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Roost characteristics as indicators for heterothermic behavior of forest-dwelling bats

Abstract Many forest-dwelling bats spend their diurnal inactivity period in tree cavities. During this time bats can save energy through heterothermy. A heterothermic response (torpor) is characterized by a lowered body temperature, reduced metabolic rate, and reduction of other physiological processes, and can be influenced by the microclimatic conditions of roost cavities. The thermal and physical characteristics of roosts used by the sympatric, ecologically, and morphologically similar bat species *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus* were compared. These three species differ in their heterothermic behavior, with the lowest skin temperatures observed for *P. auritus*. Therefore, we hypothesized that roosts occupied by the three species should differ in roost characteristics and microclimatic conditions, whereby *P. auritus* should select colder and thermally less stable roosts. The results showed that horizontal depth of the cavity, diameter of the roost tree, and microclimatic conditions within roosts differed among species. Roosts of *P. auritus* had the lowest horizontal depth, lowest thermal stability, and lowest mean minimum roost temperatures. Height of the roost, diameter of the roost tree, and vertical depth were also shown to influence microclimatic conditions. With increasing diameter of the tree and increasing horizontal depth, mean minimum roost temperature increased and thermal stability improved. Furthermore, with ascending height above ground insulation and mean roost temperatures increased. Our results imply that species such as *P. auritus*, which use pronounced torpor as a primary energy saving strategy, prefer colder cavities that support their heterothermic strategy.

Keywords Chiroptera · Forest · Microclimate · Torpor · Tree cavity

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Abbreviations

T_b	Body temperature
T_a	Ambient temperature
T_r	Roost temperature
$T_{r\,min}$	Minimum roost temperature
$T_{r\,mean}$	Mean roost temperature
$T_{r\,max}$	Maximum roost temperature
T_s	Skin temperature
HI	Heterothermy index
S_r	Thermal stability
I_r	Insulation value

Introduction

Bats shelter in roosts during their diurnal inactivity period to endure periods of low food availability. For many temperate, forest-dwelling bats this shelter can be provided by decomposition cavities, tree crevices, or woodpecker cavities (Dietz et al. 2009). However, bats are also known to roost in artificial dwellings such as bat boxes, building crevices and attics (Entwistle et al. 1997; Kerth et al. 2001a; Smith and Racey 2005; Dietz et al. 2009). During their inactivity period, bats are able to show physiological (heterothermic) responses such as torpor, one of the most effective energy-saving mechanism in bats (Geiser 2004). Torpor is induced by an actively controlled lowering of metabolism, body temperature (T_b), and other physiological processes (Heldmaier and Ruf 1992; Geiser 2004; Geiser et al. 2014; Ruf and Geiser 2014). Torpor can be distinguished into three stages: 'entry', 'maintenance', and 'arousal'. During 'entry' the T_b declines to values often close to surrounding temperatures, whereas relatively stable T_b are usually found during 'maintenance'. During 'arousal' the T_b increases to normothermic levels (Wojciechowski et al. 2007). The arousal phase is the most energy-demanding phase during torpor and can be either active or passive (Geiser and Baudinette 1990; Lovegrove et al.

1999; Geiser et al. 2004). Active arousal from torpor is very energy-demanding while passive rewarming following ambient temperatures (T_a) can lead to substantial energy savings (Chruszcz and Barclay 2002; Geiser et al. 2004; Currie et al. 2015).

Torpor in bats is mainly influenced by food availability (Wojciechowski et al. 2007; Matheson et al. 2010) and T_a (Wojciechowski and Jefimow 2006; Dzal and Brigham 2012). Temperature within the roost (T_r) is therefore a decisive factor, but also factors related to social organization of the bats may be relevant (Turbill and Geiser 2006; Willis and Brigham 2007). Huddling in large groups, influences energetic requirements as a larger group size increases T_r more rapidly and to higher levels compared to smaller groups (Willis and Brigham 2007). In larger groups the gradient between T_b and T_r, which is the major reason for heat loss, decreases and the cooling process is slowed (Hayes et al. 1992; Speakman 2001; Willis and Brigham 2007). Solitary animals, such as the neotropical hoary bat (*Lasiurus cinereus*), roost in open foliage. As an adaptation, this species has a thicker insulating pelt than other bat species (Shump and Shump 1980), which is likely a compensation for the lack of an insulating roost (Willis et al. 2006a). Roosting in open foliage or use of less well insulated roosts can sometimes be advantageous (Turbill 2006; Doucette et al. 2011). Thus animals in open foliage or within less insulating roosts can better benefit from passive rewarming. Well insulated roosts, on the other hand, provide more stable microclimatic conditions with the advantage of higher T_r at night (Sedgeley 2001; Chruszcz and Barclay 2002; Lausen and Barclay 2003). However, more studies are needed that investigate roost choice, thermal properties of roosts and heterothermy in bats (Boyles 2007; Willis 2008).

Objectives of the present study were to investigate roost characteristics and microclimatic conditions of roosts occupied by three sympatric bat species, *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus*, and to link their heterothermic behavior to roost choice. Even though the study species are ecologically and morphologically very similar (Dietz et al. 2009), they show distinct and species-specific heterothermy (Otto et al. 2013, 2015). Therefore, thermal and physical characteristics of roosts of these species were studied.

The three species are similar in body mass (6–10 g), life history, and roosting habits (Dietz et al. 2009). Within our study area, they roost in groups, with *P. auritus* having the smallest group size of 6–15 individuals. *Myotis bechsteinii* and *M. nattereri* form larger groups with 11–19 and 11–37 individuals, respectively (Otto et al. 2013). A previous analysis of the heterothermic behavior revealed differences among the three species (Otto et al. 2013; 2015). Lowest skin temperatures (T_s) and the highest heterothermy index (HI: a metric to assess temporal fluctuations in T_b or T_s over a given period of time) (Boyles et al. 2011) was found in *P. auritus*. Even during periods of high energy requirement like pregnancy, *P. auritus* displays lower T_s and higher HI than the other two species (Otto et al. 2015). *Plecotus auritus* uses pronounced heterothermy as the primary energy saving strategy, whereas, *M. bechsteinii* and *M. nattereri* probably use other strategies (Otto et al. 2013). Even in artificial roosts used by *P. auritus* (Entwistle et al. 1997) and by *M. nattereri* (Smith and Racey 2005), lower T_r were observed for *P. auritus*. These results indicate that *P. auritus* prefers cold roosts with unstable microclimatic conditions to meet its heterothermic needs for low temperatures to fully utilize its primary energy saving strategy. These needs should be satisfied by e.g. low-diameter trees, due to the lack of a buffering layer of wood or bark (Derby and Gates 1966; Nicolai 1986). We assume that heterothermic behavior should determine roost choice and therefore hypothesized that characteristics and microclimatic conditions of natural roosts should differ among species.

Materials and methods

Study site and roost characteristics

The study was conducted in April and May 2013 within a small deciduous forest near Frankfurt am Main, Germany (50°27′N 8°49′E). Data loggers (DS1921G Thermochron iButton, Maxim Integrated Products, Sunnyvale, CA, USA, resolution 0.5 °C) were installed in known tree roosts of *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus* to analyze microclimatic conditions within the cavity. Each species is represented by six roosts. However, one of the roosts in the study was used by both *M. bechsteinii* and *M. nattereri*, but during different times of the year. Therefore, when analyzing roost characteristics among species 18 roosts were included, whereas the analysis of differences among roost types was performed on 17 roosts. Prior to installation, cavities were checked for absence of animals with an endoscope (Endoscope camera TF 2809, Kraft Werkzeuge, Salzburg, Austria), as data loggers emit ultrasonic sounds which can disturb animals, especially bats (Willis et al. 2009). Roost volume was determined following Sedgeley & O'Donnell (1999a). Recorded cavity characteristics were cavity type, horizontal depth, vertical depth and height, and horizontal width of the cavity. Subsequently, data loggers were mounted on a wire and placed close to the ceiling of the cavity. To compare T_r with outside T_a another data logger was placed at the trunk at the same height facing north. Temperatures were recorded every 30 min. Obtained parameters to describe and compare the roosts were diameter of the roost tree, cardinal direction and height of the entrance hole, and canopy coverage above the cavity. Tree species was excluded as factor from the analysis, as some species were underrepresented. Since group size affects roosting ecology (Willis and Brigham 2007), this factor (*P. auri-*
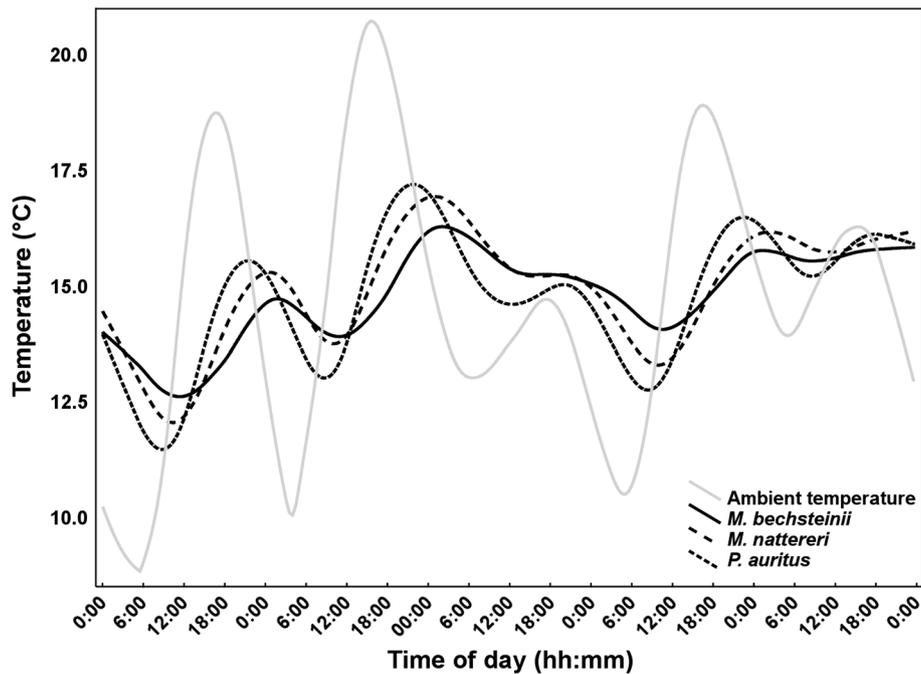
Fig. 1 Locally weighted scatterplot of temperatures in roosts occupied by *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus* during the course of five 24 h periods (120 h of measurements). Note that peaks in roost temperature are delayed relative to peaks in ambient temperature

tus = small, *M. bechsteinii* = medium, and *M. nattereri* = large) was included as potential predictor in the analyses. Before analyzing the data, T_r were checked for abnormalities, such as spontaneous increases in T_r during night and day. These increases indicate that the roost was very likely occupied by cavity-dwelling animals like dormice or birds and consequently, days with abnormalities were excluded from the analysis. Thus the data set contained 20 full days for all roosts (24 h, 28.04.2013–17.05.2013). As an indicator for thermal stability of the roost (S_r) the quotient of the range of T_r ($T_{r\ max}$–$T_{r\ min}$) and T_a ($T_{a\ max}$–$T_{a\ min}$) was determined for each day (24 h). Higher values indicate a lower thermal stability and lower values describe more stable roosts. For each day, mean T_r–T_a difference was calculated to assess insulation characteristics of the roost (I_r). Low values of I_r indicate better insulation. Furthermore, the means of S_r, I_r, $T_{r\ mean}$, and $T_{r\ min}$ were determined for each roost.

Statistical analyses

Statistical analyses were done with the Statistica 12 software package (StatSoft, Tulsa, Oklahoma, USA). The criterion for statistical significance was $P < 0.05$. Data were checked for normal distribution using the Shapiro–Wilk test. Normally distributed data are given as mean ± standard deviation (SD), whereas non-normally distributed data are given as median (min–max and 25–75 % percentiles). No data transformation was applied. Normally distributed roost characteristics (di-

ameter of the roost tree, horizontal depth, vertical height, cardinal direction of the entrance hole, and canopy coverage) were compared with an ANOVA, whereas non-normally distributed data (vertical depth, height of the entrance hole, and volume) were compared with a Kruskal–Wallis-ANOVA (KW-ANOVA). Overall, 18 roosts (*M. bechsteinii*: n = 6, *M. nattereri*: n = 6, and *P. auritus*: n = 6) were included in the analysis. Microclimatic differences were assessed by a comparison of S_r, I_r, $T_{r\ mean}$, and $T_{r\ min}$ among species with a KW-ANOVA (*M. bechsteinii*: n = 120, *M. nattereri*: n = 120, and *P. auritus*: n = 120). General linear models (GLM) with backward stepwise selection of predictors were used to determine influential predictors on mean S_r, mean I_r, mean $T_{r\ mean}$, and mean $T_{r\ min}$ (n = 17). Subsequently, a post hoc unequal *N* test was used to test for differences among roost types. The contribution of each predictor to the model is indicated by the sum of squares (SS) and the standardized effects of the predictor on the variable by parameter estimates (PE).

Results

During the study period T_a ranged from 3.5 to 24.5 °C with a median of 12.0 °C (mean 12.1 ± 3.6 °C). The overall range of T_r was 4.3 to 21.0 °C with a median of 12.5 °C [*M. bechsteinii*: 12.8 °C (4.3–21.0 °C), *M. nattereri*: 12.8 °C (5.0–18.3 °C), *P. auritus*: 12.5 °C (4.3–21.0 °C)]. Daily and nightly peaks of T_r lagged behind those of T_a (Fig. 1). Difference between T_r and

Table 1 Values (median, min, max, 25, and 75 % percentile) of thermal stability (S_r), insulation (I_r), mean roost temperature ($T_{r\ mean}$), minimum roost temperature ($T_{r\ min}$), heterothermy index (HI), and minimum skin temperature ($T_{s\ min}$) for *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus* (Otto et al. 2013, 2015, and unpublished data)

Variable	Species	Median	Min	Max	25 % percentile	75 % percentile
	Myotis bechsteinii[a]	0.26	0.04	1.50	0.18	0.43
S_r (°C)	*Myotis nattereri*[a]	0.33	0.00	1.08	0.22	0.44
$P < 0.001$	*Plecotus auritus*[b]	0.45	0.08	1.25	0.30	0.63
	Myotis bechsteinii	−0.01	−2.15	3.87	−0.50	1.02
I_r (°C)	*Myotis nattereri*	0.08	−2.45	4.35	−0.61	1.31
$P > 0.05$	*Plecotus auritus*	0.23	−2.11	3.13	−0.38	1.11
	Myotis bechsteinii	12.76	6.79	16.44	10.71	14.15
$T_{r\ mean}$ (°C)	*Myotis nattereri*	12.82	5.86	16.79	10.53	14.21
$P > 0.05$	*Plecotus auritus*	12.91	5.85	16.41	10.40	13.99
	Myotis bechsteinii[ab]	11.25	4.25	15.50	9.63	13.25
$T_{r\ min}$ (°C)	*Myotis nattereri*[a]	11.63	5.00	16.50	9.75	13.00
$P < 0.05$	*Plecotus auritus*[b]	10.63	4.25	15.50	8.88	12.00
	Myotis bechsteinii[a]	4.42	1.11	23.82	2.33	9.97
HI (°C)	*Myotis nattereri*[a]	8.66	1.37	20.32	3.59	13.26
$P < 0.01$	*Plecotus auritus*[b]	15.49	1.52	30.61	8.37	18.77
	Myotis bechsteinii[a]	26.67	9.92	34.87	19.81	30.79
$T_{s\ min}$ (°C)	*Myotis nattereri*[a]	21.52	6.21	32.54	17.44	29.68
$P < 0.05$	*Plecotus auritus*[b]	16.92	8.95	33.55	13.75	23.79

Different characters denote significant differences ($P < 0.05$) among species. P values are shown under each variable label

T_a was lowest in roosts of *P. auritus* and highest in those of *M. bechsteinii* (Fig. 1).

Data on HI and $T_{s\ min}$ (Otto et al. 2013; 2015, and unpublished data, Table 1) showed significant differences among species. Highest HI was found in *P. auritus* and differed from those of *M. bechsteinii* (KW-ANOVA: $H = 29.074$, $P < 0.001$) and *M. nattereri* (KW-ANOVA: $H = 29.074$, $P < 0.01$). The comparison between *M. bechsteinii* and *M. nattereri* revealed no significant difference (KW-ANOVA: $H = 29.074$, $P < 0.05$). For *P. auritus* $T_{s\ min}$ was significantly lower compared to *M. bechsteinii* (KW-ANOVA: $H = 21.916$, $P < 0.001$) and *M. nattereri* (KW-ANOVA: $H = 21.916$, $P < 0.05$). Between *M. bechsteinii* and *M. nattereri* no significant difference was detectable (KW-ANOVA: $H = 21.916$, $P > 0.05$).

Comparison of microclimatic conditions revealed that S_r differed significantly among bat species (KW-ANOVA: $H = 30.291$, $P < 0.001$; Table 1). Highest values were observed for roosts of *P. auritus* (Table 1), which differed significantly from those of *M. bechsteinii* ($P < 0.001$) and *M. nattereri* ($P < 0.001$). No significant difference existed between *M. bechsteinii* and *M. nattereri* ($P > 0.05$). Minimum T_r differed significantly between *P. auritus* and *M. nattereri* (KW-ANOVA: $H = 8.434$, $P < 0.05$; Table 1). I_r (KW-ANOVA: $H = 0.534$, $P > 0.05$) and $T_{r\ mean}$ (KW-ANOVA: $H = 0.449$, $P > 0.05$) did not differ significantly among species.

Of the roost characteristics, only horizontal depth differed significantly among species (ANOVA: $SS = 5886.125$, $P < 0.001$). Roosts of *P. auritus* had the lowest horizontal depth (Table 2) and differed significantly from those of *M. nattereri* ($P = 0.029$). The other comparisons revealed no significant differences (ANOVA: $P > 0.05$; KW-ANOVA: $P > 0.05$).

There were no significant differences in mean S_r (ANOVA: $SS = 2.786$, $P > 0.05$; cavity type: $SS = 0.116$, $P > 0.05$), mean I_r (ANOVA: $SS = 1.485$, $P > 0.5$; cavity type: $SS = 0.812$, $P > 0.05$), mean $T_{r\ mean}$ (ANOVA: $SS = 2405.691$, $P < 0.001$; cavity type: $SS = 0.547$, $P > 0.05$), and mean $T_{r\ min}$ (ANOVA: $SS = 1885.887$, $P < 0.001$; cavity type: $SS = 3.900$, $P > 0.05$) among cavity types.

Mean S_r (GLM: $SS = 0.493$, $P < 0.001$, $R^2 = 0.74$; Table 3) and mean $T_{r\ min}$ (GLM: $SS = 11.479$, $P < 0.001$, $R^2 = 0.76$; Table 3) were significantly influenced by diameter of the roost tree and horizontal depth. The post hoc unequal N test revealed no significant differences among roost types ($P > 0.05$). GLM analysis revealed that thermal stability increased (described by lower values of S_r) with increasing diameter ($SS = 0.260$, $P < 0.001$) and increasing horizontal depth ($SS = 0.094$, $P = 0.015$). Mean $T_{r\ min}$, however, increased with increasing horizontal depth ($SS = 2.545$, $P = 0.007$) and diameter ($SS = 5.617$, $P < 0.001$).

The only predictor affecting mean I_r was cavity height (GLM: $SS = 0.812$, $P = 0.022$, $R^2 = 0.30$; Table 3), with I_r increasing with increasing height. Mean $T_{r\ mean}$ was likewise positively related to height of the cavity (GLM: $SS = 0.557$, $P = 0.012$, $R^2 = 0.35$; Table 3).

Discussion

This study revealed differences among characteristics of tree roosts and microclimatic conditions within roosts of the three bat species. Roosts of *P. auritus* had the lowest horizontal depth, thermal stability, and mean minimum roost temperature, whereas *M. bechsteinii* and *M. nattereri* used roosts with more stable microclimatic conditions. These results are in line with the use of

Table 2 Percentages of used roost tree species, cavity type (decomposition cavity = DC, tree crevice = TC, woodpecker cavity = WC), and characteristics of identified roosts separated by species

Variable	M. bechsteinii				M. nattereri				P. auritus			
Percentages tree species	Oak (50 %)				Oak (50 %)				Oak (50 %)			
Percentages cavity type	WC (67 %)				WC (50 %)				DC/TC/WC (33 %)			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
Diameter of tree (cm)	55.2	27.6	14.3	100.3	43.9	14.7	31.5	62.7	36.8	12.9	24.5	56.7
Roost height (m)	9.0	2.3	5.0	11.0	8.8	2.2	5.8	11.0	6.5	4.0	1.0	11.3
Horizontal depth (cm)	19.5	9.4	6.0	31.0	22.4*	6.9	14.0	33.0	12.3*	4.7	5.0	19.0
Vertical depth (cm)	21.7	17.9	0.0	47.0	17.3	15.0	0.0	37.0	13.0	20.9	0.0	55.0
Vertical height (cm)	18.2	16.7	0.0	39.0	26.7	30.4	0.0	75.0	43.3	25.8	20.0	80.0
Horizontal width (cm)	7.2	1.6	5.0	9.0	9.1	4.5	14.0	4.4	9.1	3.0	12.0	3.5
Volume (dm³)	5.87	4.52	1.80	12.27	12.82	15.16	2.16	34.32	6.39	5.33	1.20	15.30
Cardinal direction (°)	103.7	108.9	4.0	282.0	133.7	86.2	32.0	280.0	223.7	100.0	100.0	358.0
Canopy coverage (%)	89.1	2.8	84.8	93.2	92.2	4.2	84.8	96.0	91.2	5.9	80.1	96.5

The cardinal direction was assessed in degree (°) with north being '0°', east '90°', south '180°', and west '270°'. The asterisk (*) denotes significant differences between *Myotis nattereri* and *Plecotus auritus*

Table 3 Results of the general linear models (GLM) with the depending variables mean thermal stability (S_r), mean insulation (I_r), mean temperature of roosts ($T_{r\ mean}$), and mean minimum temperature of roosts ($T_{r\ min}$)

Predictor	Mean S_r			Mean I_r			Mean $T_{r\ mean}$			Mean $T_{r\ min}$		
	SS	P	PE	SS	P	PE	SS	P	PE	SS	P	PE
Intercept	1.450	<0.001	0.875	0.167	0.265	−0.287	289.337	<0.001	11.924	145.592	<0.001	8.770
Group size		n.s.			n.s.			n.s.			n.s.	
Cavity type		n.s.			n.s.			n.s.			n.s.	
Diameter of tree	0.260	<0.001	−0.007		n.s.			n.s.		5.617	<0.001	0.031
Horizontal depth	0.094	0.015	−0.010		n.s.			n.s.		2.545	0.007	0.051
Vertical depth		n.s.			n.s.			n.s.			n.s.	
Vertical height		n.s.			n.s.			n.s.			n.s.	
Horizontal width		n.s.			n.s.			n.s.			n.s.	
Cardinal direction		n.s.			n.s.			n.s.			n.s.	
Height		n.s.		0.812	0.022	0.075	0.557	0.012	0.062		n.s.	
Canopy coverage		n.s.			n.s.			n.s.			n.s.	
Volume		n.s.			n.s.			n.s.			n.s.	
Error		0.172			0.281			1.026			3.582	
Model SS		0.493			0.812			0.557			11.479	
Model P		<0.001			0.022			0.012			<0.001	
Model R^2		0.742			0.302			0.352			0.762	

Predictors used in the analysis are listed in the first column. Sum of squares (SS) is the contribution of each predictor to the model and parameter estimates (PE) are the standardized effects of the predictor on the variable

heterothermy of the three species, where *P. auritus* showed the lowest median skin temperatures and the highest HI during torpor. Cavity type had no effect on microclimatic conditions. Therefore, *P. auritus* has no preference for a distinct cavity type but for the conditions within.

Bats prefer different roost characteristics and/or microclimates depending on physiological conditions, such as reproductive state (e.g. Sedgeley and O'Donnell 1999a, b; Chruszcz and Barclay 2002; Lumsden et al. 2002; Kalcounis-Rüppell et al. 2005; Vonhof and Gwilliam 2007; Willis and Brigham 2007; Lučan et al. 2009; Webala et al. 2010; Clement and Castleberry 2013a, b). Sedgeley and O'Donnell (1999a) and Willis & Brigham (2007) found that roost volume and roost type had no effect on the microclimate of roosts. Cavity volume correlated with group size, with larger roosts being used by larger groups (Willis et al. 2006b; Lučan et al. 2009). Willis and Brigham (2007) claim that social aspects like group size have a bigger effect on roosting ecology than roost characteristics, as surface-to-volume area of a group is reduced by huddling compared to all its members (Hayes et al. 1992). This assumption is supported by results regarding the group sizes of these three species, being smallest in *P. auritus* (Otto et al. 2013). Small groups, as found for *P. auritus*, are likely to cool faster than bigger ones due to their lower thermal capacity and should profit from low T_r by a faster torpor entry. However, as T_s and T_r were not recorded simultaneously in this study, group size had no effect on any

predictor in this study. It is supposed that social organization of the three studied species affects roosting ecology and plays a key role in thermoregulation as well and more data on group size, roost volume, and rewarming capabilities are needed to prove this.

A preference for a particular roost microclimate might be supported by the species-specific heterothermy of the three species and in our observations that $M. bechsteinii$ and $M. nattereri$ used the same roost at different times of the year. The roost was used during pregnancy by $M. bechsteinii$, whereas $M. nattereri$ used it during post-lactation. This difference in roost choice might be caused by periods of harsh weather and low food availability during pregnancy. The ensuing energetic benefits of using cold roosts during pregnancy might ensure successful reproduction by slowing fetal development (Kerth et al. 2001b; Willis et al. 2006a; Stawski et al. 2014). $Plecotus\ auritus$ was not found in roosts used by the other two species (Otto et al. 2013). Roosts occupied by $M. bechsteinii$ and $M. nattereri$ had a lower S_r with more stable microclimatic conditions, which reflects and should be the reason for the lower HI and higher minimum T_s of $M. bechsteinii$ and $M. nattereri$ compared to $P. auritus$. Furthermore, lower temperatures within roosts were recorded for $P. auritus$ compared to $M. bechsteinii$ and $M. nattereri$ (Entwistle et al. 1997; Smith and Racey 2005; Otto et al. 2013), as shown by the comparison of HI with S_r and $T_{s\ min}$ with $T_{r\ min}$.

More stable roosts provide higher temperatures during the nocturnal activity of bats, which might be an advantage when females return to the roost to nurse their pups. This assumption is supported by Chruszcz and Barclay (2002) who observed that lactating bats use warmer roosts than pregnant ones. This preference for particular roost characteristics and microclimatic conditions seems to be fundamental and is displayed in the distinct heterothermy of the three species. One of the problems resulting from deforestation of their habitats could be that bats are forced to use unfit roosts or roost sites (Sedgeley and O'Donnell 1999b). Continuous inhabitation of unfit roosts could cause a decrease in productivity and viability of bat populations (Brigham and Fenton 1986).

The less stable roost conditions might enable $P. auritus$ to achieve lower body temperatures compared to the other species. Roosts with a low horizontal depth should facilitate the cooling process. A low horizontal depth results in a small buffering distance and in consequence a low temperature difference between cavity and outside air. This buffering capacity depends on e.g. thermal characteristics of the bark (Nicolai 1986) that influences insulation characteristics, and microclimatic conditions within the roost. In case of less-efficient insulation low T_b can be reached faster at low T_a at night or during periods of inclement weather. This could be beneficial, as lower T_r could promote the primary energy saving strategy of $P. auritus$. Furthermore, roosts with low insulation allow for fast arousal rates from torpor by passive rewarming, which should be beneficial as this is the most energy demanding phase of torpor (Chruszcz and Barclay 2002; Geiser et al. 2004; Currie et al. 2015). Edworthy and Martin (2014) observed that cavity depth increases yearly, as decay or renovation could be responsible for the increase. Therefore, insulation capacity and thermal stability decrease over time. This should favor species like $P. auritus$, but be adverse for more thermophilous species.

To conclude, this study showed that thermal characteristics of roosts can be linked to heterothermic behavior and could be an indicator for roost choice of cavity-using animals. Factors affecting roost choice are more varied than commonly appreciated. For forest-dwelling bats, not only woodpecker cavities in tall, thick trees but thin trees with crevices are important, as the latter may provide the optimal shelter for a particular species. Hence, even crevices in inconspicuous trees should be taken into account in forest management practices.

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