



# Stage of pregnancy dictates heterothermy in temperate forest-dwelling bats



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## ABSTRACT

Bats face high energetic requirements, as powered flight is costly and they have a disadvantageous surface-to-volume-ratio. To deal with those requirements energy saving mechanisms, such as heterothermy (torpor), have evolved. Torpor during pregnancy, however, reduces rates of foetal development and consequently prolongs pregnancy. Therefore, heterothermy has a great effect on reproduction, as an unhindered parturition can only be assured by high body temperatures. Regardless of these adverse affects of torpor the energetic requirements of bats during reproduction urge for energy savings and bats are known to enter torpor during pregnancy. The species in the current study differ in their torpor patterns and thus their heterothermic strategy. However, we hypothesized, that species-specific heterothermic behaviour should be revoked at the end of pregnancy. We analyzed skin temperatures of *Myotis bechsteinii*, *Myotis nattereri* and *Plecotus auritus* during pregnancy and found no differences in torpor depth between species during the last phase of pregnancy. Furthermore, we could show that individuals entered torpor frequently during pregnancy and only minimized torpor during the last stage of pregnancy. This suggests that close to the end of pregnancy, heterothermy is restricted but not species-specific and the required energy is allocated otherwise.

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## 1. Introduction

Successful reproduction is the ultimate goal of animal life history. The reproductive stages include fertilization, pregnancy, and lactation (Campbell and Reece, 2009). Pregnancy in mammals follows three stages: cleavage, gastrulation, and organogenesis. During organogenesis the organs develop (Campbell and Reece, 2009) and therefore, this stage is likely to be the most energy demanding one. As shown for ungulates (Robbins and Robbins, 1979), rodents (Ibsen, 1928), and small insectivorous mammals (Mover et al., 1988; Studier et al., 1973; Studier and O'Farrell, 1972) most of foetal mass increase occurs in the second half of pregnancy. Hence, additional energy expenditures arise due to foetal growth and later on production of maternal tissue and milk (Kurta et al., 1989; Speakman and Racey, 1987). The increased energy demand of reproduction can be covered by e.g. higher food intake (Johnson et al., 2001), as for most species parturition is timed to the periods with abundant food availability, enhancing survival of mother and offspring (Bronson, 1985; Fietz et al., 2004; Townsend

et al., 2008). Therefore, one factor affecting reproduction in mammals is body condition (Clutton-Brock et al., 1989), as animals with better body condition might be more successful in defending offspring or cope with the increased energy demands associated with pregnancy and lactation.

Besides reproduction bats face high energetic requirements, as powered flight is costly. Furthermore, they have a disadvantageous surface-to-volume-ratio and both of which result in a high mass-specific energy demand (Alexander, 2002; Schmidt-Nielsen, 1972; Speakman, 1997). To deal with those energetic requirements several regulatory mechanisms of the energy budget, as changes in activity pattern (Clark et al., 1993; Encarnação, 2012; Swift, 1980), energy intake (Becker et al., 2013b; Kunz et al., 1995; McLean and Speakman, 1999), digestive efficiency (Barclay et al., 1991; Becker et al., 2012; Roswag et al., 2012), metabolic compensation (Becker et al., 2013a; McLean and Speakman, 1999; Speakman and Racey, 1987), and torpor (Geiser, 2004) exist in bats. Torpor is one of the most effective energy saving mechanisms (Geiser, 2004). It is induced by a controlled lowering of metabolism (Heldmaier and Ruf, 1992) and characterized by the passively lowered body temperature ( $T_b$ ). Main drawbacks, however, of low  $T_b$  during pregnancy are developmental abnormalities (Wiegand et al., 1989), embryonic diapause (Mead, 1993), or, during lactation, a reduced milk production (Wilde et al., 1999). Further strategies to cope

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<b>Nomenclature</b>		HI	Heterothermy index
		$J_c$	Temperature corrected Julian day
$T_{sm}$	Minimum skin temperature		

with the increased energetic demands during reproduction are energy allocation from activity (Slonaker, 1925) or metabolism (Mellish et al., 2000). These strategies might allow for normothermic  $T_b$ , which assure undelayed parturition if necessary and are likely to be seen as adaptations to ensure successful reproduction.

Besides ambient temperature ( $T_a$ ) (Dzal and Brigham, 2012; Wojciechowski and Jefimow, 2006) torpor in bats is mainly influenced by food availability (Matheson et al., 2010; Wojciechowski et al., 2007), body mass (Geiser and Ruf, 1995; Stawski and Geiser, 2010), habitat (Encarnação et al., 2012), roost characteristics (Boyles et al., 2007; Willis and Brigham, 2005; Willis et al., 2006b), and social organisation (Turbill and Geiser, 2006; Willis and Brigham, 2007). As hibernating and nocturnal mammals of temperate latitudes (Dietz et al., 2009) the almost exclusively insectivorous bats are confronted with seasonal and daily fluctuations in weather-dependant food availability (Esch, 1988; Taylor, 1963). Most temperate bats give birth to only one, relatively large young (Badwaik and Rasweiler IV, 2000; Dietz et al., 2009). The long pregnancy and short lactating period might reflect a strategy in which the offspring benefits from energetic input in relation to seasonal food availability (Encarnação et al., 2010; Racey and Entwistle, 2000). Therefore, undelayed and successful reproduction can only be assured by high  $T_b$  and sufficient energy i.e. food (Racey, 1973). These characteristics and how bats negotiate given conditions make them ideal model organisms for studying heterothermy and energy balancing mechanisms.

Heterothermy during reproduction was addressed by several studies before and all studies could show that torpor during reproduction occurs (e.g. Audet and Fenton, 1988; Chruszcz and Barclay, 2002; Daniel et al., 2010; Hamilton and Barclay, 1994; Johnson and Lacki, 2014; McAllan and Geiser, 2014; Stawski, 2010; Studier et al., 1973; Studier and O'Farrell, 1972; Willis et al., 2006a). Furthermore, bats tend to switch heterothermic patterns during pregnancy depending on stage of pregnancy and  $T_a$  (Daniel et al., 2010; Studier et al., 1973; Studier and O'Farrell, 1972). Due to the high energetic requirements of bats the aim of the present study was to investigate heterothermy in relation to progress of pregnancy in sympatric forest-dwelling bat species in the temperate zone. The focus of this study was laid only on the second half of pregnancy as most of the foetal mass increases during this half (Studier et al., 1973; Studier and O'Farrell, 1972) and therefore, differences in heterothermy between species are expected in the second half of pregnancy. As to their ecological and morphological similarities (Dietz et al., 2009; Oxberry, 1979) pregnant individuals of *Myotis bechsteinii*, *Myotis nattereri*, and *Plecotus auritus* were

chosen as study species. These three species are similar in body mass (6–10 g), life history (reproductive cycle with one pup), pregnancy length (about 60 days), and roosting habits (mostly tree roosts) (Dietz et al., 2009; own data). However, a difference between the three species is the foraging strategy, as all three are gleaning bat species but *M. bechsteinii* and *P. auritus* are passive gleaning species, whereas *M. nattereri* is an active gleaner. Furthermore, these three species differ in their heterothermic strategy. It could be shown that *P. auritus* exhibited the lowest minimum skin temperatures ( $T_{sm}$ ) during torpor, suggesting that *P. auritus* uses pronounced torpor as primary energy saving mechanism, whereas the other two species rely on other energy saving mechanisms (Otto et al., 2013). Therefore, we hypothesized that, due to the high energetic requirements of pregnancy, species-specific differences in heterothermic behaviour should be revoked in the last phase of pregnancy. We predicted that with advancing pregnancy torpor temperatures will increase, whereas the range of skin temperatures will decrease for all three species, leading to species-transcending heterothermic behaviour.

## 2. Materials and methods

### 2.1. Study site

The study was conducted from April 27th to May 13th in 2011 (Julian day: 117–133) and from May 4th to May 12th in 2012 (Julian day: 125–133) within a deciduous forest in Germany (50°27'N 8°49'E), where all three species occur sympatrically and form their nursery colonies. Data loggers (DS1921G Thermochron iButton, Maxim Integrated Products, Sunnyvale, CA, USA, accuracy  $\pm 1.0$  °C, resolution 0.5 °C) were used to record  $T_a$  2 m above the ground (for details see Otto et al., 2013) and the minimum  $T_a$  ( $T_{am}$ ) was determined for each day from official sunrise to official sunset, as this time frame matches the bat's diurnal inactivity period. In 2011 insect abundance between stages of pregnancy was assessed by air ecollectors (modified after Behre, 1989) to correct for potential influences of food availability on heterothermy. Three traps were randomly scattered in the forest and checked weekly. Caught insects were dried at 60 °C until constant mass was reached and insect dry masses were determined.

### 2.2. Animals

Bats were caught by mist netting or roost trapping. Body mass and forearm length (Table 1) were measured with a digital balance

**Table 1**  
Sample size and morphological data of the investigated species and results of the comparisons between species. Bat days is the mean amount of recorded days for a species. Values are given as mean  $\pm$  SD.

	<i>M. bechsteinii</i>	<i>M. nattereri</i>	<i>P. auritus</i>	Comparison p		
<b>n (individuals)</b>	7	7	7		<i>M. bechsteinii</i>	<i>M. nattereri</i>
<b>Bat days/individual</b>	4.3 $\pm$ 1.7	4.5 $\pm$ 3.4	3.7 $\pm$ 1.9		<i>M. nattereri</i>	<i>P. auritus</i>
<b>Body mass (g)</b>	9.1 $\pm$ 0.3	8.1 $\pm$ 0.7	7.8 $\pm$ 0.5	0.01	0.002	n.s.
<b>Forearm (mm)</b>	43.2 $\pm$ 0.9	41.3 $\pm$ 0.9	38.9 $\pm$ 1.1	n.s.	< 0.001	0.078
<b>BCI</b>	9.0 $\pm$ 0.2	7.8 $\pm$ 1.0	7.9 $\pm$ 0.5	0.012	0.009	n.s.
<b><math>T_s</math> flying bats (°C)</b>	35.7 $\pm$ 0.5	36.2 $\pm$ 0.7	36.6 $\pm$ 0.5	0.009	< 0.001	n.s.

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