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CHARACTERISTICS OF WINTER BAT AGGREGATIONS IN POLAND: A REVIEW

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Abstract

The distribution of natural wintering roosts of bats in Poland is not homogenous, they are found almost exclusively in the south of Poland. Manmade underground shelters, on the other hand, are found across the country, including areas outside the range of natural caves. Based on literature data and my own observations, the size and species composition of winter bat aggregations occupying natural and artificial roosts were compared. The data analysed include records that were both published and collected between 1992 and 2019. The starting date of the range has been assumed due to the well-established formula of nationwide bat monitoring, which started in 1988, while the end date was based on the availability of publications. I arbitrarily adopted 50 individuals as the minimum number of bats in a certain wintering site, found on a minimum of one occasion during the study period. In total, I collected data on 128 wintering sites: 42 natural and 86 manmade. The overall size of the analysed aggregations is a minimum of 88 800 individuals, with manmade roosting sites accounting for a minimum of 77 600 individuals, and natural sites almost 12 200 individuals. The most abundant bat aggregations were recorded in manmade underground sites (up to 38 594 individuals), while in natural sites there were only up to 2900 individuals. However, the average aggregation size did not differ greatly between the two types of shelters (169 vs. 156, F = 3.368, df = 1.128; p = 0.069). In contrast, the number of species wintering in natural shelters is higher than in manmade ones (8 vs. 6 species, F = 9.785, df = 1.128, p = 0.002179). *P. pipistrellus* was found only in anthropogenic shelters. In addition, this type of shelter is characterised by a higher proportion of *M. daubentonii* (16.4% vs. 3.7%), *M. myotis* (42.0% vs. 29.1%), *M. nattereri* (26.4% vs. 16.5%), and *B. barbastellus* (11.3% vs. 7%), as well as species recorded incidentally: *P. austriacus* (0.09% vs. 0.04%) and *E. serotinus* (0.17% vs. 0.07%). In contrast, *R. hipposideros* (16.7%) and *M. emarginatus* (5.7%) were recorded almost exclusively in caves, and *M. brandtii*/*mystacinus* (15.6% vs. 0.3%) and *P. auritus* (4.2% vs. 1.9%) were clearly predominant in these shelters. Some of these differences could be explained by the effect of geographical location: some species are found only in the south of the country (*R. hipposideros*, *M. emarginatus*). On the other hand, artificial shelters are usually characterised by a more dynamic microclimate, which is preferred by species rarely found in natural shelters.

Cite as

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Характеристика зимових скупчень кажанів у Польщі: огляд

Томаш Постава

Резюме. Розподіл природних місць зимівлі кажанів у Польщі є неоднорідним і охоплює майже виключно південь Польщі. З іншого боку, штучні підземелля трапляються по всій країні, включаючи території поза межами природних печер. На основі літературних даних та власних спостережень порівняно розміри та видовий склад зимових скупчень рукокрилих, які займають природні та штучні місця зимівлі. Дані стосуються як опублікованих раніше знахідок, так і зібраних у період з 1992 по 2019 рік. Початкову дату діапазону прийнято через усталену формулу загальнонаціонального моніторингу кажанів, який розпочався у 1988 році, тоді як кінцева дата базувалася на наявності публікацій. Ми довільно прийняли 50 особин як мінімальну кількість кажанів на певному місці зимівлі, знайдену як мінімум раз протягом періоду дослідження. Загалом зібрано дані про 128 місць зимівлі: 42 природних і 86 штучних. Загальний розмір проаналізованих скупчень сягає щонайменше 88 800 особин, з яких у штучних місцях зимівля виявлено щонайменше 77 600 особин, а у природних — майже 12 200 особин. Найбільш численні скупчення кажанів виявлено у підземних сховищах штучного походження — до 38 594 особин, тоді як у природних місцях — лише до 2900 особин, але середній розмір скупчень між двома типами сховищ не відрізнявся (169 проти 156, F = 3,368, df = 1,128; p = 0,069). З іншого боку, кількість видів, які зимують у природних укриттях є вищою за кількістю видів, що зимують у сховищах штучного походження (8 проти 6 видів, F = 9,785, df = 1,128, p = 0,002179). *P. pipistrellus* виявлено лише в антропогенних укриттях. Крім того, цей тип сховищ характеризується більшою часткою *M. daubentonii* (16,4% проти 3,7%), *M. myotis* (42,0% проти 29,1%), *M. nattereri* (26,4% проти 16,5%) та *B. barbastellus* (11,3% проти 7%), а також випадково зареєстрованих видів: *P. austriacus* (0,09% проти 0,04%) та *E. serotinus* (0,17% проти 0,07%). Навпаки, *R. hipposideros* (16,7%) і *M. emarginatus* (5,7%) були зареєстровані майже виключно у печерах, а *M. brandtii/mystacinus* (15,6% проти 0,3%) і *P. auritus* (4,2% проти 1,9%) явно переважали в цих сховищах. Деякі з цих відмінностей можна пояснити ефектом географічного положення: деякі види трапляються лише на півдні країни (*R. hipposideros, M. emarginatus*), з іншого боку, штучні укриття зазвичай характеризуються більш динамічним мікрокліматом, якому, у свою чергу, надають перевагу види, які рідко трапляються в природних сховищах.

Ключові слова: фауна, моніторинг, зимові скупчення кажанів, Польща.

Introduction

The strategy for surviving the winter food shortage, especially the shortage of invertebrates, which are an important part of predators' diet, is to migrate or hibernate [Heldmaier & Klingenspor 2010]. In the temperate zone, insectivorous bats are subject to periodic fluctuations in food availability [Geiser 2011]. The start and end of the hibernation period is highly species specific, and it depends on the type of food preferred [Speakman & Rowland 1999]. Moreover, microclimatic parameters are important: some bat species require stable conditions during hibernation (the greater mouse-eared bat *Myotis myotis*, the lesser horseshoe bat *Rhinolophus hipposideros* [Nagel & Nagel 1991]), while others winter in the near-entrance zone, where conditions are largely determined by external parameters (*Plecotus* sp., *Barbastella barbastellus*). Typical hibernation sites in nature are underground cavities—caves [Furey & Racey 2016]. The appearance of natural caves is strictly conditioned by the occurrence of karstic (karstic caves), sulphate or sandstone rocks (tectonic). In Poland, the presence of caves is limited to the south of the country: the Kraków–Wieluń Upland, the Sudetes, the Carpathian and the Świętokrzyskie Mountains [PGI-NRI 2022]. In addition to natural cavities, there are a number of other underground shelters of anthropogenic origin—bunkers, cellars, mines, or even factories—which can provide wintering sites for bats [Wołoszyn 1996]. Contrary to most natural shelters, the vast of anthropogenic undergrounds have more than one entrance, frequently with additional ventilation openings. As a result, artificial underground sites often have a much larger dynamic zone range than caves [Lesiński 1996]. Differences in microclimates also have unequal attractiveness to bats: individual species differ in their thermopreferendum [Nagel & Nagel 1991]. In fact, a number of sites of anthropogenic origin gather large aggregations of wintering bats.

Certain sites, such as the Miedzyrzecki Rejon Umocniony (MRU), represent important wintering refuges of not only national, but also European importance [Mitchell-Jones 2016].

In 1988, the first census of wintering bats in Poland was conducted, called 'the Decade' (DSN): monitoring was to take place during the first ten days of February [Wołoszyn 1994]. A summary of the first five years of monitoring resulted in a variety of important information—it identified important wintering locations, and comparison with historical data allowed the identification of trends, both locally and nationally [Wołoszyn 1996]. The action was initially based on the amateur chiropterology network, and in the course of time, universities and other associations joined in, with a database being established at CIC ISEZ PAN in Krakow (CIC—Chiropterological Information Center). After 1992, most regional chiropterological groups were functioning independently of the CIC.

While discoveries of new natural sites have been rare in recent years are rare [Nowak & Grzywiński 2017; author's data], many man-made underground sites are constantly being explored and impressive hibernation aggregations are being found [Wojtaszyn *et al.* 2013*a*]. This article summarises the available information on bat wintering roosts in Poland, and it provides a preliminary comparison of the fauna of natural and artificial roosts.

Materials and Methods

This overview uses data from my own winter bat monitoring (Kraków–Wieluń Upland) and materials available in the literature (see Annex). The compilation includes sites with more than 50 wintering individuals recorded during the period from 1992 to 2019. I arbitrarily adopted 50 individuals as the minimum number of bats in a certain wintering site, found on a minimum of one occasion during the study period. The start date of the range was assumed due to the well-established formula of nationwide bat monitoring, which started in 1988 (important factor: correctness of species identification), while the end date was based on the availability of publications. The underground sites were divided according to their genesis into: natural—caves (karst, flysh); manmade: wartime (bunkers, fortress), and non-wartime (cellars, mines, drainage systems). Some natural underground sites have been transformed during mining activities. Hence, the appropriate category was determined by the proportion of remaining natural cavities: if this was less than half it was considered to be an artificial site [Bochotnica: Kowalski & Dróżdż 2002], while if it was over half it was regarded as a natural one [Szachownica cave: Ignaczak 2017].

For every site, the bat fauna was described by: (i) maximum abundance of each species in the surveyed year range (indeterminate excluded); (ii) maximum abundance of all species (including indeterminate); and (iii) number of species found. The species of most individuals were determined by external diagnostic features (bats were not removed from the walls). For hard-to-determine species such as *M. alcathoe*/*M. brandtii* and *M. mystacinus*, they were treated together as *Mbra/Mmys*, while all *Pipistrellus* were categorised as *Pipistrellus* sp. Moreover, each underground object was described based on: (i) its origin: natural (caves) on manmade (shafts, mines, forts, bunkers, cellars); (ii) its latitude and longitude; and (iii) bibliographic data (author, journal/source).

Statistical analyses

Differences in maximum bat abundance and the number of wintering species between natural and artificial wintering sites were tested by one-way ANOVA after log-normal transformation. In addition, cluster analysis (Ward's method) was used to visualise the similarity of the proportion of the fauna of wintering bats. To determine the similarities of the diets between bat species, cluster analysis (Ward's method) with bootstrapping was performed using the R package. The distances of objects were calculated in Euclidean space, using the average linkage method.

In this analysis, the eight most numerous wintering bat species were used: *Rhinolophus hipposideros*, *Barbastella barbastellus*, *Myotis brandtii*/*M. mystacinus*, *M. daubentonii*, *M. emarginatus*, *M. myotis*, *M. nattereri*, *Plecotus auritus*, plus any other bat species (when determined at species level—'indeterminate' was excluded). All the analyses were carried out using RStudio, version 4.1.0 [R Core Team 2020].

Fig. 1. Distribution of bat hibernation sites in Poland (n > 50 individuals). Data available from literature, from 1992–2019. Underground sites: white—manmade, black—natural.

Рис. 1. Розподіл місць зимівлі кажанів у Польщі (n > 50 особин). Дані з літератури за 1992–2019 рр. Підземелля: білі — рукотворні, чорні — природні.

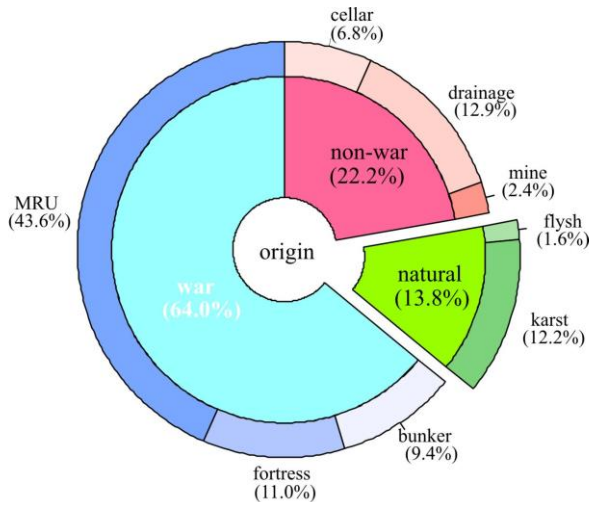


Fig. 2. The number of wintering bats in each type of wintering site: war—war-related; anthropo—non-war; and natural—caves.

Рис. 2. Кількість зимуючих кажанів у кожному типі місць зимівлі: war — пов'язані з війною (мілітарні); anthropo — не пов'язані з війною; natural — печери.

Results

Based on our own data and those from the literature, at least 128 bat wintering sites gathering more than 50 hibernating individuals have been identified in Poland, of which 42 sites are natural underground, while 86 are of anthropogenic origin (Fig. 1). The largest proportion of wintering sites is war related (38.1%), dating from around the World War II period (20.6%), as well as fortresses from before World War I (17.5%). Natural objects, that is, caves (33.3%), were the second most abundant, followed by manmade non-military objects (28.6%): cellars (11.1%), drainage (9.5%), and mines (7.9%). Wintering sites of natural origin are not homogeneously distributed and dominate in southern Poland: Tatra Mts. (4 karstic caves), Sudetes Mts. (1 karstic cave), Western Beskids (1 cave, tectonic), Świętokrzyskie Mts. (1 karstic cave), Sudeten Foothills (1 karstic cave), Beskidzkie Foothills (1 tectonic cave), and Kraków–Wielun Upland (6 karstic caves). On the other hand, wintering sites in manmade structures are fairly equally distributed throughout the country. Nine manmade wintering sites were mines, 22 were anthropogenic/technical (drainage systems, cellars), and 44 were associated with abandoned wartime fortifications (bunkers and fortresses).

For the period of 1992–2019 (27 years), the highest number of bats counted was over 88 800 individuals, from two families: Rhinolophidae (2 species) and Vespertilionidae (15 bat species). The average number of bats in a winter assemblage was slightly higher for manmade sites ($x = 168$ ind., max = 38 584) than for natural sites ($x = 153$ ind., max = 2902), and the differences are nearly significant (one-way ANOVA, $F = 3.37$, $df = 1.128$, p-value = 0.069) (Fig. 3a). The largest manmade wintering roost in terms of hibernating bats gathers almost 39 000 bats: Miedzyrzecki Rejon Umocniony (MRU). The remaining anthropogenic hibernacula hold numbers within the following ranges: 4000–3000—3 underground sites; 3000–2000—1 underground site; 2000–1000—4 underground sites; and less than 100—79 underground sites.

Among the natural sites, the largest wintering one held slightly more than 2000 bats (Szachownica Cave), while only 2 caves held between 2000 and 1000 bats, and the remaining 39 caves housed less than 1000. In total, artificial wintering roosts gather more than 6 times the number of wintering bats (76 603 individuals) than natural underground sites (12 197 individuals). Nearly half of the bats hibernated in wartime undergrounds sites dating back to WWII, while considerably lower numbers were found in fortresses from before WWI—only 11%.

On the other hand, among the manmade non-war structures, drainage systems were the most important, followed by cellars, and finally, with a small contribution, mines. In contrast, the smallest proportion of bats overwintered in natural sites, the vast majority in karst caves (Fig. 2).

In the underground sites used in the analysis, 17 bat species were found to be hibernating. The most numerous species was *M. myotis*, while less abundant were *M. nattereri*, *M. daubentonii*, and *B. barbastellus*. Small percentages were recorded for *R. hipposideros*, *P. auritus*, *M. brandtii/mystacinus*, *M. emarginatus*, and *P. pipistrellus*. The species *M. dasycneme*, *M. bechsteinii*, *E. serotinus*, *E. nilssonii*, *P. austriacus*, and those known from single individuals—*N. noctula* and *R. ferumequinum*—were found incidentally. The number of bat species found wintering in the natural underground sites was 7 on average, and this was significantly higher than the number of species wintering in manmade sites, with an average of >5 species (one-way ANOVA: F = 9.79, df = 1.128 DF, p-value: 0.0022) (Fig. 3).

The one species found only in anthropogenic shelters was *Pipistrellus* sp. (most probably *P. pipistrellus*), but it was present in low proportions. In manmade shelters, the highest proportion of bats among species *M. daubentonii*, *M. myotis*, *M. nattereri*, *P. austriacus*, *E. serotinus*, and *B. barbastellus*. In the caves, on the other hand, there was a clear predominance of *M. brandtii*/*mystacinus*, *M. bechsteinii*, *P. auritus*, and *M. dasycneme*. Several bat species were recorded almost exclusively in caves: *R. hipposideros*, *M. emarginatus*, *E. nilssonii*, and *N. noctula*, while only single individuals of *R. hipposideros* and *M. emarginathus* were found in manmade underground sites. The species composition of hibernating bats therefore differentiates between natural and manmade roosts (Fig. 4).

Wintering sites of natural and artificial origin are grouped into separate clusters: caves are characterised by a higher proportion of *R. hipposideros*, *M. brandtii*/*mystacinus*, *M. emarginathus*, and in some cases *M. myotis*, while manmade sites are characterised by a predominance of *M. nattereri*, *M. daubentonii*, and *B. barbastellus* (Fig. 5).

Discussion

In Poland, the regular monitoring of hibernating bats, which was established in 1988 [Wołoszyn 1996], initially covered known wintering sites—mostly caves, but also artificial sites. The latter were mostly war systems—fortresses built in the 19th century: Gdańsk [Ciechanowski *et al.* 2006], Toruń and Grudziądz [Kasprzyk *et al.* 2002; Kasprzyk & Leszczyński 2008], Poznań fortress [Jurczyszyn *et al.* 2002], Kostrzyń [Lesiński & Kowalski 2002], Modlin fortress [Fuszara & Fuszara 2002]; or bunkers from World War II [Urbańczyk 1991; Sachanowicz 2003].

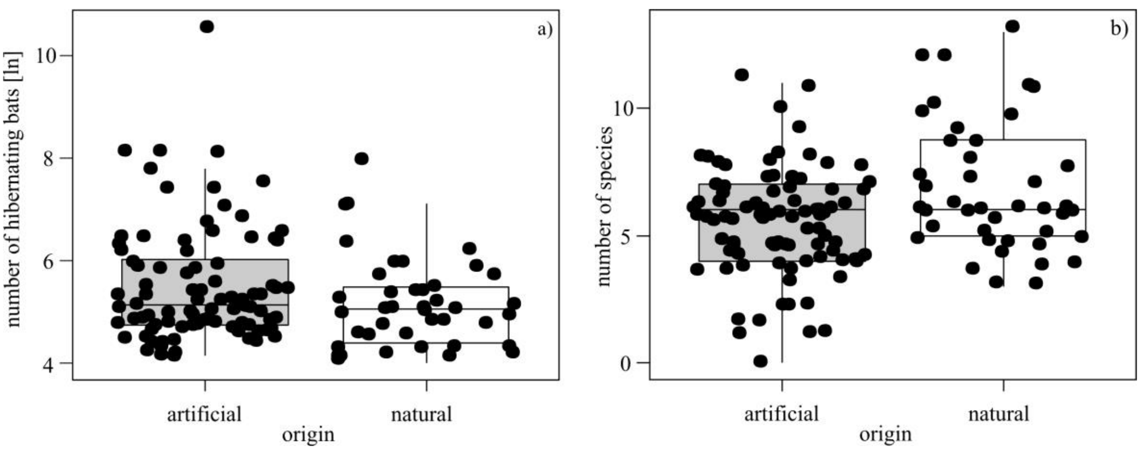


Fig. 3. Maximum abundance of winter bat aggregations (logarithmic scale) (*a*), and number of bat species at a given wintering site (*b*).

Рис. 3. Максимальна чисельність зимових скупчень кажанів (логарифмічна шкала) (*a*) та кількість видів кажанів на даному місці зимівлі (*b*).

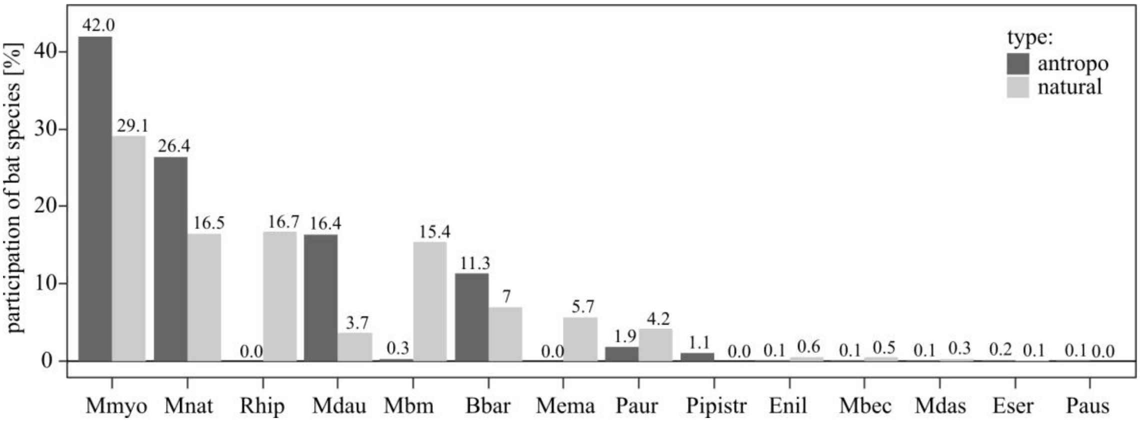


Fig. 4. Species composition of winter bat assemblages in underground sites: manmade (bunkers, fortresses, cellars, mines, and drainage systems), and natural (caves).

Рис. 4. Видовий склад зимових угруповань кажанів у підземних об'єктах: штучних (бункери, фортеці, підвали, шахти та дренажні системи) та природних (печери).

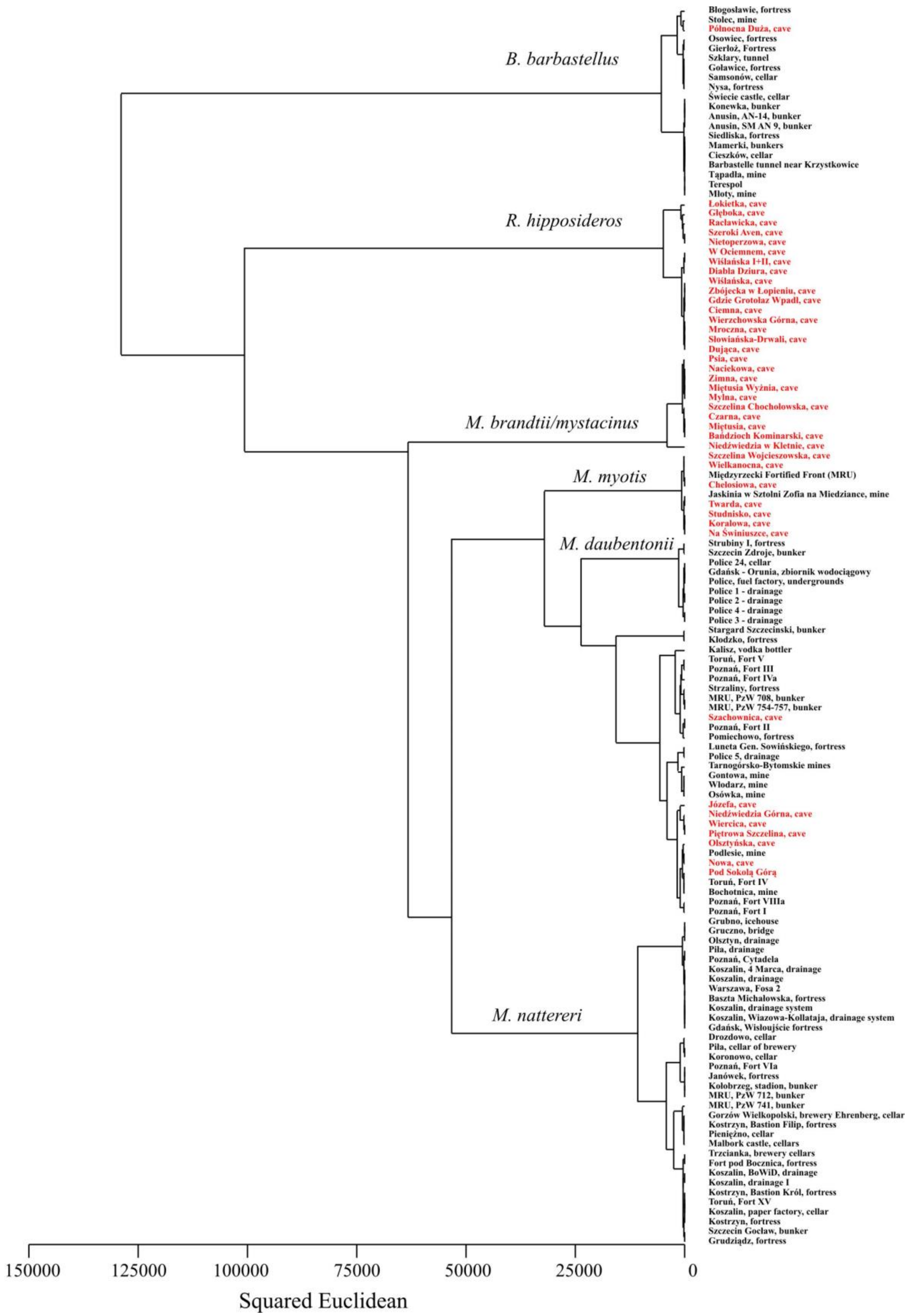
Abandoned military facilities with their extensive underground corridors are therefore very suitable roosts for the wintering of many bat species [Voigt *et al.* 2014]. Most of the bat wintering sites used in the analysis have been known since the first winter counts, but recent years have brought a very impressive discovery of new winter aggregations, ranging from several hundred to even several thousand: the drainage systems of Koszalin [2004: Wojtaszyn *et al.* 2008], Krzystkowice [2005: Wojtaszyn *et al.* 2013*b*], Police [2006: Dzięgielewska *et al.* 2007]; the drainage systems of Olsztyn [2006: Wojtaszyn *et al.* 2013*a*], the drainage systems of Piła [2008: Wojtaszyn *et al.* 2010]; and the bunker in Stargard Szczeciński [2012: Wojtaszyn *et al.* 2014]. The only natural site is the Niedźwiedzia Cave in Kletno, where the discovery of new sections has also resulted in an increase in bat counts from 240 to more than 1100 individuals [Furmankiewicz *et al.* 2016].

In Poland, the numbers of bats wintering in manmade underground sites are high; in total, these roosts have recently accounted over 86% of the bats at analysed wintering sites. Most impressive is the Międzyrzecki Rejon Umocniony (MRU), accounting for almost 39 000 individuals from 12 bat species in winter [Cichocki *et al.* 2020]. It is currently the 8th or 9th largest bat hibernaculum in Europe [(Eurobats 2014]. MRU, with other military sites—both pre- and post-World War I—provides shelter for over three-fifths of the bats wintering in Poland. However, other winter aggregations at military sites are not as considerable, and only in three locations do they exceed 1000 individuals: Michałowska Bastion [Lesiński *et al.* 2008], Grudziądz [Kasprzyk & Leszczyński 2008], and Strzaliny [Bernard *et al.* 2019].

Of the manmade underground sites, however, the urban drainage systems gather bat populations in their thousands. While similar sites in Central Europe have already been mentioned [Godlevsky 2000], initially this information was rare and the abundances recorded at the time were not as high [Grzywiński & Kmiecik 2003]. Interestingly, only a small part of the drainage system of Poznań provided a wintering site for bats comparable to the largest above-ground sites located in the Poznań Fortresses [Grzywiński & Kmiecik 2003].

Fig. 5 (→). Hierarchical clustering dendrogram of hibernating bat species composition (Ward's method). Bat fauna composition was described in terms of percentage occurrence in each hibernaculum. Name of bat species—predominant bat species. Black colour: war-made, blue colour: manmade, and red colour: natural.

Рис. 5 (→). Дендрограма ієрархічної кластеризації видового складу зимуючих кажанів (метод Уорда). Склад фауни рукокрилих описаний у відсотках зустрічальності в кожному зимівнику. Вказана назва виду — переважаючий вид кажанів. Чорний колір — об'єкти військового призначення, синій — інші антропогенні, червоний — природні.


B. barbastellus
R. hipposideros
M. brandtii/mystacinus
M. myotis
M. daubentonii
M. nattereri
Błogosławie, fortress
Stolec, mine
Północna Duża, cave
Osowiec, fortress
Gierłoż, Fortress
Szklary, tunnel
Goławice, fortress
Samsonów, cellar
Nysa, fortress
Świecie castle, cellar
Konewka, bunker
Anusin, AN-14, bunker
Anusin, SM AN 9, bunker
Siedliska, fortress
Mamerki, bunkers
Cieszków, cellar
Barbastelle tunnel near Krzystkowice
Tąpadła, mine
Terespol
Młoty, mine
Łokietka, cave
Głęboka, cave
Racławicka, cave
Szeroki Aven, cave
Nietoperzowa, cave
W Ociemnem, cave
Wiślańska I+II, cave
Diabla Dziura, cave
Wiślańska, cave
Zbójecka w Łopieniu, cave
Gdzie Grotołaz Wpadl, cave
Ciemna, cave
Wierzchowska Górna, cave
Mroczna, cave
Słowiańska-Drwali, cave
Dująca, cave
Psia, cave
Naciekowa, cave
Zimna, cave
Miętusia Wyżnia, cave
Mylna, cave
Szczelina Chochołowska, cave
Czarna, cave
Miętusia, cave
Bańdzioch Kominarski, cave
Niedźwiedzia w Kletnie, cave
Szczelina Wojcieszowska, cave
Wielkanocna, cave
Międzyrzecki Fortified Front (MRU)
Chelosiowa, cave
Jaskinia w Sztolni Zofia na Miedziance, mine
Twarda, cave
Studnisko, cave
Koralowa, cave
Na Świniuszce, cave
Strubiny I, fortress
Szczecin Zdroje, bunker
Police 24, cellar
Gdańsk - Orunia, zbiornik wodociągowy
Police, fuel factory, undergrounds
Police 1 - drainage
Police 2 - drainage
Police 4 - drainage
Police 3 - drainage
Stargard Szczecinski, bunker
Kłodzko, fortress
Kalisz, vodka bottler
Toruń, Fort V
Poznań, Fort III
Poznań, Fort IVa
Strzaliny, fortress
MRU, PzW 708, bunker
MRU, PzW 754-757, bunker
Szachownica, cave
Poznań, Fort II
Pomiechowo, fortress
Luneta Gen. Sowińskiego, fortress
Police 5, drainage
Tarnogórsko-Bytomskie mines
Gontowa, mine
Włodarz, mine
Osówka, mine
Józefa, cave
Niedźwiedzia Górna, cave
Wiercica, cave
Piętrowa Szczelina, cave
Olsztyńska, cave
Podlesie, mine
Nowa, cave
Pod Sokolą Górą
Toruń, Fort IV
Bochotnica, mine
Poznań, Fort VIIIa
Poznań, Fort I
Grubno, icehouse
Gruczno, bridge
Olsztyn, drainage
Piła, drainage
Poznań, Cytadela
Koszalin, 4 Marca, drainage
Koszalin, drainage
Warszawa, Fosa 2
Baszta Michałowska, fortress
Koszalin, drainage system
Koszalin, Wiazowa-Kollataja, drainage system
Gdańsk, Wisłoujście fortress
Drozdowo, cellar
Piła, cellar of brewery
Koronowo, cellar
Poznań, Fort VIa
Janówek, fortress
Kołobrzeg, stadion, bunker
MRU, PzW 712, bunker
MRU, PzW 741, bunker
Gorzów Wielkopolski, brewery Ehrenberg, cellar
Kostrzyn, Bastion Filip, fortress
Pieniężno, cellar
Malbork castle, cellars
Trzcianka, brewery cellars
Fort pod Bocznica, fortress
Koszalin, BoWiD, drainage
Koszalin, drainage I
Kostrzyn, Bastion Król, fortress
Toruń, Fort XV
Koszalin, paper factory, cellar
Kostrzyn, fortress
Szczecin Gocław, bunker
Grudziądz, fortress
150000
125000
100000
75000
50000
25000
0
Squared Euclidean

The monitoring of drainage systems is neither simple nor secure: there is the potential presence of carbon dioxide, methane, or even hydrogen sulphide, and there are no plans or maps for most of them. However, new large wintering sites are found year after year: currently, record abundances have been recorded mainly in the cities in northern Poland: in Olsztyn, with 3412 ind. [Wojtaszyn *et al.* 2013a], in Piła, with 3403 ind. [Wojtaszyn *et al.* 2013*a*], and in Koszalin, with 955 ind. [Wojtaszyn *et al.* 2008]. It can therefore be hypothesised that these systems, considering their extent, represent some of the most important wintering habitats in areas where natural shelters are lacking.

On the other hand, the bat fauna found up to now in these wintering sites is quite sparse in species: *M. nattereri* dominate with up to 97% [Grzywiński & Kmiecik 2003; Wojtaszyn *et al.* 2008, Wojtaszyn *et al.* 2013*a*] and *M. daubentonii* account for up to 85% [Dzięgielewska *et al.* 2007], while other species, *P. auritus* and *B. barbastellus*, were found incidentally.

Cellars, often the remains of factories, also gather large aggregations of wintering bats (e.g. in Police [Dzięgielewska *et al.* 2007]), but they are less numerous than the other categories. The least numerous among the manmade wintering sites are mines, and they do not gather large groups of bats. The reason for their lower importance as wintering habitats may be that they are mostly located in the mountains and highlands of southern Poland, where there is also an abundance of natural shelters [Kowalski 1953; Postawa & Zygmunt 2000; Szkudlarek *et al.* 2008; Piksa & Nowak 2013; Furmankiewicz *et al.* 2016].

On the other hand, among the sites of natural origin, only three of them provide shelter for more than one thousand individuals: Szachownica Cave [Ignaczak 2017], Niedźwiedzia Cave in Kletno [Furmankiewicz *et al.* 2016], and Studnisko Cave [author data], while the next in size do not exceed a few hundred individuals. Low abundance, on the other hand, may be the result of the much higher density of natural shelters than of manmade underground sites: only the upland and the Carpathians have to date inventoried over 8000 natural underground sites of various types [PGI-NRI 2022]. Despite lower winter aggregation, caves are one of the most important roosts—they are target wintering sites for bats from southern and central Poland [Wojtaszyn *et al.* 2019]. The abundance of wintering bats in Poland is probably several times higher than the value obtained, because: (i) bats overwinter in many places such as cellars or wells (small numbers, but objects are numerous); and (ii) many wintering sites are unknown to us, as demonstrated by discoveries, for example, in Niedźwiedzia Cave in Kletno, or other new caves with wintering aggregations of more than 100 individuals (Niedźwiedzia Górna Cave [author data], Twarda Cave [Nowak & Grzywiński 2017]).

The results of winter censuses of bats confirm the trend observed for more than two decades of increasing numbers of these mammals in Poland (start 1999, [Sachanowicz *et al.* 2006]). However, the dynamics of change are species specific [Piksa & Nowak 2013; Lesiński *et al.* 2011; Ignaczak 2017; Bernard *et al.* 2019], and numbers also vary at different times and even between different regions [Gottfried *et al.* 2019]. Despite a continuous increase in numbers, the population of wintering bats has not returned to the abundance it had before the collapse of the 1960s–1970s, when abundances were much higher [Kowalski 1953].

The species composition of wintering bats clearly differentiates natural from artificial roosts, while only slightly between artificial shelters: of war and no-war function. This is probably the result of a geographical trend: in the south, especially in areas rich in natural underground sites, there are many more species than in the north of Poland [Sachanowicz *et al.* 2006]. On the other hand, most manmade underground sites are characterised by a dynamic microclimate (or its dominance): artificial shelters were built for human use and in most of them ventilation was important (hence the predominance of a dynamic microclimate). Natural objects, on the other hand, have an unpredictable pattern, and static microclimates predominate for the most part, which is preferable for most temperate bat species [Nagel & Nagel 1991].

Currently, some of these sites are protected as reserves, Natura 2000 areas, or even documentary sites. However, many are still at risk, especially manmade ones: several constructions have become utilised commercially, abandoned, or demolished. Restoration works are starting in some of them in order to save their historical values, but this could present serious threats for wintering bats (see: [Wojtaszyn *et al.* 2015]). Drainage systems appear to be especially difficult to protect—their function conflicts with bat conservation, and renovations can result in the loss of microhabitats and/or a change in microclimate.

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Annex

Anusin, bunker AN-14, bunker: 216 ind. [Sachanowicz 2003]; Anusin, bunker SM AN 9, bunker: 102 ind. [Sachanowicz 2003]; Bańdzioch Kominarski, cave: 139 ind. [Piksa & Nowak 2013]; Barbastelle tunnel near Krzystkowice, drainage: 1885 ind. [Wojtaszyn *et al.* 2013]; Baszta Michałowska, fortress: 3363 ind. [Lesiński *et al.* 2008]; Błogosławie, fortress: 114 ind [Fuszara & Fuszara 2002]; Bochotnica, mine: 622 ind. [Kowalski & Dróżdż 2002]; Chelosiowa cave: 224 ind. [Wołoszyn 1994]; Ciemna cave: 393 ind. [Nowak & Grzywiński 2017]; Cieszków, cellar: 224 ind. [Gottfried *et al.* 2020]; Czarna cave: 580 ind. [Piksa & Nowak 2013]; Diabla Dziura cave: 127 ind. [Mleczek 2002]; Drozdowo, cellar: 118 ind. [Lesiński & Kowalski 2002]; Dująca cave: 54 ind. [Mysłajek *et al.* 2008]; Fort pod Bocznica, fortress: 85 ind. [Wojtowicz *et al.* 2014]; Fort Pomiechowo, fortress: 82 ind. [Lesiński *et al.* 2008]; Gdańsk — Orunia: 594 ind. [Ciechanowski & Przesmyska 2009]; Gdańsk — Wisłoujście fortress: 313 ind. [Ciechanowski *et al.* 2006]; Gdzie Grotołaz Wpadł cave: 194 ind. [Szkudlarek *et al.* 2008; Mleczek 2015]; Gierłoż, cellar:

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