



Winter activity of boreal bats

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Abstract

Natural hibernation sites used by bats in areas that lack cave features have long remained unresolved. To investigate hibernation site selection and winter activity of boreal bats, we recorded bat calls using passive acoustic monitoring at 16 sites in South-Western Finland. These sites included four rock outcrops with crevices and cave features, three glacial erratics or boulder fields, three ancient shores, three root cellars and three control sites where we did not expect bats to be overwintering. Our results revealed echolocation calls of *Eptesicus nilssonii*, *Plecotus auritus* and *Myotis* sp. We recorded significantly more activity near rock outcrops compared to other habitats, excluding root cellars. We also found that ambient temperature had a positive effect on bat activity and found evidence that *P. auritus* may be using low barometric pressure as a proxy for suitable foraging conditions during the winter. Our results suggest that rock outcrops may be more important to bats than previously acknowledged, highlighting the need to take these sites in account in planning of conservation measures. Furthermore, our findings underline the suitability of using acoustic monitoring in homing on hibernation sites that are not otherwise accessible.

Keywords Chiroptera · Hibernation · Winter activity · Acoustic identification · Winter habitat

Introduction

Insectivorous bats living at high latitudes face enormous fluctuations in the seasonal availability of food. Bats can respond to this challenge either by migrating to warmer areas, where food is occasionally available throughout the winter and hibernation is less risky (Popa-Lisseanu and Voigt 2009), or they can hibernate in situ, by utilizing fat reserves accumulated before the winter (Geiser 2013). The hibernation period of temperate bats can last more than 8 months (Norquay and Willis 2014) and is elapsed in underground hibernation sites, hibernacula. Hibernation consists

of extended bouts of torpor, during which bats lower their body temperature close to ambient temperature of the hibernaculum and decrease their metabolic rate (Geiser 2004; Guppy and Withers 2007). Torpor is interrupted with euthermic bouts—arousals—which allow the bat to counter the ecological and physiological costs caused by torpor (Thomas et al. 1990; Humphries et al. 2003; Boyles and Brack 2009; Bouma et al. 2010; Lilley et al. 2017). Arousals are energetically costly, and amount to 80–90% of total energy expenditure during the winter (Thomas et al. 1990). Due to the long winters at high latitudes, bats must shift their microclimate preference towards colder ambient temperatures and longer torpor bouts to conserve energy (Dunbar and Brigham 2010). Therefore, results of winter activity studies conducted in milder climates, where food is available throughout the winter, are not applicable in the north (Hope and Jones 2012).

During arousals, bats also have an opportunity to drink, copulate and switch places within the hibernaculum (Guilday 1948; Speakman and Racey 1989; Wermundsen and Siivonen 2010). Sometimes bats also leave the hibernation site entirely (Avery 1985; Whitaker and Rissler 1992). While information on the activities that bats undertake outside the hibernaculum is scarce (Boyles et al. 2006), foraging has often been suggested as the primary driver for winter activity

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(Avery 1985; Dunbar et al. 2007; Zahn and Kriner 2016). It is unlikely that aerial hawking bats at northern latitudes are able to feed during the coldest months, as there are almost no nocturnal aerial insects available. However, bats that also glean for terrestrial arthropods have an increased probability of foraging success even during the coldest winter months (Hays et al. 1992; Hope et al. 2014). Bats may also need to relocate to a new hibernaculum during hibernation, which can be due to disturbance, unfavorable changes in abiotic conditions, or a shift in balance between the need to save energy versus minimize cost of torpor (Boyles et al. 2006; Masing and Lutsar 2007; Wermundsen and Siivonen 2010; Johnson et al. 2017). Masing and Lutsar (2007) reported that ambient winter temperatures that are low enough to reduce the temperature inside the hibernacula caused *Eptesicus nilssonii* to arouse and switch to another hibernaculum, while *Myotis daubentonii*, *M. nattereri* and *Plecotus auritus* found in similar open hibernacula (e.g., small root cellars with missing doors) often froze to death.

Bats can benefit from timing their activity to nights with elevated ambient temperature, as this both increases the probability of flying insects being active (Paige 1995) and leads to a decrease in the energetic costs of activity for the bats (Klüg-Baerwald et al. 2016). Indeed, several studies have reported a positive relationship between bat activity and temperature during the winter (Avery 1985; Zahn and Kriner 2016; Klüg-Baerwald et al. 2016). However, most of the time hibernacula are well protected against changes in outside temperatures, and therefore, bats cannot sense these fluctuations. Unlike the outside temperature, changes in barometric pressure can be detected from inside the hibernaculum. Bats, like many other mammals, can sense changes in barometric pressure and they are known to utilize these cues in many circumstances (Paige 1995; Cryan and Brown 2007; Czenze and Willis 2015). Studies on the effect of barometric pressure on bat activity have reported conflicting results, with some studies describing increased activity with falling or low barometric pressure (Paige 1995; Czenze and Willis 2015), and other studies reporting a positive correlation between bat activity and barometric pressure (Berková and Zúkal 2010; Bender and Hartman 2015). The different outcomes likely stem from methodological differences, as well as geographical and seasonal factors affecting both bat ecology and the relationship between weather conditions and barometric pressure.

The geology of Fennoscandia is defined by Svecofennian orogeny, an environment devoid of karst-elements associated with bat hibernacula in scientific literature. The majority of previously known hibernacula in Fennoscandia are anthropogenic (e.g., bunkers, cellars and mines) while very little is known about the use of natural formations as hibernacula. A telemetry study carried out in Norway, found *Eptesicus nilssonii* and *Myotis mystacinus* hibernating in rock scree

and rock crevices, even though anthropogenic structures suitable for hibernation were also available (Michaelsen et al. 2013). Studies in North America have found bats utilizing natural sites, such as rock crevices, for hibernation (Neubaum et al. 2006; Perry et al. 2010; Johnson et al. 2017; Lemen et al. 2017; Klüg-Baerwald et al. 2017; Neubaum 2018). Johnson et al. (2017) documented bats using ground level rock crevices, rock walls, scree slopes and rock fields also during late autumn. Currently there are no estimates on the population sizes of bats in Finland but, given that only some thousands of bats are observed during the census each winter, it is likely that most bats hibernate in yet unidentified sites. Due to the glacial history and geology of Finland, there is a strong likelihood these hibernation sites are associated with a variety of rock formations. Because of the probability of attempting to forage or shift hibernacula during the hibernation period described above, acoustic monitoring in the vicinity of potential sites could provide a means to gather information on the nature of sites that are utilized by bats.

Of the eight bat species known to overwinter in Finland (Siivonen and Wermundsen 2008; Wermundsen and Siivonen 2010; Blomberg et al. 2020), five, including *E. nilssonii*, *P. auritus*, *Myotis daubentonii*, *M. brandtii* and *M. mystacinus* are considered common in South-Western Finland, where we conducted our study (Tidenberg et al. 2019; Vasko et al. 2020). To study the use of natural rock formations as hibernacula and factors affecting the winter activity of these boreal bats, we conducted acoustic monitoring of bat activity at locations we suspected were suitable hibernation sites. Our monitoring was conducted across all seasons to highlight winter activity at the sites. We selected our sites based on the findings in Norway (Michaelsen et al. 2013) and North America (Lausen and Barclay 2006; Johnson et al. 2016; Klüg-Baerwald et al. 2017). To augment these, we used anecdotal evidence of bats hibernating in boulder fields in Ostrobothnia and our previous knowledge of root cellars and some caves being used by bats in the winter. The abiotic conditions of the hibernacula affect the overwintering success of bats (Boyles and Brack 2009). Finding suitable hibernacula is vital for the survival of bats in colder climates, which is why we can predict that the location of hibernacula determines much of the spatial distribution of bats during the winter. Therefore, we consider bat activity at a given location to be a proxy for hibernation sites.

We predicted that we would detect more bat activity during the winter months outside potential natural hibernation sites (ancient shores, rock outcrops, and glacial erratic formations) and root cellars compared to sites that do not have geological formations or structures suitable for hibernation. Second, we predicted that bats would be more active during warm nights, when insect food is more likely to be available (Avery 1985; Zahn and Kriner 2016). We also predicted that

low barometric pressure increases bat activity. During the winter, barometric pressure can function as a proxy for mild outside temperature, which bats can sense from within their hibernacula (Paige 1995; Czenze and Willis 2015). Finally, we predicted *E. nilssonii* and *P. auritus* would be more active during the winter compared to *Myotis* species. Due to their higher mass and proportional fat-stores, these species can attempt to minimize the negative physiological effects of hibernation by arousing more frequently (Boyles et al. 2020). Therefore, the probability of encountering *E. nilssonii* or *P. auritus* during the winter is higher than encountering *Myotis*, although all bats most likely utilize activity to drink, forage or switch between hibernacula.

Materials and methods

Acoustic monitoring

We monitored year-round bat activity at 16 sites in southwestern Finland using 11 SongMeter SM2 + BAT (Wildlife Acoustics) and 4 AnaBat SD2 (Titely Scientific) passive detectors from 12 November 2017 to 31 April 2019. The two different types of recorder were evenly distributed across monitoring site classes to avoid sampling bias. Monitoring site classes selected for the studies included ancient shores ($N=3$), rock outcrops with caves and/or crack features ($N=4$, Fig. 1), glacial erratic formations or boulder fields ($N=3$), and root cellars ($N=3$), of which the latter were known to be used by bats during the winter as hibernation sites. Ancient shores are post-glacial rebounds, upthrusts, where the continuously rising land causes the



Fig. 1 Geological formations monitored for bat activity over two consecutive winters included **a** rock outcrops, **b** glacial erratics, and **c** ancient shores

sea to retreat further from the continent leaving rocks and pebbles (approximate $\phi = 50\text{--}100$ cm) where the seashore resided historically. The group consisting of glacial erratics or boulder fields included two glacial erratics, which in our case consisted of multiple glacially deposited rocks differing in size and type of rock native to the area in which they rest, and one anthropogenic boulder field, covered by large residual rocks from an old quarry. In all the above-mentioned environments, the potential hibernation sites are in crevices under the rocks. Feeding sites ($N=3$) used by bats in the summer were used as control sites for the study (Fig. 2). These sites were devoid of geological features in the immediate surroundings. All sites were selected based on their potential suitability for bats and accessibility for research purposes, because during the coldest and darkest period of winter, the batteries in the devices had to be changed every other week. At the sites, we placed microphones at 1.5-m height on a tree or a pole in semi-open environment with enough flying space for the bats.

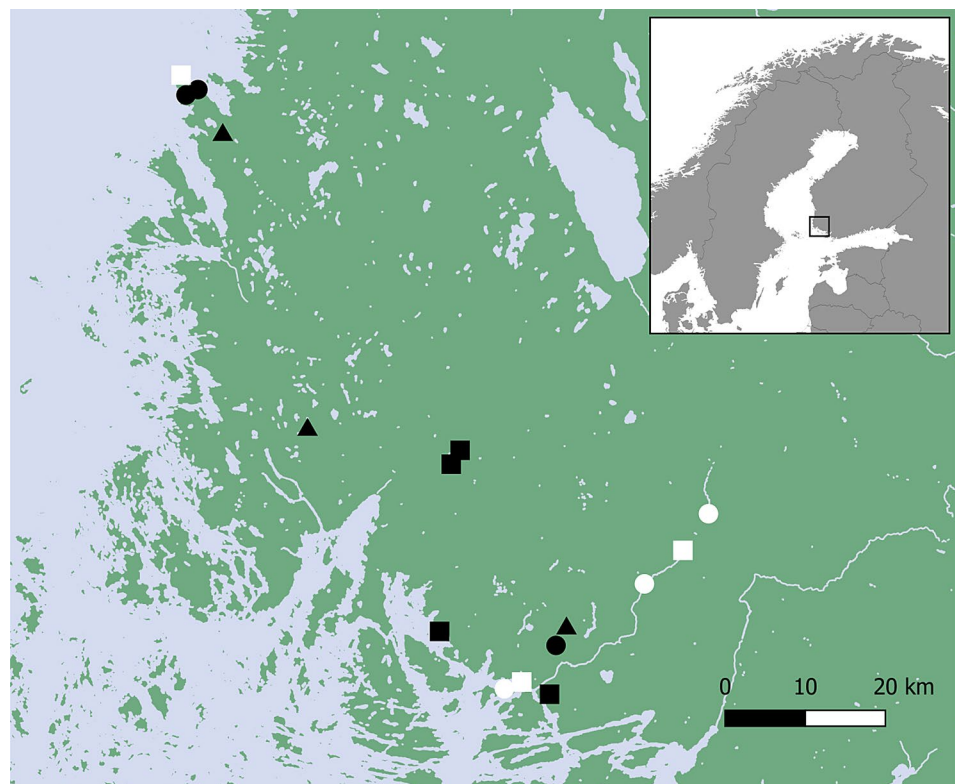
We programmed the SongMeters to begin monitoring half an hour before sunset and end monitoring half an hour after the sunrise. We adjusted the monitoring schedule of the AnaBats manually each month so that it matched the schedule of the SongMeters. We collected the data in WAV format (SongMeters) and ZeroCrossing format (AnaBats). Due to the harsh weather conditions, all multidirectional ultrasound microphones were fitted with a protective

covering to keep them from getting wet or covered with snow. We used SMX-US microphones for the SongMeters and tested their sensitivity both before and after the monitoring. Microphones with sensitivity below -15 dB at 40 kHz were not used, as recommended by the manufacturer. The AnaBats were tested by comparing them with a SongMeter in a side-by-side setup for two nights before and after the study. We obtained weather data from the Finnish Meteorological Institute. For the analysis, we used weather data from the closest weather station to the survey sites (Fig. 2).

Species identification

We used Kaleidoscope Pro (Version 5.3.8., Wildlife Acoustics) for filtering and organizing the data. We chose not to discard non-bat (noise) files suggested by the program from wintertime to ensure that all recorded bat calls were included in the analysis. From the summer months, noise files were discarded, because checking them manually would have been too laborious. After initial filtering, we then manually viewed acoustic files and identified species. Due to the uncertainty of identifying *Myotis* to species level, we chose to pool all recordings of the genus *Myotis* for analysis.

Fig. 2 Map of study area. White circles = control sites, white squares = root cellars, black circles = ancient shores, black squares = outcrops, black triangles = glacial erratics, star = weather station



Statistical analysis

We considered winter months as those from November to March (Finnish Meteorological Institute). All together, we recorded 53 656 hours of audio data during the two winters for all sites. We gathered 35 min of *Myotis* activity, 182 min of *E. nilssonii* activity and 66 min of *P. auritus* activity. We investigated the differences in bat activity between sites, habitats and species during the winter with a generalized linear mixed model (Proc GLIMMIX in SAS, SAS Institute Inc. 2013). In the model, we used normal error distribution with identity link function. For each site, we calculated a monthly activity index for *E. nilssonii*, *P. auritus* and pooled *Myotis* species by dividing the number of active minutes (minutes with bat activity) by the number of total recorded hours (number of hours the equipment was recording and functioning properly). This was done to account for any interruptions caused by battery failures. We used this activity index with a log₁₀-transformation as the response variable and species, habitat type and site nested under habitat type as fixed effects. In cases where we recorded zero minutes during a month at a site, we replaced the zero with 0.001 min to conduct the log₁₀-transformation for the activity index. The F test statistic measures the ratio of explained variance to unexplained variance ($F = \text{factor mean square/error mean square}$). We also investigated the differences in activity between habitats and species using the Tukey–Kramer method.

Furthermore, we investigated the effect of ambient temperature and barometric pressure on the activity of *E. nilssonii*, *P. auritus* and the pooled set of *Myotis* species, and all bat activities (all species pooled) using generalized linear models. We used the mean ambient temperature and mean barometric pressure of the previous 24 h, as well as their interaction as explanatory variables. We used mean barometric pressure of the previous 24 h, as low barometric pressure in the winter brings cloudy and rainy, yet mild weather to

our study area. We standardized all fixed factors prior to analysis and checked for multicollinearity using variance inflation factors (VIFs). VIFs were < 3 in all instances, suggesting that no or very minimal multicollinearity between fixed factors existed. We used backward stepwise model selection, retaining the variables that produced the lowest AIC-values, to select the best model for each species and species group. We considered P values < 0.05 significant for all tests.

Results

Levels of bat activity differed between habitats ($F_{(4, 405)} = 9.91$; $P < 0.001$), species ($F_{(2, 405)} = 19.29$; $P < 0.001$) and sites ($F_{(11, 405)} = 2.11$; $P = 0.019$). Most bat activity during the winter took place at rock outcrops (Table 1). Rock outcrops had significantly more bat activity than ancient shores ($t = 4.51$; $df = 405$; $P < 0.001$), glacial erratics ($t = 4.19$; $df = 405$; $P < 0.001$) and control sites ($t = 5.09$; $df = 405$; $P < 0.001$). Second highest activity was measured outside root cellars, in which we previously knew bats were overwintering. Root cellars had significantly more activity in the winter than control sites, which were selected because they were known foraging areas in the summer ($t = 3.29$; $df = 405$; $P = 0.01$). The difference in activity between root cellars and ancient shores approached statistical significance ($t = 2.67$; $df = 405$; $P = 0.06$). Furthermore, our results revealed significantly more calls of *E. nilssonii* ($N = 182$) than *P. auritus* ($N = 66$; $t = 5.17$; $df = 405$; $P < 0.001$) and *Myotis* species ($N = 34$; $t = 5.56$; $df = 405$; $P < 0.001$; Table 2).

Total bat activity increased with higher ambient temperature and barometric pressure (Table 3). However, we found that total activity decreased faster with decreasing temperatures if barometric pressure was low (Fig. 3a). Activity of *E. nilssonii* was positively affected by increasing barometric

Table 1 Differences of LS-means for total bat activity measured at different habitats during the winter

Habitat	Habitat	Estimate	SE	DF	t Value	Pr> t	Adj P	Alpha	Lower	Upper	Adj lower	Adj upper
Ancient shore	Outcrop	-0.991	0.219	405	-4.51	<0.001	<0.001	0.05	-1.423	-0.559	-1.593	-0.389
Ancient shore	Glacial erratic	-0.034	0.243	405	-0.14	0.889	0.910	0.05	-0.513	0.444	-0.701	0.633
Ancient shore	Root cellar	-0.738	0.276	405	-2.67	0.008	0.060	0.05	-1.280	-0.195	-1.494	0.020
Ancient shore	Control site	0.217	0.252	405	0.86	0.390	0.911	0.05	-0.278	0.711	-0.473	0.906
Outcrop	Glacial erratic	0.957	0.228	405	4.19	<0.001	<0.001	0.05	0.508	1.406	0.331	1.582
Outcrop	Root cellar	0.253	0.263	405	0.96	0.336	0.871	0.05	-0.263	0.770	-0.467	0.974
Outcrop	Control site	1.207	0.237	405	5.09	<0.001	<0.001	0.05	0.741	1.674	0.558	1.857
Glacial erratic	Root cellar	-0.703	0.283	405	-2.49	0.013	0.096	0.05	-1.260	-0.147	-1.479	0.072
Glacial erratic	Control site	0.251	0.259	405	0.97	0.334	0.870	0.05	-0.259	0.760	-0.459	0.961
Root cellar	Control site	0.954	0.290	405	3.29	0.001	0.010	0.05	0.384	1.524	0.159	1.749

Bat activity was measured at each site with a monthly activity index (minutes with recordings/number of recorded hours)

Table 2 Differences of LS-means for monthly activity indexes of *Eptesicus nilssonii*, *Plecotus auritus* and a pooled set of *Myotis* species (*M. daubentonii*, *M. brandtii*, *M. mystacinus*, and *M. nattereri*) recorded during the winter

Species	Species	Estimate	SE	df	t Value	Pr > t	Adj P	Alpha	Lower	Upper	Adj lower	Adj upper
<i>E. nilssonii</i>	<i>Myotis sp</i>	1.028	0.185	405	5.56	<0.001	<0.001	0.05	0.665	1.391	0.593	1.462
<i>E. nilssonii</i>	<i>P. auritus</i>	0.955	0.185	405	5.17	<0.001	<0.001	0.05	0.592	1.318	0.521	1.389
<i>Myotis sp</i>	<i>P. auritus</i>	-0.073	0.185	405	-0.39	0.694	0.918	0.05	-0.436	0.290	-0.507	0.362

Table 3 Results of generalized linear model on the effect of weather conditions on total bat activity ($N=318$ min with activity), activity of *Eptesicus nilssonii* ($N=182$ min with activity), activity of *Plecotus auritus* ($N=66$ min with activity) and activity of *Myotis* sp. (pooled for four species; *M. daubentonii*, *M. brandtii*, *M. mystacinus*, *M. nattereri*, $N=35$ min with activity)

Species	Weather variable	Estimate	Std. error	z value	Pr(> z)
Total bat activity	(Intercept)	-2.092	0.078	-26.650	<0.001
Total bat activity	Temperature	0.982	0.092	10.649	<0.001
Total bat activity	Barometric pressure	0.292	0.073	3.996	<0.001
Total bat activity	Temperature:pressure	-0.166	0.074	-2.240	0.025
<i>E. nilssonii</i>	(Intercept)	-3.281	0.128	-25.542	<0.001
<i>E. nilssonii</i>	Temperature	0.859	0.139	6.192	<0.001
<i>E. nilssonii</i>	Barometric pressure	0.232	0.123	1.880	0.06
<i>P. auritus</i>	(Intercept)	-5.319	0.444	-11.982	<0.001
<i>P. auritus</i>	Temperature	2.010	0.529	3.800	<0.001
<i>P. auritus</i>	Barometric pressure	0.910	0.359	2.536	0.01
<i>P. auritus</i>	Temperature:pressure	-1.434	0.331	-4.338	<0.001
Pooled <i>Myotis</i>	(Intercept)	-5.031	0.272	-18.504	<0.001
Pooled <i>Myotis</i>	Temperature	0.663	0.307	2.162	0.031
Pooled <i>Myotis</i>	Pressure	0.245	0.293	0.834	0.404
Pooled <i>Myotis</i>	Temperature:pressure	0.726	0.337	2.156	0.031

pressure and ambient temperature (Table 3). Similar to *E. nilssonii*, the activity of *P. auritus* increased with higher mean ambient temperature (Table 3). The effect of temperature on the activity of *P. auritus* was stronger at low barometric pressure (Fig. 3b). Contrary to *P. auritus*, the activity of *Myotis* species increased more steeply with ambient temperature at high barometric pressure (Fig. 3c). The lowest hourly temperature where a bat was recorded was -9.8 °C (*E. nilssonii*). The lowest temperature for the *Myotis* and *P. auritus* were -3.1 and -5.6 °C, respectively.

Discussion

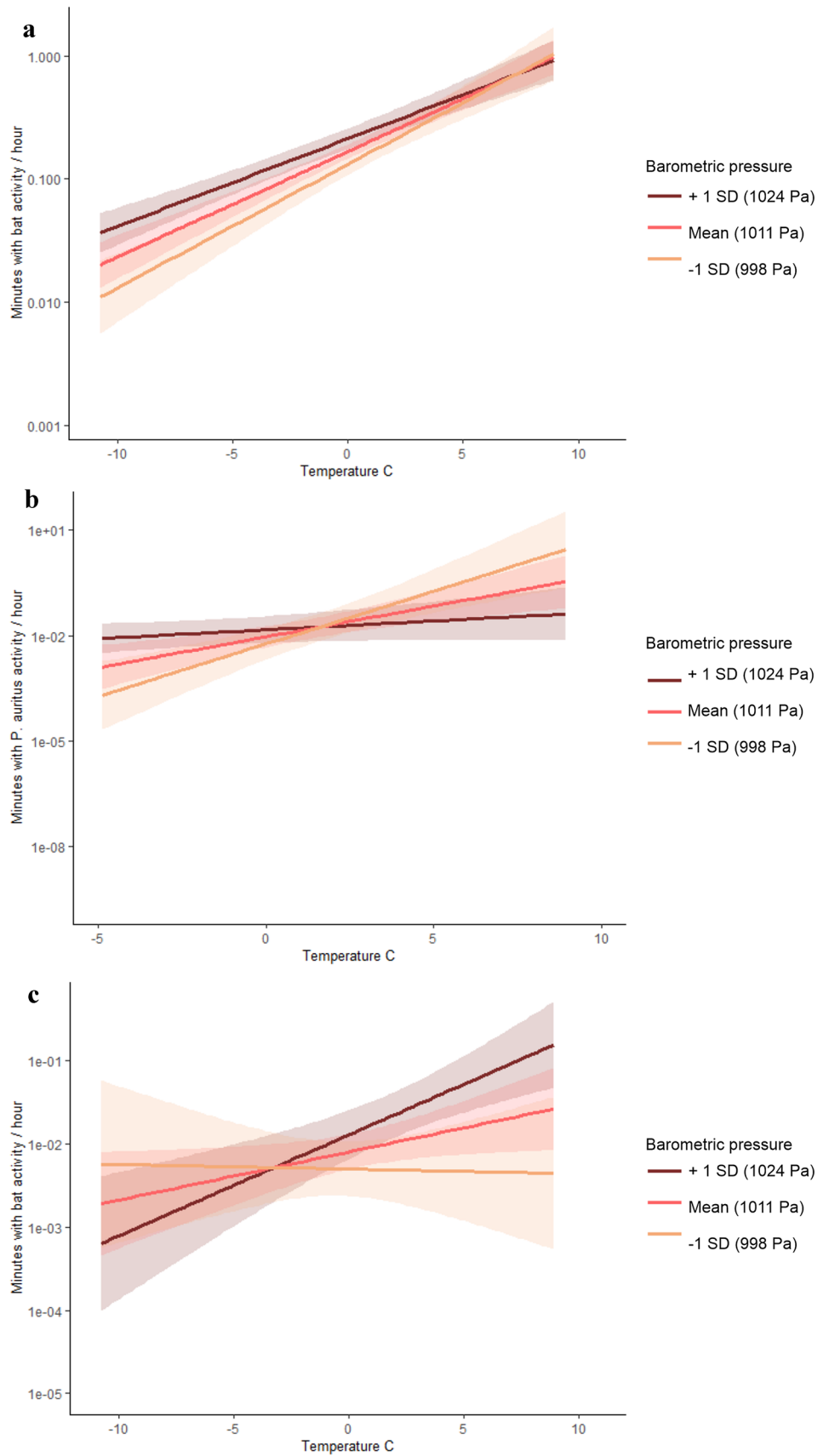
Our results revealed greater bat activity at rock outcrops compared to root cellars, which have been considered one of the most important hibernacula in many areas of the boreal zone (Rydell 1989; Lesiński et al. 2004; Vintulis and Pētersons 2014). Rock outcrops and boulder fields constitute up to 2.5% of Finland's land area (Kontula et al. 2018). Most of these are located in South-Western Finland, making them available as hibernacula to bats in our study area. However, the utilization of other natural sites in Fennoscandia should be considered in more detail (although, see Michaelsen et al. 2013). Almost all of the hibernation

sites known in Finland prior to this study are manmade, but the number of individuals observed at these sites each winter likely resembles only a fraction of the true populations (Wermundsen and Siivonen 2010). Our results suggest that natural formations may be more important to hibernating bats than previously considered.

Eptesicus nilssonii were observed significantly more often than pooled *Myotis* species or *P. auritus*. The species is well adapted to the cold and long winters of the north, hibernating in colder environments than other species, leading to longer bouts of torpor which help them save more energy (Anufriev and Revin 2006; Siivonen and Wermundsen 2008). Furthermore, *E. nilssonii* have a higher body mass than *P. auritus* and *Myotis* species, which enables them with greater fat reserves for the winter (Rydell 1993). Larger body size further increases energy saving through relatively lower levels of heat loss, as their surface area to volume ratio is lower (Worthy and Edwards 1990). These factors may allow *E. nilssonii* to spend more energy on locomotion during the winter and permit them to forage when conditions are suitable. Lausen and Barclay (2006) reported a similar pattern of higher activity of *Eptesicus fuscus* compared to *Myotis* species during the winter in Canada.

While our results can indicate that *E. nilssonii* are more active during the winter compared to the other species

Fig. 3 Effect of ambient temperature on **a** the total winter bat activity ($N=318$ min with activity) **b** activity of *Plecotus auritus* ($N=66$ min with activity) and **c** *Myotis* species (pooled for four species; *M. daubentonii*, *M. brandtii*, *M. mystacinus*, *M. nattereri*, $N=35$ min with activity) in different mean barometric pressures. Unit for activity is the predicted number of minutes with recordings/night. Shaded areas represent 95% confident intervals. Temperature and barometric pressure are mean values of previous 24 h



monitored, it is important to note that this difference may also be explained by other factors. Currently, there are no estimates on population sizes of bats in Finland, and we, therefore, cannot determine whether our results are indeed reflecting differences in the activity or population size, or differences in hibernation habitat preferences. Furthermore, the acoustic detectability varies between the species. Detectability is influenced by the intensity of calls as well as the frequency, as high frequency sounds attenuate more quickly in the atmosphere (Griffin and Galambos 1941; Lawrence and Simmons 1982), leading to species such as *E. nilssonii* with high intensity and low frequency calls having a higher probability of occurring in acoustic data compared to species with higher pitch and/or more faint calls (Schnitzler and Kalko 2001). Bat species also differ in their preference for abiotic conditions of the hibernacula and it is known that both *E. nilssonii* and *P. auritus* often hibernate in conditions that are colder and less humid than conditions preferred by many *Myotis* species (Wermundsen and Siivonen 2010). Given the ability of *E. nilssonii* to take advantage of hibernacula not suitable for other species (Masing and Lutsar 2007), it is also possible that the hibernacula studied here are not suitable for species requiring higher ambient humidity and temperature. For instance, we cannot disclose the possibility that other hibernation habitats, not included in our study, may be more suitable for *Myotis* species.

We predicted that ambient temperature would have a positive effect on bat activity, and that activity would be greater at low barometric pressure. In accordance with our hypothesis, we found that an increase in ambient temperature had a positive effect on the activity of *E. nilssonii*, *P. auritus* and *Myotis* species during the winter months. Furthermore, we found that total bat activity as well as the activity of *P. auritus* increased more rapidly with rising ambient temperature when barometric pressure was low. In Finland, low-pressure systems during the winter often conjure mild temperatures together with cloudy, rainy weather, while high pressure systems usually arrive from the east, bringing cold yet clear weather (Similä 1981). We suggest that this result indicates that in general, bats may indeed use low barometric pressure as a proxy for suitable conditions to leave the hibernaculum, leading them to be more active during warm, often cloudy, nights. Due to the siting of our passive detectors and the structure of most of the habitats studied, with no single, obvious entrance to the hibernacula, we were likely to only record bats that left the hibernacula entirely and continued flying outside for a period of time. Because *P. auritus* is known to forage during the winter (Hays et al. 1992), we suggest that this species may benefit from detecting changes in barometric pressure from within the hibernaculum. In contrast, we found that activity of *Myotis* species increased more rapidly with temperature in high barometric pressure, while the activity of *E. nilssonii* increased in high barometric

pressure. We propose that these results show that the activity of *Myotis* species and *E. nilssonii* is determined rather by the timing of their arousals than by foraging possibilities.

We suggest that a proportion of the winter activity we recorded was due to bats relocating to different hibernacula. Bats can benefit from timing these movements to warm nights, as this leads to reduced energy loss, corresponding with our model predicting more activity at warm ambient temperature (Klüg-Baerwald et al. 2016). *E. nilssonii* may be more prone to shifting between hibernation sites compared to *Myotis*, as suggested by Masing and Lutsar (2007). This is due to the larger body size and fat reserves of the species, which enables more energy to be allocated to activity. This is consistent with our result of *E. nilssonii* being active in colder temperatures than *Myotis* species.

In addition to their abundance, sites such as rock outcrop formations may offer additional advantages. For instance, it is likely that human disturbance is scarce, if nonexistent, in these environments compared to root cellars, bunkers, and other anthropogenic structures. Furthermore, Michaelsen et al. (2013) suggested that using hibernacula such as rock scree might help bats avoid predators during hibernation and emergence. Despite the acoustic evidence of bat activity in many locations, we only found a single hibernating bat in the natural study sites (*M. brandtii* inside a cave at a rock outcrop), which highlights the difficulty of visually observing hibernating bats in areas that lack large caves. Our results indicate that hibernation sites not accessible to humans, and thus understudied, are more important for bats than previously acknowledged. Most research on hibernation behavior thus far has been conducted on species that hibernate in caves in karst regions, often in large numbers, leaving the majority of species not encountered in these environments understudied. Recently, the use of acoustic monitoring and studies utilizing temperature sensing radio tags has brought new insight to the hibernation behavior of more elusive species (e.g., Lausen and Barclay 2006; Lemen et al. 2017; Ossa et al. 2020), to which our results add. However, climate change may affect the usability of these sites for bats, as the loss of snow cover is likely to have a great impact on the microclimates of these hibernacula. Furthermore, our results also highlight the need of taking bats into account in land use, when sites with rock outcrops are altered.

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Author contributions ASB, TML, VV and TE designed the study; ASB and VV collected the data; ASB, VV, TE and MBM analyzed the data; ASB wrote the first draft of the manuscript; JSJ edited the first draft; all the authors contributed to the final version.

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Availability of data and material The datasets generated during and/or analyzed during the current study are available in Dryad, <https://doi.org/10.5061/dryad.zgmsbcc9w>.

Code availability The code used in the analysis during the current study is available from the corresponding author upon request.

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

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