ACTA ZOOLOGICA BULGARICA

Acta Zool. Bulg., 75 (3), September 2023: 395-406
Published online 30 June 2023
DOI: https://doi.org/10.71424/azb75.3.002678

Conservation Biology
Research Article

Lower Montane Bat Assemblage in a Central European Protected Area: A Case Study in the Świętokrzyski National Park, Poland

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Abstract. Świętokrzyski National Park protects a low forested mountain range in SE Poland. Its bat fauna is understudied, with ten species listed from the area so far but with no knowledge of their reproductive status and distribution. We recorded 15 species, eight of them reproducing in the park. For seven species, the present study is the first record in the park. Among the netted bats, *Myotis brandtii* and *Barbastella barbastellus* were the most numerous. The ultrasound recordings were dominated by the small *Myotis* spp., with only a little share of *Pipistrellus* spp. We found predominance of *Myotis mystacinus/brandtii/alcathoe* complex and significantly male-skewed sex ratio, both features typical for the bat assemblages of the higher mountain ranges (e.g., Carpathians). Comparison of individual rarefaction curves with the two other Polish montane national parks revealed, however, much faster species accumulation due to the lower altitude and milder climate. Capture data suggest elevational gradient of bat species composition, with a shift in the structure of the bat assemblages around 330 m a.s.l., resulting in formation of two zones. These zones roughly correspond to the belt of lowland oak-hornbeam forests and montane beech and fir forests. However, no such pattern was revealed by the acoustic survey.

Key words: Chiroptera, Vespertilionidae, fauna, mountains, temperate climate, vertical distribution

Introduction

National parks are crucial elements of the system of protected areas in Poland and the only protected territories in which all nature is subjected to conservation. Thus, they are the most likely to possess broad-scale inventories of biodiversity and one may expect that at least data about the species and groups to which the highest conservation value is assigned will be available. This is, however, not the case, and in many national parks of Poland even legally protected species are not fully surveyed, including the small but charismatic groups like mammals, which are well known to the society and for which a relatively high number of research specialists is available. Among mammals, bats (Chiroptera) are the order considered of supreme conservation significance, as all the species are strictly protected in Po-

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land and the European Union, and included in a pan-European international agreement solely devoted to them (EUROBATS). However, among the 23 Polish national parks, published results of at least partial bat surveys are available only for 15 (Jurczyszyn 1994, Kowalski & Lesiński 1995, Paszkiewicz et al. 1998, Lesiński 2001, Rachwald et al. 2001, Grzywiński 2003, Domagała & Karwowska 2009, Kmiecik et al. 2010, Piksa & Gubała 2011, Sachanowicz & Wower 2013, Bartonička et al. 2015, Grzywiński et al. 2020, Piskorski 2015, Piksa et al. 2017, Gottfried et al. 2020).

The Świętokrzyski National Park (ŚPN), although being the third national park in Poland (since 1950), has remained an area with only scarce data about the bat fauna (similarly to the entire Świętokrzyskie Mountains region). The first systematic studies on bat fauna of the region were conducted by Wołoszyn (1962); however, they were restricted to the caves and none of the sites were located in the national park itself. The first information on bat fauna of the ŚPN appeared already in the original evaluation of its area, where four species were mentioned (Čmak et al. 1959). Čmak (1968) listed ten bat species from the ŚPN, while the checklist of Huruk (1992) mentioned 12 species. The following two papers that explored the park's mammalian diversity contained information of only ten species (Huruk & Huruk 1996, Huruk & Jabłoński 2000). The species lists are not consistent among the papers mentioned above. Ten taxa appeared in the last four publications: *Myotis myotis*, *M. nattereri*, *M. dasycneme*, *M. daubentonii*, *Vespertillio murinus*, *Eptesicus nilssonii*, *E. serotinus*, *Pipistrellus pipistrellus*, *Nyctalus noctula* and *Barbastella barbastellus*; all of these were considered to be elements of the park's fauna in a previous monograph (Huruk & Jabłoński 2000). *Eptesicus nilssonii* was mentioned only in the last three publications (Huruk 1992, Huruk & Huruk 1996, Huruk & Jabłoński 2000). The first three papers (Čmak et al. 1959, Čmak 1968, Huruk 1992) mentioned two additional taxa, '*Plecotus auritus*' and '*Myotis mystacinus*'. Those, however, were later split into pairs of morphologically similar species (Wilson & Mittelmeier 2019) and, therefore, it is impossible to establish the taxonomic status of their records due to lack of preserved museum specimens. Later taxonomic development (Dietz et al. 2009) put into question the validity of '*P. pipistrellus*' mentioned in already published checklists. Any detailed information about the reproductive status, distribution, habitat preferences and contribution of particular bat species to the local assemblages in the area of the ŚPN is lacking. Only six species were listed based on single undated records, while for the majority of them any details of records (localities, dates, methods) are completely lacking. This casts significant doubts on the identification of some taxa, especially those, the preferred habitats of which the park is devoid of, a problem already mentioned by Huruk (1992). Concluding, the data about bats of the ŚPN must be considered of very low quality and even their checklist requires clarification.

The aim of this study was to establish species composition, distribution and status of bats in the Świętokrzyski National Park, with special emphasis on vertical patterns in their occurrence as well as to provide a critical synopsis of all available bat records for that crucial but understudied protected area.

Materials and Methods

The Świętokrzyski National Park (7626.45 ha) is located in south-eastern Poland. Its main part covers the highest range of the Świętokrzyskie Mountains, Łysogóry, with its highest peaks (Łysica and Agata – 613 m a.s.l., Łysa Mt. – 595 m a.s.l.), the adjacent part of the Klonowskie Range (peaking at Bukowa Mt. – 467 m a.s.l.) and parts of the Wilkowska and Dębniańska Valleys between them. Two large exclaves belong to the park, covering the isolated Chełmowa Mt. (347 m a.s.l.) and Serwis Forest (Buchholz et al. 2020). Small, scattered exclaves include buildings of the park management with adjacent vegetation in the Bodzentyn Town (275 m a.s.l.) and foresters' lodges in surrounding villages.

The majority of the ŚPN consists of the old mountains of the Palaeozoic Age, which are composed mostly of various, non-karstic sedimentary rocks: quartzitic sandstones, claystones and siltstones. Due to their age, those mountains are heavily eroded, revealing a smooth relief and a pattern of parallel hill ranges. Rocky outcrops are extremely scarce and restricted to few low crags in the summit parts of the Łysogóry and Klonowskie Ranges, while caves are virtually lacking. Despite the relatively low altitude, the climate is harsher than in the surrounding areas. The mean annual temperature is 6.6°C on Łysa Mt. and 7.7°C in Bodzentyn, mean January temperature is -3.7°C and -2.4°C, respectively, while while mean July temperature is 17.0°C and 18.1°C, respectively. The mean annual precipitation varies from 757 mm on Łysa Mt. to 577 mm in Bodzentyn. Surface waters are restricted mostly to a dense network of narrow streams (recently often drying out in summer), discharging from numerous springs and peat bogs. The only small river in the

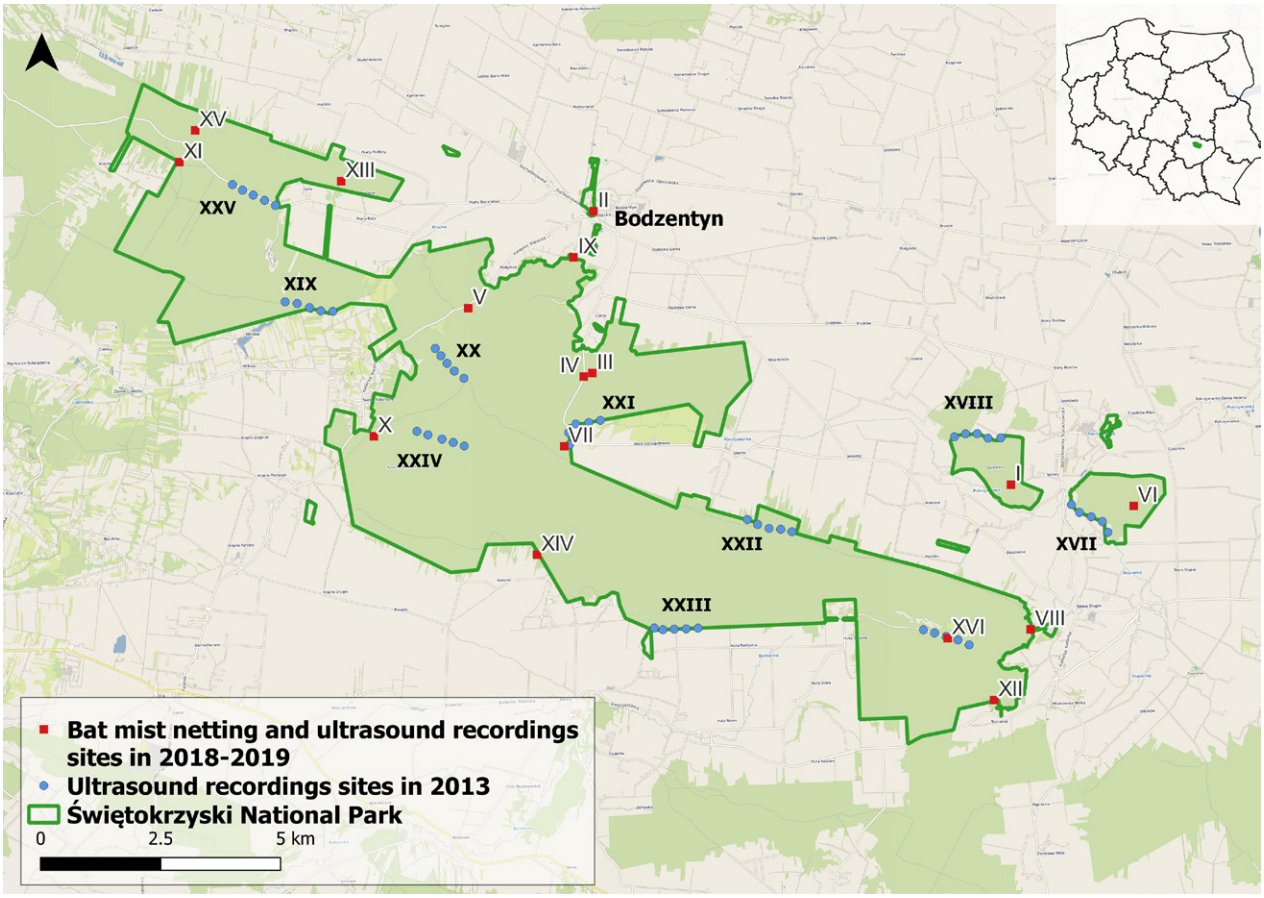

Fig. 1. Distribution of sites where bat mist-netting and broadband full-spectrum ultrasound recording (2018–2019) and zero-crossing frequency-divided ultrasound recording (2013) were performed within the borders of the Świętokrzyski National Park.

ŚPN is the Czarna Woda, except a short section of the Psarka River, crossing the exclave in Bodzentyn. Standing waters are even scarcer; the most notable are beaver ponds on Czarna Woda. The area of the park is mostly covered by forests (95 %), generally old (on average 103 years, locally extending to 200 years), built up predominantly by European silver fir *Abies alba*, European beech *Fagus sylvatica* and Scotch pine *Pinus sylvestris*. Dominant woodland communities are upland fir forest *Abietetum polonicum* and fertile montane beech forest *Dentario glandulosae-Fagetum*. In the lower parts of the valleys, a pine-oak forest *Querco-Pinetum* is common, while the warm exclave of the Chełmowa Mt. is covered by subcontinental oak-hornbeam forest *Tilio-Carpinetum*, with numerous, often 300-year-old Polish larch *Larix decidua* var. *polonica* (Buchholz et al. 2020). No villages are located in the ŚPN borders and only a few buildings are present, these are: a Benedictine abbey on the peak of the Łysa Mt., few small wooden chapels and various administrative buildings of the park. There are no abandoned mines within the park borders and the only anthropogenic structures that might serve as bat hibernacula are cellars and an underground cistern of the monastery.

To determine the species composition and distribution of bats in the Świętokrzyski National Park, we conducted overnight mist-netting of bats at 18 sites on 10–20 July 2018 and 2019 (Fig. 1). These sites were located either on forest roads and tourist trails, over small rivers and streams or small pools (Annex 1). Usually, 4–6 mist nets were set up at every site and controlled every 15–30 minutes from dusk until dawn. We determined species of the captured individuals based on both non-metric features and biometrics (Dietz et al. 2009). Additionally, we determined sex, age and reproductive status of every caught bat and then immediately released the individual at the same place where it was captured.

We recorded bat calls at most mist netting sites in 2018–2019 with the use of Wildlife Acoustics EM3+ and Pettersson D-1000X broadband ultrasound detectors, working in high-frequency (full spectrum) mode. All recordings of echolocation and social calls were analysed using the BatSound 3.31

program to determine the bat species, based on both metric and non-metric features (Russ 2012). Those calls that might represent several taxa with strongly overlapping bioacoustic parameters were uploaded to Wildlife Acoustics Kaleidoscope Pro 5 software that included automatic classifiers for all European bat species, based on maximum-likelihood estimator applied by Coleman et al. (2014). We chose Conservative (+1) level of sensitivity for the Auto ID function that produced less identifications but tended to have them more accurate. Due to the low probability of correct identification, we left calls of representatives of genus *Myotis* unidentified to the species level, with the exception of *M. myotis* and *M. alcathoe*.

Bat echolocation calls were also recorded in the park in the summer of 2013. During that season, we used the Titley Scientific Anabat SD-2 detector with the two types of microphones (standard and low frequency), working in zero-crossing mode. In total, ten recording sites were selected at the forest edges, surroundings of villages, streams and water bodies (Annex 1). Each site contained five points, distributed evenly along a line, approximately 1 km long. Thirty recordings (lasting 30 minutes at every site) were conducted; the total time of all recordings amounted 1800 minutes. Echolocation call sequences were analysed and identified using AnaLook software (Russ 2012). We calculated the number of Anabat files with calls of particular species per hour as a bat activity index, comparable among sites (Seidman & Zabel 2001).

Additionally, in 2019 we inspected all buildings within the borders of the park, mainly forester's lodges with adjacent farm buildings but also small chapels in search of daytime bats' roosts. During the two last hours before sunrise on the 18th of July 2019, we observed the buildings of the monastery on Łysa Mt. in search of swarming behaviour, also to detect daily shelters. On the 12th of January 2019 we checked also the underground cisterns and cellars of the monastery, as well as cellars of the forester's lodges, to establish if they were used by bats for hibernation.

Table 1. Checklist of bat species recorded in the Świętokrzyski National Park, with their frequency of occurrence, comments on their distribution and conservation status. Abbreviations: vc – very common (11–13 localities), c – common (6–10 localities), r – rare (3–4 localities), vr – very rare (1–2 localities), HD II – Annex II of the Habitat Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora), PL – Polish Red Data List (Głowaciński 2002), EU – European Red Data List (Temple & Terry 2007), Glo – global Red Data List (IUCN 2023), VU – vulnerable, NT – near threatened, DD – data deficient, LC – least concern.

Scientific name	Number of localities			Distribution status	Conservation status
	Total	Mist netting	Breeding		
Myotis myotis (Borkhausen, 1797)	10	4	-	c	HD II, EU LC, Glo LC
Myotis nattereri (Kuhl, 1817)	2	2	-	vr	EU LC, Glo LC
Myotis mystacinus (Kuhl, 1817)	4	4	2	r	EU LC, Glo LC
Myotis alcathoe (O. von Helversen et K.-G. Heller, 2001)	7	6	2	c	EU DD, Glo DD
Myotis brandtii (Eversmann, 1845)	6	6	3	c	EU LC, Glo LC
Myotis daubentonii (Kuhl, 1817)	2	2	-	vr	EU LC, Glo LC
Vespertilio murinus Linnaeus, 1758	1	1	-	vr	PL LC, EU LC, Glo LC
Eptesicus nilssonii (Keyserling et Blasius, 1839)	4	1	-	r	PL NT, EU LC, Glo LC
Eptesicus serotinus (Schreber, 1774)	11	3	1	vc	EU LC, Glo LC
Pipistrellus pygmaeus (Leach, 1825)	-	2	-	vr	EU LC, Glo LC
Pipistrellus nathusii (Keyserling et Blasius 1839)	2	1	-	vr	EU LC, Glo LC
Nyctalus noctula (Schreber, 1774)	7	3	1	c	EU LC, Glo LC
Nyctalus leisleri (Kuhl, 1817)	8	2	2	c	PL VU, EU LC, Glo LC
Plecotus auritus (Linnaeus, 1758)	3	3	2	r	EU LC, Glo LC
Barbastella barbastellus (Schreber, 1774)	13	7	6	vc	HD II, PL DD, EU VU, Glo NT

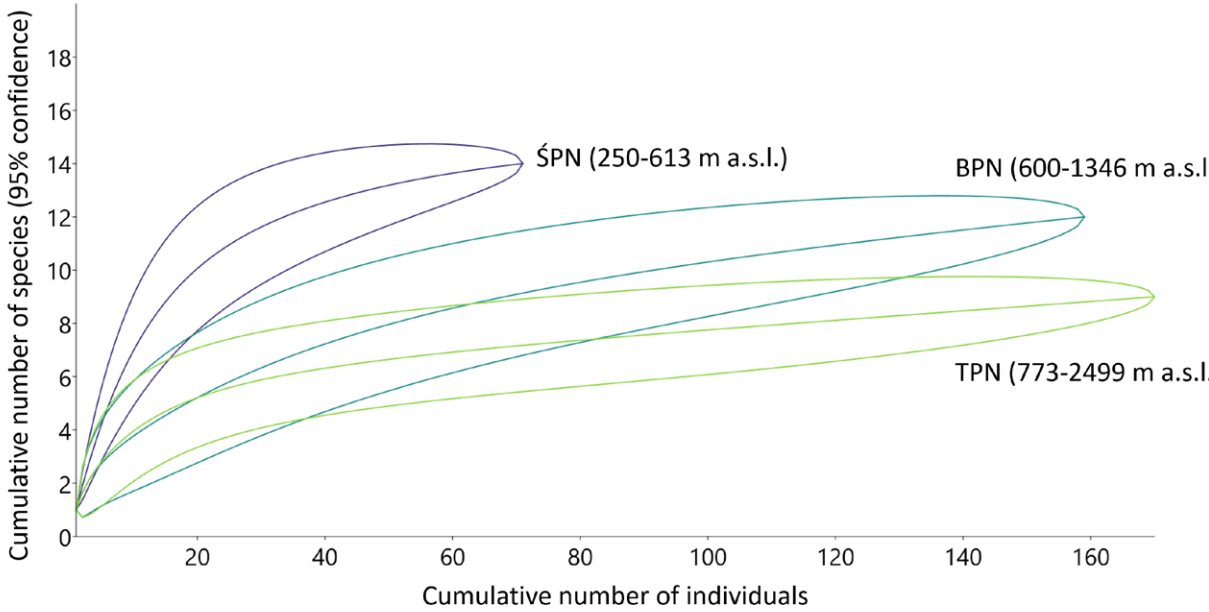

Fig. 2. Rarefaction curves for cumulative numbers of species plotted against numbers of bats captured in three Polish montane national parks of various altitudes. ŚPN – Świętokrzyski National Park (this study), BPN – Bieszczady National Park (Sachanowicz & Wower 2013), TPN – Tatrzański National Park (Piksa et al. 2017).

We used capture data only to compute the expected species richness, based on individual abundance rarefaction (species accumulation curve), using PAST ver. 4.07b (Hammer et al. 2001). This method allowed the in-detail comparison of species diversity of bats of the ŚPN with the two other Polish montane national parks where bats were extensively mist-netted (Bieszczady NP – Sachanowicz & Wower 2013, Tatra NP – Piksa et al. 2017). To test the difference between the obtained sex ratio and expected 1:1 value, we applied Pearson's chi-squared test for 2×2 tables.

Results

In total, 15 species of bats, belonging to seven genera, exclusively of the family Vespertilionidae, were recorded recently (2013–2019) within the borders of the ŚPN. Among them, 14 species were captured in mist nets, represented by 71 individuals and eight species appeared to breed in the park, based on the captures of lactating females or juveniles. Six species were represented solely by adult males, while *P. pygmaeus* – exclusively by echolocation and social calls. Two species were classified as very common, five as common, three as rare and five as very rare. The most frequent species, regarding the number of localities, appeared to be *B. barbastellus*, while the highest number of individuals was netted for *M. brandtii* (Table 1). An annotated synopsis of all available records can be found in Annex 1.

We successfully netted bats at all 16 (100 %) localities. The median number of captures per night was 3.5 (25 %–75 % quartiles: 2–4, min–max: 1–14). Among the 14 netted species, ten had been already recorded by 40 captures and after ten out of 18 sampling nights. Afterwards, detection of new species slowed down (Figs. 2–3) and, at least, a curve of individual rarefaction reached a plateau (Fig. 2). Sex ratio was significantly skewed towards males (♂♂ : ♀♀ 1.6 : 1, chi-square goodness-of-fit test 4.07, p=0.04) and seven species were not represented by any females at all. Bat assemblages were dominated by small, morphologically similar species of *Myotis* belonging to the *mystacinus* group (*M. mystacinus*, *M. brandtii*, *M. alcathoe*). In 2018–2019, they were represented by 25 of 71 captured individuals (35 %); we documented their presence at 11 out of 15 localities (Table 2). Additionally, small unidentified (or identified to the pair of species) bats of *Myotis* were recorded acoustically at 19 out of 25 localities, they also comprised 36.8 % of calls recorded in 2013. Unidentified *Myotis* spp. revealed also the highest index of activity among the distinguished taxa (Table 3). We recorded high frequency of occurrence and abundance of *B. barbastellus* (Tables 2, 3).

The species composition of bats appeared to reveal a shift around 330 m a.s.l., based on combination of both methods applied in 2018–2019. All captures of *N. leisleri*, the only cases of breeding *N. noctula* and the only captures of *P. nathusii*, *E.*

Table 2. Results of mist-netting and acoustic survey of bats in the Świętokrzyski National Park in 2018–2019. Shaded cells indicate breeding at a particular site, revealed by capturing of lactating females or juveniles. Abbreviations: d – calls recorded with ultrasound detector.

Altitude	Site	Species																Total
		Myotis myotis	*Myotis nattereri*	*Myotis mystacinus*	*Myotis alcathoe*	*Myotis brandtii*	*Myotis daubentonii*	small unidentified *Myotis*	*Vespertilio murinus*	*Eptesicus nilssonii*	*Eptesicus serotinus*	*Pipistrellus pygmaeus*	*Pipistrellus nathusii*	*Nyctalus noctula*	*Nyctalus leisleri*	*Plecotus auritus*	*Barbastella barbastellus*	
<330 m	I	-	1	-	-	-	-	d	-	-	1	-	-	-	-	-	-	2
	II	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	3
	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	IV	-	-	1	-	1	-	d	1	2	d	-	-	1	4	1	2	13
	V	-	-	-	1	-	-	d	-	-	d	d	-	-	-	-	-	1
	VI	-	-	-	-	-	-	d	-	-	-	-	1	2	4	-	-	7
	total	-	1	1	1	1	3	d	1	2	1	d	1	3	8	1	3	27
>330 m	VII	-	-	1	-	-	-	d	-	-	1	-	-	-	-	-	-	2
	VIII	-	-	4	-	3	-	-	-	-	-	-	-	1	-	5	1	14
	IX	-	-	-	1	1	-	d	-	-	-	-	-	-	-	-	-	2
	X	1	-	1	-	1	-	d	-	-	1	-	-	-	-	-	1	5
	XI	2	1	-	1	3	-	d	-	-	d	-	-	-	-	-	1	8
	XII	-	-	-	1	-	-	d	-	d	-	-	-	-	-	-	-	1
	XIII	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	XIV	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	4
	XV	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	4
	XVI	-	-	-	d	-	-	d	-	d	d	d	-	d	-	1	2	3
	Total	6	1	6	7	9	-	d	-	-	2	d	-	1	-	6	6	44
Total		6	2	7	8	10	3	d	1	2	3	d	1	4	8	7	9	71

Table 3. Species composition and index of activity of bats recorded with Anabat SD-2 ultrasound detector in 2013.

Altitude	Site	Species									
		Myotis myotis	*Myotis mystacinus/ brandtii*	*Myotis* sp.	*Eptesicus nilssonii*	*Eptesicus serotinus*	*Pipistrellus nathusii*	*Nyctalus noctula*	*Nyctalus leisleri*	*Barbastella barbastellus*	**Unidentified**
<330 m	XVII	1.2	3.6	1.2	-	4.8	-	0.4	4.4	-	-
	XVIII	0.4	7.6	-	-	-	-	-	2	0.8	-
	XIX	0.4	1.6	25.6	-	0.4	-	-	1.2	9.2	-
	XX	-	3.2	3.2	-	-	-	-	-	-	-
	XXI	-	-	12.8	-	-	-	-	-	12	1.2
>330 m	XXII	19.6	-	4.4	-	-	-	-	-	6	-
	XXIII	2.4	4	7.6	-	-	-	-	4.4	4.4	-
	XXIV	-	6.4	-	34.4	-	0.8	-	-	-	-
	XXV	-	2.8	1.2	-	10.4	-	-	0.8	3.2	-
	XVI	0.4	2.8	-	6.4	23.6	-	0.4	2.8	0.4	0.8
All points		2.1	2.8	4.7	3.4	3.2	0.3	0.3	1.1	2.7	1.1
% recordings		10.2	13.7	23.1	16.8	15.8	0.3	0.3	5.3	13.4	1.1

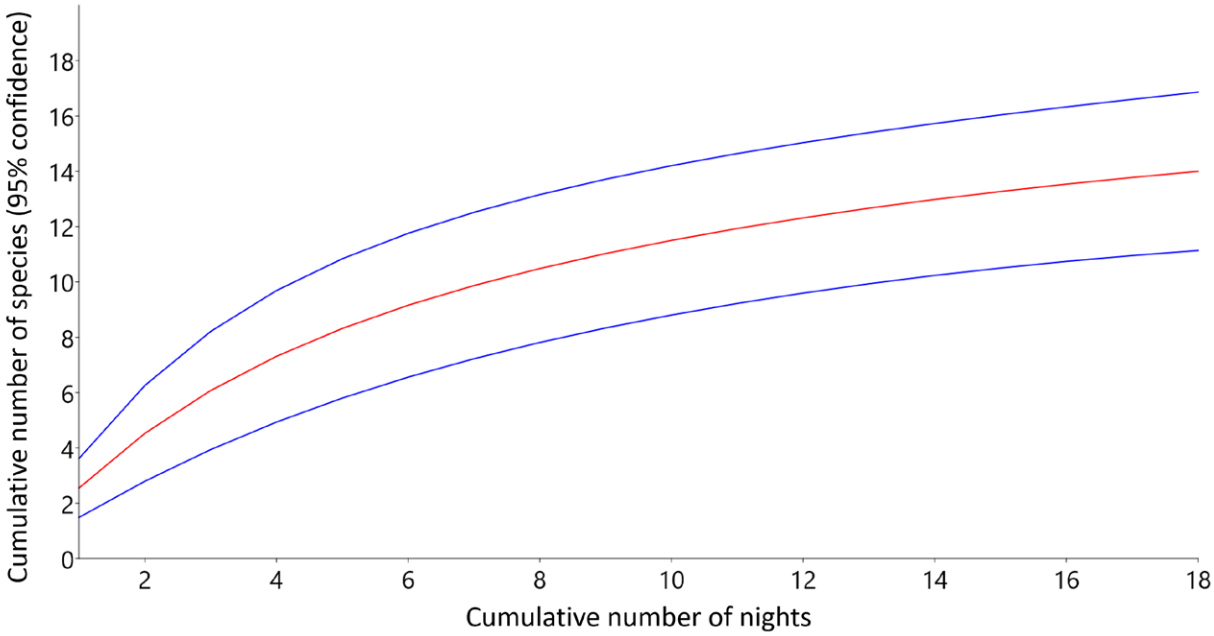

Fig. 3. Rarefaction curve for cumulative numbers of species plotted against sampling nights in the Świętokrzyski National Park, 2018–2019. Red – the line of trend, blue – confidence interval.

nilssonii and *V. murinus* were noted below that altitude. The lower zone hosted 14 species, including 13 captured in mist nets. All the captures of *M. myotis* and the only cases of breeding of *M. mystacinus* and *M. brandtii* were recorded above 330 m a.s.l. The higher zone hosted only ten species, including nine species captured in mist nets. However, even at the summits of both main ranges (sites XV–XVI), nine species were recorded (Table 2). No similar altitudinal pattern, neither qualitative nor quantitative, was revealed during the Anabat acoustic survey in 2013; *P. nathusii* was recorded at 391 m a.s.l. in Święta Katarzyna (site XXIV), while *N. leisleri* was recorded even at the highest sites (XXV and XVI) (Table 3). Notably, *B. barbastellus* was distributed evenly across the altitudinal gradient, from the valleys to the summits (Tables 2, 3).

No roosting bats in summer were found in the forester's lodges and surveyed wooden chapels. We did not find any bats hibernating within the borders of the park either. The underground water cistern near the abbey on the Łysa Mt. was not used by bats, despite the potentially suitable microclimate, while conditions in cellars under the abbey were not even favourable for wintering. Interviews with members of the monastic community during a visit in January 2019 revealed that the cellars had been submitted to large-scale renovation during the last few years and later had been extensively used.

Discussion

Based on our survey and critical review of earlier publications, we may assume that the bat fauna of the ŚPN consists of at least 15 species. One of them, *P. pygmaeus*, was reported for the first time for the area of the park. The presence of *M. brandtii*, *M. alcathoe*, *P. nathusii* and *N. leisleri* was discovered only during our studies in 2013 and/or 2018–2019 but had been previously reported in the newest monograph on the park's fauna (Buchholz et al. 2020). Two bat species, *P. auritus* and *M. mystacinus*, have to be treated as new for the ŚPN since 2018–2019, due to clarification of their taxonomic status, even if their names appeared in the earliest checklists (Čmak 1968, Huruk 1992). Their unclear status was probably the reason why they were omitted in the previous monograph (Huruk & Jabłoński 2000). We also confirmed the presence of eight species reported in the last three published checklists (Huruk 1992, Huruk & Huruk 1996, Huruk & Jabłoński 2000). We did not manage to confirm the occurrence of two other species mentioned in those publications. The first of them, *P. pipistrellus*, was reported from the Chełmowa Mt. by Čmak (1968), who even provided detailed information about its occurrence in particular forest habitats but no data about the methods applied for the bat survey. That information was repeated by every later checklist. *Pipistrellus pipistrellus* is a species easily detected and identified by its echolocation calls, yet not recorded in the ŚPN despite intensive acoustic

surveys. However, no ultrasound detectors were used in the 1960s, thus earlier reports might be an effect of wrong identification. The second species that we were not able to confirm was *M. dasycneme*, also reported for the first time by Čmak (1968) but without any details of location within the park. That species was again mentioned in all later publications (Huruk 1992, Huruk & Huruk 1996, Huruk & Jabłoński 2000). It is strictly associated with large water bodies, used as foraging habitats during reproduction (Ciechanowski et al. 2007), thus, it is unlikely to form any breeding population in the ŚPN, a fact already discussed by Huruk (1992). However, adult males and non-reproductive females can occur in regions devoid of larger waters during summer (Ciechanowski et al. 2007), while all individuals may undertake migrations up to 350 km between summer and winter roosts (Dietz et al. 2009). Two individuals were even found hibernating in 2000 in the adit on Bukowa Mt., less than 500 m outside the border of the park (M. Gwardjan in: Ciechanowski et al. 2007). Thus, we cannot exclude the seasonal occurrence of single *M. dasycneme* in the ŚPN, at least in some years but it should be kept out of the park's faunal checklists until any reliable evidence emerges.

Astonishingly, no author ever reported the occurrence of *Myotis bechsteinii* (Kuhl, 1817) in the ŚPN and we failed to capture it recently, despite netting in preferred habitats (broadleaved forests, see Wilson & Mittelmeier 2019). Although it is a rare and threatened species, its presence in the park is highly probable. Hibernating individuals of *M. bechsteinii* were spotted several times in the Łagowska Cave, about 8 km outside the borders of the ŚPN (Wołoszyn 1962, 1994), i.e., much closer than the longest distances covered by this extremely sedentary species during its summer-winter movements (Dietz et al. 2009). Another species that has not recorded but may appear in the ŚPN is *Plecotus austriacus* (Fischer, 1829). Its hibernating individuals were found in small cellars in the Masłowice-Scholasteria Village, about 3 km outside the borders of the park (Ł. Misiuna, G. Gołębniak, unpubl. data). Although the species roosts mostly in attics, it may forage in forests if they are adjacent to open areas (Dietz et al. 2009), i.e., dominant habitat class within the park's borders. Finding any further bat species within the park's borders in summer would require, however, a significant increase in sampling effort (perhaps, at least, twofold), as the rarefaction curve, representing the cumulative number of species against the number of captured individuals almost flattens well before our sample size was obtained.

The bat fauna of the ŚPN consists of several species considered to be of special conservation interest. Two species are included in Annex II of the Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora (the so-called Habitat Directive) as taxa that require establishment of Special Areas of Conservation within the Natura 2000 network. Four species are included in the Polish Red Data List (Głowaciński 2002), one is classified as threatened in the European Red Data List (Temple & Terry 2007) and the global IUCN Red Data List (IUCN 2023). Breeding of *B. barbastellus*, frequently recorded at many sites, irrespectively of altitude and forest communities as well as the high abundance of *N. leisleri* are distinct features of the park's bat fauna of significant conservation value. Both species, obligatory tree-dwellers, might be regarded as indicators of natural or semi-natural forests (Ruczyński & Bogdanowicz 2008, Wilson & Mittelmeier 2019). *Eptesicus nilssonii* is a typical boreal-alpine species, whose breeding and relatively high abundance of wintering individuals in Poland is mostly restricted to the regions of colder continental climate (Sachanowicz et al. 2006). Even in the Świętokrzyskie Mts, only three localities of *E. nilssonii* were found, all of them being hibernacula. One is located in the above-mentioned adit on the Bukowa Mt., while the other two – about 18 km and 30 km outside the borders of the park (Gubała & Kasza 1999, Misiuna & Gołębniak 2019). Another species of interest is *V. murinus* with a patchy distribution in Poland (Sachanowicz et al. 2006). Huruk & Jabłoński (2000) already mentioned hibernation of that species in the cellars of the abbey in Łysiec, which appears highly improbable as the species usually hibernates in buildings above the ground (Dietz et al. 2009), while no details of that observation were provided. It might be just a result of misidentification. Thus, we decided not to include it among the historical records of bats from the ŚPN, even if the presence of the species in summer was recently confirmed.

Myotis alcathoe, described as a new species only recently from Greece (Wilson & Mittelmeier 2019), requires special attention. Until recently, it was restricted to the southern part of Poland (Bashta et al. 2011); the northernmost known locality was found in the Silesian Lowland at 51°39'N (Kmiecik et al. 2020). In Europe, it extends its northern range as far as Sweden (Ahlén 2010), thus, it might be expected to occur on the entire Polish territory. However, no published records of that species in the Świętokrzyskie Mts. were available before our study. *Myotis alcathoe* is a forest specialist, associated with specific, often threatened habitats, includ-

ing natural or semi-natural oak-hornbeam and beech forests. It roosts almost exclusively in tree holes located at the canopy level but not in buildings (Wilson & Mittelmeier 2019). Frequent occurrence of *M. alcathoe* in the ŚPN is a specific trait of its bat fauna and one of its greatest conservation values.

The species richness of the ŚPN bat fauna (15) is just above the average as compared to all Polish national parks. The same number of species was recorded in the Bieszczady NP (but only 12 netted – Sachanowicz & Wower 2013), while in the whole montane part of the country it varies from eight in the Magura NP (Grzywiński 2003) to 22 in the Tatra NP. The last of the parks covers, however, the only alpine range in Poland and also has numerous karstic caves, where several species hibernate and participate in autumn swarming; the summer bat fauna of the Tatra Mts. consists also of 15 species, just as in the ŚPN, but only nine were netted (Piksa et al. 2017). The species accumulation rate in the Bieszczady NP, revealed by individual rarefaction curve, is much lower than that in the ŚPN (Fig. 2), thus one may assume that the bat assemblage in the second park is much more diverse, reflecting its lower altitude, despite similar habitats (predominantly beech forests on non-calcareous rocks). The Ojców National Park, the closest to the ŚPN and being a part of the same Polish Uplands, is inhabited by at least 20 bat species, but it is located in a much warmer karstic region that is rich in limestone outcrops and caves (Grzywiński et al. 2020). The number of bat species inhabiting the national parks located in Polish lowlands is usually lower, ranging from 11 species in the Białowieża NP (Rachwald et al. 2001) to 13 in the Polesie NP (Piskorski 2015), reflecting NE-SW gradient of bat species richness in Poland (Sachanowicz et al. 2006).

The specific feature of chiropteran fauna of the ŚPN is the predominance of small, morphologically similar species of *Myotis*, representing the *mystacinus* group. In some patches of upland fir forest of the Łysogóry Range, they appear to be the most common and locally the only bat species. Their high frequency of occurrence in the ŚPN make the bat fauna of the park resemble chiropteran assemblages of higher mountain ranges, i.e., the Carpathians and the Sudetes (Sachanowicz & Wower 2013, Piksa et al. 2017, Gottfried et al. 2020). On the contrary, in Polish lowlands, species of the *mystacinus* group are either extremely rare, usually represented exclusively by *M. brandtii* (Lesiński 2001, Rachwald et al. 2001) or do not occur at all (Ciechanowski 2002, Ciechanowski et al. 2002). In the northern lowland areas, they are replaced by members of the genus *Pipistrellus* that constitute a significant part of the local bat assemblages (Rachwald et al. 2001, Ciechanowski 2002, Ciechanowski et al. 2002, Kmiecik et al. 2010). In south-eastern Poland, all pipistrelle species are often scarce in summer, while *P. nathusii* and *P. pygmaeus* even do not breed there, especially in upland and montane areas; the presence of the last two species is restricted to single adult males, a situation also confirmed in the ŚPN. That striking pattern of mutual replacement is often considered a result of interspecific competition, as both groups of taxa reveal similar hunting tactics and opportunistic roosting behaviour (Kurek et al. 2017). That hypothesis, although tempting to be accepted, is far from being properly tested; coexistence of abundant *P. pipistrellus* and members of the *M. mystacinus* group in the Sudetes appears to contradict it (e.g., Bartonička et al. 2015, Gottfried et al. 2020), while the scarcity of *P. nathusii* and *P. pygmaeus* in southern Poland might equally be explained by low availability of water bodies and wetlands, i.e., preferred foraging habitats (Ciechanowski 2015). Another specific feature of the ŚPN bat fauna is the negligible contribution of *M. daubentonii*, considered one of the most common and numerous chiropteran species in Poland (Sachanowicz et al. 2006), associated, however, with water bodies as a foraging habitat (Wilson & Mittelmeier 2019). As such habitats are scarce in the park, so is *M. daubentonii*, similarly to the other regions of Poland with a poorly developed hydrographic network (Sachanowicz et al. 2006).

Finally, the bat fauna of the ŚPN is characterised by strong predominance of males, to the point that several species that occur there, do not breed in the study area. Male-skewed sex ratios are specific for montane bat assemblages in the summer (e.g., Sachanowicz & Wower 2013). Reproductively active females of several bat species, known for their high energy needs, are constrained from roosting and foraging in high-elevational habitats, due to increased thermoregulatory costs and decreased foraging efficiency. Thus, their relative abundance decreases with altitude; thus, only adult males are able to use the sub-optimal habitats at the higher sites (Cryan et al. 2000, Russo et al. 2002, Nardone et al. 2015). The predominance of males is another feature that makes chiropteran assemblage of the ŚPN similar to those occurring in higher mountain ranges.

European bat assemblages reveal clear zonation along the elevational gradient and their species composition significantly varies with altitude (Holzheider & Zahn 2001, Piksa et al. 2011, Piksa et al. 2013). Most available examples of that phenomenon were studied in the ranges much higher

than the Świętokrzyskie Mts., usually reaching the alpine zone, like the Carpathians or Alps and one may wonder if any elevational zonation occurs in low mountains completely located within the broad-leaved woodland zone. The study along a much shorter altitudinal gradient (350–1350 m a.s.l.) in the Pol'ana Mts., being part of the Slovakian Carpathians, suggests that it might be the case (Kaňuch & Krištín 2006). Due to much smaller sample size, we could not properly test the hypothesis about the elevational zonation of bat assemblages in the ŚPN; however, some pattern appears to emerge already. The two zones distinguished by us, with shift in species composition around 330 m a.s.l., roughly correspond with the two vegetation zones distinguished in Buchholz et al. (2020: 509–510). They divided the park into two areas, indicated by the 350 m a.s.l. contour line. The higher zone is formed by montane forests, predominantly beech and beech-fir ones; it covers the whole Łysogóry range, the summit parts of the Klonowskie Range and the Miejska Mt. The lower zone, covering the remaining part of the park, including valleys and exclaves, consists of upland and lowland forests, predominantly oak-hornbeam, alder and mixed pine ones. However, these zones are supposed to be formed mostly by diverse soil conditions, while the climate affects them only to a minor extent (Buchholz et al. 2020). Some of the observed differences in bat species composition between those zones correspond to the distinction between 'highland' and 'lowland' species by Kaňuch & Krištín (2006), where *N. noctula*, *N. leisleri* and *M. daubentonii* belong to the second category. Another reason for this zonation might be, however, an effect of specific local differences in vegetation structure. All the individuals of *M. myotis* have been captured above 330 m a.s.l., but that thermophilous species of Mediterranean origin (Sachanowicz et al. 2006), is highly unlikely to strongly associate with the montane zone. In fact, all its nursery roosts near the park are located at lower altitudes, at ~260 m a.s.l. (B. Sepioł, A. Nosek, unpubl.). When hunting, however, the species prefers woodlands with sparse or lacking undergrowth, especially mature beech stands (Dietz et al. 2009), a habitat that occupies the higher locations within the borders of the ŚPN. Moreover, the results of mist netting and earlier acoustic survey hardly correspond to each other, when dealing with the hypothesis about the persistence of elevational zones in the park. *Eptesicus nilssonii*, identified as 'highland' specialist (Kaňuch & Krištín 2006), was netted by us, unexpectedly, in the lower zone only, while its abundant calls were recorded, indeed, in the higher zone only.

The Świętokrzyskie Mts. abound in winter bat roosts, mostly karstic caves and abandoned mines (Wołoszyn 1962, 1992; Gubała & Wołoszyn 1996). However, their central and the highest part, located within the borders of the ŚPN appears to be completely devoid of bat hibernacula accessible for humans. That situation is partially a result of the geological structure of the area, dominated by quartzite sandstones (Buchholz et al. 2020). Cellars under forester's lodges are too poorly insulated for hibernation, while the apparent lack of bats wintering in underground cisterns on the Mt. Łysiec might be owing to the lack of proper entrances. The only winter roost already mentioned in the literature, the cellars of the abbey on the same mountain (Čmak et al. 1959, Huruk & Jabłoński 2000) were probably destroyed by adaptation works. The closest underground bat hibernaculum is, however, located less than 0.5 km from the park (Gubała & Kasza 1999). No anthropogenic summer roosts are known to be present in the ŚPN as well, even if some of the scarce buildings might be suitable for that function. Future bat surveys in the ŚPN should focus on location of natural summer roosts in trees, as the basic faunal inventory has been almost completed, with expectation to record additional one or two species.

Acknowledgements: We are thankful to Dr Jan Reklewski, Director of the Świętokrzyski National Park, for reception of our team, issuing a permit for field study in 2018–2019 and providing us with accommodation in 2018, as well as to Paweł Szczepaniak, manager of the Department of Monitoring, Research and Analyses of the Świętokrzyski National Park for help with organisation of our project, providing us with necessary contacts, direct help with logistics and fieldwork and conducting Anabat recordings in 2013. We also thank all the participants of our research-training camps in 2018–2019: Weronika Ardzińska, Michał Bełcik, Agnieszka Kiełtyka, Estera Kornacka, Joanna Modzelewska Anna Ewa Płotka, Monika Wołczecka, Marta Szurlej and Dawid Zyskowski. The project was partially funded by means of the Polish Society for Nature Protection "Salamandra" and Green Federation GAJA, thanks to a grant obtained from the International Visegrad Fund.

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Received: 18.11.2022
Accepted: 24.02.2023

Annex 1

A) Bat mist netting sites in the Świętokrzyski National Park (2018–2019), with altitude and habitat characteristics. Numbers of sites in accordance with Fig. 1

I, 253 m a.s.l., 50°53'14.44"N, 21° 4'20.15"E, Serwis forest, a crossroad in a pine-fir-oak forest; II, 265 m a.s.l., 50°56'26.35"N, 20°57'3.16"E, Psarka River in Bodzentyn, near the park administration headquarters, an alder forest; III, 275 m a.s.l., 50°54'37.38"N, 20°56'57.35"E, Czarna Woda River, beaver ponds, road in a pine forest; IV, 276 m a.s.l., 50°54'35.27"N, 20°56'48.14"E, Czarna Woda River in an alder forest and a road in a pine forest; V, 306 m a.s.l., 50°55'23.31"N, 20°54'47.00"E, roads in a fir forest near Łąki Miłości ('Meadows of Love'); VI, 327 m a.s.l., 50°52'57.93"N, 21°6'30.46" E, Chełmowa Mt., a crossroad in an oak-beech-larch forest; VII, 331 m a.s.l., 50°53'48.62"N, 20°56'25.30"E, Wola Szczygiełkowa, roads and small stream in a fir forest; VIII, 356 m a.s.l., 50°51'36.70"N, 21° 4'36.80"E; Nowa Słupia, a tourist trail in larch-pine-fir-beech-alder forest, with small streams; IX, 357 m a.s.l., 50°55'55.73"N, 20°56'40.51"E, Miejska Mt., a road in a fir-beech forest; X, 381 m a.s.l., 50°53'58.73"N, 20°53'2.77"E, Saint Francis Spring, a water pool with wooden chapel and a tourist trail in a fir and beech forest; XI, 402 m a.s.l., 50°57'6.63"N, 20°49'42.76"E, Klonów, a crossroad in a beech forest; XII, 415 m a.s.l., 50°50'49.78"N, 21° 3'55.86"E, Trzcianka, a crossroad in a pine-spruce forest; XIII, 431 m a.s.l., 50°56'51.09"N, 20°52'34.90" E, Psary Podlesie, a crossroad in a beech forest; XIV, 458 m a.s.l., 50°52'36.06"N, 20°55'53.35"E, Kakonin, roads in a fir forest; XV, 467 m a.s.l., 50°57'27.82"N, 20°50'0.40"E, Bukowa Mt., rocky outcrops and trails in a beech forest; XVI, 573 m a.s.l., 50°51'32.28"N, 21° 3'8.25"E, Łysa Mt., surroundings of the monastery and a trail in a beech forest

B) Bat call recording sites in the Świętokrzyski National Park (2013). Numbers of sites in accordance with Fig. 1

XVII, 258 m a.s.l., Chełmowa Góra; XVIII, 259 m a.s.l., Serwis; XIX, 296 m a.s.l., Grabowa; XX, 306 m a.s.l., Podgórze; XXI, 308 m a.s.l., Wola Szczygiełkowa; XXII, 353 m a.s.l., Dębno; XXIII, 376 m a.s.l., Jastrzębi Dół; XXIV, 392 m a.s.l., Święta Katarzyna; XXV, 393 m a.s.l., Psary; XVI, 573 m a.s.l., Łysa Mt. (location identical with that used in 2019 for mist netting, thus with the same number assigned)

C) Synopsis of all records of bat species in Świętokrzyski National Park. Roman numbers refer to the number of sites from the Annex A), data about sex, age and reproductive status – to the individuals captured in mist nets. Abbreviations: RD – recent data, HD – historical data (pre-2013), ad. – adult, juv. – juveniles, lact. – lactating, act. – sexually active, d – ultrasound recording with bat detector.

M. myotis: RD: X 17.07.2018 1♂ad.; XI 12.08.2018 1♂ad., 10.07.2019 1♂ad.; XIII 11.07.2019 1♂ad.; XV 16.07.2019 2♂♂ad.; XVII 2013 d; XVIII 2013 d; XIX 2013 d; XXII 2013 d; XXIII 2013 d; XVI 2013 d. ***M. nattereri***: RD: I 19.07.2018 1♂ad.; XI 10.07.2019 1♂ad. ***M. mystacinus***: RD: IV 17.07.2018 1♂ad.; VII 13.07.2018 1♀juv.; VIII 14.07.2019 3♀♀ad. lact., 1♂ad.; X 14.07.2018 1♂ad. ***M. alcathoe***: RD: V 19.07.2019 1♀ad. lact.; IX 10.07.2018 1♂ad., d; XI 12.07.2018 1♂ad.; XII 12.07.2019 1♀ad. lact.; XIV 16.07.2018 1♀ad., 1♂ad., 1♂juv.; XV 16.07.2019 1♂ad.; XVI 18.07.2019 d. ***M. brandtii***: RD: IV 15.07.2019 1♂ad.; VIII 14.07.2019 1♀ad. lact., 1♂ad., 1♂juv.; IX 10.07.2018 1♀ad. lact.; X 14.07.2018 1♂ad.; XI 12.07.2018 1♂juv., 10.07.2019 1♀ad. lact., 1♂juv.; XIV 16.07.2018 1♂ad. ***M. daubentonii***: RD: II 11.07.2018 3♂♂ad. HD: Chełmowa Góra (Čmak 1968). ***V. murinus***: RD: IV 15.07.2019 1♂ad. ***E. nilssonii***: RD: IV 17.07.2018 2♂♂ad.; XII 12.07.2019 d; XVI 2013 d, 18.07.2019 d; XXIV 2013 d. ***E. serotinus***: RD: I 19.07.2018 1♂juv.; IV 17.07.2018 d; V 19.07.2019 d; VII 13.07.2018 1♂ad.; X 14.07.2018 1♂ad., d; XI 12.07.2018 d; XVI 2013 d, 18.07.2019 d; XVII 2013 d; XIX 2013 d; XXV 2013 d. HD: Łysiec, cellars of the abbey, hibernation site (Čmak et al. 1959, Huruk & Jabłoński 2000). ***P. pygmaeus***: RD: V 19.07.2019 d; XVI 18.07.2019 d. ***P. nathusii***: RD: VI 15.07.2018 1♂ad.; XXIV 2013 d. ***N. noctula***: RD: IV 17.07.2018 1♂ad. act.; VI 15.07.2018 1♂ad., 1♀ad. lact.; VIII 14.07.2019 1♂ad.; XVI 2013 d, 18.07.2019 d, XVII 2013 d. HD: Łysiec; vicinity of Kakonin forester's lodge; forest section 202 near Wólka Milanowska (Huruk & Jabłoński 2000). ***N. leisleri***: RD: IV 17.07.2018 3♀♀ad. lact., 1♂juv.; VI 15.07.2018 2♀♀ad. (1 lact.), 2♀♀juv.; XVI 2013 d; XVII 2013 d; XVIII 2013 d; XIX 2013 d; XXIII 2013 d; XXV 2013 d.; ***P. auritus***: RD: IV 15.07.2019 1♀ad. lact.; VIII 14.07.2019 3♂♂ad., 2♀♀ad. lact.; XVI 18.07.2019 1♂ad. ***B. barbastellus***: RD: III 17.07.2019 1♀ad. lact.; IV 17.07.2018 1♀ad. lact., 15.07.2019 1♀ad. lact.; VIII 14.07.2019 1♀ad. lact.; X 14.07.2018 1♂juv.; XI 12.07.2018 1♂juv., d; XV 16.07.2019 1♂ad.; XVI 2013 d, 18.07.2019 2♀♀ad. lact., d; XVIII 2013 d; XIX 2013 d; XXI 2013 d; XXII 2013 d; XXIII 2013 d; XXV 2013 d.