


# Activity patterns of two syntopic and closely related aerial-hawking bat species during breeding season in Białowieża Primateval Forest

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**Abstract** Temporal and spatial activity of bats is species specific and shaped by many factors such as energy requirements, climate conditions and food distribution. Pregnancy and lactation are the most energy-demanding periods throughout the female life cycle. During these periods, females have to optimize their activity patterns to maximize foraging success; however, they simultaneously need to take care of their young. In addition, daily and seasonal fluctuations of insect availability strongly affect bat foraging activity. If females, which are under strong energy constraints, belong to closely related species, they may potentially suffer from competition. One of the mechanisms that allows them to avoid competition is temporal and spatial niche partitioning. Noctule and Leisler's bats are closely related forest-dwelling species whose diet is similar and consists mainly of ephemeral insects. The aim of our study was to test if they exhibit similar patterns in relation to the time and duration of their nocturnal activity. In Białowieża Forest, we demonstrated that female nocturnal activity of both noctule and Leisler's bats was shaped mostly by reproductive period and ambient temperature. We did not observe significant differences in the activity patterns of the two noctule species, which suggests that physiological constraints connected with reproduction and environmental conditions affect these species in a similar way and outweigh the competition between species.

**Keywords** *Nyctalus noctula* · *Nyctalus leisleri* · Reproduction · Temperature · Niche segregation · Species competition

## Introduction

Bats are the only mammals capable of active flight. The ability to fly allows bats, especially aerial insectivorous species, to cover large distances during the night and decrease risk of predation (Rydell et al. 1996). Although flight ability is beneficial from an evolutionary perspective, it is also a time- and energy-consuming process (Norberg and Rayner 1987; Muijres et al. 2012). Thus, the pattern of daily flight activity should maximize energy intake and minimize the costs of flight and predation risk (Rydell et al. 1996; Speakman and Thomas 2003; Voigt et al. 2010). Temporal and spatial patterns of activity of bats are shaped by many factors, such as temporal and spatial changes in food distribution and the energetic demands of individuals (Neuweiler 2000; Dietz and Kalko 2007; Barclay and Jacobs 2011). Because the diet of bats occurring in the temperate zone contains mainly small flying invertebrates, the activity of which is known to be reliant on ambient temperature (Abdullah 1961; Taylor 1963; Bale et al. 2002), bat activity is also highly dependent on climate and weather conditions (Clare et al. 2011; Frick et al. 2012; Clare et al. 2014). Night activity of females during the breeding season is mainly connected with the necessity for foraging, parental care and roost finding (Neuweiler 2000). The most energy-demanding periods for females are pregnancy and lactation (Kunz 1974; Anthony and Kunz 1977; Racey et al. 1987; Barclay 1989). Females need to balance their time out of the roost, which is required to get enough food, with the necessity for regularly returning to feed and warm their young (Rydell 1993; Shiel and Fairley 1999; Vonhof and Betts 2010).

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Females of most bat species deal with the same constraints relating to parental care; however, nocturnal activity patterns in bats are highly species specific. Even in the same climate conditions and reproductive period, females belonging to different species may exhibit different temporal activity patterns. The differences are mainly connected with the various food preferences and hunting strategies (Neuweiler 2000; Dietz et al. 2009). Bats that feed on ephemeral insects that occur in high abundance and unpredictably in space and time usually make only one short bout per night (Racey and Swift 1985; Brigham and Fenton 1991; Shiel et al. 1999; Dechmann et al. 2009). Contrarily, bats whose food is continuously available throughout the whole night feed for a longer time and make more flights (Audet 1990; Chruszcz and Barclay 2003).

The theory of niche differentiation indicates that closely related sympatric species use the environment in a way that allows them to reduce competition for resources. The separation of resource utilization can be based on temporal or spatial partitioning (Kronfeld-Schor and Dayan 2003; Bergeson et al. 2013; Symes et al. 2013). To test if closely related insectivorous bat species exhibit similar patterns, we conducted research on two syntopic, noctule bat species: noctule bats (*Nyctalus noctula*) and Leisler's bats (*Nyctalus leisleri*). The diets of both species consist mainly of ephemeral insects and their night activity lasts only a few hours. Majority of noctule bat prey consists of swarm insects, i.e. Trichoptera, Diptera (mostly Chironomidae) and Lepidoptera. In spring and autumn, they also forage on mass emergences of large insects from Hemiptera and Coleoptera (Beck 1995; Gloor et al. 1995; Mackenzie and Oxford 1995). Leisler's bats have similar food preferences and they forage predominantly on small- and medium-sized insects forming swarms. Their diet consists primarily of Lepidoptera, Diptera (mainly Tipulidae), Trichoptera (Beck 1995; Shiel et al. 1998) and Hymenoptera (Kaňuch et al. 2005). These two bat species are dependent on forest as they roost mainly in trees (Bihari 2004; Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004). The noctule bat is widespread across its range and known to be one of the most common forest-dwelling bats in Europe, unlike Leisler's bat, which is rather rare apart from in Spain, southern France, Germany and the Balkans (Horáček et al. 2000; Dietz et al. 2009). Both species migrate seasonally from the south or southwest to Białowieża Primaeval Forest, which is one of their important breeding sites (Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004; Kaňuch et al. 2004). Aggregations last from May until August (Ruczyński and Bogdanowicz 2005). Breeding colonies usually comprise 20–60 individuals in noctule bats and 20–50 in Leisler's bats (Bogdanowicz and Ruprecht 2004). In the study area, parturitions in both species take place in mid-June and females wean young around late July (Ruczyński 2006b). Although previous surveys provided detailed information on roost utilization

(Ruczyński and Bogdanowicz 2005; Ruczyński et al. 2007; Ruczyński and Bogdanowicz 2008; Ruczyński and Bartoń 2012) and foraging activity during pregnancy and lactation (Kronwitter 1988; Jones 1995; Shiel and Fairley 1999; Shiel et al. 1999; Kaňuch et al. 2005; Kaňuch 2007; Nad'ó and Kaňuch 2015) for both species, there was no comparative study of these two species inhabiting the same forest area. Our study aims to compare the patterns of nocturnal activity of the two noctule bats in primaeval forest conditions.

We hypothesized that in both species, the temporal foraging patterns, i.e. the duration and time of nocturnal activity and number of flights, are shaped by the reproductive status of females. To test our hypotheses, we searched the bat roosts and monitored their emergences and nocturnal activity with radiotelemetry. We expected females of two *Nyctalus* species to (i) increase number of flights per night and their duration after parturitions and hasten the onset of emergence when lactating, as well as (ii) lengthen their nocturnal activity in higher ambient temperatures and (iii) exhibit similar activity patterns.

## Study area, methods and material

### Study area

Our study was conducted in the Białowieża Primaeval Forest (BPF). This large temperate mixed lowland forest covers an area of 1450 km<sup>2</sup>, partially in Poland (600 km<sup>2</sup>) and partially in Belarus. BPF in Poland (52° 45' N, 23° 50' E) is divided into Białowieża National Park (105 km<sup>2</sup>) and managed forest. The study area (100 km<sup>2</sup>) covered well-preserved stands of Białowieża National Park (BNP), as well as parts of the managed forest with old-growth remnants (over 80–100 years). The climate is continental (Olszewski 1986), with the highest average temperature in July (17.8 °C) and lowest in January (−4.7 °C). The daily temperature amplitude is high in spring and summer. During the study period, the night's duration varied from 7:05–9:25 h. The five main forest types in this area are deciduous forest (*Quercus robur*, *Tilia cordata* and *Carpinus betulus*), mixed deciduous forest (*Picea abies*, *Q. robur*, *T. cordata* and *C. betulus*), black alder bog forest and streamside alder-ash forest (*Alnus glutinosa* and *Fraxinus excelsior*), mixed coniferous forest (*Pinus sylvestris*, *P. abies* and *Q. robur*) and coniferous forest (*P. sylvestris* and *P. abies*) (Faliński 1986; Bernadzki et al. 1998). The superabundance of holes in this forest provides shelters for a wide variety of animals; there are 16 secondary cavity nesting bird species inhabiting BPF (Wesołowski 2007). The area is inhabited by 15 species of bats (Ruczyński and Ruczyńska 2008; Rachwald and Ruczyński 2015); all of which use the forest as roosting sites, foraging sites or safe commute routes.

**Table 1** ANOVA table for the top-ranked linear model (LM) assessing the effects of species (*Nyctalus noctula* and *Nyctalus leisleri*), reproductive period (pregnancy and lactation) and time of sunset on the time of emergence onset

Variable	Mean squared error	F value	p value
Time of sunset	0.003	42.06	<0.001
Species	0.0001	1.40	0.239
Reproductive period	0.001	14.46	<0.001

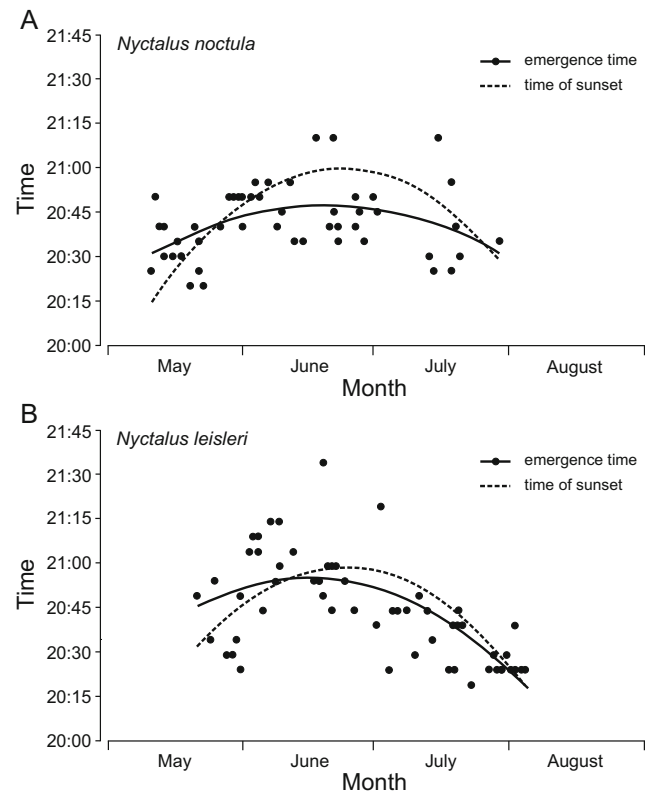
## Capture

We caught bats (1998–2002) with mist nets by small forest rivers (Lutownia, Narewka, Hwoźna and Złota) and by a little pond at the edge of the forest (BNP). We identified bats at the species level and assessed their sex, age and reproductive status. Reproductive state was classified as non-pregnant, pregnant or lactating; pregnancy was assessed by palpation of the abdomen, while the indicator for lactation was a hairless area around the nipples. Based on this information the parturition time was estimated. All handling procedures were performed under the permission from the Ministry of Environment of Poland.

## Radio tracking

We attached small transmitters (0.5 g, Biotrack, Wareham, UK, Titley Electronics Pty. Ltd., Ballina, New South Wales, Australia; 0.7 g, Titley Electronics, and Holohil System, Carp, Ontario, Canada) to the interscapular region of bats with surgical adhesive (Skin-Bond, Smithand Nephew, Largo, Florida). The mass of the applied transmitters never exceeded 5 % of the bats' body mass (Aldridge and Brigham 1988). We radio tracked a total of 26 noctule bats (10 pregnant females, 11 lactating females, 3 juvenile females and 2 juvenile males) and 25 Leisler's bats (10 pregnant females, 12 lactating females, 1 juvenile female and 2 juvenile males). We used H-shaped handmade antennae and two types of receivers (Yupiteru, MVT-700, Javiation, Bradford, West Yorkshire, United Kingdom and Yaesu FT-290R, Vertex Standard, Cypress, California) to locate the position of tagged bats. We searched roost sites from May to August in 1998–2000 and 2002 (Leisler's bat) and in 1999–2002 (noctule bat). Bats were radio tracked each day as long as signals from the transmitters were found; the average tracking period was 6.5 days (range 1–14 days) for noctule bat and 7.5 days (range 2–13 days) for Leisler's bat.

Observations of radio tracked bats allowed us to estimate the minimum time duration that animals spent in



**Fig. 1** Variation in the onset of bat emergence over the summer with reference to the time of sunset. The changes in timing of emergence in **a** noctule bat (1999–2002;  $N = 48$ ) and **b** Leisler's bat (1998–2000, 2001;  $N = 58$ ). Dashed lines denote time of sunset; black lines show polynomial trend line for the onset of bat emergence

their roosts. We checked if bats were in their roost every 10 min, from their evening emergence until sunrise. Only all-night observations were analysed further; we excluded nights with foul weather and nights when bats lost transmitters or changed their roosts. Finally, only 46 of 98 observations (21 noctule bats and 25 Leisler's bats) were analysed.

## Emergence observations

Emergence counts at dusk started 30–40 min before sunset and continued until it was totally dark. Noctule bats were observed from May to August 1999–2002 and Leisler's bats in 1998–2000 and 2002. The time of emergence of the first bat and the duration of all emergences were recorded for 48 evenings for the colonies of noctule bats and 58 evenings for Leisler's bats. The identification of species emerging from each roost was based on the presence of radio-tagged individuals. However, mixed species bat aggregations are also known in BPF (Ruczyński and Ruczyńska 2000).

**Table 2** ANOVA table for the top-ranked linear model (LM) assessing the effects of species (*Nyctalus noctula* and *Nyctalus leisleri*), reproductive period (pregnancy and lactation) and temperature on activity duration

Variable	Mean squared error	F value	p value
Temperature	70,790	13.95	0.001
Temperature <sup>2</sup>	37,100	7.31	0.010
Reproductive period	30,284	5.97	0.019
Temperature × reproductive period	327	0.06	0.801
Temperature <sup>2</sup> × reproductive period	36,828	7.26	0.010

## Statistical analysis

To verify if species considered reproductive period and ambient temperature affected duration of bat activity and number of bat flights per night, we applied a linear model (LM) and generalized linear model (GLM) for count data (Poisson family), respectively. The global models included the following: (1) the main effects of all explanatory factors (species, reproductive period and ambient temperature), (2) quadratic terms for temperature and (3) two-way interactions between all three explanatory variables. LM was also used to assess the effect of sunset time, species and reproductive period on the time of bat emergence. The global model included the main and interactive effects (two-way interaction) of all variables considered.

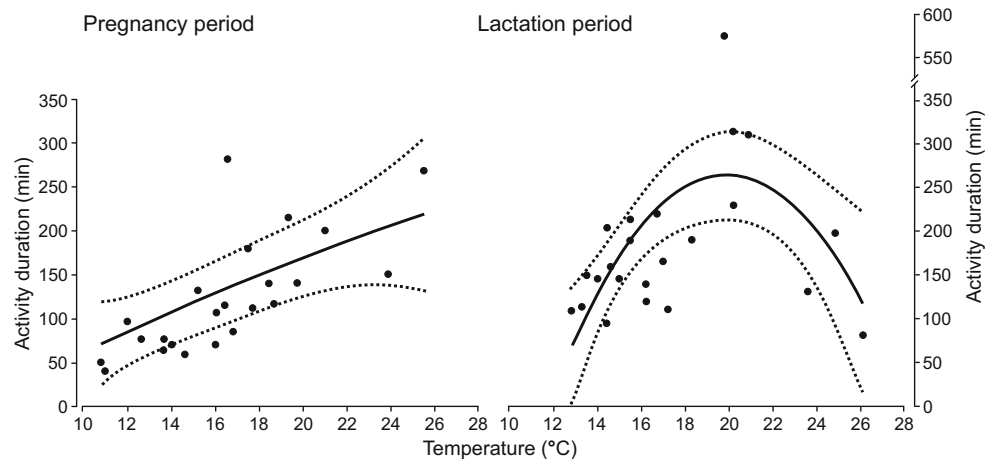
For all models, every explanatory variable was standardized to a mean of 0 and a SD of 0.5 by using the *standardize* function within the “arm” package (Grueber et al. 2011; Gelman and Su 2015). Then, we applied model ranking based on the Akaike information criterion (AIC) with a second-order correction for small sample size (AIC<sub>c</sub>) available within the *dredge* function (“MuMIn” package; Bartoń 2015)); the results are given in Table S1 (Online Resource 1). The top-ranked, most parsimonious submodels were selected as the single best models. Analyses were performed using R software version 3.2.3 (R Core Team 2015).

## Results

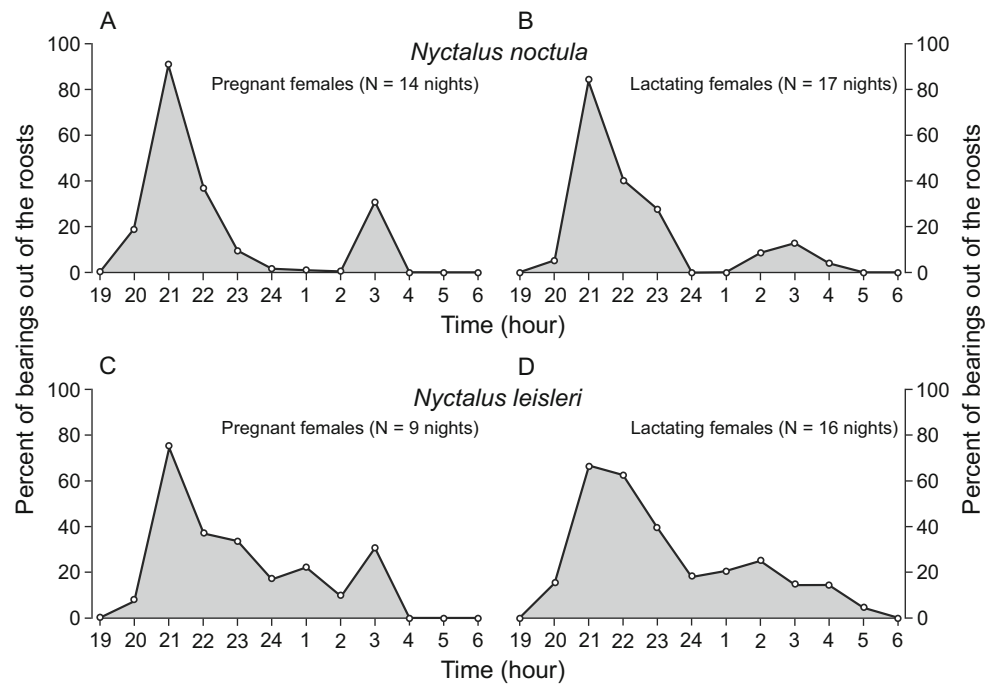
The time of sunset affected emergence onset of both bat species. The time of emergence onset increased with growing time of sunset (LM,  $R^2 = 0.36$ ,  $P < 0.001$ , Table 1). Over the summer, the daily timing of emergence did not differ between species and in both species, it changed dependently on reproductive period ( $P < 0.001$ , Table 1). Noctule bats started to leave their roosts on average ( $\pm$  SD)  $2.0 \pm 11.5$  min ( $N = 27$ ) after sunset during pregnancy, while in lactation, they emerged on average  $10.0 \pm 13.95$  min ( $N = 21$ ) before sunset. In Leisler’s bat, the observed onset of emergence during pregnancy was on average  $6.0 \pm 13.3$  min ( $N = 19$ ) after sunset and during lactation on average  $5.0 \pm 12.5$  min ( $N = 39$ ) before sunset. At the end of July, the observed onset of emergence was later in both species (Fig. 1).

In noctule bats, the average total time spent outside the roost during the night ( $\pm$  SD) was  $119 \pm 45$  min during pregnancy, increasing to  $137 \pm 34$  min after parturition. A similar pattern was observed in Leisler’s bats; time out of the roost varied from  $132 \pm 93$  min during pregnancy to  $190 \pm 91$  min after parturition. Duration of bat activity (both species) was significantly affected by the interactive effect of temperature and reproductive period (LM,  $R^2 = 0.463$ ,  $P < 0.05$ , Table 2, Fig. 2). As the temperature increased, the length of time that the animals spent out of the roosts almost linearly extended in

**Fig. 2** Influence of mean daily ambient temperature on the activity duration of noctule and Leisler’s bats in pregnancy and lactation periods. Dotted lines denote 95 % confidence intervals



**Fig. 3** Variation in the percentage of radio telemetry bearings, when bats were out of the roosts over the night for noctule bat in pregnancy (a) and lactation periods (b) and for Leisler's bat in pregnancy (c) and lactation periods (d)



pregnancy period, while during lactation, duration of activity increased at moderate temperatures (13.5–21 °C) and decreased when temperature exceeded 21 °C (Fig. 2). We did not observe species-related differences in effect of ambient temperature on activity duration.

Both before and after parturitions, two peaks of nocturnal activity were observed in noctule bats, when bats spent significant amount of time away from the home roost. During the first peak of activity (9 pm–10 pm), up to 91 % of radio telemetry bearings were out of the roosts, while during the second peak (2 am–4 am), 31 %. In Leisler's bat, only one noticeable peak of activity was observed, from 9 pm to 10 pm. In subsequent hours, animals spent progressively less time out of their roosts (Fig. 3).

Pregnant noctule bat females performed on average ( $\pm$  SD)  $1.6 \pm 0.6$  ( $N = 14$ ) flights per night, similarly to Leisler's bats  $1.5 \pm 0.8$  ( $N = 9$ ). After parturitions, the number of flights per night increased significantly (GLM,  $P < 0.05$ ), to  $2.0 \pm 1.2$  ( $N = 7$ ) in noctule bat and  $3.0 \pm 1.9$  ( $N = 16$ ) in Leisler's bat. The species and ambient temperature did not affect the number of flights per night.

In noctule and Leisler's bat, we did not find any significant correlation between the number of flights and the time spent outside the roost ( $R = 0.05$  and  $R = 0.20$ , respectively). The first flight was the longest and for noctule bat was on average 99 min in pregnancy and during lactation 113 min. Subsequent flights were shorter and lasted on average 3 to 17 min. In Leisler's bat, the mean duration of the first flight for females was 77 min during pregnancy and 139 min after parturitions. The next foraging bouts lasted on average 1 to 43 min.

## Discussion

Our studies demonstrated that female nocturnal activity of two closely related species noctule and Leisler's bats is shaped mostly by reproductive period and ambient temperature. Bats spent more time foraging after parturitions (longer flights and earlier emergences), while the duration of activity also increased with higher temperatures. We did not observe any significant differences in the activity patterns of the two noctule species, which suggests that physiological constraints connected with reproduction and environmental conditions affect these species in a similar way. This may indicate that competition between these species does not have a significant impact on their activity patterns which can suggest that niche segregation is not based on shifting of temporal activity.

Our studies showed that energetic demands connected with reproduction costs are crucial for shaping activity of noctules. Pregnant females emerged later, and their duration of activity was shorter in comparison to lactating females. Possibly, lactating females, due to their higher energetic requirements, start foraging earlier and elongate time of activity, even if potential insect availability during the lactation period is higher (Anthony and Kunz 1977). These observations are comparable to studies conducted on noctule bats and other species of aerial-hawking bats, e.g. *Myotis lucifugus* and *Eptesicus nilsonii* (Kunz 1974; Anthony and Kunz 1977; Rydell 1993; Jones 1995; Duverge et al. 2000; Shiel and Fairley 2000). However, some authors suggest that there is no correlation between foraging and reproductive season because insect abundance is higher during lactation (higher mean ambient



temperatures) and lower female wing loading after parturition, which makes foraging a less energy-consuming process (Kunz 1974; Anthony and Kunz 1977). Females of noctule and Leisler's bats increase the number of flights after parturition which is probably affected by the parental care, i.e. warming up of young and the necessity of feeding them during the night. A higher number of bouts in lactating females was also observed in Indiana bats *Myotis sodalis*, which during pregnancy never come back to the roost before dawn, while after parturitions 2–4, flights were recorded (Murray and Kurta 2004). In Leisler's bats, an increasing number of flights was documented by Shiel et al. (1999), where the first bout was always the longest, irrespective of the reproductive period. In our studies, the first flight was also always the longest and its duration was prolonged after parturition.

Insect activity is highly positively correlated with ambient temperature (Abdullah 1961; Taylor 1963; Bale et al. 2002). Low temperature constrains insect activity patterns, so insect density becomes much lower soon after sunset, when temperature decreases (Kunz 1973; Racey and Swift 1985; Rydell et al. 1996; Polakowski et al. 2014). A second peak of insect density starts at the end of the night (Racey and Swift 1985; Rydell et al. 1996). It is known that bat activity is also highly dependent on ambient temperature and insect availability (Racey and Swift 1985; Speakman and Thomas 2003; Wolbert et al. 2014). In view of this, bats should emerge earlier and elongate their night activity to match the periods of the highest density of insects. The relatively cold climate of BPF could explain noctule bats engaging in earlier emergences, even before estimated parturition time; while in other studies, this pattern overlapped with the onset of lactation (Kunz 1974; Jones 1995; Shiel et al. 1999; Duverge et al. 2000). Benefits of reaching the feeding areas before insect abundance depletion have to outweigh the risk of predation (Barclay 1989; Barclay 1991; Shiel and Fairley 1999; Shiel et al. 1999; Frick et al. 2012) and food competition with diurnal birds (Speakman 1991; Speakman 1995). Noctule bats in our studies started their emergences as much as 25 min before sunset. This is consistent with observations by Polakowski et al. (2014) over the Siemianowka reservoir, where noctule bats started to forage as much as 15 min before sunset. In both noctule and Leisler's bats, ambient temperature determined also the duration of being out of the roost. Rising ambient temperature (up to 21 °C) increased the total time of bat activity—the pattern commonly observed in other bat species (Anthony et al. 1981; Kronwiter 1988; Maier 1992; Catto et al. 1995). In a pregnancy period, the activity duration extended almost linearly with the growing temperature, while during lactation, it decreased after the temperature exceeded 21 °C. A decrease in activity duration in lactating period can result from the fact that lactating tree-roosting females may use torpor more often than pregnant females. Females of *Eptesicus fuscus* became torpid more frequently after nights with a shorter activity

duration (Rintoul and Brigham 2014). Longer and deeper torpor bouts are potentially more profitable for lactating than for pregnant females. The saved energy can be used in milk production (Studier and Ofarrell 1972; Dzal and Brigham 2013). Yet, there are studies reporting opposite relationship, where pregnant females use torpor more often than lactating individuals (e.g. Audet and Fenton 1988; Dietz and Kalko 2006). Interestingly, Bell et al. (1986) showed that time that bats (*Macrotus californicus*) have to spend foraging is inversely correlated with the roost temperature which is remarkably associated with ambient temperature (Ruczyński 2006a). This phenomenon may be explained by higher water loss in lactating females (Kurta et al. 1990) or by the heat dissipation limit hypothesis, providing that lactating active animals, when facing high temperatures, cannot increase their food intake or milk production, because they are not able to dissipate body heat generated as a by-product of milk production (Król and Speakman 2003).

The lack of prominent differences between the activities of the two studied species can be explained by their similar ecology and the similar physiological and environmental constraints shaping their behaviour. Both species belong to the aerial-hawking bats, feeding mainly on ephemeral insects, whose availability changes over the night (Safi 2008). Moreover, both noctules are strictly tree-dwelling bats in BPF, which occupy similar roosts (Ruczyński and Bogdanowicz 2005). The thermal properties of roosts affect bat thermoregulatory behaviours similarly, so energetic requirements are also probably comparable. The lack of prominent differences in the activity of the bats also indicates that food niche segregation is not based on the shifting of temporal activity. Being active during a time of lower food availability can negatively affect the fecundity of animals. Therefore, mechanisms based on segregation in space, such as those observed among males and females of Daubenton's bats, seem to be more efficient (Senior et al. 2005; Encarnação 2012; Nardone et al. 2015). Bats may also choose different foraging sites in relation to their prey detection strategy and manoeuvrability (Norberg and Rayner 1987; Siemers and Schnitzler 2004). Although both species are opportunistic consumers of flying insects and their flying technique is quite similar—the flight is usually direct and very fast (Jones 1995; Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004; Kaňuch et al. 2005), they slightly differ in selection for habitats to forage. Unlike noctule bats, beside open landscapes, Leisler's bats utilize large woodlands, where they forage predominantly in the forest clearings (Kowalski and Ruprecht 1981; Kronwiter 1988; Rachwald 1992; Sachanowicz and Ciechanowski 2005). However, selection of foraging sites for both species highly depends on study site (Shiel et al. 1998; Shiel and Fairley 1999; Dietz et al. 2009). Based on authors' experience, in BPF, *N. leisleri* hunts predominantly in forest

stands, while they occurred rarely over the water bodies or in open areas. This may suggest that spatial segregation mechanism of food niche segregation could prevail over temporal one.

In summary, we showed that during pregnancy and lactation, both noctule and Leisler's bats exhibit similar patterns of activity, which are mainly dependant on the development level of young and ambient temperature. Further studies including the relative density of insects in different periods of the breeding season would help to answer the questions about differences in the feeding patterns of these two closely related species in BPF.

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