

Do the thermal conditions in maternity colony roost determine the size of young bats? Comparison of attic and cave colonies of *Myotis myotis* in Southern Poland

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Abstract. Body weight and forearm length measurements were taken from the bats from two reproductive colonies of *Myotis myotis*: a church attic (50° 54' 18" N; 18° 56' 16" E) and a cave (50° 43' 45" N; 19° 16' 31" E) in 2001–2003. During pregnancy air temperatures outside these shelters were more variable than during lactation. Mean 24 hour temperatures in the attic never drop below mean daily temperatures outside and the rate of temperature change inside the roosts resulting from outside temperature fluctuations were four times higher than in the cave. Temperatures from the cave showed 24 hour oscillations which did not differ significantly between the years of study. Forearm lengths and body weight of the young did not show any correlation with roost location but varied with the year of study. Differences in the size of the young were explained by cool weather during pregnancy resulting in food shortage for the mothers and reduced growth rate of their fetuses. Low roost temperatures also induced torpor. Forearm length in the adult females varied between roost but was independent of year of study. The number of clustering females is probably crucial for the persistence of colonies of *Myotis myotis* located in caves in the northern Carpathians.

Key words: nursery colony, microclimate, roost adaptation, greater mouse-eared bat

Introduction

Bats of the temperate zone are thought to be guided by the thermal conditions inside the roost whilst choosing a site for a maternity colony. Thermal conditions could be reflected in delayed implantation and embryogenesis and consequently in parturition (Racey et al. 1987, Mowat & Andrews 1995). Low temperatures can also prolong postnatal development of young bats, e.g. by exerting an influence on food resources and by the induction of torpor (Racey et al. 1987, Heidinger et al. 1989, Zahn 1999, Rodrigues et al. 2003). Lausen & Barclay (2002, 2003) have shown that torpor is much rarer in *Eptesicus fuscus* during pregnancy and earlier lactation than during late lactation. Kunz (1973) did not find any differences in growth rate between young *Myotis velifer* from underground and aboveground sites, but showed significant differences between seasons. A maternity colony consisting of hundreds or more individuals accumulates energy which may compensate the influence of low temperature (Dwyer & Harris 1972, Tuttle 1975, Kurta 1985, Kunz 1987). *Myotis myotis* (Borkhausen, 1797) is found in western, southern and central Europe, excluding most of Scandinavia, the British Isles, and nearly all of European Russia (Guttinger et al. 2001). The northeastern boundary is demarked by the Vistula and Bug rivers in Poland (Sachanowicz & Ciechanowski 2005) and the eastern borders of Podolya in Ukraine (Godlevska 2002) (Fig. 1).

In southern Europe females gather to form maternity colonies mostly in caves, whereas individuals north of the Alps, Sudety Mts. and Carpathians form colonies almost exclusively

in attics. This can be explained by a lack of underground chambers (cavities) meeting their temperature demands (H o r á ě e k 1984, R o d r i g u e s et al. 2003). In Central Europe parturitions take place from the middle of June till the beginning of July (R o d r i g u e s et al. 2003), and juveniles attain adult size after two months (P a n d u r s k a 1998, A r l e t a z et al. 1991). It is assumed that north of the Carpathian Mts. *M. myotis* appeared as a result of migrations from southern Europe (Iberian Peninsula), the northern edges of the Alps and the foreland of the Sudety Mts. (R u e d i & C a s t e l l a 2003), or through the Moravian Gate and the depression in Beskid Niski (Dukielska pass) (W o ł o s z y n 1989). Adaptation to attics that took place about 200 years ago is thought to have provided independence from underground sites for this species and allowed it to expand in a northern direction (H o r á ě e k 1984, Z a h n 1999). The maternity colony of *M. myotis* in Nietoperzowa Cave – existing at the turn of the 19th and 20th centuries (W a g a 1855, K o w a l s k i 1953, H a r m a t a 1973), and a colony known from the 1970's located in the Nietoperek undergrounds (U r b a n c z y k 1990) indicate the possibility of reproduction in cool places despite the availability of attics. Evidence for the reproduction of *M. myotis* in southern Poland comes from the subatlantic period (P o s t a w a 2004). The easternmost maternity colony of this species located in a cave (G a s & P o s t a w a 2001) has been observed since 1998 in Studnisko Cave (southern Poland). If thermal condition of the roost influence pregnancy and juvenile development, differences in size between attic and cave colonies are expected. The primary objective of this study was to examine i) if there are differences in body size between young bats from cave and attic colonies and ii) if so, which thermal parameters (temperatures) play a key role.

Material and Methods

Study area

Krakowsko-Wieluńska Upland is a part of Southern Poland Uplands. It forms a narrow belt, 12 to 50 km wide and about 160 km long, with the area of about 3 000 km², extending longitudinally from 49°48'N to 51° 14'N. It consists of Upper Jura limestone, but in north part (Wieluńska Upland) it is covered by glacial deposits (about 300 m a. s. l.). In the north part it reaches about 450 m (the highest elevation: 512 m a. s. l.) and overtops neighbouring areas of about 100 m. Summary of annual precipitation ranges between 650–700 mm, whereas mean temperature is estimated to 7.5°C and is lower about 0.5–1.0°C comparing to adjacent areas. Winter period lasts about 100 days, ice-sheet lays 80 days on average, but in shadowed places and in the bottom of valleys can sustain even 100 days (K o n d r a c k i 2001). There are numerous caves and rock shelters, which have been catalogued to the number of about 1 000 (G r a d z i Ń s k i & S z e l e r e w i c z 2004). The surveys were conducted in a maternity colony of the greater mouse-eared bat *M. myotis* in a cave and a colony situated on church attic was taken as a control (distance about 30 km, Fig. 1):

- The Studnisko Cave (Częstochowa Upland, 346 m a.s.l., 19°16'E, 50°43'N): the cave 77.5 m deep and 337 m length, a static microclimate, mean air temperature 7.5°C (S k a l s k i 1995). Between 1998 and 2002 a maternity colony of *M. myotis* was located in a chimney in the main chamber ceiling about 5 m below the entrance, in 2003 it moved into less accessible chimney about 5 m below entrance. The colony was formed in 1998 and currently numbers over 200 bats.

- Kłobuck (Wieluń Upland, 245 m a.s.l., 18°56'E, 50°54'N) situated 15 km to the north – east from Częstochowa. The maternity colony of *M. myotis* is located in a church attic, in 3 m high aisle with a southern roof exposition. The colony counts from 60 to 100 individuals and has been constantly monitored from 1993.

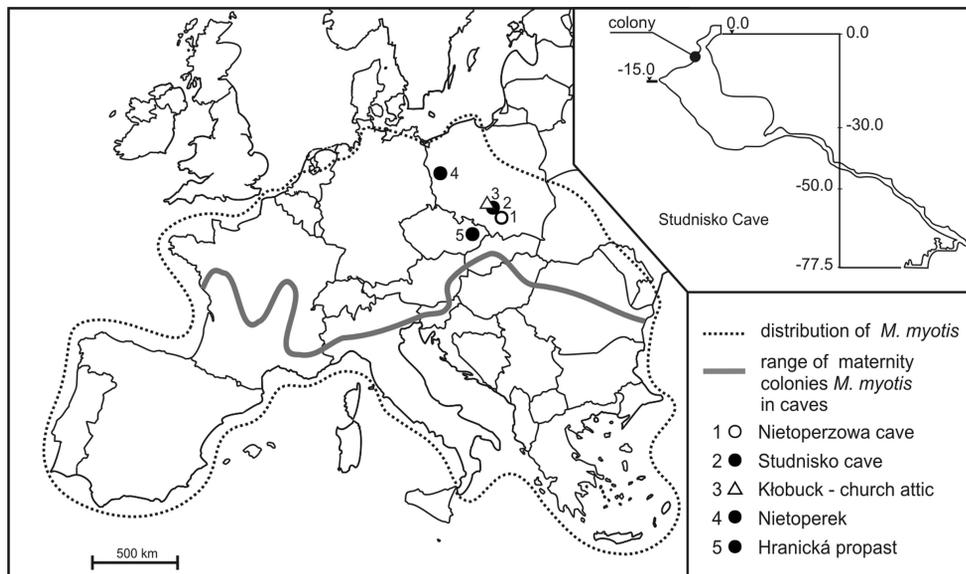


Fig. 1. Localization of the investigated maternity colonies of *M. myotis*: the church attic in Kłobuck (3) and the Studnisko Cave (2); remaining underground maternity colonies: existing (4) and historical (1), and scheme of the Studnisko Cave with the colony localization. Occurrence of *M. myotis* in Europe after: G ü t t i n g e r et al. (2001), Godlewska (2002), Sachanowicz & Ciechanowski (2004); range of maternity colonies in caves after Horáček (1984).

Nettings and morphometric measurements

Bats from both maternity colonies (*M. myotis*) were captured when young were volant, every year in the same time: 30–31 July. In that time – about 40 days after parturition, juveniles of *M. myotis* attain 85–90% of adults size (P andurska 1998, Arletta et al. 1991). Mist nets and harp trap were used (Studnisko Cave) or animals were caught directly from the colony (Kłobuck). The forearm length fl (0.01 mm) and body weight m (0.25 g) measurements were taken. The age (juv – the current year individuals, ad – older than one year) was determined on the basis of the presence of chin-spot, fur color (young have gray fur) and epiphyses ossification (Kunz 1988). Reproductive status of adult females was determined upon lack of fur around nipples (lactating/non lactating). To avoid bias connected with mass changes during foraging (that could increase body weight in night time), measurements were conducted while bats were leaving the roost in foraging purpose (the Studnisko Cave) or in late afternoon (Kłobuck).

For young bats fl (x) and m (y) relations were tested. For males and females from the colony situated in the Studnisko Cave and also males from the colony in Kłobuck statistically significant values were obtained – respectively: $y=0.56x-9.77$, $r^2=0.45$ ($F_{1,27}=21.4$, $p<0.0001$); $y=0.75x-21.62$; $r^2=0.63$ ($F_{1,22}=35.2$, $p<0.0001$); $y=0.71x-18.52$, $r^2=0.38$ ($F_{1,18}=10.5$, $p<0.005$). For females from Kłobuck colony relations were not statistically significant: $y=0.16x+13.91$, $r^2=0.007$ ($F_{1,17}=0.1$, $p=0.746$).

Because one of above-mentioned linear regressions was not significant, bci (body condition index: m/fl: (S p e a k m a n & R a c e y 1986) was excluded from analyses and therefore body weight [g] and forearm length [mm] were tested separately.

During nettings, bats were marked with yellow aluminum rings with numbers: Bxxxxx CIC KRAKOW (5.2 x 5.5 mm, *Lambournes*, Birmingham, UK), males on the right and females on the left forearm. 68 adult females, 37 young females and 46 young males were ringed. Colonies of *M. myotis* situated in attics in 30 km radius range were investigated. In winter, the caves of Krakowsko-Częstochowska Upland were checked as well, in order to confirm or eliminate bat exchange between roosts.

Mortality within juveniles of *M. myotis* in the Studnisko Cave turned out to be impossible to assess because of the chamber size and the complicated sill form (blocks and rock pieces). Therefore this aspect has not been taken into account.

Microclimate

Day and night temperatures could determine the frequency of conversion into torpor or can influence the foraging activity (i.a. A u d e t 1990, R y d e l l 1993, H i c k e y & F e n t o n 1996, L a u s e n & B a r c l a y 2003). That is why several thermal parameters were distinguished: T_{an} – mean nightly temperature outside, T_{ad} – mean daily temperature outside, T_{ad-n} – mean day-night temperature outside; T_{cave} – temperature inside the Studnisko Cave; T_{attic} – temperature inside the attic in the church in Kłobuck. Temperature measurements were recorded by an automatic logger HOBO 8 (± 0.7 °C, Onset Computer Corp., USA), situated in about 0.5 m distance from the aggregation of *M. myotis*. The recording frequency was 1 per hour. Measurements in the Studnisko Cave were conducted from 11 June to 23 August every year (2001–2003); in the church attic, due to a logger malfunction, data spread over only a period of 30 July to 23 August 2001. In the Studnisko Cave the measurements were limited to a lactation period, because in May pregnant females resided in a smaller aggregation in different parts of the cave (G a s & P o s t a w a 2001).

Ambient temperature data come from a meteorological station in Częstochowa. Pregnancy period was estimated to 46–59 days according to the literature data (S k l e n á ř 1963), whereas a delivery term – about 15 of June on the basis of our own observations. The investigated period was divided into 2 parts: pregnancy (2 May – 15 June) and lactation (16 June – 31 July).

Statistical analyses

Results were presented as mean \pm SD (Standard Deviation). We applied the linear regression and the significance correlation test to define the relation between the temperature within the colony and the outside temperature; one-way ANOVA to test differences of mean temperatures in pregnancy and lactation periods among years (separately for the attic colony and the cave colony); two level nested ANOVA to test differences of body weight and forearm length of *M. myotis* between the type of roost (cave vs attic) and also among years for different roosts. Analysis were performed separately for every sex – age group: adult females (Fad), young females (Fjuv) and young males (Mjuv). Juveniles (both sexes) were taken separately because of sexual dimorphism (A r l e t t a z e t al. 1991, B e n d a 1994). For every ANOVA Tukey's *post-hoc* tests were conducted. For nested ANOVA results were given only for the pairs cave –

attic and also between ages, separately for each of the colonies (principal and nested factors). Hypotheses were tested at $p=0.05$.

Surveys were conducted with the permission issued by the Polish Ministry of Environment: OPog. 4201/197/98, OPog. 4201/198/99, DLOPiKog. 4201/157/00, BOA-A-75-1018/01/RP and DLOPiKog.-4201-04A-3/2002.

Results

Morphometry of *M. myotis*

Measurements were performed on 115 individuals captured in the maternity colony in the Studnisko Cave and also on 57 individuals from maternity colony situated in the church attic in Kłobuck (Fig. 2).

Adult females

Forearm length was dependent on the colony type (nested ANOVA: $F_{1,81}=16.52$, $p=0.0001$), but it did not depend on a particular year (nested ANOVA: $F_{4,81}=1.14$, $p=0.346$). Every year females from the Studnisko Cave colony were smaller than those from the colony located in the church attic in Kłobuck, significant differences occur only in 2003: 60.5 ± 1.65 vs $63.3 \text{ mm} \pm 2.40$ ($p=0.041$) (Tukey's pairwise comparison). Body weight was independent on both the roost (nested ANOVA: $F_{1,81}=0.5$, $p=0.48$) and the year (nested ANOVA: $F_{4,81}=2.11$, $p=0.088$).

Young females

Forearm length was not dependent on the colony type (nested ANOVA: $F_{1,35}=3.30$, $p=0.078$), however it depended significantly on the year (nested ANOVA: $F_{4,35}=10.07$; $p<0.001$). In 2001 individuals from the Studnisko Cave were smaller than individuals from the colony in Kłobuck ($58.0 \pm 2.55 \text{ mm}$ vs $62.8 \pm 1.04 \text{ mm}$, $p=0.0004$). In the Studnisko Cave specimens from 2001 were significantly smaller than the specimens both from 2002 ($58.0 \pm 2.55 \text{ mm}$ vs $62.4 \pm 1.64 \text{ mm}$, $p=0.0007$) and those from 2003 ($58.0 \pm 2.55 \text{ mm}$ vs $63.0 \pm 1.47 \text{ mm}$, $p=0.0002$) (Tukey's pairwise comparison). Mean body weight was independent on the colony type (nested ANOVA: $F_{1,35}=0.2$, $p=0.656$), whereas it depended on the year (nested ANOVA: $F_{4,35}=5.98$, $p=0.001$). Individuals from the Kłobuck colony in 2002 were significantly heavier than those from 2001 ($26.5 \pm 1.76 \text{ g}$ vs $22.5 \pm 1.55 \text{ g}$, $p=0.024$) as well as those from 2003 ($26.5 \pm 1.76 \text{ g}$ vs $22.2 \pm 1.33 \text{ g}$, $p=0.012$) (Tukey's pairwise comparison).

Young males

Forearm length did not depend on the colony type (nested ANOVA: $F_{1,41}=4.75$, $p=0.035$), but it depended on the year (nested ANOVA: $F_{4,41}=20.58$; $p<0.0001$). In 2001 specimens from Studnisko Cave were smaller than individuals from the colony situated in Kłobuck ($54.2 \pm 2.27 \text{ mm}$ vs $59.3 \pm 0.83 \text{ mm}$, $p=0.0002$). In the Studnisko Cave specimens from 2001 were significantly smaller than specimens from both 2002 ($54.2 \pm 2.27 \text{ mm}$ vs $60.9 \pm 1.47 \text{ mm}$, $p=0.0001$) and those from 2003 ($54.2 \pm 2.27 \text{ mm}$ vs $60.3 \pm 0.88 \text{ mm}$, $p=0.0002$) (Tukey's pairwise comparison). Mean body weight did not depend on the colony (nested ANOVA: $F_{1,41}=2.32$, $p=0.14$), but depended on the year (nested ANOVA: $F_{4,41}=12.352$, $p<0.0001$). In 2001 individuals from the Studnisko Cave were lighter than the individuals from the colony from Kłobuck ($19.8 \pm 0.52 \text{ g}$ vs $23.1 \pm 1.34 \text{ g}$; $p=0.012$). In the Studnisko Cave specimens from

2001 were significantly lighter than the specimens captured in 2002 (19.8 ± 0.52 g vs 24.9 ± 1.86 g, $p=0.0002$) as well as those from 2003 (19.8 ± 0.52 g vs 24.5 ± 1.29 g, $p=0.002$) (Tukey's pairwise comparison).

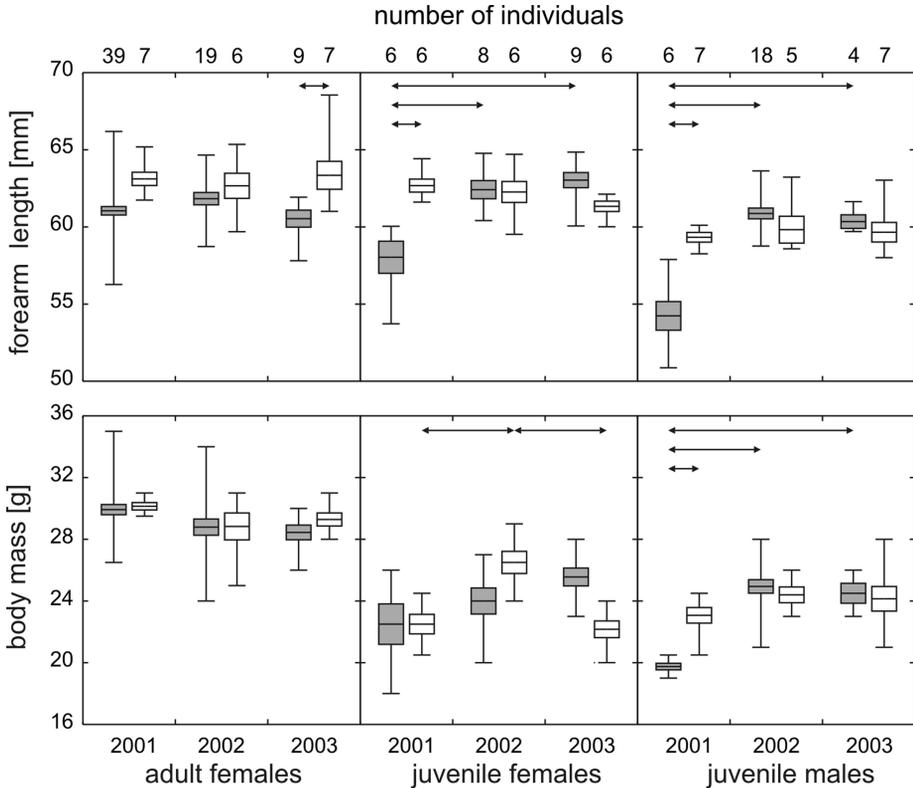


Fig. 2. Box plots of forearm length and body mass of *M. myotis* collected during 2001–2003 in the Studnisko Cave (grey box) and the Kłobuck attic (white box). Box: Standard Error, horizontal line: mean, whiskers: min. – max., horizontal arrow: statistically significant differences (p values in text).

Air temperatures outside the roost

During the pregnancy period T_{an} differed significantly among years (one-way ANOVA: $F_{2,132} = 39.7$, $p < 0.00001$). The 2001 was cooler than 2002 ($p = 0.00002$) and 2003 ($p = 0.00002$) (Tukey's pairwise comparison). Whereas during the lactation period T_{an} were similar within all 3 years (one-way ANOVA: $F_{2,135} = 0.965$, $p = 0.383$). T_{ad} during pregnancy differed significantly between years (one-way ANOVA: $F_{2,135} = 8.65$, $p = 0.0003$). The 2001 were cooler than 2002 ($p = 0.0007$) as well as 2003 ($p = 0.0014$) (Tukey's pairwise comparison). T_{ad} during lactation differed significantly among years (ANOVA: $F_{2,135} = 7.36$, $p = 0.001$). The year 2002 was warmer than both 2001 ($p = 0.02$) and 2003 ($p = 0.0007$) (Tukey's pairwise comparison) (Table 1).

Microclimate of Studnisko Cave

The lowest temperature was noted in 2001, whilst the highest in 2003. Twenty four hour amplitudes of temperature were marginal and fluctuated from 0.0 to 1.6°C in 2001

(mean=0.6°C), from 0.0 to 1.2°C in 2002 (mean=0.4°C), and from 0.0 to 2.7°C in 2003 (mean=1.2°C) (Table 1). For the lactation period temperature inside cave differed significantly among years (one-way ANOVA: $F_{2,129} = 24.95$, $p=0.001$). In 2001 temperature was lower from both 2002 ($p=0.04$) and 2003 ($p=0.00002$); in 2002 temperature was lower than in 2003 ($p=0.00004$) (Tukey's pairwise comparison).

Table 1. Outside temperatures (T_{ad} and T_{an}) and the temperature of the maternity colony surroundings (T_{cave}) in the Studnisko Cave during the pregnancy and lactation period.

		$T_{s, day}$		$T_{s, night}$		T_{cave}	
		min. + max.	aver. ± SD	min. + max.	aver. ± SD	min. + max.	aver. ± SD
2001	pregnancy	12.0±25.0	19.0±3.50	-2.0±12.0	6.7±3.40		
	lactation	10.0±30.0	23.3±3.77	10.0±18.0	13.8±1.97	8.7±13.0	11.0±1.38
2002	pregnancy	15.0±27.0	21.9±3.07	7.0±18.0	10.9±2.41		
	lactation	19.0±32.0	25.3±3.60	9.0±19.0	13.7±2.41	10.2±13.2	11.7±0.78
2003	pregnancy	10.0±29.0	21.7±4.33	3.0±17.0	12.1±3.13		
	lactation	16.0±31.0	22.5±3.46	10.0±21.0	14.3±2.61	10.9±16.4	13.0±1.64

Influence of outside temperature on the roost microclimate

Studnisko – the lactation period

Temperature inside the cave collected from the neighbourhood of *M. myotis* colony in the Studnisko Cave was significantly dependent on mean day-night temperature outside (T_{ad-n}) – respectively: $y=0.379x+4.09$, $r^2=0.485$, $p<0.0001$ (2001); $y=0.134x+9.13$, $r^2=0.23$, $p=0.001$ (2002); $y=0.399x+5.66$, $r^2=0.397$, $p<0.0001$ (2003). Every 10°C increase in T_{ad-n} induced respectively: for 3.8°C, 1.3°C, and 4.0°C increasing temperature inside the cave.

Studnisko vs Kłobuck (30 July – 20 August 2001)

For temperature inside the cave (T_{cave}) and attic (T_{attic}) overall measurements, a statistically significant relation was obtained both for Studnisko: $y=0.114x+10.16$, $r^2=0.344$

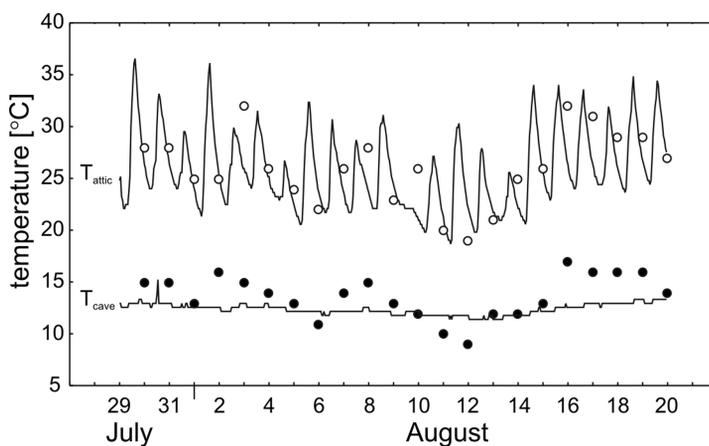


Fig. 3. Fluctuations of temperature in 29 July – 20 August 2001 in the church attic in Kłobuck (T_{attic}) and in the Studnisko Cave (T_{cave}), mean outside temperatures: white dots - daily temperatures, black dots – night temperatures.

($p=0.0026$), and for the attic in Kłobuck: $y=0.494x+15.94$, $r^2=0.47$ ($p=0.0002$). The 10°C increase of Tad-n has induced the T cave rise of 1.1°C and the T attic rise of 4.9°C: the rate of changes is about 4.3 times faster in the attic than in the cave. Twenty four hour T attic fluctuated from 3.1°C to 14.8°C. Mean T attic was similar to mean Tad-n: $25.8 \pm 3.63^\circ\text{C}$ vs $19.8 \pm 2.76^\circ\text{C}$ ($p<0.001$) (Tukey's pairwise comparison). Twenty four hour amplitudes of temperature oscillated from 0.0 to 2.7°C (Fig. 3). T cave was similar to T an: $12.4 \pm 0.53^\circ\text{C}$ vs $13.7 \pm 2.10^\circ\text{C}$ ($p=0.35$), but differed significantly from mean T ad-n: $12.4 \pm 0.53^\circ\text{C}$ vs $19.8 \pm 2.76^\circ\text{C}$ ($p<0.001$) (Tukey's pairwise comparison).

Discussion

Thermal conditions and reproduction of bats in caves

Underground shelters (caves, mines) can be partitioned into three thermal (microclimatic) zones: i) a dynamic zone in which the twenty four hour amplitude of temperature exceeds 5°C, ii) a intermediate zone, with the twenty four hour amplitude of temperature oscillating between 1–5°C, and iii) a static zone in which the twenty four hour amplitude does not exceed 1°C (Kwiatkowski & Piasecki 1989). The temperature prevailing within a static zone corresponds to the mean year temperature in a given area (Kowalski 1953). There exists a temperature gradient between the floor and the roof of an underground site, caused by air circulation, that can reach up to several degrees (Postwa 2000).

Cave maternity colonies of *M. myotis* are found most frequently within the dynamic or half dynamic zone, rarely the static one. The ambient temperatures around the colony range from 9.2 to 22.0°C in Bulgaria (Pandurska 1998), from 12 to 20°C (median=15°C) in Portugal, with 3–5°C fluctuations during the season (Rodrigues et al. 2003). The maternity colony in Nietoperzowa Cave (Poland) resides in the static zone, with a temperature of 8.7°C (Harmata 1973). A situation similar to this is known from the nearest maternity colonies of *M. myotis* localized in caves (Slovakia), i.e. aggregations are situated in the static zone, and the mean temperature remains around 10°C: Plavecká Cave (240 m a.s.l.; Lehotská & Lehotský 1998, pers.com.) and Drienovska Cave (245 m a.s.l.; Matiš 2000). In Studnisko Cave, the colony stays in the half dynamic zone in which twenty four hour amplitudes rarely exceed 1.5°C, the temperature is several degrees higher than the mean yearly temperature and is also higher than the temperature prevailing in the static zone. An attic microclimate is apparently more strongly influenced by outside conditions, and the differences between the floor and the roof can even reach 10°C (Heidinger et al. 1989, Zahn 1999). The temperature in the Kłobuck attic is similar to the mean daily temperature, whereas the twenty four hour amplitude reaches 15°C. In caves, twenty four hour amplitudes are 10 times smaller than those in attics, and the rate of change caused by outside temperature fluctuations is over 4 times lower. The investigated reproduction sites of *M. myotis* differ significantly from each other in the temperature prevailing in the roost, the amplitude of temperatures, and in the reaction to the changes of outside climatic conditions. Studnisko cave is a shelter with a cool but stable climate, whereas the attic in Kłobuck is warm but labile. Differences in body size of *M. myotis* between the cave and the attic were tested each year for the duration of the study i), and also between seasons within a given shelter ii). For young bats, we obtained a significant correlation with the investigated year, however the differences between the colonies were not

statistically significant. Similar results were reported by U h r i n & K a ň u c h (2007) who compared *M. myotis* maternity colonies in attics and caves.

The differences in the size of the juveniles could be induced by delayed fertilization, delayed embryogenesis and delayed parturition, and also by the extension of postnatal development (i.e. R a c e y et al. 1987, M c O w a t & A n d r e w s 1995, Z a h n 1999). In conclusion, directly or indirectly, temperature plays a crucial role in the differentiation of the size of *M. myotis* progeny. In 2001, greater differences in the sizes of the young bats within a single colony and between colonies were noted. In 2001 mean day and night temperatures during pregnancy were lower than during the other years. Differences were detected only in day temperatures throughout the lactation period, and were significantly higher in 2002 than in the other years.

P r e g n a n c y

In many bat species of the temperate zone, unfavourable climatic conditions influence embryogenesis. Not only is the temperature inside the maternity colony a significant factor, but also the thermal conditions prevailing outside are important. This is connected with food availability because the activity of insects depends significantly on air temperature (T a y l o r 1963, H i c k e y & F e n t o n 1996). During a temporal lack of food (precipitation, low temperatures) females in the shelters may fall into torpor. But induction of torpor is energetically expensive and has to last a certain time in order to be profitable (K u r t a 1985, 1987, K u r t a et al. 1991). Further surveys revealed that torpor occurred less frequently in pregnant females than in lactating ones, but was deeper in the former (L a u s e n & B a r c l a y 2002, 2003). This strategy saves energy but at the same time delays fetus development.

In *Pipistrellus pipistrellus* low temperature prolongs early pregnancy and delays parturition (R a c e y 1973, R a c e y & S w i f t 1981, R a c e y et al. 1987). In *Rhinolophus ferrumequinum* the temperature of April influences ovulation and fetus implantation, and moreover, low temperatures lead to an insufficient food base (M c O w a t & A n d r e w s 1995). Reduction of activity has been observed for *M. myotis* females, e.g. when temperatures were lower than 10°C pregnant females stayed in the maternity colony, whereas at higher temperatures they foraged longer than during the lactation and post-lactation period (A u d e t 1990). Females of *M. myotis* fall into torpor only when a cool period (temperature below 12°C) persists for several days (H e i d i n g e r et al. 1989). In cave maternity colonies of *M. myotis* in which the ambient temperature is constantly at the same low level, juveniles should be smaller than those from attic colonies, and this pattern should be consistent from year to year. K u n z (1973) investigated the growth rate of *M. myotis* juveniles from attic and cave maternity colonies with results similar to ours: within one shelter there were differences between years but no differences between shelters within one year. The author explained the lack of differences by the saving of energy through the aggregation of bats in caves, as suggested by others authors as well (D w y e r & H a r r i s 1972, T u t t l e 1975, K u r t a 1985, K u n z 1987).

Differences in the size of young *M. myotis* found in 2001 may be caused by the interaction of two factors: the relative cool temperatures during pregnancy and differences in the temperature between the attic and the cave. Sustained cool temperatures caused a lack of food and consequently the females fell into torpor to save energy. Differences between roosts (temperature inside attic corresponds to the mean daily temperature which is higher than the

temperature inside a cave) prompted a deeper and longer torpor of the cave dwelling females. This explains the differences in the size of young *M. myotis* in the same environmental conditions. The lack of a longer period of low temperatures within two subsequent years explains the lack of significant differences between the shelters (as observed previously).

Lactation

After parturition females fall into torpor during a temporary lack of food (chill, precipitation), whereas young *M. myotis* gather in distinct aggregations, sustaining a higher temperature (Heidinger et al. 1989). Sometimes females leave their non-flying young without food for several days and move to other roosts. This triggers torpor of the young and causes a higher mortality rate (Heidinger et al. 1989, Audet 1990). Zahn (1999) has shown that the juveniles of *M. myotis* born in colonies at a higher mean temperature were significantly larger than individuals derived from cooler attics, and the maximum growth rate is attained at temperatures up to 24°C. The author explains this observation by a remarkable influence of temperature during the first weeks of life (temperatures at the end of June), that might slow down development in the first days of life. In our study, higher temperatures after parturition were noted in 2002 (T ad). In that year young females from the attic were significantly heavier than in other years, supporting the aforementioned hypothesis. However, discrepancies in the mean temperatures between years were only in the range of 2–3°C, and the sizes of young males were similar throughout the study. According to this notion, greater differences should occur between the attic and the cave in which differences in temperature reach several degrees. However, in the cave colonies young bats form dense aggregations (Pańdurska 1998, Rodrigues et al. 2003, our data) and this type of thermoregulation may limit the effect of the ambient temperature on growth rate. The mitigation of ambient temperature by thermoregulation is in need of further studies.

Morphometry of adult females

The adult females from the Studnisko Cave colony showed a constant decrease in size in consecutive years compared to the females from the church attic in Kłobuck. By marking the captured bats we excluded the possibility of an exchange of individuals between these colonies. Constant movement of females between colonies was shown for roosts located within a radius of 30 km, and the number of swaps was negatively correlated with distance (Horiček 1985), and positively correlated with colony size – the larger the aggregation the more individuals immigrating (Zahn 1999). Among 151 specimens ringed in the Studnisko Cave only several individuals hibernated in this cave or in its surroundings (the Sokole Góry reserve). Flights to hibernacula in caves situated to the north were observed; the longest distance recorded was 45 km (Gas 2003). Therefore, the population that comprises the maternity colony of the Studnisko Cave uses other hibernacula, whereas during winter other specimens hibernate in this cave. The recent formation of this colony (Gas & Postawa 2001) and migrations to hibernacula situated in the south suggest that this is a different and separate population which has lately started migrating to the north. Probably for this reason small but significant differences in size between the adult females from the investigated colonies were observed. More studies of this distinct population are needed, including surveys based on molecular methods (microsatellite DNA) similar to those conducted by Ruedi & Castella (2003).

Why reproduce in caves if attics are available?

In southern Europe most *M. myotis* maternity colonies are located in underground cavities, whereas to the north of the Alps and Carpathians, lofts of buildings are preferred. This can be explained by high temperature demands during the pregnancy period (H o r á ě k 1984, R o d r i g u e s et al. 2003). Reproduction of *M. myotis* in Nietoperzowa cave (Kraków – Częstochowa Upland) in both the subatlantic period (P o s t a w a 2004) and in historical times (W a g a 1855, H a r m a t a 1973), indicates a weaker correlation with the climate than was previously suggested (H o r á ě k 1984, Z a h n 1999). This notion is confirmed by the appearance of a maternity colony in the undergrounds of the Nietoperek reserve in the 1970's (U r b a ŋ c z y k 1990), and in the Studnisko Cave at the end of the 1990's (G a s & P o s t a w a 2001). Both colonies are small and belong to the lower range of size of typical cave colonies; the average census size is estimated at about 500 individuals, a number possibly associated with thermoregulation mechanisms (P a n d u r s k a 1998, R o d r i g u e s et al. 2003).

Colonies from attics are generally smaller and dense aggregations are formed less frequently than in caves (H e i d i n g e r et al. 1989, Z a h n 1999). The formation of the colony in Studnisko cave coincides with the slow restitution of the *M. myotis* population in Poland (G a s & P o s t a w a 2001, K o z a k i e w i c z 2003, W o ł o s z y n et al. 2005). Similar trends are also observed on the southern side of the Carpathian arch (Ř e h á k 1997, B i h a r i & G é c z i 2000, M a t i s 2000) where a new cave maternity colony of *M. myotis* was established in 2000 (Rotunda cave, Hranická propast: Ř e h á k 2006).

The gradual increase of the population size of this species will probably suffice for the maintenance of underground maternity colonies.

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