (*P. k. lepidus*, Sachanowicz et al. 2017; Hukov et al. 2020) that has moved from Central Asia and Transcaucasia to Central and Eastern Europe over the last 50-40 years (Strelkov et al. 1985; Sachanowicz et al. 2009; Sachanowicz et al. 2017; Hukov et al. 2020). Further, currently there is an ongoing *Hypsugo savii*'s range expansion from west to east and northeast (Uhrin at al. 2016; Bartonichka et al. 2017). Also, *Pipistrellus nathusii* is a typical long-distance migrant bat species (Steffens et al. 2004) with the longest recorded distance of seasonal movement in Europe of 2200 km (Alcalde et al. 2020). This species is now recorded more frequently during the cold season in human settlements of Central (Sachanowicz et al. 2018) and Eastern Europe (Prylutska & Vlaschenko 2013; Godlevska 2012a; Godlevska 2015) and sometimes even in Northern Europe (Blomberg et al. 2020). Further, well documented is the range expansion of *Plecotus austriacus,* inhabiting both urban and rural landscapes, that shifts northeast in Ukraine (Godlevska 2012a; Manyuk & Lahuta 2018; Zagorodniuk 2019).

This raises a number of questions like – Are these pioneer individuals recorded in new regions just randomly wintering or translocated bats or are they first inhabitants that systematically populate urban landscapes? For example, will these first records of wintering *P. nathusii* in a few decades end up with a mass winter aggregation of this species? What is the role of urban landscapes in changing the migratory status of bats?

Cases of wintering and range expansion for *H. savii* and *P. nathusii* in the last decades are already well described for Central Europe (Uhrin at al. 2016; Sachanowicz et al. 2018). However, the current status of these species in Eastern Europe (especially in Ukraine) remains largely not well presented in the literature (e.g. Sachanowicz et al. 2018) because all recent records have been published in Cyrillic (e.g. Prylutska & Vlaschenko 2013; Godlevska 2012b). Therefore, this paper aims to fill the gap in the data on the current distribution and wintering status and recent records of *H. savii*, *Pl. austriacus, Pipistrellus pygmaeus* and *P. nathusii* in urban and rural

landscapes in Ukraine (2011-2022 years) based on records made by The Bat Rehabilitation Center of Feldman Ecopark as well as on the data previously published in non-English language sources.

Materials and methods

The data for this publication were collected by the Bat Rehabilitation Center of Feldman Ecopark (BRC-FE), which is the premier organization for rescue and rehabilitation of bats in Ukraine that is gathering data about bat distribution (e.g. Vlaschenko and Prylutska 2018, Hukov et al. 2020). Citizens' reports of found bats (alive or deceased) were received by the contact-centre of BRC-FE, and the animals which could not be released immediately were brought to the BRC-FE. For all findings (both factual observations and correspondence), location, date and details of the finding were recorded (e.g. Hukov et al. 2020; Kravchenko et al. 2017).

For this paper we summarised three types of records made for four bat species in Ukraine over the period from 2011 to January 2022: (i) factual records, bats that were delivered to the BRC-FE and examined by specialists; (ii) correspondence records, bats that were identified by picture; and (iii) published records. We summarised all-year-round records for two resident species (*H. savii* and *Pl. austriacus*) and for two migratory species (*P. nathusii* and *P. pygmaeus*) for hibernation period only. For this paper we extended winter season to include the period from the beginning of November till the end of March.

Factual records of bats

Bats delivered to the BRC-FE had their sex, age category, reproductive status, forearm length (accuracy 0.1 mm) and body mass (accuracy 0.1 g) recorded and were subsequently banded according to the protocol described in Vlaschenko et al. (2020). For details of the methods used for age category classification see Kravchenko et al. (2017). The BRC-FE cared for bats that were delivered during the winter, and in spring those animals were released to the wild. Individuals with signs of injuries were examined by a veterinarian and received proper treatment. Bats that were not capable of flying after treatment, were left at the BRC-FE for life-long care and rehabilitation.

Correspondence records of bats

When a bat was not delivered to the BRC-FE, its species and sex (if possible) were determined from a picture made by a recorder (Prylutska & Vlaschenko 2013). Usually, recorders could be asked to provide any required details or additional pictures to enable an exact identification of the species. The exact species identification was based on a variety of external parameters (e.g. fur colour, size and shape of ears and tragus, etc.) (Dietz & Kiefer 2014) and the relative body size of a bat (pictures made near ruler). The final database includes only those cases where the identified bat species did not raise any doubts.

Published records

All published records of focal bat species, to the best of our knowledge, have been reviewed (Godlevska 2012a; Godlevska 2012b; Godlevska 2015; Godlevska et al. 2018; Manyuk & Lahuta 2018; Panchenko & Godlevska 2018; Zagorodniuk 2019) and data on winter records of *P. nathusii* were added to the final database. An additional table with all known published winter records of *P. nathusii* is presented in Appendix. Published records of *Pl. austiacus* are not included here as these are well presented in a recent review on *Pl. austiacus* distribution in Ukraine (Zagorodniuk 2019).

Genetic analysis

Wing membrane biopsies were obtained from *P. pygmaeus* from Kharkiv (#5 in Table 1). Two wing membrane biopsy samples were taken from captured animal using a sterile disposable 4-mm diameter biopsy punch; one biopsy sample was taken from each plagiopatagium avoiding puncturing major blood vessels (Worthington Wilmer & Barratt 1996). All wing membrane biopsies were stored in 96% ethanol solution at -20°C until genomic DNA extraction. Total genomic DNA was extracted from one of the biopsy samples according to the Mammalian Genomic DNA Miniprep Kit (GenElute™) protocol. The eluted DNA was then stored at -20°C until PCR amplification. Primer pair BatL5310 (CCTACTCRGCCATTTTACCTATG) and R6036R (ACTTCTGGGTGTCCAAAGAATCA) (Robins et al. 2007) were used to amplify a 702 bp fragment size of COI mitochondrial gene. PCR amplification was carried out in 12.5 µL reaction volume containing up to 5 µL DNA extract, 5x HOT FIREPol Blend Master Mix Ready to Load (Solis BioDyne, Estonia), and 0.25 µM of each primer, and filled up to final volume with water. PCRs were performed at the following temperature profile: pre-denaturation 94 °C for 2 min; followed by 35 cycles of 94 °C for 30 s, 60 °C for 30 s, 68 °C for 1 min and final extension at 68°C for 5 min. Se-

quencing was performed by Macrogen Europe (Amsterdam, The Netherlands) using the forward primer BatL5310. The sequence were then checked and trimmed using Chromas software (Chromas, Technelysium Pty Ltd). Then sequence similarity search and evaluation of the degree of homology was performed using the online BLAST tool.

Results

General findings

In total, 66 records of four focal bat species (*P. nathusii* n=15, *P. pygmaeus* n=3, *H. savii* n=2, and *Pl. austriacus* n=46) (Fig. 1) from 40 settlements in Ukraine made over the last 10-year period 2011-2022 were summarized. The complete list of records for each species indicating numbers of bats of each sex is provided in the Appendix. The geographical distribution of the records on the territory of Ukraine is shown in Figures 2 and 3.

Records of *P. nathusii* and *P. pygmaeus* in winter season

Wintering individuals of *P. nathusii* were recorded mostly (13 out of 15 records) in the settlements in southern Ukraine (Fig. 2; Tab. S2). One record originated from the north-western region of Ukraine (record 4, Lutsk, Fig. 2) (Godlevska 2015) and one more single record (record 5, Fig. 2) was from the region located 100 km north from southern Ukrainian cities where the most of the records were made (Fig. 2). Both these records were made in mid or late March, which may possibly indicate the beginning of the spring migration. However, most records were made over the calendar winter, i.e. from December to February (11 records). All sexed individuals of *P. nathusii* were males (7 records). Two individuals in our records were found inside buildings and one more – outside, on the ground in a city.

a

b

c

Figure 1: Pictures of some individuals of recorded bat species in Ukraine: a – *Pl. austriacus*, Kharkiv city, February 9, 2019; b - *P. pygmaeus*, Kharkiv city, January 19, 2021; c - *H. savii*, Uzhhorod city, February 9, 2020.

Table 1: Numbers of records of four focal bat species (reviewed in this paper) collected by different methods in Ukraine in 2011-2022

Type of record	*P. nathusii* Hib (F/M/Un)	*Pl. austriacus* (F/M/Un)	*H. savii* (F/M/Un)	*P. pygmaeus* Hib (F/M/Un)
Factual	-/1/-	7/9/-	-/3/-	2/1/-
Correspondence	-/1/2	4/2/5	-/-/-	-/-/-
Published	2/5/4	21/12/25	-/-/-	-/-/-
Total individuals records	 2/7/6 2/7/6	 32/23/30 19/18/17	 -/3/- -/3/-	 2/1/- 2/1/-

* Hib – recorded in the hibernation period; F – females, M – males, Un – sex not determined.

Two wintering individuals of *P. pygmaeus* were found during the same winter period (2020-2021) but in completely different parts of Ukraine: in the south – in Kherson (a female), and the north-east – in Kharkiv (a male) (Fig. 2). The *P. pygmaeus* individual from Kherson was found on the ground in the city. The individual from Kharkiv was found inside a building near a park after it had flown inside. The third recorded *P. pygmaeus* was in a group of wintering *P. kuhlii* (96 individuals) and *N. noctula* (1 individual) in a building crevice under a window frame in Poltava region (in Velyka Bahachka).

Year-round records of *H. savii* and *Pl. austriacus*

In winter season *Hypsugo savii* was found in the most western Ukrainian city – Uzhgorod – and 27 km northeast from it – in Mukachevo (Fig. 2). One of the individuals was found outside on the ground in Uzhgorod. Year-round records of *Pl. austriacus* cover the whole territory of Ukraine (Fig. 3) with equal sex ratio for sexed individuals (Table 1). Records in stairwells inside multi-story buildings were the most common (n = 13). One more record was from a private house. One individual was trapped on flypaper in a stairwell of a multi-story building (it is the first record of a bat trapped in such a way for Ukraine).

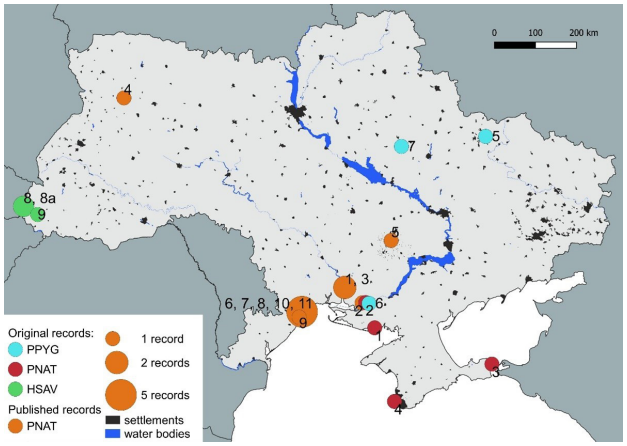

Figure 2: A map of Ukraine showing distribution of records of *H. savii* (HSAV, green dot), and winter records of *P. nathusii* (PNAT, red and orange dots) and *P. pygmaeus* (PPYG, cyan dots) in Ukraine (2011-2022).

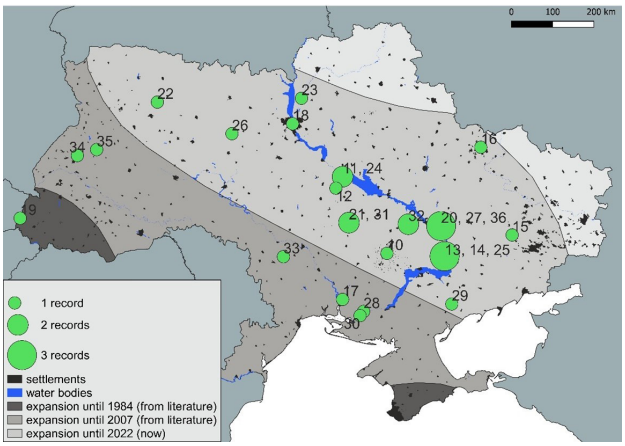

Figure 3: A map of Ukraine showing distribution of records of *Pl. austiacus* presented in this paper, and the already known margins of the species range in the country.

Confirmation of species status by genetic analysis

Since two criptic species *P. pygmaeus* and *Pipistrellus pipistrellus* (Schreber, 1774) are potentially sympathric in some parts of their range, we have analyzed DNA barcoding sequences of the specimen from Kharkiv. We have obtained *P. pygmaeus* sequence and uploaded it to the GenBank (accession number ON797423). BLAST has found our sequence to be most similar (99.70% of identity) to the sequence of *P. pygmaeus* voucher ZMMU S-167243 (accession numbers JF443085) originated from Volgograd, Russian Federation.

Discussion

Our results present new evidence, confirmed by molecular identification, of further urbanization patterns of common European bats species. Here we show that *Pl. austiacus* range already covers all the territory of Ukraine (moving from west to east), and all new records were made in human settlements. As it has already been predicted for *H. savii* (Uhrin et al. 2016), this species now undergoes range expansion to the east and we recorded the first individuals in one of the western Ukrainian cities. Records of long-distance migrant bat species in winter time in cities and towns suggest shifting of the winter range or possible start of formation of the local sedentary population. In the case of *P. nathusii*, winter-time records were made in the settlements all over the Black Sea coast steppe regions of continental Ukraine, and one isolated individual was recorded in a city in the north-western Ukraine (Godlevska 2015). The most extraordinary records presented in this paper are records of wintering individuals of *P. pygmaeus* (also in urban areas), not only in the southern but also in the north-eastern part of Ukraine. *Pipistrellus pygmaeus* has always been evaluated as an extremely long-distance migrant (in the Eastern part of the species range), for years there have been no evidence that this species may stay for hibernation in the breeding part of the range. Finally, we demonstrate the process of utilization of urban landscape by bats with different life-histories both for breeding and hibernation in the east of Europe. Possibly, bats can follow the landscape changes, and may benefit from inhabiting urban areas. While urban areas may offer more opportunities for human observers to detect a bat species. However, the presence of bats in cities does not necessarily reflect their true distribution and abundance in natural habitats. Thus, urban areas may also function as inhabited islands in the wider range of bat species, support isolated bat populations.

Focal bat species status and life-history features

Of the four focal bat species reviewed in this paper, two (*Pl. austiacus* and *H. savii*) belong to resident species, as they do not make long-distance migrations between breeding and winter areas. *Plecotus austriacus* is a quite common bat species in the territory of Ukraine, it is widespread in the western (Buchko et al. 2010), south-western and southern regions (Godlevska et al. 2012) of the country (Zagorodniuk 2019). Most of bat records are associated with human settlements (Zagorodniuk 2019), however in the southern region bats are rather often recorded in abandoned mines as well, where even breeding colonies were recorded (Godlevska et al. 2012). Since 2009, there have been records of this species in the central (Bilushenko 2009; Godlevska et al. 2016a; Manyuk & Lahuta, 2017; Godlevska & Rebrov, 2018), and even northern parts of Ukraine (Godlevskaya 2012; Godlevska et al. 2016b; Zagorodniuk 2019). Finally, taking into account new records presented here, it can be concluded that *Pl. austiacus* has extended their species range all over the country. Up to now, the only regions of Ukraine where no records of this species have been made are the most northern and eastern parts of the country (Fig. 3). *Pl. austiacus* may possibly already inhabit the regions in the Russian Federation bordering eastern Ukraine.

The second resident species in our list is *H. savii*. Local population of this species inhabits a single location in Crimea, that for decades has been known as the only one in Ukraine (Abelentsev et al. 1956; Godlevskaya et al. 2009). That population is isolated by hundreds of kilometres from the nearest known populations in Central Europe; and by Strait of Kerch from the Caucasus's population (Juste & Paunović 2016). This species was recorded using the acoustic method in several locations of western Ukraine in the period from 2009 to 2013 (Uhrin et al. 2016). Our present data finally confirms the presence of *H. savii* in that region of Ukraine. However, acoustic identification has recently revealed *H. savii* in some locations in the south-eastern part of the country in the coast of the Azov Sea (Volokh et al. 2021). These records are located nearly a thousand km away from the known records of *H. savii* in the western part of Ukraine, and two hundred km away from the above-said colony in Crimea. These records may be ex-

plained by the range expansion of other populations of *H. savii* from Caucasus or Crimea. However, more plausible reason could be a probable misidentification of the species using the acoustic method (Volokh et al. 2021). This information should be verified by factual records or disproved.

Bat species that were recorded in winter time – *P. nathusii* and *P. pygmaeus* – are typical long-distance migratory species. Strong migratory behaviour is well known for *P. nathusii* (Hutterer et al. 2005; Steffens et al. 2004). Previously, maximum translocations of 1900 km were recorded (Hutterer et al. 2005), and this was recently updated up to 2200 km (Alcalde et al. 2020), both were from one of the Baltic states (Latvia) to the south of Europe. Due to this long-distance migratory pattern, *P. nathusii* is one of the migratory bat species with the northernmost distribution in Europe (Bogdarina & Strelkov 2003; Juste & Paunović 2016). The known wintering areas of *P. nathusii* were Mediterranean countries, Balkans and Central Europe on the West (Dietz & Kiefer 2014; Sachanowicz et al. 2018) and Caucasus on the East (Rakhmatulina 2005). There are previously reported records of wintering of *P. nathusii* in the Ukrainian Transcarpathian region (Abelentsev et al. 1956) which climatic conditions are similar to those of Central European countries (Hungary, Slovakia, etc.). In Ukraine, during the breeding period, this species is common or even ubiquitous over the whole territory (e.g. Gashchak et al. 2013; Godlevska & Rebrov 2018; Kovalov et al. 2019) except south steppe regions, to which it only migrates twice a year. Summarizing the above, the winter range of *P. nathusii* in Ukraine now covers urban areas in all Black Sea coast steppe regions; that is 400-500 km further north from the previously known wintering areas (e.g. Transcaucasia, Rakhmatulina 2005). Another region of winter range expansion is the north-western part of Ukraine (Godlevska 2015). That region borders Poland where the number of winter records of *P. nathusii* is tending to increase as well (Sachanowicz et al. 2018). Recently, an acoustic record *P. nathusii* was made during the winter season even in the north of Europe – in Finland (Blomberg et al. 2020). However, the similarity of calls of *P. nathusii* and *P. kuhlii* (Zsebok et al. 2012) leaves a chance that also *P. kuhlii* could have been recorded that far north (Blomberg et al. 2020).

By contrast to *P. nathusii,* the migratory status of *P. pygmaeus* until now was not just as clear. *Pipistrellus pygmaeus* was separated from *Pipistrellus pipistrellus s.s.* in the end of 1990-ies (Barlow & Jones 1999), and the main banding efforts had been done before this taxonomic separation and in the regions cohabitated by these two species (Steffens et al. 2004; Hutterer et al. 2005). However, in terms of the eastern part of Europe *P. pipistrellus s.l.* (before the separation into two species) was previously evaluated as a migratory species that had never wintered in the territories spreading from Baltic states on the north through European Russia and Belarus in the middle to Ukraine on the south, except Transcarpathia (Strelkov 1969, 1999). Moreover, multiple surveys that were performed in those regions in the period from 2007 to 2020 did not support the presence of *P. pipistrellus s.s.* (e.g. Kruskop 2007; Gukasova et al. 2011; Vlaschenko et al. 2016; Dombrovsky et al. 2017; Godlevska & Shpak 2020; Vlaschenko et al. 2021) above 44-45th parallels north. Instead, the breeding range of *P. pygmaeus s.s.* is distributed farther north in Russia and Belarus (Strelkov 1999; Vlaschenko et al. 2016), and is also common in the northern (Gashchak et al. 2013), central (Godlevska & Rebrov 2018) and eastern parts of Ukraine (Kovalov et al. 2019; Zagorodniuk 2019). The population structure of *P. pygmaeus* s.s. in the breeding part of its range (territories of Belarus, European Russia and Ukraine) is presented almost exclusively by adult females (which is different to summer population structure of *P. nathusii*). Female-biased migration includes the movement to the north for breeding and back, whereby bats spend no longer than 4 to 5 months annually in the north of their range. Records of adult males in the breeding part of the range are extremely rare (Strelkov 1999; Vlaschenko & Gukasova 2010), suggesting the overlap between the mating and the wintering areas. In fact, all individuals of *P. pygmaeus* (adult-females and this-year-born individuals) usually just leave the breeding part of the range until mid-September. Due to the extreme extraordinariness of the case of recording, we used genetic methods for species identification. One of our first hypotheses was that it could have been *P. pipistrellus s.s.* transported north with cargo, e.g. from Caucasus (see the case with *Tadarida teneotis*, Prylutska et al. 2020). However, strong evidence of genetic identification of *P. pygmaeus s.s.* together with two additional records of this species in cities in other regions of Ukraine, have convinced us that this is indeed the first time individuals of this species stay for wintering in the Eastern part of breeding range. Of note is one previously published record of (possi-

bly) *P. pipistrellus s.l.,* made in the winter season in the Azov sea coast area of Ukraine (Mariupol) (Zagorodniuk 2018). However, that record was based on identification of *P. pygmaeus* by a photo. A group of bats were found during renovation of windows and there was one a little darkish individual among *P. kuhlii* group that looked similar to *P. pipistrellus s.l.* and which was identified as such. But not even this one individual, but the whole group's identification was performed by a photo (Zagorodniuk 2018). Taking into account a high variability in colour and size known for *P. kuhlii* (Hukov et al. 2020), a misidentification is highly likely.

Utilization of urban landscape by bats with different life-history strategies

Out of the 28-29 bat species of Ukrainian fauna (Vlaschenko et al. 2021), only two (*P. kuhlii* and *E. serotinus*) are completely tolerant to urban environment and may have year-round activity within the borders of cities and towns (Kravchenko et al. 2017; Bilushenko 2013; Hukov et al. 2020). We hypothesize that three other species (*Pl. austriacus*, *H. savii* and *P. pipistrellus*) also tolerate urban areas, with two of them found in the western part of Ukraine and in Crimea. The western margin of the *P. pipistrellus* range in Ukraine is not studied yet. However, further research into bat ecology in Ukrainian cities is needed to prove this hypothesis. There is a number of bat species that are tolerate urban environment and are common in urban forests and outskirts in summer time, e.g. *Myotis daubentonii*, *M. dasycneme*, *P. nathusii*, *P. pygmaeus*, *Pl. auritus* (Bashta 2010; Vlaschenko et al. 2012, 2021). Another two species avoid urbanized areas in Ukraine during the breeding season, but are common (*V. murinus*) or even ubiquitous (*N. noctula*) there during autumn swarming and hibernation (Kravchenko et al. 2017; Vlaschenko et al. 2020). According to the migratory status of Ukrainian bats, two forest-dwelling species (*N. lasiopterus* and *N. leisleri*) belong to strong long-distance migratory bats, and no record in the country was available of any individual during the winter time (except in the territory of Crimea). Also *P. pygmaeus* was included in this group, prior to the novel data presented here. In summary, two urban-tolerant resident species and two wintering bat species have now been added to the list of bat fauna of Ukrainian cities. However, coming back to the question we raised in the beginning of this paper – do these records mean just marginal individuals or is it a systematic repopulation of urban landscapes?

As to Kharkiv (the most well-studied and monitored in regard to bats city in Eastern Europe), we noticed that every 30 to 20 years a new bat species appear in the city area as a novel resident species or the one previously migratory one that became sedentary. We can see how the bat fauna of the Kharkiv city area has become richer within 90 to 70 years of monitoring. For example, in 1930 there was the first record of *E. serotinus*, later – the first winter record of *N. noctula* (1986 year), further – a record of *P. kuhlii* (2000 year) (Vlaschenko 2011) and currently there are records of *Pl. austriacus* and *P. pygmaeus*. There are two species (*N. noctula* and *P. kuhlii*) that demonstrated a clear pattern of populating urban areas (as seen on the example of Kharkiv) from a marginal individual at the begging to a common or even ubiquitous occurrence five or ten years later (e.g. Kravchenko et al. 2020; Sachanowicz et al. 2009; Hukov et al. 2020). By contrast, *V. murinus* has been for years known in Eastern Europe as a sporadic hibernating species (Strelkov 2001; Vlaschenko 2011; Godlevska 2013, and it has not become an ubiquitous hibernating species (Kravchenko et al., 2017). In winter time, *V. murinus* is a common species in cities of Ukraine, but nearly always it is the fourth abundant species after *N. noctula*, *E. serotinus* and *P. kuhlii* (e.g. Godlevska 2015; Kravchenko et al. 2017). Finally, two main scenarios of utilization of modern urban landscapes in Eastern Europe by bats can be described. The first one is a rapid increase in the number of individuals of the species after arrival of pioneer individuals, with formation of ubiquitous sedentary populations (as in case of *P. kuhlii*) or hibernating populations later shifting to sedentary (as in case of *N. noctula*) (Kravchenko et al. 2020; Hukov et al. 2020; Vlaschenko et al. 2020). The second scenario includes the presence of a small number of hibernating individuals while the main part of the population is migratory (as in case of *V. murinus*). Based on the species' natural history, *Pl. austriacus* and *H. savii* may possibly become common (not ubiquitous) resident species in human settlements in Ukraine. *Plecotus austriacus* will likely move to farther human settlements, towards the regions of European Russia, with their subsequent colonization. In contrast, the rate of expansion and the future eastern border of *H. savii* range are difficult to predict. We can speculate that future scenarios of wintering of *P. nathusii* and *P. pygmaeus* in urban areas may become more similar to those of *V. murinus* rather than *N.*

noctula. *Pipistrellus nathusii* and *P. pygmaeus* will most likely winter in urban areas as single individuals rather than forming ubiquitous hibernation aggregations and sedentary populations.

Conclusions

Here we summed up the records of four European bat species in the territory of Ukraine made over the last ten years. The cases of four focal species (*H. savii*, *Pl. austriacus, P. nathusii*, *P. pygmaeus*) suggest that bat species with different life histories and ecological particularities may benefit from utilization of urban landscapes. These new types of habitat provide opportunities both for bat hibernation and breeding. Finally, we interpret these cases as a part of an extensive adjustment process of bats to new landscapes (ecosystems) in the Anthropocene. We also hypothesize that urban areas are indeed the main arena of bat range shifts because of urbanization. However, little is known about bat range shifting in their natural habitats and how it is connected to the pattern seen in urbanized areas.

The urbanization of bat fauna and range expansion of urbanized species should be viewed as an outcome of two simultaneous and not mutually excluding processes. First is the colonization process, which should be viewed as the result of elevated survival rates in the marginal populations and favorable conditions in newly colonized areas within the individual activity range. Second is the outcome of emerging adjustment via selection favoring urban-adapted individuals. The second process is of great importance to forecast further changes in faunas, including the abrupt spread of the species that switch their habitat preferences. Currently, we can not disentangle the mutual importance of these two processes in the observed expansion of bat species ranges, however, speeding up expansion speed and abrupt character of emergence of a new city species are in favor of the hypothesis of strong importance of evolutionary mechanisms in range expansion.

Research ethics: The Bat Rehabilitation Center of Feldman Ecopark works under the general permission of the Kharkiv Oblast Authority of Ecology and Natural Resources.

Acknowledgements: The authors would like to thank people who rescued bats in different settlements: Gryhoriy Fomichov (Uzhhorod city), Tetyana Granat (Dnipro city), Olesya Kulyk (Zaporizhzhia city), Ksenia Lisnychuk (Kropyvnytskyi city) and others. We are also grateful to a large number of our colleagues, employers, volunteers, and alumni for putting up with the exhausting daily routine at the Bat Rehabilitation Center of Feldman Ecopark: Dr Kseniia Kravchenko, Olena Rodenko, Viktor Kovalov, Olena Holovchenko, Ihor Tovstukha, Maryna Yerofeeva, Alona Shulenko, Andriy Schnakenberg, Mykhailo Shlakhter, Natalis Shanuk, Andrey Pryhodko, Tatiana Yurieva, and all the others. We are very grateful to Dr Olena Tkachenko for correction of the English language.

This manuscript was finalised during the time of Russian-Ukrainian war. The authors would like to thank the Armed Forces of Ukraine and the People of Ukraine for their strong resistance that allow us to finish this manuscript.

Author contributions: AV, VH, OT, MM, AD, AP worked with bats in different years, OZ and VH provided the genetic analyses, VH did the visualisation, AV and AP provided the general management of the project, AV completed the first version of the manuscript, all authors wrote, contributed and approved the final version of the paper.

Research funding: The Bat Rehabilitation Center of Feldman Ecopark was funded mostly by the International Charity Foundation “Oleksandr Feldman Foundation”.

Conflict of interest statement: The authors declare that they have no competing interests.

References

Abelentsev, V.I. & Pidoplichko, I.G. (1956) The Order of Insectivores - Insectivora. Fauna of Ukraine. Volume 1: Mammals. Number 1. The Academy of Sciences of URSR Press, Kyiv. [in Ukrainian].

Ancillotto, L., Tomassini, A. & Russo, D. (2015) The fancy city life: Kuhl’s pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. Wildlife Research. 42, 598-606. DOI: https://doi.org/10.1071/WR15003

Alcalde, J.T., Jiménez, M., Brila, I., Vintulis, V., Voigt, C.C., Petersons, G. (2020) Transcontinental 2200 km migration of a Nathusius’ pipistrelle (*Pipistrellus nathusii*) across Europe. Mammalia. 85, 161–163. DOI: https://doi.org/10.1515/mammalia-2020-0019

Barlow, K.E. & Jones, G. (1999) Roosts, echolocation calls and wing morphology of two phonic

types of *Pipistrellus pipistrellus*. Zeitschrift fur Sdugetierkunde. 64, 257–268.

Bartonicka, T. Benda, P. & Juda, J. (2017) First findings and phenology of *Hypsugo savii* in the Děčín District, Czech Republic (Chiroptera: Vespertilionidae). Lynx, n. s. (Praha). 48, 5–14. [in Check with English summary]. DOI: https://doi.org/10.2478/lynx-2017-0001

Bashta, A.-T. (2010) Characteristics of bat community of the city of Lviv (Ukraine): species composition, spatial and seasonal distribution. Studia Biologica. 3, 109–124. [in Ukrainian with English summary].

Bilushenko, A.A. (2009) The first record of the grey long-eared bat, *Plecotus austriacus* (Chiroptera, Vespertilionidae), in Cherkasy region. Vestnik Zoologii 43, 120. [In Russian]

Bilushenko, A.A. (2013) The current status of Kuhl's Pipistrelle, *Pipistrellus kuhlii* (Chiroptera, Vespertilionidae), in the central forest-steppe of Ukraine. Vestnik Zoologii. 47, 343–349. DOI: https://doi.org/10.2478/vzoo-2013-0036

Blomberg, A.S., Vasko, V., Salonen, S., Pētersons, G., Lilley, T.M. (2020) First record of a Nathusius' pipistrelle (*Pipistrellus nathusii*) overwintering at a latitude above 60°N. Mammalia. 85, 74-78. DOI: https://doi.org/10.1515/mammalia-2020-0019

Bogdarina, S. & Strelkov, P. (2003) Distribution of bats (Chiroptera) in the north of European Russia. Plecotus et al. 6, 7–28. [In Russian with English summary].

Buchko, V. Vlaschenko, A., Kravchenko, K., Sudakova, M., Gukasova, A., Kusnezh, O. (2011) Contribution to bat fauna (Chiroptera) of Galytskiy National Nature Park (Ivano-Frankivsk region). Visnuk of Lviv University. Series: biology. 55, 146-159. [In Ukrainian with English summary].

Clergeau, P., Savard, J.P.L., Mennechez, G., Falardeau, G. (1998) Bird abundance and diversity along an urbanrural gradient: A comparative study between two cities on different continents. Condor. 100, 413-425. DOI: https://doi.org/10.2307/1369707

Dietz, C. & Kiefer, A. (2014). Die Fledermäuse Europas: kennen, bestimmen, schützen. Kosmos, Stuttgart.

Dombrovski, V., Fenchuk, V. & Zhurauliou, D. (2017) The bat fauna (Mammalia, Chiroptera) of Stary Zhaden zakaznik, southern Belarus. Proceedings of the Theriological School. 15, 3–9. DOI: https://doi.org/10.15407/ptt2017.15.003

Gashchak, S.P., Vlaschenko, A.S., Naglov, A.V., Kravchenko, K.A., Prylutska, A.S (2013) Bat fauna of the Exclusion Zone in concern of assessment of environmental value of its areas. Problems of Chernobyl Exclusion Zone. 11, 56–78. [in Russian with English summary].

Godlevska, L. (2012a) Expansion of *Plecotus austriacus* (Chiroptera, Vespertilionidae) Range: First Records in the Kyiv Oblast (Ukraine). Vestnik zoologii. 46, 88. DOI: https://doi.org/10.15407/pts2018.16.051

Godlevska, L. (2012b) Results of the work of the bat contact-centre (Ukraine). Scientific Notes of Taurida V.I. Vernadsky National University. Series: Biology, chemistry. 25, 12-20. [in Russian].

Godlevska, L.V. (2013) New *Vespertilio murinus* (Chiroptera) Winter Records. An Indication of Expansion of the Species' Winter Range? Vestnik Zoologii. 47, 239-244. DOI: https://doi.org/10.2478/vzoo-2013-0023

Godlevska, L. (2014) Northward expansion of the winter range of *Nyctalus noctula* (Chiroptera: Vespertilionidae) in Eastern Europe. Mammalia. 79, 315-324. DOI: https://doi.org /10.1515/mammalia-2013-0178

Godlevska, L. (2015) Results of the Work of the Kyiv Bat Contact-Centre in 2012–2015. Proceedings of the Theriological School. 13, 11–19. [in Ukrainian] DOI: https://doi.org/10.15407/ptt2015.13.011

Godlevska, L. & Shpak, A. (2020) Bats in the collection of the Zoological museum of Belarusian State University. Proceedings of the National Academy of Sciences of Belarus. Biological series. 65, 412–420. [in Russian with English abstract]. DOI: https://doi.org/10.29235/1029-8940-2020-65-4-412-420

Godlevskaya, E.V., Ghazali, M.A. & Postawa, T. (2009) A Current State of Cave Dwelling Bat Species (Mammalia, Chiroptera) of the Crimea. Vestnik zoologii. 43, 253–265. [In Russian with English summary].

Godlevska, L., Ghazali, M. & Tyshchenko, V. (2012) Results of the census of cave-dwelling bats in Podolia and Middle Dniester River region (Ukraine) in 2010–2011. Proceedings of the Theriological School. 11, 89–97. [In Ukrainian]. DOI: https://doi.org/10.15407/ptt2012.11.089

Godlevska, L., Buzunko, P., Rebrov, S., Ghazali, M. (2016a) Underground bat sites of "not-cave" region of Ukraine, on results of 2002–2015.

Visnyk of the Lviv University. Series Biology. 71, 178–189. [In Ukrainian].

Godlevska, L.V., Rebrov, S.V. & Panchenko, P.S. (2016b) New data on bat fauna of Rivne oblast (Ukraine). Zapovidna sprava. 22, 72–77. [In Ukrainian].

Godlevska, L. & Rebrov, S. (2018) Bats of the Left-Bank Dnipro Region in the northern part of Ukraine. Theriologia Ukrainica. 16, 25–50. [In Ukrainian]. DOI: https://doi.org/10.15407/pts2018.16.025

Godlevska, L., Panchenko, P., Rebrov, S., Savchenko, M., Yakovlev, M., Formanyuk, O., Ghazali, M. (2018) Knowledge of the bats on the territory of the Black Sea coast of Ukraine (AR Krim, Mykolayivska, Odeska, Kherson region) In: Materials up to the 4th edition of the Red-data book of Ukraine. Volume. 1. (pp. 196–203). Kyiv: Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine. [In Ukrainian].

Grimm, N.B., Foster, D., Groffman, P., Grove, J.M., Hopkinson, C.S., Nadelhoffer, K.J., et al. (2008) The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. Frontiers in Ecology and the Environment. 6, 264-272. DOI: https://doi.org/10.1890/070147

Gukasova, A., & Vlaschenko, A. (2011) Effectiveness of mist-netting of bats (Chiroptera, Mammalia) during the non-hibernation period in oak forests of Eastern Ukraine. Acta Zoologica Cracoviensia-Series A: Vertebrata. 54, 77-93. DOI: https://doi.org/10.3409/azc.54a_1-2.77-93

Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D., Gaston, K.J. (2011) What makes an urban bird? Global Change Biology. 17, 32-44. DOI: https://doi.org/10.1111/j.1365-2486.2010.02247.x

Hukov, V., Timofieieva, O., Prylutska, A., Rodenko, O., Moiseienko, M. Bohodist, V., et al. (2020) Wintering of an urban bat (*Pipistrellus kuhlii lepidus*) in recently occupied areas. European Journal of Ecology. 6, 102-120. DOI: https://doi.org/10.17161/eurojecol.v6i1.13629

Hutterer, R., Ivanova, T., Meyer-Cords, C., Rodrigues, L. (2005). Bat migrations in Europe: a review of banding data and literature. Bonn: Federal Agency for Nature Conservation.

Jung, K., & Threlfall, C.G. (2016) Urbanization and Its Effects on Bats - A Global Meta-Analysis. In: Voigt, C.C. and Kingston, T. (Eds.). Bats in the Anthropocene: Conservation of Bats in a Changing World (pp. 13-33). Springer, Cham. DOI: https://doi.org/10.1007/978-3-319-25220-9_2

Juste, J. & Paunović, M. (2016) *Hypsugo savii*. The IUCN Red List of Threatened Species 2016: e. T44856A22072380. Available at: DOI: https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T44856A22072380.en. (Accessed on 22 January 2022).

Kovalov, V., Hukov, V. & Rodenko, O. (2019) New record of *Nyctalus lasiopterus* (Schreber, 1780) in Ukraine with a new confirmation of carnivory. North-Western Journal of Zoology. 15, 91-95.

Krauel, J.J. & LeBuhn, G. (2016) Patterns of Bat Distribution and Foraging Activity in a Highly Urbanized Temperate Environment. PLoS ONE. 11, e0168927. DOI: https://doi.org/10.1371/journal.pone.0168927

Kravchenko, K., Vlaschenko, A., Prylutska, A., Rodenko, O., Hukov, V., Shuvaev, V. (2017) Year-round monitoring of bat records in an urban area: Kharkiv (NE Ukraine), 2013, as a case study. Turkish Journal of Zoology 41, 530-548. DOI: https://doi.org/10.3906/zoo-1602-51

Kravchenko, K.A., Vlaschenko, A.S., Lehnert, L.S., Courtiol, A., Voigt, C.C. (2020) Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes. Biology Letters. 16, 20200351. DOI: https://doi.org/10.1098/rsbl.2020.0351

Kruskop, S. V., Borisenko, A. V., Ivanova, N. V., Lim, B. K., Eger, J. L. (2007) Using of DNA barcodes to recover phylogeographical splits among East Palaearctic bats. Molecular and genetic basis for preservation of the Holarctic mammal diversity (pp. 115-121). Materials of the conference. Moscow: KMK Scientific Press.

Manyuk, V. & Lahuta, A. (2018) *Plecotus austriacus* in the valley of the Kilchen river (left bank of the Dnipro), a new stage of expansion to the East. Theriologia Ukrainica. 16, 149–151. [in Ukrainian]. DOI: https://doi.org/10.15407/pts2018.16.149

McKinney, M.L. (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems. 11, 161-176. DOI: https://doi.org/10.1007/s11252-007-0045-4

Mas, M., Flaquer, C., Puig-Montserrat, X., Porres, X., Rebelo, H., López-Baucells, A. (2022) Winter bat activity: The role of wetlands as food and drinking reservoirs under climate change.

The Science of the total environment. 828, 154403. DOI: https://doi.org/10.1016/j.scitotenv.2022.154403

Maxinová, E., Kipson, M., Naďo, L., Hradická, P., Uhrin, M. (2016) Foraging Strategy of Kuhl's Pipistrelle at the Northern Edge of the Species Distribution. Acta Chiropterologica. 18, 215–222. DOI: https://doi.org/10.3161/15081109ACC2016.18.1.012

Panchenko, P., & Godlevska, L. (2018) Data on the bat fauna of the Northern Black Sea Region based on results of the work of bat contact centres. Theriologia Ukrainica. 16, 120-126. [in Ukrainian]. DOI: https://doi.org/10.15407/pts2018.16.120

Paunović, M. & Juste, J. (2016) *Pipistrellus nathusii.* The IUCN Red List of Threatened Species 2016: e.T17316A22132621. Available at: DOI: https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T17316A22132621.en. (Accessed on 22 January 2022).

Prylutska, A.S. & Vlaschenko, A.S. (2013) Materials on bat distribution on the base of results of contact-center in Kharkiv (2008–2012). Biological systems. 5, 532-537.

Prylutska, A., Moiseienko, M., Yerofieieva, M., Hukov, V., Vlaschenko, A. (2020) Northern record for *Tadarida teniotis* (NE Ukraine) far from known species range. Journal of Bat Research & Conservation. 13, 104-108. DOI: https://doi.org/10.14709/BarbJ.13.1.2020.17

Rakhmatulina, I.K. (2005). Bats of Azerbaijan (fauna, ecology, zoogeography). Baku: Institute of Zoology of NAS Azerbaijan.

Robins, J. H., Hingston, M., Matisoo-Smith, E. Ross, H. A. (2007) Identifying *Rattus* species using mitochondrial DNA. Molecular Ecology Notes. 7, 717-729. DOI: https://doi.org/10.1111/j.1471-8286.2007.01752.x

Rodenko, E.E., Kravchenko, K.A., Vlaschenko, A.S., Chepizhnaya, A.J., Suvorova, A.D., Prylutskaya A.S. (2014) The record of *Nyctalus noctula* in winter time in Poltava city (Ukraine). Plecotus et al. 17, 43–51. [in Russian with an abstract in English]

Russo, D. & Ancilotto, L. (2015) Sensitivity of bats to urbanization: a review. Mammalian Biology. 80, 205–212. DOI: https://doi.org/10.1016/j.mambio.2014.10.003

Russo, D., Salinas-Ramos, V.B., Cistrone, L., Smeraldo, S., Bosso, L., Ancillotto, L. (2021) Do We Need to Use Bats as Bioindicators? Biology. 10, 693. DOI: https://doi.org/10.3390/biology10080693

Sachanowicz, K., Wower, A. & Bashta, A. (2009) Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in Central and Eastern Europe. Acta Chiropterologica. 8, 543–548. DOI: https://doi.org/10.3161/1733-5329(2006)8[543:FREOPK]2.0.CO;2

Sachanowicz, K., Piskorski, M. & Tereba, A. (2017) Systematics and taxonomy of *Pipistrellus kuhlii* (Kuhl, 1817) in Central Europe and the Balkans. Zootaxa. 4306, 053–066. DOI: https://doi.org/10.11646/zootaxa.4306.1.2

Sachanowicz, K., Ciechanowski, M., Tryjanowski, P., Kosicki, J.Z. (2018) Wintering range of *Pipistrellus nathusii* (Chiroptera) in Central Europe: has the species extended to the northeast using urban heat islands? Mammalia. 83, 260-271. DOI: https://doi.org/10.1515/mammalia-2018-0014

Schneider, A., Friedl, M.A. & Potere, D. (2010) Mapping global urban areas using MODIS 500-m data: new methods and datasets based on 'urban ecoregions. Remote Sensing of Environment. 114, 1733–1746. DOI: https://doi.org/10.1016/j.rse.2010.03.003

Shpak, A. (2018) Hibernating bat species of Belarus: results of the work of the Minsk bat contact centre. Theriologia Ukrainica. 16, 156–162. DOI: https://doi.org/10.15407/pts2018.16.156

Steffens, R., Zöphel, U., Brockmann, D. (2004). 40th Anniversary Bat Marking Centre Dresden — Evaluation of Methods and Overview of Results. Dresden: Saxon State Office for Environment and Geology.

Strelkov, P.P. (1969) Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. Acta Zoologica Cracoviensia. 14, 393–439.

Strelkov, P.P. (1999) Sex ratio in breeding season in adult individuals of long-distant migrant bats (Chiroptera, Vespertilionidae) of Eastern Europe and adjacent territories. Zoologicheskiy zhurnal. 78, 1441–1454. [in Russian with English summary].

Strelkov, P.P. (2000) Seasonal distribution of migratory bat species (Chiroptera, Vespertilionidae) in eastern Europe and adjacent territories: nursing area. Myotis. 37, 7–25.

Strelkov, P.P. (2002) Materials on wintering of migratory bat species (Chiroptera) on the territory of the former USSR and adjacent regions. Part. 2. *Nyctalus noctula*. Plecotus et al. 5, 35–56. [In Russian].

Strelkov, P.P. & Il'in, V. Yu. (1990) Chiropterans (Chiroptera, Vespertilionidae) of the Southern Middle and Low Volga Regions. Proceedings of the Zoological Institute of the SSSR. 225, 42–167. [In Russian].

Strelkov, P.P., Unkurova, V.I. & Medvedeva, G.A. (1985) New data on *Pipistrellus kuhlii* and dynamics of its range in the USSR. Zoologichesky zhurnal. 64, 87-97.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H.W., Gamauf, A. (2014) Hard times in the city attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. Frontiers of Zoology. 11, 13. DOI: https://doi.org/10.1186/1742-9994-11-48

Uhrin, M., Hüttmeir, U., Kipson, M., Estók, P., Sachanowicz K., Bücs, S.L., et al. (2016) Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: a review. Mammal Review. 46, 1-16. DOI: https://doi.org/10.1111/mam.12050

United Nations, Department of Economic and Social Affairs, Population Division (2014) World urbanization prospects: the 2014 revision, highlights (ST/ESA/SER.A/352).

Vlaschenko, A.S. (2011) Research history and list of records of bats (Chiroptera) in the Kharkov Region in the XIX and XX centuries. Plecotus et al. 14, 26-54. [in Russian].

Vlaschenko, A.S. & Gukasova, A. S. (2010) Bat (Chiroptera) fauna and structure of assemblage of projecting protected area "Yaremovskoe" (Kharkov region). Nature reserves in Ukraine. 16, 44-50. [In Russian].

Vlaschenko, A.S. & Plylutska, A.S. (2018) Das Bat Rehabilitation Center des „Feldman Ecoparks", Charkiw, Ukraine. Nyctalus (N.F.) Berlin. 19, 158–161. [in German].

Vlaschenko, A., Kravchenko, K., Prylutska, A., Ivancheva, E., Sitnikova, E., Mishin, A. (2016) Structure of summer bat assemblages in forests in European Russia. Turkish Journal of Zoology. 40, 876-893. DOI: https://doi.org/10.3906/zoo-1508-56

Vlaschenko, A., Kovalov, V., Hukov, V., Kravchenko, K., Rodenko, O. (2019) An example of ecological traps for bats in the urban environment. European Journal of Wildlife Research. 65, 20. DOI: https://doi.org/10.1007/s10344-019-1252-z

Vlaschenko, A.S., Prylutska, A.S., Kravchenko, K., Rodenko, O., Hukov, V., Timofieieva, O., et al. (2020) Regional recaptures of bats (Chiroptera, Vespertilionidae) ringed in Eastern Ukraine. Zoodiversity. 54, 53–66. DOI: https://doi.org/10.15407/zoo2020.01.053

Vlaschenko, A., Yatsiuk, Y., Hukov, V., Prylutska, A., Straka, T. M., Kravchenko, K. (2021) Urban forest preserves local bat species diversity, but not forest dweller specialists—renewed study 65 years later (Kharkiv city, Ukraine). Mammal Research. 66, 615-626. DOI: https://doi.org/10.1007/s13364-021-00580-9

Volokh, A., Gorlov, P., Siokhin, V., Polishchuk, I. (2021) Species diversity of bats (Chiroptera) in the Ukrainian Azov Region and features of their residence by seasons. Theriologia Ukrainica. 20, 24–36. [In Ukrainian with English summary]. DOI: https://doi.org/10.15407/TU2104

Wilmer, W.J., & Barratt, E. (1996) A non-lethal method of tissue sampling for genetic studies of chiropterans. Bat Research News. 37, 1–3.

Zagorodniuk, I. (2018) A game against natural selection: cases of hibernation of migrant bat species in their summering range in Eastern Ukraine. Theriologia Ukrainica. 16, 111-119. DOI: https://doi.org/10.15407/pts2018.16.111

Zagorodniuk, I. (2019) Range dynamics in sibling species: facts and reconstructions for the mammal fauna of Eastern Europe. Theriologia Ukrainica. 18, 20–39. DOI: https://doi.org/10.15407/pts2019.18.020

Zahn, A., & Kriner, E. (2014). Winter foraging activity of Central European Vespertilionid bats. Mammalian Biology. 81, 40–45. DOI: https://doi.org/10.1016/j.mambio.2014.10.005

Zuñiga-Palacios, J., Zuria, I., Castellanos, I., Lara, C., Sánchez-Rojas, G. (2021) What do we know (and need to know) about the role of urban habitats as ecological traps? Systematic review and meta-analysis. The Science of the total environment. 780, 146559. DOI: https://doi.org/10.1016/j.scitotenv.2021.146559

Zsebok, S., Estók, P. & Görföl, T. (2012) Acoustic discrimination of *Pipistrellus kuhlii* and *Pipistrellus nathusii* and its application to assess changes in species distribution. Acta Zoologica Academiae Scientiarum Hungaricae. 58, 199–209.

Appendix

List of new records of *Hypsugo savii* and *Plecotus austriacus* (all year-round), and winter records of *Pipistrellus nathusii* and *P. pygmaeus* in the territory of Ukraine during 2012-2022.

No.	Date	Locality, settlement name	Coordinates	Sex	Age	Details of how the animal(s) was found	Record details
Pipistrellus nathusii							
1	28.12.2012	Skadovsk, Kherson region	46.113869, 32.910852	M	un	inside a building	Correspondence
2	09.01.2018	Kherson	46.619638, 32.583397	M	ad	other	Factual
3	21.02.2014	Kerch	45.3573, 36.4683	un	un	inside a building	Correspondence
4	31.01.2019	Sevastopol	44.6166, 33.5254	un	un	on the ground	Correspondence
Pipistrellus pygmaeus							
5	19.01.2021	Kharkiv	49.999472, 36.224943	M	ad	inside a building, before flying outside	Factual
6	20.01.2021	Oleshky, Kherson region	46.3800, 32.3500	F	ad	on the ground	Factual
7	06.01.2022	Velyka Bahachka, Poltava region	49.5847491 34.5483748	F	sad	under window frame	Factual
Hypsugo savii							
8	7.11.2019	Uzhhorod	48.612255, 22.283197	M	sad	unknown	Factual
8a	09.02.2020	Uzhhorod	48.610801, 22.263625	M	ad	on the ground	Factual
9	25.02.2022	Mukachevo	48.447505, 22.750453	M	un	between window frame	Factual
Plecotus austriacus							
10	31.01.2014	Kryvyi Rih	47.9105, 33.3918	F	un	stairwell of a multi-story building	Correspondence

11	07.10.2015	Cherkasy	49.42190, 32.057468	M	ad	unknown	Factual
12	16.01.2017	Smila, Cherkasy region	49.2277, 31.8522	un	un	stairwell of a multi-story building	Correspondence
13	14.03.2017	Zaporizhzhia	47.8388, 35.1396	un	un	stairwell of a multi-story building	Correspondence
14	11.11.2017	Zaporizhzhia	47.8388, 35.1396	un	un	inside a building	Correspondence
15	09.12.2018	Pokrovsk, Donetsk region	48.281787, 37.184946	F	ad	unknown	Factual
16	09.02.2019	Kharkiv	49.951456, 36.265115	F	sad	stairwell of a multi-story building	Factual
17	06.09.2019	Mykolaiv	46.9750, 31.9946	un	un	unknown	Correspondence
18	17.09.2019	Kyiv	50.363383, 30.463759	F	ad	inside a building	Factual
19	28.09.2019	Uzhhorod	48.6208, 22.2879	M	un	porch of private house	Correspondence
20	03.10.2019	Dnipro	48.4647, 35.0462	F	un	inside a building	Correspondence
21	16.12.2019	Kropyvnytskyi	48.519242, 32.289077	F	sad	unknown	Factual
22	21.12.2019	Kostopil, Kirovohrad region	50.8791, 26.4423	un	un	trapped on flypaper, at the stairwell of a multi-story building	Correspondence
23	12.01.2020	Lutava, Chernihiv region	50.962171, 30.802682	M	un	unknown	Correspondence
24	18.09.2020	Cherkasy	49.430368, 32.082796	M	un	inside a building	Factual
25	28.12.2020	Zaporyzhzha	47.865822, 35.058877	M	ad	stairwell of a multi-story building	Factual
26	08.01.2021	Zhytomyr	50.242769, 28.622711	M	ad	stairwell of a multi-story building	Factual

27	30.01.2021	Dnipro	48.409875, 34.918746	F	ad	inside a building	Factual
28	30.01.2021	Zhovtneve, Kherson region	46.702771, 32.684668	M	sad	inside a building	Factual
29	27.02.2021	Melitopol, Zaporizhzhia region	46.872257, 35.379521	F	ad	stairwell of a multi-story building	Factual
30	18.03.2021	Kherson	46.669682, 32.618573	F	ad	unknown	Factual
31	14.09.2021	Kropyvnytsky	48.5123560, 32.2727995	F	un	stairwell of a multi-story building	Correspondence
32	2.10.2021	Volnogorsk Dnipro region,	48.4759674, 34.0087209	M	ad	stairwell of a multi-story building	Factual
33	3.10.2021	Liubashivka, Odesa region	47.8353, 30.2582	M	un	stairwell of a multi-story building	Factual
34	22.12.2021	Lviv	49.8362034, 24.0285903	M	ad	stairwell of a multi-story building	Factual
35	27.12.2021	Busk, Lviv region	49.9577849, 24.6150377	M	ad	stairwell of a multi-story building	Factual
36	13.01.2022	Dnipro	48.4923566, 35.0511378	F	un	stairwell of a multi-story building	Correspondence