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Bat activity and bat migration at the elevation above 3,000 m at Hoher Sonnblick massif in the Central Alps, Austria (Chiroptera)

Aktivita a tah netopýrů v nadmořské výšce nad 3000 m v massivu Hoher Sonnblick ve středních Alpách v Rakousku (Chiroptera)

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Abstract. Recent studies on the presence and activity of bats at high elevations show, surprisingly, that large numbers of bats cross the Alps up to 2,500 m a. s. l. This study takes the next step: to investigate bat activity at an elevation above 3,000 m a. s. l. The main study site was located on the top of Hoher Sonnblick at 3,106 m a. s. l. (Salzburg, Austria). Bat activity was monitored during September and October 2014, and permanently from March to November 2015, with an automated recording device. To compare bat activity at a lower location, a study site at 2,273 m a. s. l. was also monitored from May to October 2015. Contrary to our expectations, we found bats present at 3,106 m from mid-April to mid-September. However, periods of bat activity at these high altitudes were shorter than at lower elevations and were interrupted by longer periods with no activity. Among the recorded species there were all the long-distance migrants in Europe: *Nyctalus leisleri*, *N. noctula*, *Pipistrellus nathusii* and *Vespertilio murinus*. *Eptesicus nilssonii*, a predominantly sedentary species, was also recorded on the mountain top as well as *Pipistrellus pygmaeus*. Bat activity was linked to milder weather conditions. However, we did record bats at wind speeds of up to 12.2 m/s and temperatures as low as –2.1 °C.

Key words. Chiroptera, Austrian Alps, high elevations, phenology, climatic conditions, bat migration, mating behaviour.

INTRODUCTION

Studies on bats at altitudes above 2,000 m a. s. l. are very rare. Patterson et al. (1996) recorded bats in the Peruvian Andes up to 3,450 m a. s. l. Further proof that bats are able to inhabit very high elevations comes from Nepal, where *Plecotus auritus* was found at 3,938 m a. s. l. (Thapa et al. 2014). These records are located at different latitudes with distinct climatic conditions. In this study we focus on European bats. The alpine habitats with their extreme environmental conditions seem unsuitable for bats; and, moreover, it is difficult and harsh for researchers to work there. Because of that, high mountain regions are not among the most popular bat study sites.

Investigations in the Pyrenees revealed that bats are able to use alpine environments up to 2,800 m a. s. l. (Garin et al. 2003, Alberdi et al. 2013, 2015). Some rare records of bats at elevations above 2,000 m are known from the Alps, for example, a maternity roost of *Plecotus auritus* was found at 2,300 m in the Swiss Alps (Schober & Grimmberger 1998), *Eptesicus* *nilssonii* was caught at 2,300 m in the Hohen Tauern/Austria (Ausobsky 1970), *Pipistrellus nathusii* was recorded at an altitude of 2,200 m at the Colm de Balme/Swisse (Hausser 1995) and recently Zingg & Bontadina (2016) detected eight bat species in the Swiss Alps at the Jungfrau Joch at an elevation of over 3,000 m a. s. l.

Since only short-term studies had been conducted so far, we started systematic investigations on bats in the highest regions of the Central Alps in 2012 (Widerin 2012, Widerin & Jerabek 2014, Widerin & Reiter 2017), partly within an international project investigating bat migration throughout the Alpine Arc (Bontadina et al. 2014). With study sites located between 2,300 and 2,700 m a. s. l., a surprisingly high number of eleven bat species was detected by acoustic methods, eight of them proven by mist netting at the Weißsee region (Hohe Tauern, Salzburg, Austria; Widerin & Reiter 2017). The long-term study at Weißsee revealed that bats use high alpine habitats more intensively than previously expected. However, bats use high elevations in the Alps not only for foraging or breeding. Annual migration movements also occur there, which is demonstrated by the records of all four long-distance migrants at different Alpine locations (Bontadina et al. 2014, Widerin & Reiter 2017).

Hutterer et al. (2005) summarized the banding data on European bats, and their results illustrate broad migration mainly from northeastern to western and southwestern Europe. Some

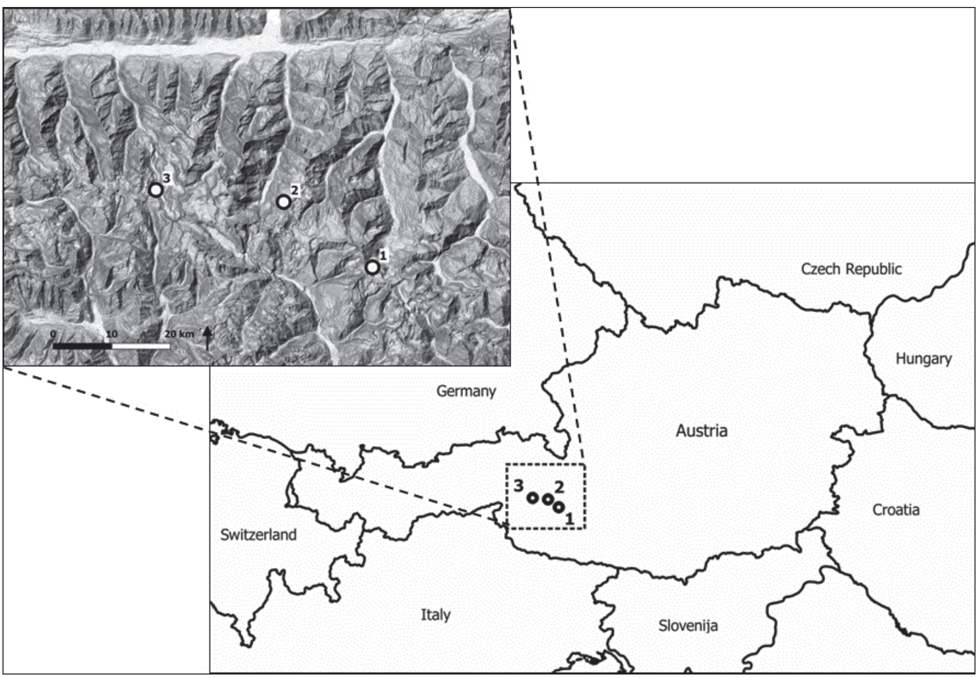

Fig. 1. Location of the study sites of Sonnblick (1) and Glockner (2) and the reference site of Weißsee (3). Map source: MapSurfer.Net.
Obr. 1. Lokalisace studovaných lokalit Sonnblick (1) a Glockner (2) a porovnávací lokality Weißsee (3). Zdroj mapy: MapSurfer.Net.

bat species exhibit long-range annual migrations between summer and winter roosts across Europe. Maximum recorded distances include 1,905 km in *Pipistrellus nathusii* (Petersons 2004), 1,787 km in *Vespertilio murinus* for (Markovets et al. 2004), 1,600 km in *Nyctalus noctula* (Strelkov 1969) and 1,568 km in *Nyctalus leisleri* (Ohlendorf et al. 2000). South of the Austrian Alps, discoveries of banded bats in wintering areas including northern Italy, the Adriatic coast in Italy and Croatia as well as in Slovenia are known. All these bats were banded in eastern Germany. These records are related to *Pipistrellus nathusii* and *Nyctalus noctula* (Hutterer et al. 2005), and the migration routes of these bats might lead across the Austrian Alps near our study sites. Both species have already been recorded at Alpine passes in Austria during former studies (Widerin & Reiter 2017). Previous results also indicated that many bats migrate across the Alpine Arc. If masses of bats cross the Alps on their annual migration routes and possibly concentrate their flyways at Alpine passes, a severe conservation problem would occur if wind farms were built in alpine areas. Knowledge of bat activity and bat migration at high elevations is still limited. More studies on diversity, phenology, behaviour and use of different elevations in high alpine areas are needed to provide arguments for the protection of migrating bats.

The overall aim of this study was to investigate bat activity and bat diversity at a very high study site in the Alps, to discover if bats are present at such high elevated habitats. For that purpose we chose the main study site on the top of Hoher Sonnblick with an elevation of 3,106 m a. s. l.

The study was designed to answer the following questions: (i) Which bat species can be found at elevations above 3,000 m? (ii) Are migratory bat species present even at this elevation? (iii) What is the phenology of bats at this elevation? (iv) What are the differences in bat activity between different elevations? and, (v) Which factors influence the activity of bats at high elevations?

MATERIAL AND METHODS

Study area and study sites

Hoher Sonnblick (3,106 m, 47.05389° N, 12.95722° E)
The main study site was situated on the summit of Hoher Sonnblick, a glaciated mountain on the main Alpine Arc. It is located in the Hohe Tauern National Park in the south of the province of Salzburg at the border between the southern and northern sides of the Austrian Alps (Fig. 1). The Hoher Sonnblick rises at the end of the north-south bound valley of Rauriser Tal. On the steep summit there is the meteorological Sonnblick Observatory, which enables investigations throughout the year.

The study site is dominated by extreme environmental conditions such as coldness, high wind speeds, fog, suddenly changing weather and short summers (for climatic data see Table 1). Rocks, snow and glaciers characterize the study site. There is no vegetation with flowering plants at this height except around the buildings on the top of Hoher Sonnblick. Small patches of alpine vegetation with blooming flowers probably arose as a consequence of the permanent human presence and its accumulated waste since the establishment of the Sonnblick Observatory in 1886.

Pilatusscharte (2,906 m, 47.05603° N, 12.95035° E)
Pilatusscharte is a wind gap, which is situated 500 m west and 200 m lower than the observatory at the Sonnblick (Fig. 2).

Glockner (Eberhard Stüber Research Centre for High-Alpine Studies in the Hohe Tauern National Park) (2273 m, 41.12249° N, 12.82128° E)

Table 1. Climatic conditions (mean values) for Hoher Sonnblick, 3,106 m a. s. l. (Climate Data for Austria, ZAMG – Zentralanstalt für Meteorologie und Geodynamik); y = year
Tab. 1. Podnebné podmínky (průměrné hodnoty na hoře Hoher Sonnblick, 3.106 m n. m. (Climate Data for Austria, ZAMG – Zentralanstalt für Meteorologie und Geodynamik); r = rok

month / měsíc	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	y/r
daily temperature / denní teplota [°C]													
	−11.7	−12.2	−10.9	−8.3	−3.3	−0.4	2.1	2.3	−0.6	−3.7	−8.3	−10.5	−5.5
highest temperature / nejvyšší teplota [°C]													
	−9.4	−9.8	−8.4	−5.7	−1.0	2.1	4.8	4.8	1.7	−1.5	−6.0	−8.2	−3.1
lowest temperature / nejnižší teplota [°C]													
	−13.8	−14.4	−13.0	−10.4	−5.4	−2.6	−0.1	0.2	−2.5	−5.5	−10.3	−12.7	−7.5
number of rainy days / počet deštivých dnů													
	14.8	14.4	18.0	19.1	16.6	18.2	17.5	16.2	13.7	12.7	15.4	16.2	192.8
wind speed / rychlost větru [m/s]													
	8.2	7.9	7.5	6.7	5.8	5.5	5.3	5.0	5.8	7.1	7.4	8.3	6.7
number of days with wind speed ≥11 m/s / počet dnů s rychlostí větru ≥11 m/s													
	15.8	14.1	14.1	11.3	7.4	7.1	6.9	6.4	8.8	12.5	13.3	16.0	133

This study site is located at the Großglockner High Alpine Road, 11 km east of Hoher Sonnblick. Since the study site was easily accessible via the road, it was also possible to gather continuous data at a lower elevation. However, winter closure of the road postponed the start of the survey until 4 May.

Methods

The period of permanent data collection at Hoher Sonnblick lasted from 19 August to 17 September 2014, and from 19 March to 22 November 2015. The Pilatusscharte study site was very difficult to reach; thus the recording of bat calls was only possible for two nights: 29 August and 30 August 2015. At the Glockner study site, data were collected continuously from 4 May to 24 October 2015, with the same methods used at Hoher Sonnblick, except for the heating system installed in 2015. We monitored bat activity with automatic ultrasound recording units ("batcorder", ecoObs), which allow continuous monitoring over long periods. Batcorders digitally record ultrasonic signals in real time (500 kHz, 16 bit) and use an online analysis to distinguish between bat calls and ultrasound signals of other origins. Further advantages of this system are the comparability of the results between different devices (calibrated sensitivity) and the omnidirectionality of the microphone (www.ecoobs.de). In order to reflect the different conditions at this elevation, the settings of the batcorder were adjusted as follows: (i) quality = 20, (ii) threshold level = –36 dB, (iii) post-trigger = 800 ms, and, (iv) critical frequency = 16 kHz. Because we expected migrating bats, we chose a long post-trigger. Bats on transfer flights often use low calls with long call intervals. Otherwise bat passes would probably be recorded with only one call which is difficult to identify. For the long-term studies, the batcorder was placed within a plastic box ("Waldbox") and the battery was recharged using a solar panel. At the end of each recording night, a GMS-module sent a status update to a mobile phone. This message contained the number of recordings of the last night, the overall number of recordings, memory capacity of the SDHC card and microphone sensitivity. The box was fixed on the top of the Sonnblick observatory and at the north-side balcony of the Eberhard Stüber Research Centre at the Glockner study site.

Due to the experience obtained during previous investigations at high alpine study sites, we knew that the ultrasound microphones cannot stand the adverse weather conditions at very high elevations for a long time. In order to achieve high quality data at the permanent recording site at Hoher Sonnblick, a self-made heating system for the microphone was invented and applied, which was run by the electricity supply of the observatory. Thus, the system was able to produce continuous data with good microphone sensitivity throughout the monitoring period.

The recorded bat calls were automatically stored and measured by the software bcAdmin 2.28 (www.ecoobs.de). Subsequently, the measurements were analyzed by the software batIdent 1.03 (www.ecoobs.de). This software compares unknown bat calls with reference calls based on a mathematical approach (package 'Random forest' in R). This system is able to achieve 95% correct classifications under training conditions (www.ecoobs.de). In the field, these conditions are rarely met and some identifications made here – especially for species such as *Vespertilio murinus* and *Nyctalus leisleri* with very similar calls – may be incorrect (Marckmann & Runkel 2010, Russo & Voigt 2016). However, both of these species are migratory and, therefore, any erroneous classification would only have a minor effect on the interpretation of the results related to the goals of this work. Furthermore, if the available information for some call sequences is insufficient, the procedure results in classifications only to OTU's (Operational Taxonomic Units), which are groups of bats which cannot be distinguished by their calls in some cases such as "Nycmi" (*Nyctalus leisleri*, *Vespertilio murinus*, *Eptesicus serotinus*) and "Nyctaloid" (*Nyctalus* spp., *Eptesicus* spp., *Vespertilio murinus*, *Tadarida teniotis*). After this automated classification, all sequences were manually checked using the sonogram bcAnalyze 1.11 (www.ecoobs.at) and compared with descriptions of bat calls of the different species (Zingg 1990, Russo & Jones 2002, Hammer et al. 2009, Skiba 2014, Barataud 2015). Collectively, this procedure resulted in a classification of each call

Fig. 2. Northward view of Hoher Sonnblick with the Observatory (S) and Pilatusscharte (P); and, the Kleinfleißkees glacier in the foreground, 27 August 2015 (www.foto-webcam.eu/webcam/sonnblick).
Obr. 2. Pohled severním směrem na horu Hoher Sonnblick s lokalitami Observatory (S) a Pilatusscharte (P); v popředí ledovec Kleinfleißkees, 27. srpna 2015 (www.foto-webcam.eu/webcam/sonnblick).

Table 2. Detected bat species and OTUs (Operational taxonomic units) and number of recorded call sequences during the study (2014–2015); species that are very unlikely to occur (taking into account the high elevation) are shown in parentheses
Tab. 2. Zaznamenané netopýří druhy či OTU (operační taxonomické jednotky) a počet zaznamenaných hlasových sekvencí během studie (2014–2015); v závorkách jsou jména druhů jejichž výskyt je velmi nepravděpobný vzhledem k velké nadmořské výšce
OTUs / OTU: Mkm = *Myotis daubentonii*, *M. mystacinus*, *M. brandtii*, (*M. bechsteinii*); Nycmi = *Nyctalus leisleri*, *Vespertilio murinus* (*Eptesicus serotinus*); Nyctaloid = *Nyctalus* spp., *Eptesicus* spp., *V. murinus*, (*Tadarida teniotis*)

species / OTU druh / OTU	Hoher Sonnblick (3,106 m) 19 VIII – 17 IX 2014	 19 III – 22 XI 2015	Pilatusscharte (2,906 m) 29–30 VIII 2015	Glockner (2,273 m) 4 V – 24 X 2015	total úhrnem
M. mystacinus / M. brandtii	0	0	0	3	3
Eptesicus nilssonii	4	142	0	571	717
Vespertilio murinus	4	18	14	2	38
Nyctalus leisleri	1	4	11	0	16
Pipistrellus nathusii / (P. kuhlii)	39	4	9	23	75
Nyctalus noctula	2	1	4	1	8
Pipistrellus pygmaeus	0	0	4	0	4
Pipistrellus pipistrellus	0	0	0	6	6
Pipistrellus pipistrellus / P. pygmaeus	1	0	0	0	1
Mkm	0	0	0	7	7
Myotis sp.	0	0	0	8	8
Nycmi	39	41	18	113	211
Nyctaloid	38	112	16	69	235
Plecotus sp.	0	0	0	16	16
Chiroptera sp.	2	6	1	5	14
total / úhrnem	130	328	77	824	1359

sequence to the lowest possible OTU. High quality meteorological data were provided by the Sonnblick Observatory (ZAMG 2018).

RESULTS

Recorded bat species

We were able to detect at least six bat species at the elevation of 3,106 m (Table 2): *Eptesicus nilssonii*, *Vespertilio murinus*, *Nyctalus leisleri*, *N. noctula*, and *Pipistrellus pygmaeus.* In one case it was not clear whether the record was related to *Pipistrellus pipistrellus* or *P. pygmaeus*. Some bat species cannot be distinguished with certainty by acoustic methods if social calls are missing, as, for example, the recorded species pair *Pipistrellus nathusii/P. kuhlii.* However, because there are no published records of *Pipistrellus kuhlii* in the country of Salzburg so far (Jerabek et al. 2005) and because of the high elevation, it is assumed that all these records belong to *Pipistrellus nathusii.* Many sequences were assigned to the Operational Taxonomic Units (OTU's) "Nycmi" and "Nyctaloid", because of the similarity of calls (Table 2).

At the Glockner study site located at 2,273 m, at least seven bat species were noticeable. Species of the genus *Myotis* and *Plecotus* were recorded only at the lower study site (Table 2).

Call activity and phenology

During the whole survey in 2014 and 2015, a total of 535 bat call sequences were recorded at the Sonnblick study sites (Table 2). The highest call activity was found for *E. nilssonii.* Other frequently recorded species were *P. nathusii*/(*P. kuhlii*), *V. murinus* and, with smaller numbers of bat passes, *N. leisleri.* Half of all sequences (52%) were assigned to the "Nycmi" and "Nyctaloid" OTUs. Concerning the high elevation of the study site, these OTUs comprise particularly *E. nilssonii*, *N. leisleri*, *N. noctula* and *V. murinus*. Species detected only rarely were *N. noctula* and *P. pygmaeus* (Table 2).

The total call activity at the lower study site was more than twice as high compared to the higher study site. However, the same ranking in the number of recorded call sequences for species and OTUs was evident. The vast majority of the recordings were assigned to *E. nilssonii.* Furthermore, the "Nycmi" and "Nyctaloid" OTUs were recorded frequently, and in smaller numbers *P. nathusii*/(*P. kuhlii*) as well as the genus *Plecotus.* All other species and OTUs were only rarely registered (Table 2).

Bats were present on the top of Sonnblick from mid-April to the end of August 2015; this period was punctuated by longer intervals with no activity (Fig. 3a). Spring activity was lower compared to that in late summer. In early spring, only single call recordings were noticeable. We monitored the first bat calls on 15 April 2015, and registered a few more (10) from early to mid-May. Thereafter, several weeks with almost no activity followed, except for two recordings on 9 June 2015. With the beginning of July, more activity was noticeable during five days. Again a few weeks without records followed until the beginning of August when the largest number of bat call sequences was recorded. During the night of 6 August 2015, 205 sequences were detected that comprise two thirds of all recordings in 2015. Call activity ceased at the end of August, followed by several weeks of bad weather. However, in 2014 bats were recorded until 17 September. Since this was the last day of the investigated period, bat activity may have lasted longer (Fig. 3). Furthermore, a comparison of the time periods from 19 August to 17 September in 2014 and 2015 revealed that the interannual variation in bat activity at such heights may be considerable. Whereas in 2015 no bat activity was registered from September onwards, two bursts of activity with relatively high numbers of recorded call sequences occurred in 2014 (Fig. 3).

Sonnblick 2014

During 30 nights of permanent monitoring from 19 August until 17 September 2014, bat activity was noticeable in 11 nights. A total of 130 bat call sequences were detected during this period (Table 2). Two gaps between periods of activity were due to wintry conditions at the study site. The first of them was on 20 August 2014, when a thunderstorm brought 15 cm of snow at night. In the sample period of 2014, most bats passed Sonnblick in the first week of September after a period of five days of cold and windy weather (see Fig. 5).

An extraordinarily high activity was registered on the night of 6 September 2014, with 68 recorded call sequences (see Fig. 4). The first burst of activity during that night consisted of seven recordings of *P. nathusii*/(*P. kuhlii*) within 20 minutes. One hour later, between 10:23 p.m. and 10:37 p.m. CET (Central European Time), 48 recordings were made in those 15 minutes. These recordings belonged particularly to the "Nycmi" and "Nyctaloid" OTUs. Three hours later at

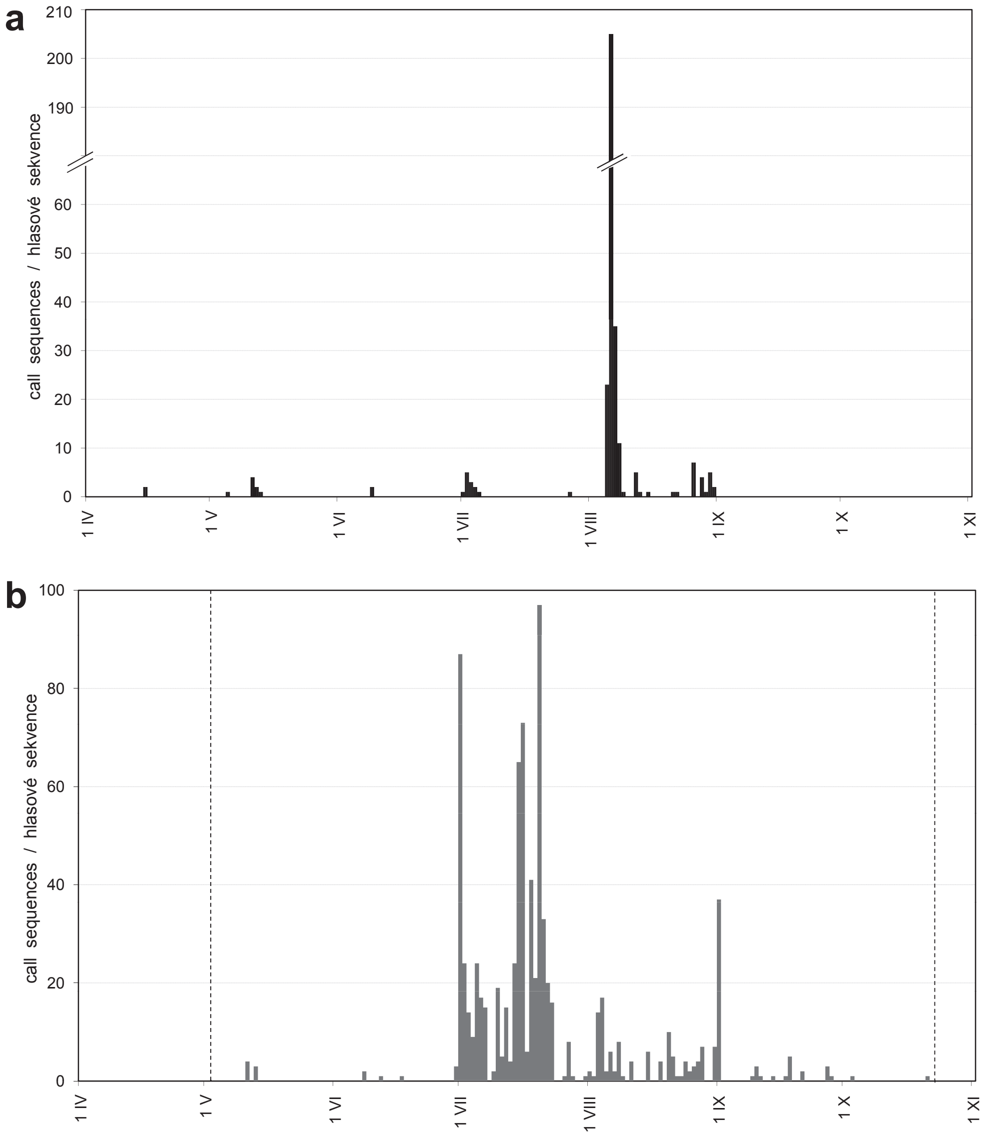

Fig. 3. Call activity of bats during 2015 (13 March to 22 November). (a): on top of Hoher Sonnblick (3,106 m); (b): at the Glockner study site (2,273 m). Note the difference in the recording period between the study sites – dashed line indicates the monitoring period at the Glockner site and the discontinuous y-axis in (a).
Obr. 3. Hlasová aktivita netopýrů v průběhu roku 2015 (13. března až 22. listopadu), (a) na vrcholu hory Hoher Sonnblick (3.106 m); (b) na lokalitě Glockner (2.273 m). Lze si povšimnout rozdílu mezi oběma místy v údobí nahrávání – přerušovaná čára ukazuje období sledování na lokalitě Glockner, jakož i přerušená osa y v části (a).

2 a.m., there was a further group of five sequences of *P. nathusii*/(*P. kuhlii*), which occurred within two minutes. Weather conditions at 10 p.m. were as follows: wind speed: 4.7 m/s; wind direction: north, temperature: +1.5 °C; relative humidity: 100% (fog). During that night, the wind speed was constantly at 4.7 m/s between 8 p.m. and 11 p.m. At midnight, wind speed increased to 6.3 m/s and remained constant till morning. Furthermore on 5 September 2014, there was a noticeable group of 10 records within three minutes from the "Nycmi" group species.

Variaton of bat activity during August and September in 2014 and 2015:
In 2014 the period of bat activity was notably longer. Interrupted by spells of poor weather, bats were recorded even during September till the last day of investigation, whereas in 2015 bat activity stopped at the end of August (Fig. 5).

Pilatusscharte – Hoher Sonnblick

For two consecutive nights we were able to compare bat activity at the mountain top of Hoher Sonnblick with that recorded in the lower wind gap of Pilatusscharte (Fig. 2). Both nights were starry without any fog. We found ten times higher call activity at the lower site (23 and 54 call sequences) compared to that at the summit (2 and 5 call sequences). Only calls of long--distance migratory species were detectable during those two nights, as well as four sequences of *P. pygmaeus*.

The data from the longitudinal acoustic monitoring yielded phenology data for species or groups of bat species (OTUs).

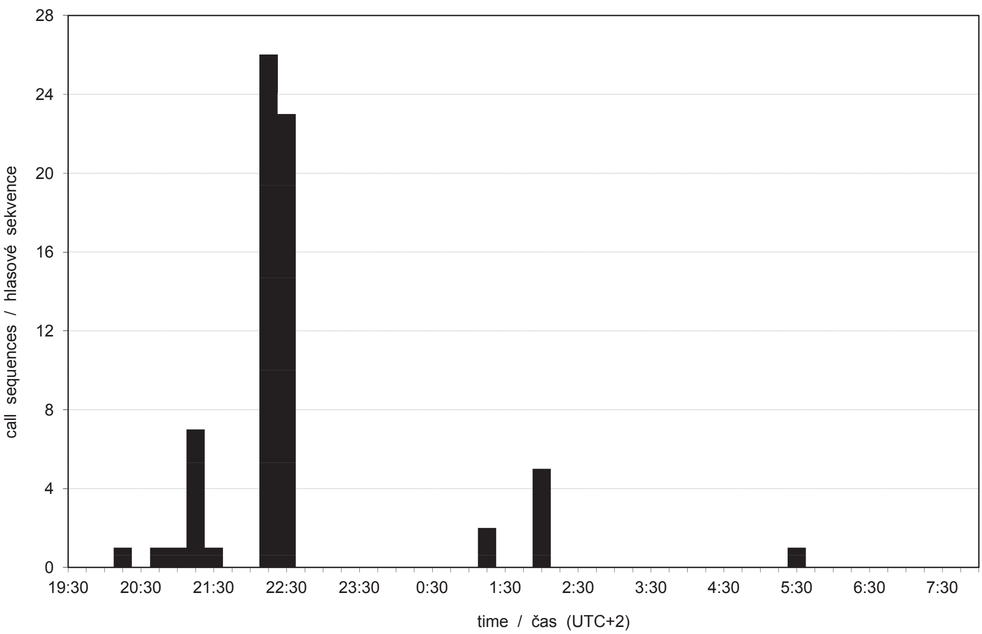

Fig. 4. Call activity of bats during the night of 6 September 2014 (7:15 p.m. till 8:00 a.m., UTC+2).
Obr. 4. Hlasová aktivita netopýrů v noci 6. září 2014 (19:15 až 8:00, SELČ).

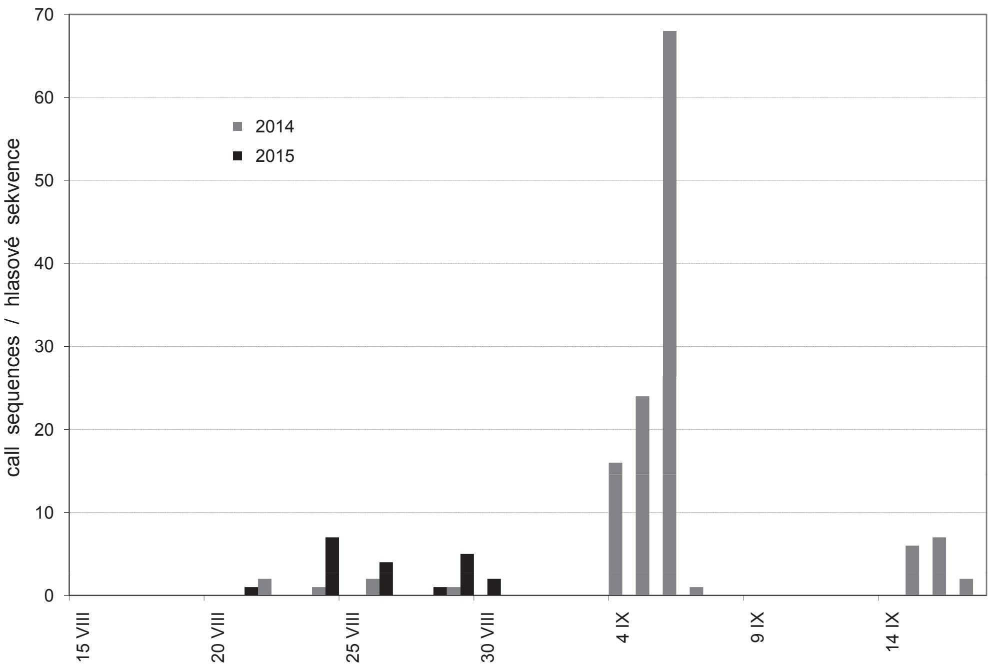

Fig. 5. Call activity of bats on the top of Hoher Sonnblick from 19 August to 17 September in 2014 and 2015.
Obr. 5. Hlasová aktivita netopýrů na vrcholu hory Hoher Sonnblick od 19. srpna do 17. září v letech 2014 a 2015.

Migratory species (*N. leisleri*, *N. noctula*, *P. nathusii*, and *V. murinus*) showed infrequent call activity in spring from mid-April to mid-May. During summer only two recordings of "Nycmi" (*V. murinus/N. leisleri)* were made on 9 June 2015. Three weeks with no bats followed until another recording at the end of July. The highest call activity of migratory species occurred during August and September.

Eptesicus nilssonii was detected only in summer and autumn although it was the species with the highest call activity. The first records of *E. nilssonii* were detected at the beginning of July for four days. The highest call activity was registered at the beginning of August, especially during one night when the extraordinary number of 205 sequences was detected (6 August 2015). In September, the activity was again much lower with only four records of this species. From 5 August until 7 August 2015, we recorded the highest call activity during our study. At least half of the 205 records during the night of 6 August could be assigned to *E. nilssonii*. This species was present more or less continuously between 1 a.m. and 4 a.m. Other species or OTUs present were *V. murinus* and the "Nycmi" and "Nyctaloid" OTUs.

Bat activity at Hoher Sonnblick was recorded from 15 April until 31 August 2015 (139 days), while at the approximately 800 m lower situated Glockner study site, bat calls were registered from 11 May until 21 October 2015 (164 days). It is important to note that monitoring at the Glockner site did not start until 4 May due to inaccessibility of the site.

We noticed 27 nights of bat activity at Hoher Sonnblick, compared to 66 nights at the Glockner site. Furthermore, 12 activity periods (continuous nights with bat activity) were registered at Hoher Sonnblick and 21 at the Glockner study site. The longest period of bat activity at Hoher Sonnblick was five consecutive nights, whereas at the Glockner site it was 15 nights.

Factors influencing bat activity

Wind speed and air temperature

By comparing call activity with meteorological data, we found that most activity occurred at air temperatures above zero, although bats were active even at –2.1 °C. Furthermore, bats preferred wind speeds between 2 and 3 m/s. However, we recorded bat calls at wind speeds up to 12.2 m/s (Fig. 6).

Wind direction

During spring migration only 13 bat call sequences were recorded on the top of Hoher Sonnblick (2015). Wind direction during the hour of recording was from the west (5 sequences), northeast (4 sequences), south (2 sequences) and northwest (2 sequences).

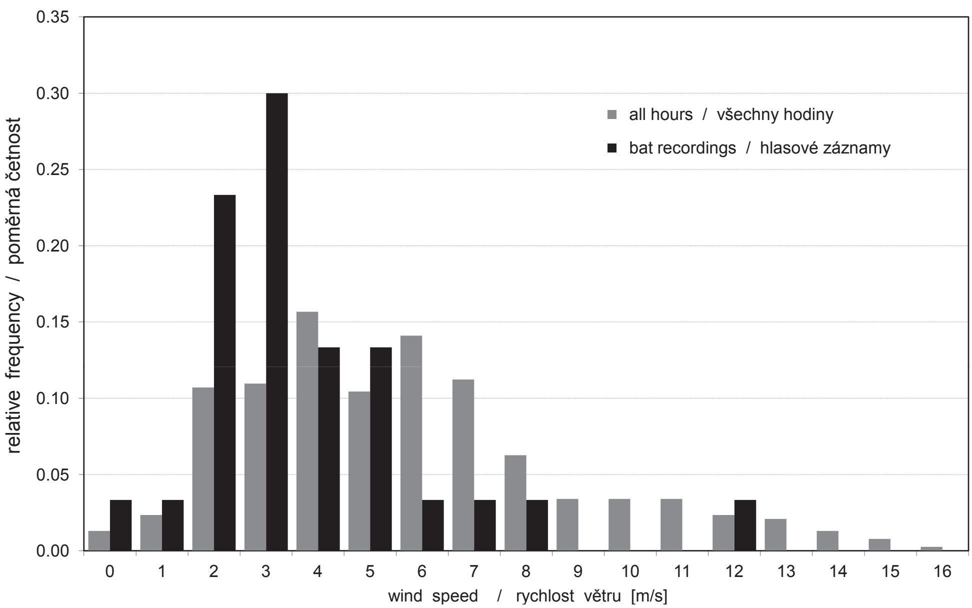

Fig. 6. Relative frequency of bat activity (n=130 call sequences) and overall wind speed from 19 August until 17 September 2014.

Obr. 6. Relativní četnost aktivity netopýrů (n=130 hlasových sekvencí) a celková rychlost větru od 19. srpna do 17. září 2014.

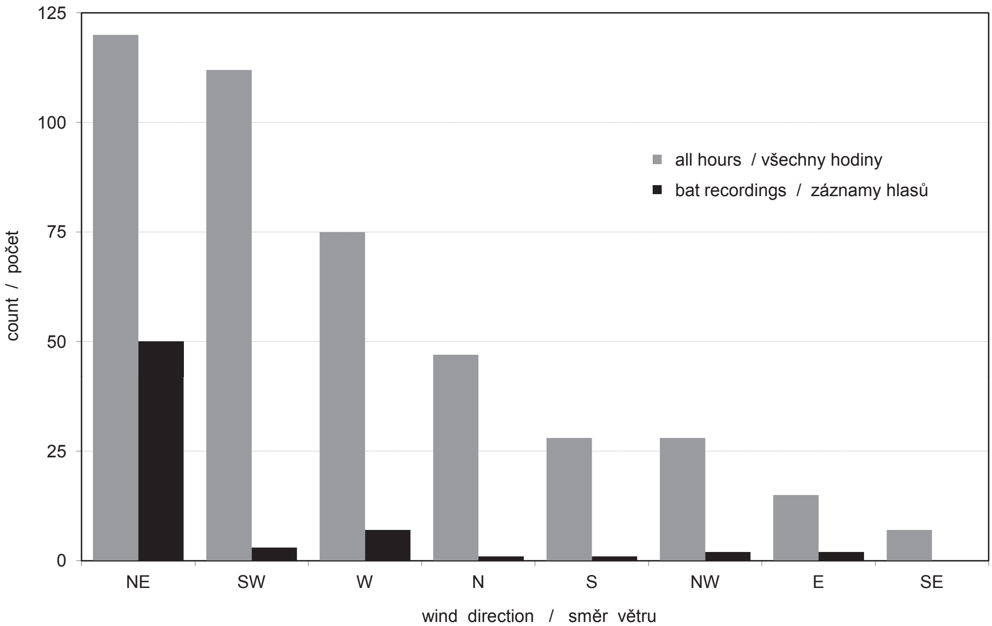

Fig. 7. Hourly wind direction during the night and call activity of migratory bat species (n=66 call sequences) during the autumn migration (27 July to 3 August 2015).
Obr. 7. Hodinový směr větru v průběhu noci a hlasová aktivita stěhovavých druhů netopýrů (n=66 hlasových sekvencí) během podzimního tahu (27. července do 3. srpna 2015).

For the autumn migration we compared all sequences of migrating bats (*N. noctula*, *N. leisleri*, *P. nathusii*, *V. murinus* and the "Nycmi" OTU) between 27 July and 31 August 2015 to hourly measured wind directions. Most bat passes were recorded with wind blowing from the northeast (Fig. 7).

During the three nights with the highest call activity in 2015 (5 to 7 August, Fig. 3a), air temperature was between 7 and 8 °C. Wind speed was mostly below 5 m/s and wind direction was predominantly from the northwest, north or northeast.

DISCUSSION

Bat species found at high elevations

Despite the harsh conditions at the elevation of 3,100 m a. s. l., we recorded at least six bat species. These comprise 21% of the currently known 28 species in Austria (Spitzenberger 2001, Dobner 2010, Reiter et al. 2016). Furthermore, it is remarkable that all four long-distance migrants in Europe (Hutterer et al. 2005) could be detected at these elevations: *N. noctula*, *N. leisleri*, *P. nathusii* and *V. murinus.* The same species were detected by Zingg & Bontadina (2016) in the Swiss Alps: at an elevation of 3,460 m a. s. l., eight species were detected by acoustic methods during 36 nights of investigation.

Although we monitored bat activity only by acoustic methods, our results are plausible considering the comparable results and experience of an extensive study at Weißsee (Salzburg) (Widerin & Reiter 2017). That study site is located only 20 km west of Sonnblick at the end of a north-south bound valley (Fig. 1). Within that study, 8 bat species were confirmed by mist-netting at elevations between 2,300 and 2,500 m a. s. l. Moreover, four bat species were mist-netted at Fuscher Törl, which is in close proximity to our Glockner study site (Reiter et al. 2016). Altogether, the mist-netting results of these studies confirmed the acoustic data.

Call activity and phenology

Our study revealed an unexpected high bat activity, considering the very high elevation. The species with the highest call activity on all study sites was *E. nilssonii* (Table 2). This bat is cold-resistant with a distribution area far into northern regions such as Scandinavia. This species even breeds above the Arctic Circle (Hutterer et al. 2005, Dietz et al. 2016) with environmental conditions similar to those in alpine regions. In the longitudinal study at Hoher Sonnblick (2015), at least 43% of all call sequences could be assigned to *E. nilssonii*. Taking into account that some calls were assigned to the "Nyctaloid" OTU, this species may be even more dominant. This finding is consistent with the results of our study at Weißsee at 2,300 m a. s. l. where *E. nilssonii* comprised more than a half of all 33,000 collected call sequences (Widerin & Reiter 2017).

E. nilssonii was present mainly during summer. No recordings were detected at Hoher Sonnblick in spring. It is usually considered to be a sedentary bat, and the migratory behaviour of *E. nilssonii* seems to be rather small-scale (Rydell 1993, Gerell & Rydell 2001, Dietz et al. 2016). Only single long flights have been recorded (Tress 1994, Hutterer et al. 2005). One documented long-distance movement in Europe is 445 km from Germany to Turrach (Styria/ Austria). This banded bat was found after six years near an alpine pass located 70 km east of Hoher Sonnblick (Tress 1994). This bat probably crossed the Alps near our study sites. Perhaps the single records of *E. nilssonii* during our previous study at Weißsee during spring migration (April–May) are related to migrating individuals. Hüppop & Hill (2016) recorded *E. nilssonii* at an offshore platform in the North Sea. In their study they hold the opinion that this species might be more migratory than is implied by the low number of recoveries of banded bats.

E. nilssonii was present on the top of Sonnblick for four days at the beginning of July 2015, and during the first days of August. The study at Weißsee yielded a comparable activity pattern for *E. nilssonii*, which was regularly recorded foraging during summer (Widerin & Reiter 2017). Thus, *E. nilssonii* is the most active bat species at high alpine regions in the Austrian Alps during summer.

In contrast to the phenology of *E. nilssonii,* the activity pattern in the long-distance migrants is different. We recorded these species in spring during the deepest wintry conditions at Hoher Sonnblick and in late summer as well as autumn, but they were absent in early summer. *P. nathusii* was the first bat in spring (15 April) but in the autumn migration period it was present only in late August 2015, and in September 2014, at Hoher Sonnblick. In our investigation at Weißsee we found a similar pattern for *P. nathusii*: being absent during summer until mid-August, although the last records in the season (3 and 21 October 2014) were assigned to this species (Widerin & Reiter 2017).

The fact that migratory bat species appeared during migration periods at an elevation of 3,100 m a. s. l. at the border between the northern and southern part of the Austrian Alps suggests that they cross the Alps. Similar results were obtained in our study at Weißsee (Widerin & Reiter 2017). Moreover, all data from high elevations in the Central Alps are consistent with the conclusion that a huge number of bats cross the Alps every year on their route between summer and winter sites (Bontadina et al. 2014, Zingg & Bontadina 2016, Widerin & Reiter 2017). This hypothesis is also supported by the fact that records of migratory species are very rare during early summer at lower elevations in the area of Salzburg (Stüber et al. 2014).

A clear difference in bat activity was evident between spring and autumn: the call activity of migratory species in spring was strikingly lower than that in autumn. This difference was obvious at the study sites at Sonnblick, as well as at Weißsee. Similar results are known from studies on wind farms (Cryan & Barclay 2009, Rydell et al. 2010, Hayes 2013, Behr et al. 2018). Cryan & Barclay (2009) discuss some explanations for this fact. One reason might be the mating behaviour of migrating bats at the masts of wind farms during autumn migration. For our alpine study sites we have no persuasive explanation for such an enormous difference in activity.

Possible reasons: (i) The study site may serve as a "stop-over" where bats interrupt their autumn migration to fill up their energy reserves, resulting in higher activity, whereas in spring the study sites in alpine habitats are under wintry conditions and bats only pass by. (ii) Flight heights may differ in spring and autumn: Furmankiewicz & Kucharska (2009) found such difference on a migration route along a river in Poland. Perhaps bats in general fly higher during spring migration even in alpine regions when they are not searching for prey. (iii) Bats may fly in different heights when approaching and leaving an alpine pass. Studies on different flight altitudes at wind turbines revealed that migratory bats such as *P. nathusii* fly between 55 m and 60 m above ground. The genera *Nyctalus*, *Eptesicus*, *Pipistrellus* and *Vespertilio* were detected at levels of 90 m to 140 m (Feltl et al. 2015). Our experience in catching bats with mist nets at alpine passes indicated that migrating bats sometimes fly low above ground, sometimes less than one meter high when they are reaching the pass (our net). When they are leaving the pass, they are at a high altitude above the slope and probably fly more or less at that altitude through the following valley. So if the recording device is placed on the slope of the alpine pass, the migrating bats are recorded on the way up to the pass, possibly flying lower than usual in lowlands. Conversely during the spring migration, bats may perhaps pass high above the batcorder beyond the hearing range of the device. (iv) The differing numbers of spring and autumn migrants could be due to the morphology of the mountains and valleys on the opposite sides of the pass leading to varied flyways; alternatively bats may be more widely dispersed on their way back. (v) The mating behaviour during autumn migration cannot be excluded as a possible factor (see below).

The rarest bat species of this study was *P. pygmaeus*. Only four recordings were made at the Pilatusscharte. On the summit of Sonnblick, we noted one sequence, which could be assigned to the species pair *P. pygmaeus*/P. *pipistrellus.* Whilst *P. pipistrellus* was common (at 2,300 m) during summer, *P. pygmaeus* was found only between mid-August and mid-September. The study at Weißsee revealed similar results for *P. pygmaeus* where only 11 sequences of the total >33,000 were assigned to this species (Widerin & Reiter 2017). The status of *P. pygmaeus* as a sedentary or migratory bat in Central Europe is unclear. This bat is very common in the city of Salzburg throughout the year (Stüber et al. 2014), whereas there are almost no records of long distance flights in Central Europe (Dietz et al. 2016). One documented record belongs to an individual which was banded in eastern Germany and was recovered one year later on the Adriatic coast at a distance of 775 km (Ohlendorf in Dietz et al. 2016). However, the recording of this bat at such high elevations in the Central Alps, as well as at the Jungfrau Joch in the Swiss Alps (Zingg & Bontadina 2016) during migration season suggests that this species may also be migratory.

Variation in species composition and bat activity

Hoher Sonnblick versus Glockner

During the period from 4 May to 24 October 2015, the study sites at 3,106 and 2,273 m a. s. l. were monitored simultaneously. We found that the call activity at the lower study site of Glockner was more than twice as high as that at the Sonnblick site. However, during the spring migration there was low bat activity at both study sites until the end of May. The most striking differences occurred in July, with weeks of constant bat activity at the lower site and almost no records at Hoher Sonnblick (Fig. 3). Alpine meadows at the elevation of 2,273 m a. s. l. offer enough insects for foraging, but habitats at 3,100 m a. s. l. are usually bare of vegetation. Moreover, our study at Weißsee revealed a very high activity of sedentary bats, mainly *E. nilssonii*, during July (Widerin & Reiter 2017). Interestingly in the present study we found the highest call activity per night at the higher study site (Fig. 3a). In summary, more activity occurred at the lower study site of Glockner, especially during July, when sedentary bats used this elevation for foraging. Above 3,000 m a. s. l., a lack of autochthone insects and bad weather conditions reduced bat activity.

The latest recordings of bats at the Sonnblick study site were made at the end of August (only 2015), whereas at the lower study site bats were still active till the end of October. Periods of bat activity at the Glockner study site are similar to our findings at Weißsee at the same elevation (Widerin & Reiter 2017).

Altogether, we found the following differences in bat activity between the study site at 3,100 m a. s. l. and the study site at 2,200 m a. s. l.: (i) a shorter period of bat activity at the higher study site; (ii) an overall lower level of bat activity at the higher study site; (iii) fewer activity periods and fewer nights with bat activity at the higher study site; (iv) shorter periods of continuous bat activity at the higher study site.

Hoher Sonnblick versus Pilatusscharte

Data collected simultaneously during two starry nights at the 200 m lower study site of Pilatusscharte and the Sonnblick-Observatory yielded a tenfold higher bat activity than at the mountain top. This preliminary result indicates that migrating bats prefer lower mountain passes. The echolocation system works only at a maximum distance of about 100 m. Bats also use visual orientation (Ulanovsky & Moss 2008). Evidence suggests that bats can navigate toward distal visual beacons such as mountains and are able even to see the starlight of individual stars (Williams et al. 1966, Childs & Buchler 1981). Their conclusions are supported by our records from the night of 6 September 2014, when a surprisingly large number of 68 bats crossed the high summit of Sonnblick. The night was foggy, so perhaps without visual orientation they missed the wind gap. However, more detailed studies are needed to verify this preliminary finding.

Factors influencing bat activity at high elevations

Weather conditions

In our study, bats were more likely to be active at temperatures above 0 °C but were still active at temperatures down to –2.1 °C. Similar findings were obtained from the long-term study at Weißsee (Widerin & Reiter 2017) with call sequences recorded at temperatures as low as –5.8 °C. Furthermore, these results are in agreement with the study at the Glockner site where the last recorded bat was flying at –5.0 °C (Reiter et al. 2016). Bats were more frequently recorded at wind speeds of 2 to 3 m/s, but with a tailwind they were even active at up to 12.2 m/s. At Weißsee they were active at up to 13 m/s (Widerin & Reiter 2017). Our results indicate that bats are more active at lower temperatures and faster wind speeds at higher elevations than in the lowlands. This fact should be taken into account when wind farms are planned and designed at these elevations.

During the autumn migration, the wind was mainly from the northeast and southwest and migrating bats preferred wind from the northeast (Fig. 7). These data match the main direction of bat migration across Europe from the northeast to southwest (Hutterer et al. 2005). Evidence suggests that bats use tailwind during migration. Tailwinds make it easier to pass over the Alps at elevations above 3,000 m a. s. l. Similar outcomes were obtained by Dechmann et al. (2017) who investigated the migration behaviour of *N. noctula* in relation to weather conditions. Their results showed that *N. noctula* preferred tailwind or slow headwind when starting their spring migration.

Food availability

The high alpine habitats (rocks, glaciers) lack vegetation, and no autochthone insects are available as food for bats at the heights above 3,000 m a. s. l. However, migrating insects together with insects blown up from lower areas are potential food sources for bats. One reason for the extraordinarily high bat activity at Weißsee was that swarms of migrating insects passed the southbound valley in August and September (Mazzucco 1967, 1975). An observation on 4 July 2015 below the Sonnblick observatory showed a great number of living and dead insects densely covering the old snowfield. Different groups of insects including plant lice, ladybugs, flying ants and butterflies had obviously been blown up from the valley and were being carried across the glacier from the southwest in a very warm afternoon. Interestingly this was during the first activity period of *E. nilssonii* at Hoher Sonnblick. This event can perhaps be interpreted as an altitudinal migration of the bat which came up from the valley and was feeding on the insects there. The survey by Heiniger (1989) on arthropods on snowfields in the Jungfrau region in the Swiss Alps (2,320 m a. s. l.) revealed a considerable density of allochthone insects accrued by passive wind transport or active migration. Future simultaneous studies on bats and insects at Hoher Sonnblick may clarify possible correlation.

Bat behaviour

During our study, we usually recorded call sequences typical for migrating species on transfer flight with lower calls and long inter-call intervals (Skiba 2014). The call sequences were mostly short because the bats quickly passed the recording device. Interestingly, many call sequences of *E. nilssonii* had a much longer duration, up to 10 seconds, supporting the idea that they were not only passing. This fact became obvious during the night with the overall highest activity (6 August 2015), mainly due to this species being present for hours around the observatory which has a high mast on its roof. Although we sampled almost 100 calls of this species, no feeding buzz was recorded. In a few files, at least two individuals were recorded simultaneously. Social calls were also registered. Thus, the presence of *E. nilssonii* could be explained in the context of mating behaviour. The mating season in *E. nilssonii* starts already in July (Dietz et al. 2016), and this bat appears at swarming sites from mid-July to mid-August (Meschede & Rudolph 2004) with a peak at the beginning of the swarming period (Piksa et al. 2011). Mating behaviour is generally known to occur at caves, rock walls, church steeples or high objects such as towers or masts of wind turbines (Cryan & Barclay 2009, Dietz et al. 2016). However, more detailed research is needed to clarify the presence of sedentary species at these heights.

Conclusion for bat conservation

Based on our findings, we strongly recommend that bats and their requirements are examined and taken into account when planning the construction of wind farms at high alpine elevations.

Environmental conditions at alpine habitats are much more adverse than those in lowlands. Bats have adjusted their activity to lower temperatures as well as to higher wind speeds. So if measures are applied to mitigate adverse effects of wind farms on bats, the results of studies at lowlands have to be reconsidered.

The investigated activity at one study site can vary greatly over the years mainly due to changing weather conditions. Further studies are needed in order to obtain more information and understand reasons for bats being present at such high elevations.

SOUHRN

Sučasné výzkumy aktivity netopýrů ve vysokých nadmořských výškách Alp překvapivě ukazují, že velké počty netopýrů přeletují Alpy až do nadmořské výšky 2.500 m. Cílem této studie je další krok: zkoumat aktivitu netopýrů v nadmořské výšce nad 3.000 m. Hlavní studovanou lokalitou byl vrchol hory Hoher Sonnblick ve výšce 3.106 m nad mořem (Solnohrady, Rakousko). Aktivita netopýrů zde byla monitorována pomocí automatické záznamové stanice během září a října 2014, a soustavně pak od března do listopadu 2015. Pro srovnání s aktivitou v níže položeném místě byla monitorována v květnu až říjnu 2015 také druhá lokalita v nadmořské výšce 2.273 m. Oproti našim předpokladům jsme zjistili přítomnost netopýrů ve výšce 3.106 m nad mořem od střední části dubna do střední části září. Ovšem periody aktivity netopýrů v této velké výšce byly kratší než v nižších polohách, a byly přerušovány delšími obdobími bez aktivity. Naše data ukazují velkou variabilitu v úsecích aktivity během roku v závislosti na povětrnostních podmínkách. Jarní migrace byla nápadně nižší ve srovnání s migrací podzimní a migrující netopýři se několikrát objevili ve skupinách.

Mezi zaznamenanými druhy byli všichni dálkoví migranti obývající Evropu: *Nyctalus leisleri*, *N. noctula*, *Pipistrellus nathusii* a *Vespertilio murinus*. *Eptesicus nilssonii*, převážně sedentární druh, byl také na horském vrcholu zaznamenán, stejně jako *Pipistrellus pygmaeus*. Aktivita netopýrů souvisela s mírnějšími povětrnostními podmínkami. Avšak netopýry jsme zaznamenali i při rychlosti větru až 12,2 metru za sekundu a nízké teplotě až do –2,1 °C.

Mimořádná hlasová aktivita *Eptesicus nilssonii* byla zjištěna v noci 5. srpna 2015, kdy byl tento sedentární druh přítomen na vrcholu po několik hodin. Není jasné, zda tato vysoká aktivita byla způsobena tím, že zde netopýři lovili migrující nebo nafoukaný hmyz, či zda měla souvislost s pářením.

Na základě našich zjištění důrazně doporučujeme, aby netopýři a jejich ochrana museli být bráni v úvahu, když jsou plánovány nebo budovány větrné elektrárny ve velkých nadmořských výškách. Navíc ochranné podmínky, vycházející z kritických hodnot rychlosti větru a teploty, vymezené ke zmírnění nežádoucích účinků nížinných parků větrných elektráren na netopýry, musejí být ve vysokých nadmořských výškách přehodnoceny.

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