Journal of Thermal Biology 125 (2024) 103999

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

The interplay of temperature and circadian periodicity in winter activity of non-cavernous hibernator, *Nyctalus noctula*

Kseniia Kravchenko [a,b,c,*], Joanna Furmankiewicz [b]

[a] Ukrainian Bat Rehabilitation Center of NGO "Ukrainian Independent Ecology Institute", Plekhanov St., 40, 61001 Kharkiv, Ukraine
[b] Department of Behavioral Ecology, University of Wrocław, Wrocław, Poland
[c] University of Luxembourg, Belval Campus 2, place de l'Université, L-4365 Esch-sur-Alzette, Luxembourg

ARTICLE INFO

Keywords:
Bats
Winter activity
Circadian cycle
Photoperiod
Ambient temperature
Climate change

ABSTRACT

Winter activity of hibernating mammals is likely to be influenced by climate change. Our study focuses on *Nyctalus noctula*, a non-cavernous hibernator using artificial roosts in a recently colonized winter region. Using continuous acoustic monitoring and temperature measurements inside and outside the roosts, we found that bats exhibit a circadian cycle (active at night, resting during the day) even during hibernation season. Activity duration and intensity changed in response to ambient temperature, photoperiod, and hibernation progression. Warm ambient temperatures led to increased nighttime activity, extending the duration of the active phase. As photoperiod increased, the rest phase lengthened, while the overall magnitude of activity decreased from the beginning to the end of the hibernation period. Below 0 °C vocal activity was nearly zero indicating a minimal probability of bat activity during both day and night. The species recent success in extending its hibernation range northward may be attributed to its flexible adjustment to prevailing environmental conditions. Nevertheless, it remains uncertain whether engaging in daily activity at temperatures above 0 °C confers any advantages at northern latitudes to prevent premature energy depletion. The persistence of circadian activity during winter could be a relic behavior, adapted from historical patterns of wintering in insect-rich and warm southern latitudes.

1. Introduction

Periodicity by animals is an inescapable trait common across ecosystems. The life of most animals exists in an alternate shift of two behavioral stages - rest and activity (Halle and Stenseth, 2012). The trade-off between energy gain and expenditure during these stages is performed on a tidal, daily, monthly, or annual basis. This delicate balance is particularly crucial for many small mammals, necessitating the adoption of heterothermy as a strategy for energy regulation (Stawski et al., 2014). Heterothermic mammals are capable of torpor - a state of profound and controlled decrease in metabolic rate (McNab, 2002; Ruf and Geiser, 2015). A variety of torpor patterns, such as daily torpor, hibernation, and short-term hibernation, are broadly represented in different species of mammals. However, the pattern of torpor and extent to which individuals use it depends on many factors: body size, dietary specialization and food source availability, type of roosts, geographical distribution, and seasonality (Ruf and Geiser, 2015; Körtner and Geiser, 2000).

Bats of temperate zones are predominantly small; insectivores and their annual cycle of activity depends on prey availability (Dietz et al., 2009). Therefore, temperate zone bats spend the cold period with low prey availability in hibernation, using fat stored prior to winter (Stawski et al., 2014). However, bats exhibit periodic arousals during hibernation, sometimes even emerging from their hibernacula (Jonasson and Willis, 2012; Boyles et al., 2006). The reasons for such arousals are thought to be related to removing metabolic byproducts, copulation, switching hibernacula, feeding, drinking, and potentially avoiding muscle atrophy (Strelkov, 1969; Boyles et al., 2006; Lee et al., 2008, 2010; Hope and Jones, 2012; Czenze et al., 2013; Ben-Hamo et al., 2013; Lyman et al., 1982). Winter activity is costly for bats, as they spend up to 80–90% of energy sources from fat deposit to sustain periodic active states during hibernation (Geiser, 2004; Reeder et al., 2012). Nevertheless, a crucial role of periodic rewarming appears to be the adjustment of biological rhythms to environmental oscillations. Both duration and function of winter activity are moderated by: 1) latitude and in particular average winter temperatures of the hibernacula (Thomas

* Corresponding author. Ukrainian Bat Rehabilitation Center of NGO "Ukrainian Independent Ecology Institute", Plekhanov St., 40, 61001 Kharkiv, Ukraine.
E-mail addresses: a.kravchenko@gmail.com, kseniia.kravchenko@uni.lu (K. Kravchenko).

https://doi.org/10.1016/j.jtherbio.2024.103999
Received 16 February 2024; Received in revised form 9 October 2024; Accepted 15 October 2024
Available online 2 November 2024

et al., 1990); 2) type of hibernacula in terms of its microclimatic stability –caves and mines maintain more stable temperatures than trees and buildings, where temperatures are more variable (Boyles et al., 2006); 3) physiological, ecological and behavioral features of the species and even of the particular population (Jones et al., 1995).

Non-cavernous hibernacula, such as tree cavities, foliage, rock crevices, and anthropogenic structures, are typically smaller in space and more climatically unstable than caves (Klüg-Baerwald et al., 2017; Kunz and Lumsden, 2003). Bats using non-cavernous hibernacula exhibit more frequent physical activity during the winter compared to cavernicolous species (Boyles et al., 2006; Klüg-Baerwald et al., 2024). However, knowledge about their winter activity remains limited (Boyles et al., 2006; Boyles and Robbins, 2006; Klüg-Baerwald et al., 2024). Some species switch hibernacula frequently during the winter likely as an attempt to find more suitable microclimate conditions for hibernation, especially when temperatures fluctuate significantly in poorly insulated hibernacula (Boyles et al., 2006; Boyles and Robbins, 2006; Boyles and McKechnie, 2010). Therefore, overwintering in above-ground hibernacula is often restricted to latitudes with mild winter conditions (average temperature above zero). Species which use poorly insulated cavities all year round in the Northern hemisphere perform seasonal southward migration (Fleming and Eby, 2003; Cryan and Veilleux, 2007). Mild winter temperatures also increase insect availability and may lead to periodic arousals for feeding synchronized with the circadian cycle (Jones et al., 1995; Hope and Jones, 2012; Park et al., 2000). However, recent evidence for *Eptesicus fuscus* hibernating in rock crevices showed that they exhibit circadian activity without signs of foraging (Klüg-Baerwald et al., 2024). In contrast, cavernicolous species at northern latitudes with severe winter conditions have no possibility to feed outside the caves and do not synchronize arousal activity with circadian cycle (Speakman and Thomas, 2003; Czenze et al., 2013; Hayman et al., 2017). While many aspects of winter activity remain unclear, we can nevertheless, highlight two distinct patterns of winter activity: 1) prolonged torpor bouts and free-ranging cycles without the possibility of feeding and 2) shorter torpor bouts with pronounced circadian activity with compensation of energy needs by occasional feeding.

Global environmental processes such as climate change affect species distribution range, phenology, and physiology (Walther et al., 2002). Some aboveground hibernating species, such as *Nyctalus noctula* now prefer to overwinter on the breeding grounds which are significantly north of previously known hibernacula (Kravchenko et al., 2020). *Nyctalus noctula* has been defined as a long-distant migrant since the middle of the 20th century (Strelkov, 1969). Mark recapture data show that *N. noctula* migrate 1200–1600 km from northern breeding territories in summer to south-western hibernation sites (Panutin, 1980; Hutterer et al., 2005). However, over the last 30 years, several studies provide evidence of northward expansion of the hibernation range of this species (Strelkov, 1969; Schmidt, 2010; Godlevska, 2015; Kravchenko et al., 2020). Currently, *N. noctula* hibernates in buildings and bat boxes across Central Europe (Lupicki et al., 2007; Kanuch and Celuch, 2000; Gebhard, 1984; Avery, 1986; Zahn and Clauss, 2003; Schmidt, 2010; Voigt et al., 2014; Kravchenko et al., 2017). Around 80% percent of *N. noctula* in hibernation sites in Central and Eastern Europe originate from local populations (Voigt et al., 2014; Kravchenko et al., 2020). Investigating how climate-driven range shifts are shaping the winter activity and hibernation strategies of these animals is crucial to understanding their ability to survive in changing environments.

To shed light on the question of adjustment of winter behavior periodicity to the environment, we hypothesized that this former "migratory" species, which now overwinters in poorly insulated roosts at northern latitudes, will exhibit a flexible behavioral pattern determined by temperature and circadian periodicity. We predicted that warm spells during winter would stimulate circadian activity, whereas cold spells would promote prolonged multi-day torpor. Additionally, we hypothesized that the course of hibernation shapes the magnitude of activity, with higher activity levels at the beginning and end of the hibernation period. According to the energy maximization hypothesis (Avery, 1985), bats should be more active at the beginning of hibernation (November, December), when fat reserves are highest and offer the most significant energy gain, enabling the energy-intensive arousals from torpor needed for essential activities. Similarly, they are more active at the end of hibernation (March) when energy and water replenishment are necessary after the coldest period (Speakman and Racey, 1989).

2. Material and methods

2.1. Study site

Our study was conducted in the city of Wroclaw (51°06′N, 16°53′E, 121 m a.s.l.) in southwestern Poland. Wroclaw is situated in the Silesian Lowlands on the Oder River, which is known as a migration route of *N. noctula* (Furmankiewicz and Kucharska, 2009). Wroclaw has a marine west coast climate that is temperate with mild winters, warm summers, no dry seasons and moderate seasonality (http://www.wroclaw.climatemps.com). The mean air temperature in the warmest month is +18.8 °C (July) and in the coldest month is −0.4 °C (January) (Dubicki et al., 2002). The early winter (average air temperatures between 0 and 5 °C) starts from 8 November and lasts till the 18 December. The winter thermal period (average air temperatures fall below 0 °C) lasts from 19 December till the 21 February (total duration of up to 65 days per year). This period is characterized by large temperature fluctuations (up to 15.6 °C) within a single year. The early spring (average air temperatures are the same as for early winter) thermal period is from 22nd of February till the 27th of March (Dubicki et al., 2002).

The winter aggregation of *N. noctula* we studied inhabited a single large brick building, the Lower Silesian Governor's Office (LSGO), located in the center of the city along the Oder River. The roost was in a space between the wall and ceiling at the level of the third floor (14–15 m above ground). We estimated from emergence counts that approximately ~120 individuals hibernated there.

2.2. Recording of bat activity

We recorded vocalizations of bats at the roost, continuously from November 17, 2011 until March 30, 2012 with Anabat SD1 bat detector (Titley Scientific, QLD, Australia). The detector was constantly operating under default zero-crossing mode. The detector stored bat calls on a CompactFlash card and was connected to a 12 V battery. We changed the battery every two weeks and at the same time downloaded the data. We made no recordings between 7th and 22nd of March due to premature battery drain. We placed the detector in a plastic box to protect it from unfavorable weather conditions. We placed the detector on the outside windowsill 1.5 m from the roost. The microphone was directed towards the roost entrance.

2.3. Temperature measurements

We measured temperature each hour with two i-Button temperature data loggers (iButtons, Maxim Integrated Products, Dallas, TX, USA) with temperature range from −40 to +85 °C and an accuracy ±0.5 °C. One logger was placed inside the roost and the second was placed outside the roost on the windowsill near the detector to measure ambient temperature. The indoor logger was placed 50 cm deep from the roost entrance and was placed into the plastic mesh grid to prevent direct contact of individuals with the logger.

2.4. Analyses of recordings

We analyzed audio recordings with AnalookW software program (version 3.5 m; C. Corben, Titley Scientific, QLD, Australia). Two types

of vocalizations of *N. noctula* were distinguished. The first one were echolocation sequences emitted by passing bats, i.e. flying out of the roost in the open space with the range of frequency of maximum energy between 20 and 24 kHz (we call these F calls or "flight"). The second type were shorter echolocation pulses emitted by bats close to the roost entrance (bats entering/exiting roost or sitting close to roosts entrance) and from the roost (bats resting in the roost), with a frequency range between 25 and 60 kHz (we termed it R calls or "roost") (Furmankiewicz et al., 2011) (Fig. 1). It was not possible to make a distinction between two subcategories of R calls because we did not conduct continuous video recording of bat behavior, but only undertook visual observation of the colony activity during the study and linked observed behavior with emitted calls. R calls were unambiguously emitted by bats in the roost because they were also recorded during the day when no bats were seen flying around the roosts entrance.

The level of each type of vocal activity (F/R) emitted by bats was counted and converted to activity units. The activity unit was defined as the number of sequences of each type of echolocation in a 5 s period. If the sequence lasted more than 5 s, then the number of activity units we counted as a number which is obtained by division of total duration time of the sequences by 5 (rounding to the highest whole number) (Fig. 1). In cases when up to three individuals vocalized simultaneously the number of individuals was determined based on the number of sequences and the activity unit was multiplied by the number of vocalizing bats. If many individuals vocalized simultaneously and it wasn't possible to identify the sequences for each of them, the number of sequences was multiplied by 3 to avoid overestimating the number of individuals (Kepel et al., 2011). Bats also emitted low-frequency social calls (with the average frequency of maximum energy 13.4 kHz) when they rested in the roost (Furmankiewicz unpublished data.), similar to the vocalization in the summer roosts (Pfalzer and Kusch, 2003; Furmankiewicz et al., 2011). However, they were sporadic and infrequent, and we did not include them in the analysis.

2.5. Statistical analysis

Statistical analyses were carried out in R version R i386 3.5.0 (R Core Team (2021)). First, we checked the relationship between the two types of activity (F and R) using a Spearman's rank correlation test. The data on activity units of both call types showed a right-skewed distribution with a large proportion of zero values. Our raw activity data were potentially pseudo replicated, as it was not possible to distinguish how many individuals were vocalizing simultaneously. Therefore, the degree of activity based on absolute activity unit counts was not biologically relevant according to experimental setup (observation and recording on the group level with many individuals), as more calls within the same numerical order did not necessarily reflect more individuals vocalizing. Taking this into account, we considered the binomial distribution of

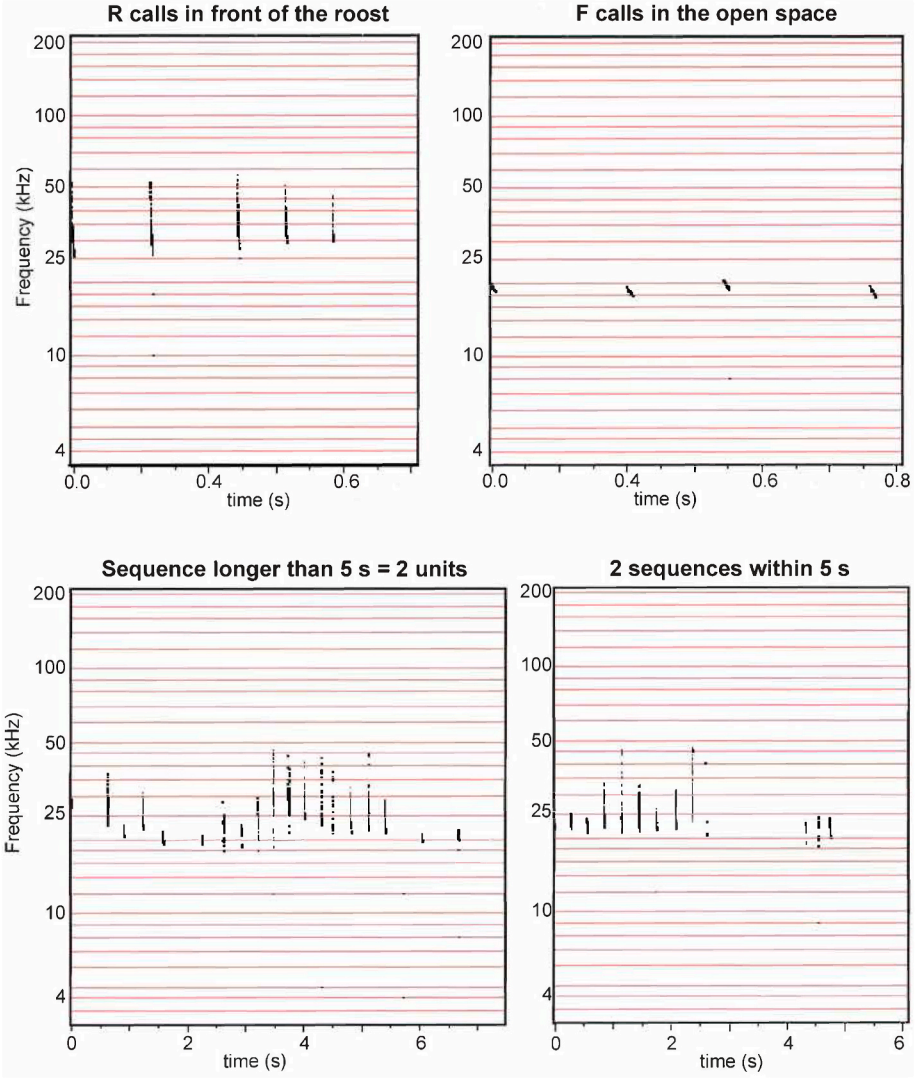

Fig. 1. Examples of calls and activity units of *Nyctalus noctula* recorded by Anabat SD1 detectors and visualized with Analook v 3.5 m software.

data. For F calls, zero was equal to the absolute absence of activity units and one was equal to one or more activity units. For R calls, zero was equal to a range between zero and ten activity units and one was equal to eleven or more activity units. We arbitrarily defined a threshold in 10 activity units for R calls, as in many cases calls from the roost were single and infrequent, which reflected a single individual vocalizing, rather than the activity of the whole colony.

To understand the impact of T_a and course of hibernation period on circadian activity cycles we used Fourier series (Nievergelt, 2013). A Fourier based approach comes from trigonometric algebra and allows the decomposition of a periodic function into a linear combination of simple oscillating functions (sines and cosines) parameterized by Fourier coefficients (see example in Rickard et al., 2012). We modeled time of day was modeled as sines and cosines of time in radians and then added this to the model as an interaction with T_a and variable called Time_rel. Time_rel in our case was a continuous vector of interval numbers from beginning to end of the study period representing course of hibernation period. We used autocorrelation function "AR1" applied to Time_rel vector. The model was fitted with "fitme" function from "spaMM" package (Rousset and Ferdy, 2014). The coefficients and structures of all applied models are provided in Supplementary Material 1.

To assess the insulation properties of the roost, we tested the effect of T_a on the temperature in the roost (T_{roost}) using linear regression. Also, we checked whether activity level in the roost affected T_{roost}. Then we compared two models with "anova" function from "stats" package (R Core Team (2021)), which performs likelihood ratio test for nested models.

3. Results

3.1. General activity and roost insulation properties

Bats were active in the roosts during most of the study period from November until mid-March, with inactivity primarily observed on days when the temperature was below 0 °C. In total, we recorded 633,060 sound sequences within the roost (R calls) and 93,441 flying calls (F calls) in this period. R activity was positively correlated with F activity during the study period (Spearman rank correlation, $r_s = 0.83$, $p < 0.001$).

T_a had a significant effect on T_{roost} and explained 81% of the variation with an intercept of 5.18, which means that T_{roost} was on average approximately 5 °C higher than T_a (see Supplemental material 1). R activity had also correlated with T_{roost} and the model which included T_a and R activity variables provided the best fit according to the likelihood ratio test ($F = 128.7$, $p < 0.001$). Based on this we only used T_a as a predictor of bat activity.

3.2. Circadian cycle of bat activity in relation to temperature and phase of hibernation season

Both F and R activity had a similar pattern over the course of the study, although there were some differences in the significance of coefficients in the models (see a summary of models in Supplementary material 1). The probability of F and R activity was correlated with T_a and time of the day. Bats exhibited circadian activity patterns. Both types of activity were higher at night, and fewer calls happened in the daytime (Fig. 2A and B). During nighttime the probability of activity was high with higher temperatures. At temperatures below 0 °C the probability of activity was almost zero throughout the day and night.

For F activity, Sin1, which represents the Sine time of day in radians and shaped the maximum and minimum values of the function on the y-axis, had a significant effect. The interaction of T_a with Sin1 had a significant effect on F activity as well and showed that temperature along with the time of the day impacted the probability of activity. The Time_rel factor had a negative tendency ($p = 0.08$), meaning that the probability of a flying activity tended to decrease over the course of hibernation. However, the interaction of Cos1, which shaped the probability of activity function along the x-axis, and Time_rel was not significant and indicating that maximum probability of flying activity occurred at the same time during the season.

For R activity, the effect of Sin1 was evident only when the

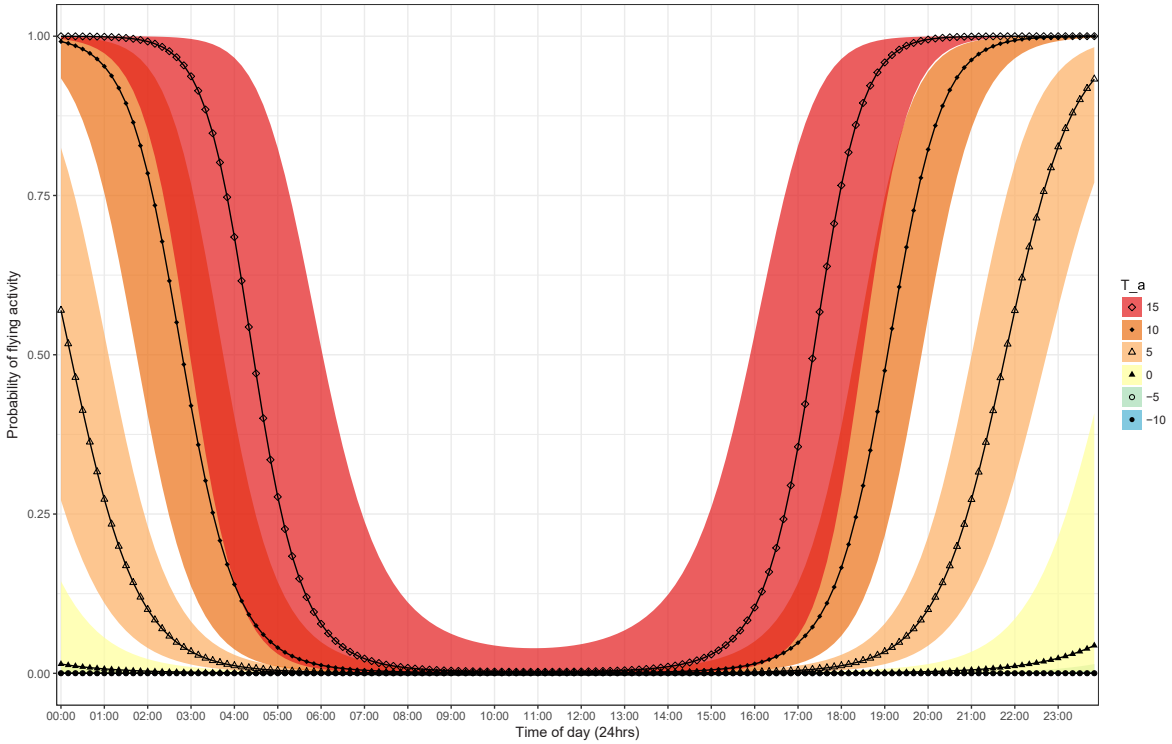

Fig. 2a. Probability of flying activity (F) in relation to Ta. The probability is modeled for middle time of hibernation season (27th of January).

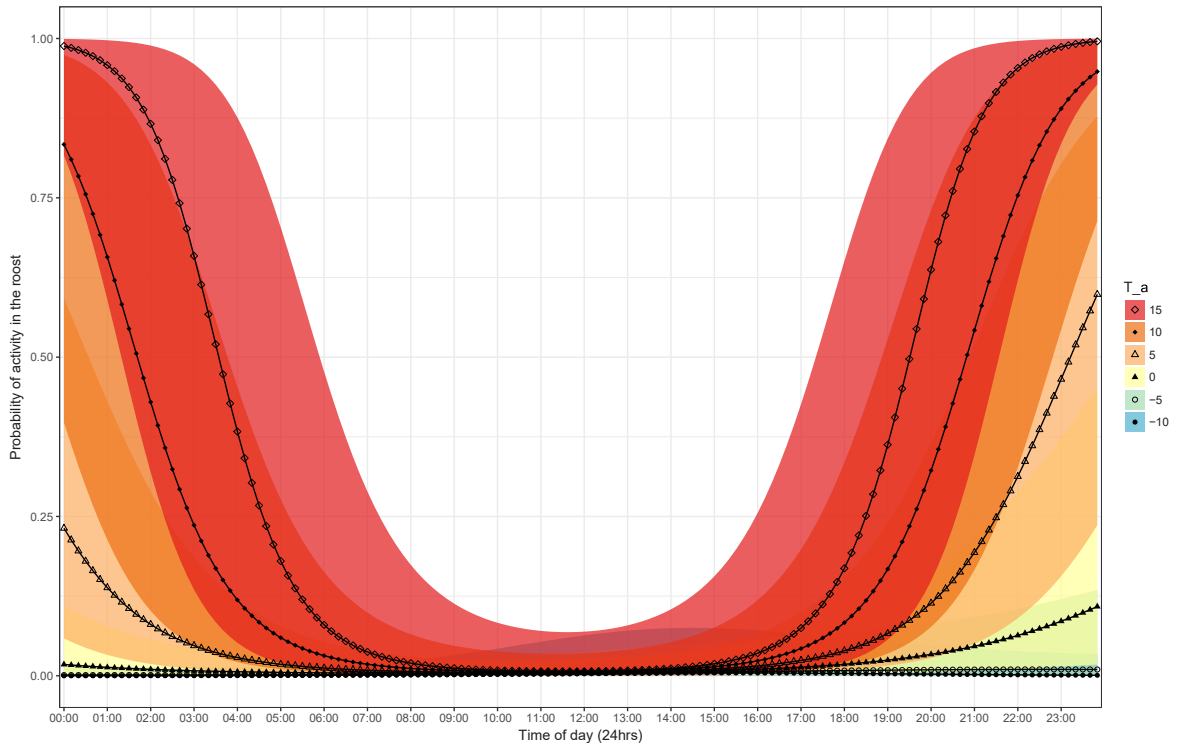

Fig. 2b. Probability of activity in the roost (R) in relation to Ta. The probability is modeled for middle time of hibernation season (27th of January).

interaction of Sin1 and T_a was retained. The interaction between Cos1 and Time_rel factor had a marginally significant effect ($p = 0.03$) with negative coefficients on activity in the roost, as well as the interaction between Sin1 and Time_rel ($p = 0.04$). This suggests that the duration of active vocalization and activity decreased in course of hibernation (Fig. 3A and B).

In general R activity was several times higher in terms of the number of recorded calls than F activity. Specifically, F activity occurred steadily, from sunset to sunrise, while R activity within the roost peaked a few times, particularly 1–2 h after sunset, close to midnight, and up to 1 h before sunrise (see Supplementary Fig. 4). The steady pattern of F activity suggests an initial emergence of the bats from the roost followed by continuous activitynear the roosts. In contrast, the distribution of R activity indicates that bats had distinct periods of elevated activity in the

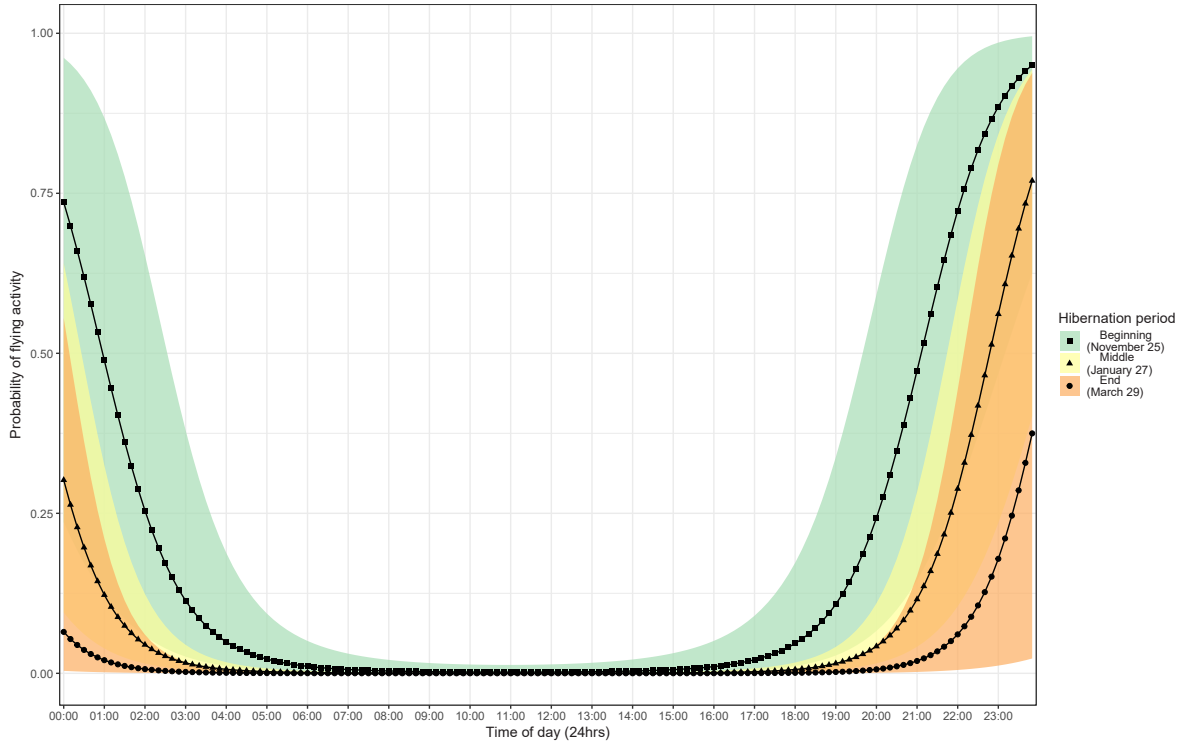

Fig. 3a. Probability of flying activity F (A) in relation to time during hibernation season. The probability is modeled for the avarage over season T_a 3.7 °C.

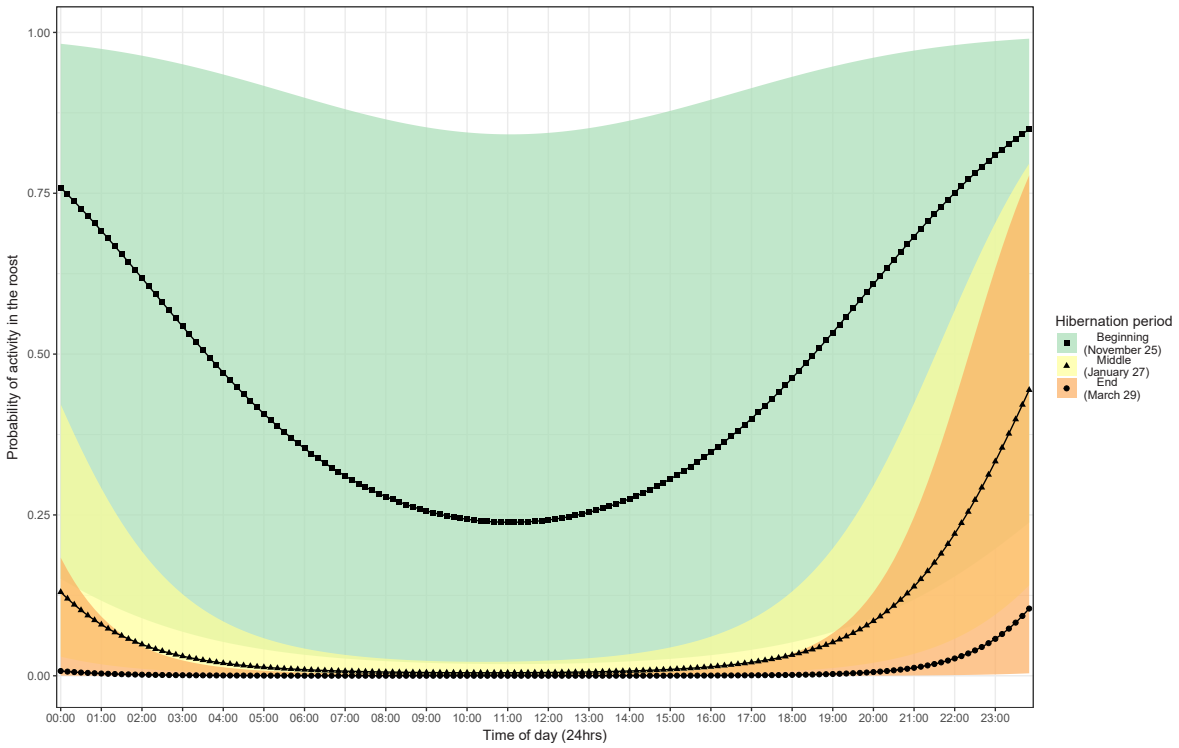

Fig. 3b. Probability of activity in the roost R (B) in relation to time of hibernation season. The probability is modeled for the avarage over season T_a 3.7 °C.

roost.

4. Discussion

Our study demonstrates the activity patterns of a non-cavernous hibernator was related to ambient temperature, circadian periodicity, and course of winter. As predicted, winter activity of *N. noctula* was related to ambient temperature and followed a circadian rhythm with an active phase during the night and a rest phase during the day. These findings are the first to show the winter activity pattern of migratory bats from a newly occupied northern hibernation range. However, bats maintained the circadian periodicity only at warm temperatures. Below 0 °C activity levels were minimal with no circadian pattern, suggesting that bats remain active only when it is energetically profitable. Given that energetic costs of flight increase as temperatures drop (Racey and Speakman, 1987; Klüg-Baerwald et al. 2016), flying is beneficial during warm nights when insect availability is higher (Williams, 1961; Zahn and Kriner, 2016) and the cost of flying is compensated by the benefit of feeding (Speakman and Racey, 1989). Furthermore, the energy costs for rewarming during arousals from torpor decrease at mild T_a (Geiser et al., 2004; Turbill and Geiser, 2008). Therefore, when temperatures fall below 0 °C, bats most likely remain in state of deep torpor. An important question is whether warm spells with similar temperature values during winter, occurring in both the northern and southern parts of the species hibernation range offer similar opportunities for occasional feeding. The case of Big brown bats (*Eptesicus fuscus*) from North America is illustrative. At lower latitudes, these bats forage during winter (Bernard et al., 2021). However, at higher latitudes, even during warm nights, they exhibit periodic circadian-synchronized flights without foraging (Klüg-Baerwald et al., 2024). Further studies on insect winter activity in relation to climate conditions are necessary to test weather warm temperatures serve as indicators of feeding opportunities and therefore trigger the winter activity patterns of non-cavernous hibernators.

The activity pattern followed a circadian rhythm. The maintenance of this circadian cycle during hibernation has been reported for bats that spend winter in mild climates (Boyles et al., 2006; Park et al., 1999; Hope and Jones, 2012, 2013). Our study revealed that *Nyctalus noctula* exhibited a distinct circadian activity in a newly occupied area for hibernation, but only when T_a was above 0 °C. The fact that displaying a circadian rhythm depends on temperature indicates a flexible adjustment of the active mode to environmental conditions, which might explain the species' recent success in expanding its hibernation range northward.

One indication suggesting that winter arousal is for feeding, is the synchronization of activity with sunset time. (Hope and Jones, 2012). Several studies (Turbill, 2008; Turbill and Geiser, 2008; Zahn and Clauss, 2003; Georgiev and Stoycheva, 2006) have shown that bat activity during winter at temperate latitudes gradually decreases with time after sunset, influenced by temperature loss and insect availability. When ambient temperatures were above 0 °C, bats were expected to fly near the roost throughout the night, not just in the first few hours after sunset. Turbill and Geiser (2008) demonstrated that during hibernation, bats in roosts can arouse several times per night. Since the bat aggregation was large, the constant activity near the roost throughout the night can be attributed to the alternating behavior of individual bats, with some remaining active while others remain in torpor. Furthermore, due to the small daily amplitude of T_a during winter, we suggest that photoperiod rather than T_a was the main zeitgeber triggering the synchronization of activity phase with nighttime. Thus, while Ta moderated the degree of activity, day length affected the duration of the rest phase versus activity.

The course of hibernation shapes the magnitude of activity. As predicted by the energy maximizing hypothesis, the probability of activity decreases throughout hibernation. The notably higher bat activity early in winter may result from the behavior of bat aggregations. They tend to gather in winter roosts at the start of the hibernation period and emit loud, low-frequency social calls (Furmankiewicz, unpublished data). According to Gebhard (1995), *N. noctula* mate in November. Mating behavior, followed by loud calls from the roost, likely provides crucial information to newcomers about the wintering group's location (Gebhard, 1995).

Winter activity patterns have been previously studied only in

southern and western populations of *N. noctula* from Slovakia, Bulgaria, and England (Celuch and Kanuch, 2005; Georgiev and Stoycheva, 2006; Avery, 1986). These regions are characterized by mild winters and pronounced insect activity during warm spells, favoring active behavior of non-cavernous hibernators. In our study, the colony was located at 51°N in central Europe and has been used for hibernation by *N. noctula* only for the last few decades (Strelkov, 1969; Lupicki et al., 2007; Godlevska, 2015). Although winter temperatures are mild, there are periods of several weeks with below 0 °C temperatures and significant snow cover (Dubicki et al., 2002). Maintaining activity without available food under these conditions should be costly. Additionally, the effect of global climate change increases the likelihood of extreme weather events in mid-latitudes (Cohen et al., 2014). For example, the so-called Early 2012 European cold wave from the North-East, reported in winter 2011/2012 (WMO report 2013), brought three weeks of temperatures below 0 °C in January and February and was associated with significant snowfall across Europe, especially in Central and Eastern Europe. Considering such periodic cold spells in Europe and the active behavior of winter aggregations of *N. noctula* in poorly insulated aboveground roosts, we suggest that Central European populations, accustomed to mild winters, may be more dependent on temperature amplitudes and thus more vulnerable than Western and Southern European populations.

Insulation properties of winter cavities are an additional crucial factor shaping winter activity in non-cavernous hibernators. According to Speakman and Racey (1989), temperature fluctuation in tree hibernacula is crucial as it allows animals to gauge outside conditions regarding food availability and the availability of unfrozen drinking water. Thus, roost temperature may directly impact the survival rate of winter colonies during hibernation (Speakman and Racey, 1989). It has been observed in Western, Central, and Southern Europe that *N. noctula* choose poorly insulated roosts for hibernation in various types of cavities such as trees (Sluitter and Heerdt, 1964), bat boxes (Horn, 2015), and buildings (Zahn et al., 2000). Simultaneously, cavities with temperatures above 0 °C are required for optimal hibernation (Gazarian, 2002). In our study, internal roost temperature was positively correlated with external temperature. The internal roost temperature was consistently 5 °C higher than the external temperature. The choice of poorly insulated cavities for hibernation made by *N. noctula* at more northern latitudes could be a consequence of behavioral predisposition (Bihari, 2004) rather than physiological requirements. However, several studies (Ruf and Arnold, 2000; Willis and Brigham, 2007; Czenze et al., 2013) have reported that social thermoregulation of bat aggregations, rather than the roost's microclimate itself, affects energy expenditure within a colony of cavity-roosting bats. Social thermoregulation provides benefits by allowing bats to share body heat, reducing the individual energy expenditure required to maintain body temperature. Noctule bats hibernating in groups awoke less frequently and had more prolonged torpor bouts compared to solitary bats (Moiseienko and Vlaschenko, 2023). Gazarian (2002) reported that a winter aggregation of more than 40–50 individuals of *N. noctula* could endure freezing temperatures, even below −10 °C for up to a week, while aggregations of fewer individuals in the same roost conditions did not survive. Therefore, bats may benefit from the poor insulation of winter cavities during warm spells, even at northern latitudes, as it allows passive rewarming (Currie et al., 2014), and they may compensate for heat loss during cold periods by clustering in aggregations.

Little is known about behavioral changes of species adjusting to new environmental conditions, at the same time this information is essential for understanding of ecological challenges and conservation needs for species in question (Wong and Candolin, 2015). The high activity level, occupancy of poorly insulated roosts, and maintenance of the circadian cycle during winter lead us to characterize *N. noctule* as an opportunistic hibernator relying on mild winter conditions. However, below-freezing temperatures limits activity and might force prolonged torpor bouts, while extreme cold spells can also increase arousal probability. Due to climate change, winters are becoming shorter and milder in Europe, which may promote the survival of bats by reducing the impact of harsh weather conditions. Interestingly, there is an interplay with circadian periodicity, which remains constant compared to temperature changes. We suppose that warmer temperatures and longer northern nights in winter at high latitudes may provide the larger time window for activity yet may not offer adequate opportunities for replenishing fat stores. This raises the question of whether observed activity in poorly insulated roosts allows bats to avoid premature energy depletion at high temperature at northern latitudes. The activity we recorded may be relic behavior, adapted from historical patterns of wintering in insect-rich, warm regions with 10–12-h nights. Further comparative studies along a latitudinal gradient are required to better understand the ecological challenges and direction of selection pressure on the winter behavior of non-cavernous hibernators. This will allow for the adjustment of conservation management strategies to species needs in the current era of rapid environmental changes.

5. Conclusion

The activity patterns of non-cavernous hibernators, focusing on *Nyctalus noctula*, in relation to ambient temperature, circadian rhythms, and seasonal dynamics. We found that winter activity in *N. noctula* is influenced by ambient temperature, showing a circadian rhythm with increased activity at night and rest during the day. These represent the first documentation of winter activity patterns for migratory bats in the recently colonized northern part of their hibernation range.

Changes in *N. noctula* activity patterns were primarily influenced by ambient temperature, with bats maintaining their circadian periodicity only at temperatures above 0 °C. This interplay of the ambient temperature with circadian periodicity highlights the flexibility of *N. noctula* winter behavior, However, it remains unclear whether similar temperature values in the northern range of the species wintering grounds have the same impact on insect activity as observed in southern regions and could provide noctules with compensatory energy through foraging. The northward expansion of *N. noctula* raises conservation concerns as warmer temperatures and longer northern nights in winter may not provide adequate opportunities for replenishing fat stores. Understanding these dynamics is crucial for developing effective conservation strategies to support *N. noctula* in adapting to a changing climate. Our study underscores the importance of further research to understand the ecological challenges and conservation needs of this species in the face of ongoing environmental changes.

CRediT authorship contribution statement

Kseniia Kravchenko: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Joanna Furmankiewicz:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Funding sources

Kseniia Kravchenko was supported by the Teraz Wroclaw program (http://study-in-wroclaw.pl/) for full tuition coverage for the Master's program at Wroclaw University.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the administrative staff of the Lower Silesian Governor's Office for providing regular access to bat roosts. We are grateful to Dr. Shannon Currie and Sara Troxell for their manuscript proofreading and valuable comments. Special thanks to Dr. Alexandre Courtiol and Dr. Viktoriia Radchuk for their help and guidance with statistical analysis. We also extend our gratitude to the three anonymous reviewers and editors, whose thoughtful comments greatly improved this manuscript. The first author additionally thanks the Teraz Wroclaw project (http://study-in-wroclaw.pl/) for supporting the Master's program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2024.103999.

References

Avery, M.I., 1985. Winter activity of pipistrelle bats. J. Anim. Ecol. 54, 721–738. https://doi.org/10.2307/4374.

Avery, M.I., 1986. The winter activity of noctule bats *(Nyctalus noctula)*. J. Zool. 209, 296–299. https://doi.org/10.1111/j.1469-7998.1986.tb03590.x.

Ben-Hamo, M., Munoz-Garcia, A., Williams, J.B., Korine, C., Pinshow, B., 2013. Waking to drink: rates of evaporative water loss determine arousal frequency in hibernating bats. J. Exp. Biol. 216, 573–577. https://doi.org/10.1242/jeb.078790.

Bernard, R.F., Willcox, E.V., Jackson, R.T., Brown, V.A., McCracken, G.F., 2021. Feasting, not fasting: winter diets of cave hibernating bats in the United States. Front. Zool. 18, 1–13. https://doi.org/10.1186/s12983-021-00434-9.

Bihari, Z., 2004. The roost preference of *Nyctalus noctula* (Chiroptera, Vespertilionidae) in summer and the ecological background of their urbanization. Mammalia mamm 68, 329–336. https://doi.org/10.1515/mamm.2004.032.

Boyles, J.G., McKechnie, A.E., 2010. Energy conservation in hibernating endotherms: why "suboptimal" temperatures are optimal. Ecol. Model. 221 (12), 1644–1647. https://doi.org/10.1016/j.ecolmodel.2010.03.018.

Boyles, J.G., Robbins, L.W., 2006. Characteristics of summer and winter roost trees used by evening bats (*Nycticeius humeralis*) in Missouri. Am. Midl. Nat. 155, 210–220. https://doi.org/10.1674/0003-0031(2006)155[0210:COSAWR]2.0. CO;2.

Boyles, J.G., Dunbar, M.B., Whitaker, J.O., 2006. Activity following arousal in winter in North American vespertilionid bats. Mamm Rev. 36, 267–280. https://doi.org/10.1111/j.1365-2907.2006.00095.x.

Celuch, M., Kanuch, P., 2005. Winter activity and roosts of the noctule (*Nyctalus noctula*) in an urban area (Central Slovakia). Lynx 36, 39–45.

Cohen, J., Screen, J.A., Furtado, J.C., Barlow, M., Whittleston, D., Coumou, D., et al., 2014. Recent Arctic amplification and extreme mid-latitude weather. Nat. Geosci. 7 (9), 627. https://doi.org/10.1038/ngeo2234.

Cryan, P.M., Veilleux, J.P., 2007. Migration and use of autumn, winter, and spring roosts by tree bats. In: Lacki, M., Hayes, J., Kurta, A. (Eds.), Conservation and Management of Bats in Forests. John Hopkins University Press, Baltimore, MD, pp. 153–175.

Currie, S.E., Noy, K., Geiser, F., 2014. Passive rewarming from torpor in hibernating bats: minimizing metabolic costs and cardiac demands. Am. J. Physiol. Regul. Integr. Comp. Physiol. 308 (1), R34–R41. https://doi.org/10.1152/ajpregu.00341.2014.

Czenze, Z.J., Park, A.D., Willis, C.K., 2013. Staying cold through dinner: cold-climate bats rewarm with conspecifics but not sunset during hibernation. J. Comp. Physiol. B 183, 859–866. https://doi.org/10.1007/s00360-013-0753-4.

Dietz, C., Nill, D., von Helversen, O., 2009. Bats of Britain, Europe and Northwest Africa. A & C Black.

Dubicki, A., Dubicka, M., Szymanowski, M., 2002. Klimat wrocławia. In: Smolnicki, K., Szykasiuk, M. (Eds.), Środowisko Wrocławia—Informator. Dolnośląska Fundacja Ekorozwoju, Wrocław, pp. 9–20 (In Polish.).

Fleming, T.H., Eby, P., 2003. Ecology of bat migration. In: Kunz, T.H., Fenton, M.B. (Eds.), Bat Ecology. University of Chicago Press, Chicago , Illinois, pp. 156–208.

Furmankiewicz, J., Kucharska, M., 2009. Migration of bats along a large river valley in southwestern Poland. J. Mammal. 90, 1310–1317. https://doi.org/10.1644/09-MAMM-S-099R1.1.

Furmankiewicz, J., Ruczynski, I., Urban, R., Jones, G., 2011. Social calls provide tree-dwelling bats with information about the location of conspecifics at roosts. Ethology 117, 480–489. https://doi.org/10.1111/j.1439-0310.2011.01897.x.

Gazarian, 2002. Наблюдения за зиМовкой рыЖих вечерниї в дуплах деревьев в предкавказье. Plecotus 5, 28–34.

Gebhard, J., 1984. *Nyctalus noctula* – Beobachtungen an einem traditionellen Winterquartier in Fels. Myotis 21–22, 163–170.

Gebhard, J., 1995. Observations on the mating behaviour of *Nyctalus noctula* (Schreber, 1774) in the hibernaculum. Myotis 32–33, 123–129.

Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu. Rev. Physiol. 66, 239–274. https://doi.org/10.1146/annurev.physiol.66.032102.115105.

Geiser, F., Drury, R.L., Kortner, G., Turbill, C., Pavey, C.R., Brigham, R.M., 2004. Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes, B.M., Carey, H.V. (Eds.), Life in the Cold: Evolution, Mechanisms, Adaptation, and Application. Inkworks, Fairbanks, AK, pp. 51–62.

Georgiev, D.G., Stoycheva, S.B., 2006. Flight activity of *Nyctalus noctula* bats (SCHREBER, 1774) (Mammalia: chiroptera) close to their winter colonies in the town area of Stara Zagora, Southern Bulgaria. Animalia 42, 161–166.

Godlevska, L.V., 2015. Northward expansion of the winter range of *Nyctalus noctula* (chiroptera: vespertilionidae) in eastern Europe. Mammalia 79, 315–324. https://doi.org/10.1515/mammalia-2013-0178.

Halle, S., Stenseth, N.C. (Eds.), 2012. Activity Patterns in Small Mammals: an Ecological Approach, vol. 141. Springer.

Hayman, D.T., Cryan, P.M., Fricker, P.D., Dannemiller, N.G., 2017. Long-term video surveillance and automated analyses reveal arousal patterns in groups of hibernating bats. Methods Ecol. Evol. 8 (12), 1813–1821. https://doi.org/10.1111/2041-210x.12823.

Hope, P.R., Jones, G., 2012. Warming up for dinner: torpor and arousal in hibernating Natterer's bats (*Myotis nattereri*) studied by radiotelemetry. J. Comp. Physiol. B 182, 569–578. https://doi.org/10.1007/s00360-011-0631-x.

Hope, P.R., Jones, G., 2013. An entrained circadian cycle of peak activity in a population of hibernating bats. J. Mammal. 94, 497–505. https://doi.org/10.1644/12-MAMM-A-095.1.

Horn, J., 2015. Temperaturuntersuchung in winterquartierkasten. Mitteilungen des LFA. Saugetierkunde Branderburg-Berlin 23, 2–3.

Hutterer, R., Ivanova, T., Meyer-Cordes, C., Rodrigues, L., 2005. Bat migrations in Europe—a review of banding data and literature. Naturschutz, Biologie und Vielfalt 28.

Jonasson, K.A., Willis, C.K.R., 2012. Hibernation energetics of little brown bats. J. Exp. Biol. 215, 2141–2149. https://doi.org/10.1242/jeb.066514.

Jones, G., Duverge, P.L., Ransome, R.D., 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symp. Zool. Soc. Lond. 67, 309–324. https://doi.org/10.1093/oso/9780198549451.003.0020.

Kanuch, P.I., Celuch, M., 2000. Výskyt *Nyctalus noctula* v panelových budovách mesta Prešov v rokoch 1998–1999 (The occurrence of *Nyctalus noctula* in prefab houses in Prešov in 1998–1999 (E-Slovakia)). Vespertilio 4, 146–148 (in Slovak with English abstract).

Kepel, A., Ciechanowski, M., Jaros, R., 2011. Wytyczne dotyczące oceny oddziaływania elektrowni wiatrowych na nietoperze. Generalna Dyrekcja Ochrony Środowiska, Warszawa (In Polish).

Klüg-Baerwald, B.J., Lausen, C.L., Willis, C.K., Brigham, R.M., 2017. Home is where you hang your bat: winter roost selection by prairie-living big brown bats. J. Mammal. 98 (3), 752–760. https://doi.org/10.1093/jmammal/gyx039.

Klüg-Baerwald, B.J., Lausen, C.L., Burns, S.M., Brigham, R.M., 2024. Physiological and behavioural adaptations by big brown bats hibernating in dry rock crevices. J. Comp. Physiol. B, 1–10. https://doi.org/10.1007/s00360-024-01546-4.

Körtner, G., Geiser, F., 2000. The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. Chronobiol. Int. 17 (2), 103–128. https://doi.org/10.1081/cbi-100101036.

Kravchenko, K., Vlaschenko, A., Prylutska, A., Rodenko, O., Hukov, V., Shuvaev, V., 2017. Year-round monitoring of bat records in an urban area: kharkiv (NE Ukraine), 2013, as a case study. Turk. J. Zool. 41, 530–548. https://doi.org/10.3906/zoo-1602-51.

Kravchenko, K.A., Vlaschenko, A.S., Lehnert, L.S., Courtiol, A., Voigt, C.C., 2020. Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes. Biol. Lett. 16 (9), 20200351. https://doi.org/10.1098/rsbl.2020.0351.

Kunz, T.H., Lumsden, L.F., Fenton, M.B., 2003. Ecology of cavity and foliage roosting bats. Bat ecology 1, 3–89.

Lee, K., Park, J.Y., Yoo, W., Gwag, T., Lee, J.W., Byun, M.W., Choi, I., 2008. Overcoming muscle atrophy in a hibernating mammal despite prolonged disuse in dormancy: proteomic and molecular assessment. J. Cell. Biochem. 104, 642–656. https://doi.org/10.1002/jcb.21653.

Lee, K., So, H., Gwag, T., Ju, H., Lee, J.W., Yamashita, M., Choi, I., 2010. Molecular mechanism underlying muscle mass retention in hibernating bats: role of periodic arousal. J. Cell. Physiol. 222, 313–319. https://doi.org/10.1002/jcp.21952.

Lupicki, D., Szkudlarek, R., Cichocki, J., Ciechanowski, M., 2007. Zimowanie borowca wielkiego *Nyctalus noctula* (Schreiber, 1774) w Polsce. Nietoperze 8, 27–38.

Lyman, C.P., 1982. Mechanisms of arousal. In: Lyman, C.P., Willis, J.S., Malan, A., Wang, L.C.H. (Eds.), Hibernation and Torpor in Mammals and Birds. Academic Press, New York, pp. 104–123.

McNab, B.K., 2002. The Physiological Ecology of Vertebrates: a View from Energetics. Cornell University Press.

Moiseienko, M., Vlaschenko, A., 2023. Deep torpor patterns and body mass loss of above-ground hibernating bats (*Nyctalus noctula*) in captivity—effects of sex, age, and grouping. Acta Chiropterol. 25 (2), 299–310. https://doi.org/10.3161/15081109acc2023.25.2.009.

Nievergelt, Y., 2013. Fourier series for periodic functions. In: Wavelets Made Easy. Birkhäuser, New York, NY, pp. 175–201. https://doi.org/10.1007/978-1-4614-6006-0_6.

Park, K.J., Jones, G., Ransome, R.D., 1999. Winter activity of a population of greater horseshoe bats (*Rhinolophus ferrumequinum*). J. Zool. 248, 419–427. https://doi.org/10.1111/j.1469-7998.1999.tb01041.x.

Park, K.J., Jones, G., Ransome, R.D., 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). Funct. Ecol. 14, 580–588. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00460.x.

Pfalzer, G., Kusch, J., 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. J. Zool. 261, 21–33. https://doi.org/10.1017/S0952836903003935.

Racey, P.A., Speakman, J.R., 1987. The energy costs of pregnancy and lactation in heterothermic bats. In: Loudon, A.S.I., Racey, P.A. (Eds.), Reproductive Energetics in Mammals. Symp Zool Soc Lond, vol. 57, pp. 107–125.

Reeder, D.M., Frank, C.L., Turner, G.G., Meteyer, C.U., Kurta, A., Britzke, E.R., et al., 2012. Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. PLoS One 7, e38920. https://doi.org/10.1371/journal.pone.0038920.

Rousset, F., Ferdy, J.B., Courtiol, A., 2014. spaMM: Mixed-Effect Models, with or without Spatial Random Effects. https://doi.org/10.32614/CRAN.package spaMM.

Ruf, T., Arnold, W., 2000. Mechanisms of social thermoregulation in hibernating alpine marmots (Marmota marmota). In: Life in the Cold: Eleventh International Hibernation Symposium. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 81–94.

Ruf, T., Geiser, F., 2015. Daily torpor and hibernation in birds and mammals. Biol. Rev. 90 (3), 891–926. https://doi.org/10.1111/brv.12137.

Schmidt, A., 2010. Zum Überwinterungsverhalten des Abendseglers *Nyctalus noctula* in Ostbrandenburg. Nyctalus 15, 223–234.

Sluiter, J.W., Van Heerdt, P.F., 1964. Distribution and abundance of bats in S. Limburg from 1958 till 1962. Natuurhist. Maandbl. 53 (11/12), 164–173.

Speakman, J.R., Racey, P.A., 1989. Hibernal ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. J. Anim. Ecol. 58, 797–813. https://doi.org/10.2307/5125.

Speakman, J.R., Thomas, D.W., 2003. Physiological ecology and energetics of bats. In: Kunz, T.H., Fenton, M.B. (Eds.), Bat Ecology. University of Chicago Press, Chicago, pp. 430–490.

Stawski, C., Willis, C.K.R., Geiser, F., 2014. The importance of temporal heterothermy in bats. J. Zool. 292 (2), 86–100. https://doi.org/10.1111/jzo.12105.

Strelkov, P.P., 1969. Migratory and stationary bats (chiroptera) of the European part of the soviet union. Acta Zoologica Cracoviensia 14, 393–440.

Thomas, D.W., Dorais, M., Bergeron, J., 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. J. Mammal. 71, 475–479. https://doi.org/10.2307/1381967.

Turbill, D.W., 2008. Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. J. Zool. 276, 285–290. https://doi.org/10.1111/j.1469-7998.2008.00487.x. London.

Turbill, C., Geiser, F., 2008. Hibernation by tree-roosting bats. J. Comp. Physiol. B 178, 597. https://doi.org/10.1007/s00360-007-0249-1.

Voigt, C.C., Lehnert, L.S., Popa-Lisseanu, A.G., Ciechanowski, M., Estók, P., Gloza-Rausch, F., Kramer-Schadt, S., 2014. The trans-boundary importance of artificial bat hibernacula in managed European forests. Biodivers. Conserv. 23, 617–631. https://doi.org/10.1007/s10531-014-0620-y.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., et al., 2002. Ecological responses to recent climate change. Nature 416, 389–395. https://doi.org/10.1038/416389a.

Williams, C.B., 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 244, 331–378. https://doi.org/10.1098/rstb.1961.0011.

Willis, C.K., Brigham, R.M., 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behav. Ecol. Sociobiol. 62, 97–108. https://doi.org/10.1007/s00265-007-0442-y.

Wong, B.B.M., Candolin, U., 2015. Behavioral responses to changing environments. Behav. Ecol. 26, 665–673. https://doi.org/10.1093/beheco/aru183.

Zahn, A., Clauss, B., 2003. Winteraktivität des Abendseglers (*Nyctalus noctula*) in Südbayern. Nyctalus 9, 99–104.

Zahn, A., Kriner, E., 2016. Winter foraging activity of Central European Vespertilionid bats. Mammalian Biology-Zeitschrift für Säugetierkunde 81, 40–45. https://doi.org/10.1016/j.mambio.2014.10.005.

Zahn, A., Christoph, C., Christoph, L., Kredler, M., Reitmeier, A., Reitmeier, F., Schachenmeier, A., Schott, T., 2000. Die Nutzung von Spaltenquartieren an Gebäuden durch Abendsegler (*Nyctalus noctula*) in Südostbayern. Myotis 37, 61–76.