



Do European bats react to climate warming more rapidly than expected? further winter range expansion of *Pipistrellus pygmaeus* in Eastern Europe

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Abstract

Ongoing climate change is rapidly altering winter conditions across Europe. This results in northward range expansions and the establishment of new sedentary populations in migratory volant vertebrates. Here we report the first large winter aggregation of *Pipistrellus pygmaeus* in central Ukraine - and, to our knowledge, in the entire Eastern European Plain. Over the winters of 2021/22–2024/25, we recorded 11 wintering events involving more than 1200 individuals. The largest was a single hibernaculum in a municipal building in Cherkasy (49.43° N, 31.99° E; central Ukraine), where 231 bats were found alive and approximately 1000 were found dead. The bat colony was strongly female-biased and included both adult and this-year-born individuals; the body mass of bats in March was at its lowest seasonal point, notably lower than summer values. Our findings indicate not only a rapid northward shift in the species' winter range, but also a reorganization of spatial sexual segregation. This shift may be interpreted as a response to the shortening and warming of winters in the region. Our results highlight the critical importance of systematic winter monitoring of urban hibernating bats to understand the mechanisms and broader ecological consequences of climate-driven range dynamics in bats.

Keywords Bats · Chiroptera · Eastern Europe · Species distribution · Climate change · Urbanisation

Introduction

One of the most conspicuous fingerprints of ongoing climate change is the progressive warming and shortening of winters in the Northern Hemisphere (Wang et al. 2021;

Gottlieb and Mankin 2024). Consequently, many volant vertebrates, such as birds and bats, that once undertook long-distance seasonal migrations can now remain farther north, sometimes forming new sedentary populations and in other cases driving a northward expansion of their winter ranges.

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Among birds, Eurasian blackcaps now regularly overwinter in Britain and Ireland rather than Africa (Van Doren et al. 2021). European robins have shortened their median migration distance across the continent (Ambrosini et al. 2016). Bewick's swans exhibit winter "short-stopping", with their range shifting eastward from the United Kingdom to the Baltic (Nuijten et al. 2020). Among European long-distance migratory bats, one of the best-documented examples is *Nyctalus noctula*, which historically migrated to winter almost exclusively south of 45° N. However, by the late 1990s - early 2000s, it had already become a regular hibernator at latitudes up to 50° N (Strelkov 2002, Godlevska 2015; Kravchenko et al. 2017). Current data indicate its winter limit is near 55° N (Shpak 2018), and modelling predicts a further northward advance (Kravchenko et al. 2025). Owing to its tendency to form large urban aggregations, *N. noctula* has become the numerically dominant species in urbanised areas of Ukraine in winter within just three decades (Prylutska et al. 2023; Vlaschenko et al. 2025). Another European long-distance migrant bat, *Pipistrellus nathusii*, has also shifted its winter range northward by approximately 300 km across central and eastern Europe since the early 2000s (Sachanowicz et al. 2018; Vlaschenko et al. 2023a). Together, these cases illustrate that the winter ranges of volant vertebrates can be displaced by several hundred kilometres within a few decades, underscoring how swiftly contemporary climate warming (Wang et al. 2021) is reshaping species distributions.

The focal species in this study is *Pipistrellus pygmaeus* (Leach, 2023), one of the smallest Europe-wide distributed bat species, reaching high local abundances patchily across the continent (Dietz et al. 2018; Vlaschenko et al. 2022; Jones and Froidevaux 2023; Ciechanowski et al. 2024). After the late-1990s, *Pipistrellus pipistrellus* complex was split into two species *P. pipistrellus* (Schreber, 1774) s.s. and *P. pygmaeus* (Barlow and Jones 1999). Later, expert-drawn range maps in field guides and atlases depicted the two taxa as broadly sympatric across Europe, extrapolating the Western European pattern of sympatry eastward despite the near-absence of verified records from east of the Carpathians (as discussed in detail by Godlevska and Gazaryan 2024). The recently published synthesis of a two-decade survey of *P. pipistrellus* complex distribution in Eastern Europe shows that in the east of the Carpathians, the complex is composed exclusively of *P. pygmaeus*, with *P. pipistrellus* s.s. present in Moldova, Crimea, and the Caucasus only (Godlevska and Gazaryan 2024). Unlike the largely sedentary *P. pipistrellus* s.s., *P. pygmaeus* is characterised as a long-distance migrant (Godlevska and Gazaryan 2024). Articles from the late 1990s on *P. pipistrellus* s.l. (Strelkov 1999) showed a striking seasonal sex-age segregation: only adult females reached the northern part of the range for reproduction, arriving in

May and departing with their volant young by late August, whereas adult males remained in the southern regions (e.g. Crimea and the Caucasus) (Strelkov 1999). Historical phenological notes from Ukraine describe *P. pipistrellus* s.l. as one of the first bat species to leave post-breeding areas, with the last captures recorded in the final days of August (Moskovskiy 1941, Abelentsev and Popov 1956).

During the first quarter of the twenty-first century, summer records of *P. pygmaeus* adult males became regular across eastern Europe (Godlevska and Gazaryan 2024), the last autumn detections shifted into mid-October (UBRC datasets, unpublished), and - most notably - solitary overwintering individuals were reported from 2021 onwards (Vlaschenko et al. 2023a). Hence, within roughly 30 years (after the last published reviews, Strelkov 1999), the species appears to have not only shifted the northern limit of its winter distribution poleward but also begun a reorganisation of spatial sexual segregation.

Our earlier report of the first solitary winter records of *P. pygmaeus* in eastern Europe led us to hypothesise that the species would persist only as solitary individuals rather than in large hibernation groups (Vlaschenko et al. 2023a). In contrast to our predictions, a colony of more than a thousand *P. pygmaeus* was discovered in early March 2025 in central Ukraine. In this report, we (i) provide the first description of a numerous winter aggregation of *P. pygmaeus* in eastern Europe, (ii) summarise all additional winter records of the species documented in Ukraine over the last five years, and (iii) discuss whether the observed winter range expansion may be linked to the recent shortening and warming of the cold season in the region.

Methods

The Ukrainian Bat Rehabilitation Center (UBRC) has operated a network of volunteers that record urban bat findings throughout Ukraine, varying from 3000 to 6000 bats per year (Vlaschenko and Prylutska 2018; Prylutska et al. 2023; Vlaschenko et al. 2025). Whenever feasible, alive or dead bats are transported either to UBRC headquarter in Kharkiv or to one of its volunteer branches located in big Ukrainian cities, where they undergo species confirmation, ringing, and veterinary assessment following Prylutska et al. (2021). All species identifications follow the illustrated keys of Dietz and von Helversen (2004) and Dietz and Kiefer (2014).

During a rescue call to UBRC helpline on 3 March 2025 in Cherkasy city (49.43° N, 31.99° E) a large *P. pygmaeus* colony (here and after Cherkasy colony), part of which had crowded into a window-trap and required extrication (Fig. 1c). First, all alive bats were rescued and subsequently

Fig. 1 Winter records of *P. pygmaeus* in Ukraine (2021/22–2024/25) and the Cherkasy colony case; **a** - geographic distribution of the 12 winter records within Ukraine compiled in this study (purple circles - newly reported solitary records, yellow circles - previously reported solitary records, green triangle - the mass hibernaculum in Cherkasy city; **b** - exterior of the building in Cherkasy where the hibernaculum was discovered; **c** - the window-trap on the second floor; **d** - alive bats from the site immediately after rescue, in transport boxes; **e** - bat carcasses collected at the site following the rescue (Pictures M. Radevych)



transported to Kharkiv (Fig. 1d) for examination and first aid (later, bat carcasses (Fig. 1e) also were collected and transported to Kharkiv for detailed examination).

For this report, we put together all records of *P. pygmaeus* in the winter season (1 November – 31 March) made in the frame of the ongoing work of UBRC since January 2021 (first documented winter record of *P. pygmaeus* (Vlaschenko et al. 2023a) (Supplementary, Table S1). This period (1 November – 31 March) corresponds to the hibernation season as defined by long-term year-round monitoring of urban bat phenology in Ukraine, during which winter city bat aggregation fully formed by early November and spring emergence begins in late March - early April (Kravchenko et al. 2017; Vlaschenko et al. 2023b). We call them here and after: (i) “solitary records” - solitary individuals that were found in different regions of Ukraine; and (ii) “Cherkasy

colony” - the exact record of the numerous colony in March 2025. Age identification followed the protocol described previously by Kravchenko et al. (2017); bats were divided into: (i) adult individuals (ad) - older than one year, (ii) “this-year-born bats” - younger than one year (sad), and (iii) individuals for which it was not possible to identify their age category (un).

Our analyses addressed three questions. First, we characterised the sex and age composition of winter records using binomial tests and chi-square tests to determine whether the observed structure deviated from expected ratios. Second, we compared body mass of bats from the winter colony with values obtained during the summer reproductive season. Third, we assessed factors affecting mortality during rehabilitation using binomial logistic regression with likelihood-ratio tests. All statistical analyses were performed in Python



Fig. 1 (continued)

3.x using the SciPy library for binomial and chi-square tests, and the statsmodels package for logistic regression.

Sex ratios were tested against the expected 1:1 ratio using two-tailed binomial tests, with 95% confidence intervals calculated using the Wilson score method. Differences in sex ratio between alive and dead individuals in the Cherkasy colony were analyzed using a two-proportion Z-test. Age structure (adult, subadult, unknown) was compared separately for each sex using Chi-square tests of independence, with effect sizes quantified using Cramér's V. Where significant, post-hoc pairwise chi-square tests with Bonferroni correction (adjusted $\alpha=0.017$) were used to identify which age categories differed. We note that the assumption of independent detection underlying binomial tests is not fully met for the Cherkasy colony, where all individuals were discovered in a single rescue event. The tests applied to colony data should therefore be interpreted as descriptive

characterisations of the sample rather than inferences about population-level parameters. For solitary records, where each bat was found independently at a different location and time, this assumption is more reasonably satisfied.

Morphometric measurements were taken for all live individuals and for a part of the carcasses. Forearm length (Ra) was measured with a digital calliper (0.1 mm accuracy), and body mass (W) was measured with a portable electronic scale with 0.1 g precision (Supplementary Table S2a).

To assess factors affecting mortality during rehabilitation, we analysed 229 individuals with complete data for survival status, body mass, sex, and age using binomial logistic regression with a logit link: $\text{mortality} \sim W + \text{Sex} + \text{Age}$, where W is body mass (g), Sex (female, male), and Age (adult, subadult, unknown). The unique contribution of each predictor was evaluated using likelihood-ratio tests (Type II ANOVA), comparing the full model with reduced models.

To place winter body mass values in a seasonal context, we used data collected by the UBRC team between 2017 and 2024. We note that the winter and summer datasets differ in both spatial coverage (winter: Cherkasy only; summer: Kirovohrad, Poltava, Kyiv, and Kharkiv oblasts) and temporal span (winter 2025 vs. summers 2017–2024), and therefore the comparison is treated as descriptive only. These consisted exclusively of adult ($n=93$) and this-year-born ($n=250$) females (Supplementary Table S2b) mist-netted in summer (June–July) across multiple regions of Ukraine: central (Kirovohrad and Poltava oblasts), northern (Kyiv oblast), and eastern (Kharkiv oblast). Only non-pregnant bats whose body mass was measured within 10 h after capture were included in the dataset.

A detailed description of the bat rehabilitation protocols (housing conditions, feeding regimes, and triage procedures) is presented in the Supplementary.

We acknowledge that all winter records of *P. pygmaeus* reported here are based on opportunistic rescue calls to the UBRC helpline network and are therefore not standardised in sampling effort across space and time. Detection probability is inherently higher in areas with active UBRC volunteers and in larger settlements, and reporting effort has increased over the study period as the volunteer network expanded.

Results

During the four most recent winters (2021/22–2024/25), we documented 11 winter records of *P. pygmaeus* in Ukraine (Fig. 1a). Ten findings were single-bat encounters spread across 10 settlements. In contrast, the colony in Cherkasy consisted of more than 1000 (231 alive) individuals. Together, these findings represent 242 *P. pygmaeus* transported alive to the UBRC facilities (the full list is given in Supplementary, Table S1, and their spatial distribution is mapped in Fig. 1).

The eleven winter records of *P. pygmaeus* documented in Ukraine originated from a wide range of settlement types, spanning large cities, mid-sized towns, and small rural villages (Supplementary, Table S1). Settlement area ranged from 2 km² (Korobivka, Cherkasy region; 1155 inhabitants) to 350 km² (Kharkiv, 1.42 million inhabitants). Human population size varied by three orders of magnitude, from fewer

than 1000 residents (Melnyky, Cherkasy region; 905 inhabitants) to more than one million in Kharkiv. The records span a broad geographic gradient across Ukraine (Fig. 1a).

The winter colony in Cherkasy was discovered in a municipal two-storey, Soviet-era brick building set within a sparsely wooded parkland (Fig. 1b) on the city's periphery. The majority of overwintering bats were found crowded within a window trap on the second floor (Fig. 1c), where numerous torpid individuals were visible among accumulated remains of conspecifics (Fig. 1c). Visual examination of carcasses from the Cherkasy colony suggested that mortality had occurred over an extended period. Based on external appearance, carcasses were roughly categorised into four decomposition stages: freshly dead (ca. 150 individuals), recently dead with early signs of decomposition (ca. 450), decomposed (ca. 250), and completely desiccated mummies (ca. 150) (Fig. 1e). Although precise timing of death cannot be determined without microclimatic data from the site, the range of decomposition stages is consistent with mortality events spanning weeks to possibly several months. Only 231 individuals were found alive and viable for rescue and further examination. The window trap evidently functioned as a lethal ecological trap, due to the bats' inability to escape once inside.

Sex- and age-class structure differed markedly between groups. Sex ratios deviated significantly from the expected 1:1 ratio in the Cherkasy colony (alive: $z=10.86$, $p<0.001$; dead: $z=5.15$, $p<0.001$) and overall dataset ($z=7.84$, $p<0.001$), with females comprising 74.5%, 58.3%, and 61.3% respectively. In contrast, solitary records showed no significant deviation from 1:1 ($z=0.30$, $p=0.754$) (Table 1). Sex and age composition differed significantly between alive and dead individuals. Females comprised a significantly higher proportion of alive (74.5%) versus dead (58.3%) bats ($Z=5.11$, $p<0.001$). Age structure differed between alive and dead groups for both females ($\chi^2=109.85$, $df=2$, $p<0.001$, Cramér's $V=0.389$) and males ($\chi^2=15.21$, $df=2$, $p<0.001$, Cramér's $V=0.183$). Post-hoc pairwise chi-square tests with Bonferroni correction revealed that, among females, all three age categories differed significantly from each other in their proportions found alive (ad: 46.0%, sad: 28.1%, un: 7.6%; all $p<0.001$). Among males, adults and subadults showed similar proportions (20.8% vs. 18.7%; $p=0.844$), but both differed significantly from the unknown-age category (6.6%; both $p<0.001$). The high

Table 1 Sex- and age-class structure of *P. pygmaeus* winter records in Ukraine (2021/22–2024/25) (F - females, M - males, ad - adult individuals, sad - this-year-born individuals, un - individuals with unidentified age or sex)

Group	F ad	F sad	F un	F total	M ad	M sad	M un	M total	Un	Total
Solitary records	3	1	1	5	4	0	2	6	0	11
Cherkasy colony (alive)	75	74	23	172	15	29	15	59	0	231
Cherkasy colony (dead)	88	189	279	556	57	126	214	397	67	1020
Overall	166	264	303	733	76	155	231	462	67	1262

proportion of unknown-age individuals among dead bats reflects the difficulty of ageing decomposed carcasses rather than a distinct biological group. The proportion found alive was highest for adult females (46.0%) and lowest for subadult males (18.7%), with females showing approximately twice the proportion of males overall.

Within the Cherkasy colony, forearm length in females ranged from 29.0 to 32.4 mm, while in males it varied from 28.0 to 31.1 mm (Supplementary Table S2a). Body mass exhibited broader variation, particularly among females, with values spanning 3.5–5.2 g; the corresponding range for males was narrower at 3.1–4.6 g. Notably, the majority of females weighed over 4.0 g, whereas most males were below this threshold.

Body mass of adult and subadult females captured in summer (Supplementary Table S2b) was consistently higher, averaging 5.40 ± 0.49 g (4.3 – 6.4 ; $n=93$) in adults and 4.54 ± 0.50 g (3.0 – 6.0 ; $n=250$) in subadults. When pooled, all females weighed on average 4.76 ± 0.62 g (3.0 – 6.4 ; $n=343$). These comparisons indicate that the mean body mass of females from the Cherkasy colony (4.32 ± 0.34 g) was notably lower than that of conspecifics measured in summer, especially adult females. The overall proportion of survivors during rehabilitation (March 6–20) was 72.4% (163 of 225 individuals). Logistic regression revealed that body mass was the strongest predictor of mortality (LR $\chi^2(1)=12.68$, $p<0.001$), with heavier individuals having significantly lower mortality risk. Sex also contributed significantly (LR $\chi^2(1)=5.80$, $p=0.016$), while age class showed no significant effect (LR $\chi^2(2)=3.71$, $p=0.156$). Of 163 bats released on 21 March in Cherkasy, 115 flew successfully (70.6%); 48 required return to Kharkiv for additional care, of which 32 were subsequently released. Overall, 147 bats (63.6% of the original 231) were successfully released to the wild.

Discussion

In this report, we document the first numerous winter aggregation of *P. pygmaeus* in central Ukraine and across the entire extent of eastern Europe. Taken together with all the records presented in this study, it demonstrates that within the past five years, *P. pygmaeus* has expanded its wintering range in Ukraine, altering our understanding of its seasonal distribution and migratory behaviour. We hypothesise that this change is linked to the documented shortening of the winter season and extension of the warm period in the Northern Hemisphere (Wang et al. 2021; Gottlieb and Mankin 2024), although a formal climatic analysis is beyond the scope of this study. The sex and age structure of the Cherkasy colony was distinctly female-biased. While the commonly

accepted hypothesis suggests that males are usually the first to colonize new regions (Kerth and Petit 2005; Kerth 2008; Kravchenko et al. 2020), early male colonists, in this case, may have been present but remained undetected due to their solitary behaviour.

The significantly higher survival of females, particularly adults, in the Cherkasy colony may reflect several non-mutually exclusive factors. Females may have entered hibernation with greater fat reserves, as suggested by their higher body mass compared to males (4.32 ± 0.34 g vs. 3.87 ± 0.42 g). Second, physiological differences in hibernation strategy could contribute to differential overwinter survival (Czenze et al. 2017). The substantially lower survival of subadults compared to adults (22.5% vs. 35.2% overall) is consistent with patterns documented in other bat species, where inexperienced this-year-born individuals face higher mortality during their first winter due to insufficient fat reserves (Kokurewicz and Speakman 2006).

The lower body mass of wintering females compared to summer values is expected, as measurements were taken in early March at the end of hibernation, when fat reserves are typically depleted to their seasonal minimum. Although mean body mass of wintering females (4.32 ± 0.34 g) was only moderately lower than summer values (4.76 ± 0.62 g), this difference was associated with substantial mortality. This resulted in substantial mortality: of approximately 1230 totally collected bats, only 147 survived to release (see Supplementary: rehabilitation results). The origin of the Cherkasy colony remains unclear. One possibility is that bats summering in the area did not undertake autumn migration and instead settled in the building for hibernation; alternatively, individuals may have actively selected this site during autumn. Although *P. pygmaeus* is common in the Cherkasy region in summer (Godlevska et al. 2022), no colony was found in this particular building in summer 2025, and neither hypothesis can be tested with the available data. At the same time, their persistence can plausibly be attributed to a response to climate warming, and in particular to the pronounced shortening of the cold season now observed across the region (Wang et al. 2021; Gottlieb and Mankin 2024; Ruosteenoja et al. 2016). Taken together, these results suggest possible changes in both the winter range and seasonal sex distribution of *P. pygmaeus*, although further data are needed to confirm whether these patterns represent a lasting reorganisation. Nevertheless, the species remains highly vulnerable to extreme weather events and habitat disruption, which can severely reduce survival during harsh winters, even though milder winters may temporarily enhance its persistence and local population success.

Recent analyses demonstrate a sustained warming trend and a shortening of the winter season across Europe (Wang

et al. 2021; Gottlieb and Mankin 2024; Ruosteenoja et al. 2016). Such changes extend the temporal window favourable for insectivorous bat activity and fat accumulation at higher latitudes (Godlevska 2015; Zahn and Kriner 2016), thereby reducing the energetic constraints that historically enforced long-distance migration (Kravchenko et al. 2025). In this context, whereas the first winter records (2021–2023) were limited to Kharkiv and southern Ukraine (Vlaschenko et al. 2023a), the records reported here (2023–2025) extend across a much broader area of central Ukraine, from Kyiv oblast in the north to the Cherkasy and Poltava regions. Although the opportunistic nature of the data does not allow us to calculate a formal rate of range advance, the rapid appearance of winter records across such a wide geographic area is noteworthy when compared with the slower range shifts typically reported for temperate bats (Rebello et al. 2010; Roche et al. 2019; Festa et al. 2022). However, these studies typically focus on shifts in the overall species distribution, often using presence data from the breeding season or the entire year, and rarely address the complexity of changes occurring within population and range structure at a finer scale. Our findings highlight that possible climate-driven responses may involve not just a simple northward movement of the range margin, but also a reorganisation of local sex-age spatial structure, wintering strategies, and the emergence of novel aggregation patterns.

We hypothesise that regional climatic warming, combined with local microclimatic refugia created by human infrastructure, underpins this recent shift. Urban heat islands and the relatively stable thermal regimes within buildings may provide conditions suitable for overwintering in various bat species (Vlaschenko et al. 2019, 2025; Hukov et al. 2020; Kravchenko et al. 2025). However, no microclimatic measurements were taken at the Cherkasy site, which formally limits our ability to evaluate the thermal conditions experienced by the colony. At the same time, the Cherkasy case illustrates the potential costs: the discovery of hundreds of mummified carcasses in a window trap shows that such structures may act as ecological traps, simultaneously enabling survival for some bats while leading to mass mortality in others. Our data show a clear seasonal contrast in body condition: wintering *P. pygmaeus* in Cherkasy were markedly lighter than individuals measured in summer. Because body mass integrates pre-hibernation fattening, this pattern is consistent with the high mortality observed at the site and suggests that many bats entered winter close to, or below, the body-mass threshold needed to complete hibernation without additional feeding, or lost their fat resources too quickly because of colder weather conditions than the species had already adapted to. We speculate that climate warming may be creating conditions that allow overwintering attempts in central Ukraine, but the high mortality

observed at the Cherkasy site suggests that the energetic capacity of many individuals has not yet matched these new opportunities.

Thus, the broad spatial and demographic spectrum of winter records suggests that *P. pygmaeus* may be increasingly attempting to overwinter across Ukraine, using both large cities and small settlements as novel winter sites. However, this expansion is accompanied by increased exposure to anthropogenic risks, highlighting the dual role of human-modified environments as both facilitators and hazards in the ongoing climate-driven reorganisation of the species' range.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13364-026-00863-z>.

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Author contributions AV, KK, and AP conceived the idea; MY, MR, AS, KZ, AK, AB and VP collected data and rescued bats; AV, MY, AS, KZ, AK, KK, VP and AP analysed the data and wrote the manuscript. All authors approved the final version of the manuscript.

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Data availability All required data/information is provided in the manuscript and Supplementary materials.

Declarations

Competing interests The authors declare no competing interests.

References

- Abelentsev VI, Popov BM (1956) Order Chiroptera, or bats. In: Pidplichko IG (ed) Fauna Ukrainy, Vol. 1: Mammalia. Academy of Sciences of the Ukrainian SSR, Kyiv, pp 229–446
- Ambrosini R, Cuervo JJ, Møller AP, de Lope F, Saino N, Rubolini D (2016) Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis. *J Anim Ecol* 85:749–760. <https://doi.org/10.1111/1365-2656.12496>

- Barlow K, Jones G (1999) Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*. *Zoologische Mededelingen* 73:257–268
- Ciechanowski M, Wikar Z, Borzym O et al (2024) Exceptionally uniform bat assemblages across different forest habitats are dominated by single hyperabundant generalist species. *Forests* 15:337. <https://doi.org/10.3390/f15020337>
- Czenze ZJ, Jonasson KA, Willis CKR (2017) Thrifty females, frisky males: winter energetics of hibernating bats from a cold climate. *Physiol Biochem Zool* 90:502–511. <https://doi.org/10.1086/692623>
- Dietz C, Kiefer A (2014) *Bats of Britain and Europe*. Bloomsbury Publishing, London
- Dietz C, von Helversen O (2004) Illustrated identification key to the bats of Europe. Electronic publication, Version 1.0. Tübingen and Erlangen, Germany
- Dietz M, Brombacher M, Erasmý M, Fenchuk V, Simon O (2018) Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest. *Acta Chiropterologica* 20:117–127. <https://doi.org/10.3161/15081109ACC2018.20.1.008>
- Festa F, Ancillotto L, Santini L et al (2022) Bat responses to climate change: a systematic review. *Biol Rev* 97:1853–1879. <https://doi.org/10.1111/brv.12868>
- Godlevska LV (2015) Northward expansion of the winter range of *Nyctalus noctula* (Chiroptera: Vespertilionidae) in Eastern Europe. *Mammalia* 79:315–324. <https://doi.org/10.1515/mammalia-2014-0027>
- Godlevska L, Gazaryan S (2024) Near or far: revision of distribution, breeding and winter ranges of two sibling *Pipistrellus* species (Chiroptera, Vespertilionidae) in Eastern Europe and the Caucasus. *Mammal Rev* 54:122–147. <https://doi.org/10.1111/mam.12325>
- Godlevska L, Rebrov S, Vorobei P et al (2022) Bats of Central Ukraine: a synopsis. *Zoodiversity* 56:203–222. <https://doi.org/10.15407/zoo2022.03.203>
- Gottlieb AR, Mankin JS (2024) Evidence of human influence on Northern Hemisphere snow loss. *Nature* 625:293–300. <https://doi.org/10.1038/s41586-023-06859-2>
- Hukov V, Timofieieva O, Prylutska A et al (2020) Wintering of an urban bat (*Pipistrellus kuhlii lepidus*) in recently occupied areas. *Eur J Ecol* 6:102–120. <https://doi.org/10.17161/eurojocol.v6i2.13522>
- Jones G, Froidevaux JSP (2023) Soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825). In: Russo D (ed) *Handbook of the Mammals of Europe: Chiroptera*. Springer, Cham, pp 591–615. https://doi.org/10.1007/978-3-319-47829-6_46-1
- Kerth G (2008) Causes and consequences of sociality in bats. *Bioscience* 58:737–746. <https://doi.org/10.1641/B580810>
- Kerth G, Petit E (2005) Colonization and dispersal in a social species, the Bechstein's bat (*Myotis bechsteinii*). *Mol Ecol* 14:3943–3950. <https://doi.org/10.1111/j.1365-294X.2005.02719.x>
- Kokurewicz T, Speakman JR (2006) Age related variation in the energy costs of torpor in Daubenton's bat: effects on fat accumulation prior to hibernation. *Acta Chiropterologica* 8:509–521. [https://doi.org/10.3161/1733-5329\(2006\)8\[509:ARVITC\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2006)8[509:ARVITC]2.0.CO;2)
- Kravchenko KA, Vlaschenko AS, Prylutska AS et al (2017) Year-round monitoring of bat records in an urban area: Kharkiv (NE Ukraine), 2013 as a case study. *Turkish J Zool* 41:530–548. <https://doi.org/10.3906/zoo-1512-10>
- Kravchenko K, Vlaschenko A, Lehnert L et al (2020) Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes. *Biol Lett* 16:20200351. <https://doi.org/10.1098/rsbl.2020.0351>
- Kravchenko K, Voigt CC, Volkholz J et al (2025) Shorter and warmer winters expand the hibernation area of bats in Europe. *Ecol Lett* 28:e70119. <https://doi.org/10.1111/ele.70119>
- Moskovsky G (1941) Materials on the fauna of bats (Chiroptera) in the Kharkiv region. Manuscript, 15 pp. (in Russian).
- Nuijten RJM, Wood KA, Haitjema T et al (2020) Concurrent shifts in wintering distribution and phenology in migratory swans: individual and generational effects. *Glob Change Biol* 26:4263–4275. <https://doi.org/10.1111/gcb.15140>
- Prylutska A, Vlaschenko A, Domanska A, Hukov V (2021) Guidebook on bat rehabilitation. Tsifrapynt, Kharkiv, Ukraine. (in Ukrainian)
- Prylutska A, Yerofeieva M, Bohodist V et al (2023) The dataset of bat (Mammalia, Chiroptera) occurrences in Ukraine collected by the Ukrainian Bat Rehabilitation Center (2011–2022). *Biodivers Data J* 11:e99243. <https://doi.org/10.3897/BDJ.11.e99243>
- Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Glob Change Biol* 16:561–576. <https://doi.org/10.1111/j.1365-2486.2009.02021.x>
- Roche N, Langton S, Aughney T et al (2019) Climate change, species traits and bat distributions: modelling abundance and occurrence in a continental context. *Biol Conserv* 237:60–72. <https://doi.org/10.1016/j.biocon.2019.06.017>
- Ruostenoja K, Räisänen J, Jylhä K et al (2016) Projections for the duration and degree days of the thermal growing season in Europe derived from CMIP5 climate models. *Int J Climatol* 36:3039–3055. <https://doi.org/10.1002/joc.4549>
- Sachanowicz K, Ciechanowski M, Tryjanowski P, Kosicki Z (2018) Wintering range of *pipistrellus nathusii* (Chiroptera) in Central Europe: has the species extended to the north-east using urban heat islands? *Mammalia*. 83:260–271. <https://doi.org/10.1515/mammalia-2017-0060>
- Shpak A (2018) Hibernating bat species of Belarus: results of the work of the Minsk bat contact centre. *Theriologia Ukrainica* 16:156–162. <https://doi.org/10.15407/pts2018.16.156>
- Strelkov PP (1999) Sex ratio during the breeding season in adult migratory bat species (Chiroptera: Vespertilionidae) of eastern Europe and adjacent territories. *Zoologicheskii Zhurnal* 78:1441–1454 (in Russian with English summary)
- Strelkov P.P. (2002) Materials on wintering of migratory bat species (Chiroptera) in the former USSR and adjacent regions. Part 2: *Nyctalus noctula*. *Plecotus* et al 5:35–56
- Van Doren BM, Conway GJ, Phillips RJ et al (2021) Human activity shapes the wintering ecology of a migratory bird. *Glob Change Biol* 27:2715–2727. <https://doi.org/10.1111/gcb.15578>
- Vlaschenko A, Prylutska A (2018) The Bat Rehabilitation Center of the Feldman Ecopark, Kharkiv, Ukraine. ResearchGate preprint. <https://doi.org/10.13140/RG.2.2.12508.03205>
- Vlaschenko A, Kovalov V, Hukov V, Kravchenko K, Rodenko O (2019) An example of ecological traps for bats in the urban environment. *Eur J Wildl Res* 65:20. <https://doi.org/10.1007/s10344-019-1252-z>
- Vlaschenko A, Kravchenko K, Yatsiuk Y, Hukov V, Kramer-Schadt S, Radchuk V (2022) Bat assemblages are shaped by land cover types and forest age: a case study from Eastern Ukraine. *Forests* 13:1732. <https://doi.org/10.3390/f13101732>
- Vlaschenko A, Hukov V, Timofieieva O et al (2023a) Leaping on urban islands: further summer and winter range expansion of European bat species in Ukraine. *Eur J Ecol* 9:70–85. <https://doi.org/10.17161/eurojocol.v9i2.18383>
- Vlaschenko A, Shulenko A, But A et al (2023b) The war-damaged urban environment becomes deadly trap for bats: case from Kharkiv City (NE Ukraine) in 2022. *J Appl Anim Ethics Res* 5(1):27–49. <https://doi.org/10.1163/25889567-bja10035>

- Vlaschenko A, Shulenko A, Yerofeieva M et al (2025) Urban bat rescue crisis in Eastern Europe: a new challenge for bat conservation. *Anim Conserv*. <https://doi.org/10.1111/acv.70018>
- Wang J, Chen C, Wang C et al (2021) Changing lengths of the four seasons by global warming. *Geophys Res Lett* 48. <https://doi.org/10.1029/2020GL091753>. e2020GL091753
- Zahn A, Kriner E (2016) Winter foraging activity of Central European vespertilionid bats. *Mammalian Biology* 81:40–45. <https://doi.org/10.1016/j.mambio.2015.07.008>

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