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Source: Folia Zoologica, 60(1) : 5-16

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v60.i1.a2.2011

Folia Zool. – 60 (1): 5–16 (2011)

Thermoregulation of tree-dwelling temperate bats – a behavioural adaptation to force live history strategy

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Received 30 June 2010; Accepted 1 October 2010

Abstract. Metabolic rate and body temperature (T_b) reduction during torpor can provide significant energy savings for bats during inclement weather and food scarcity. However, torpor use may slow down biochemical processes including fetal and juvenile development and sperm production. Sex-differences in the timing of reproductive activity of bats in the temperate climate zone should result in differences of the thermoregulation behaviour by males and females during summer. To test this hypothesis, we studied thermoregulation of free-ranging, tree-dwelling gleaning bats (*Myotis bechsteinii*) and trawling bats (*M. daubentonii*) during different reproductive periods. Gleaners and trawlers are able to forage on prey which is sitting on vegetation and the ground (gleaning) or which is slowly moving over water bodies (trawling). This prey is characterized by lower ambient temperature (T_a) dependent abundance than flying prey. We used temperature-sensitive radio transmitters to measure skin temperature (T_{sk}). Temperature telemetry over 144 census days revealed a significant effect of reproductive period and sex on T_{sk}. Pre-spermatogenic males exhibited a significantly greater T_{sk} reduction than females in early pregnancy. Males at the beginning of sperm production and in main spermatogenesis exhibited much more frequent and deeper temperature reductions than females in late pregnancy and in lactation. Lactating females maintained the highest T_{sk} of all bats. Post-lactating females reduced T_{sk} to the same extent or even more than males in advanced spermatogenesis.

Our findings indicate that the thermoregulation of gleaning and trawling temperate bats is likely to be much less influenced by environmental conditions than that of aerial hawking bat species. We suggest that both sexes of Bechstein's bats and Daubenton's bats primarily adapt their thermoregulation in response to current reproductive activity.

Key words: Chiroptera, *Myotis bechsteinii*, *Myotis daubentonii,* reproduction, thermoregulation, torpor

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Introduction

Small-sized endotherms with large relative surface areas generally lose considerable heat when maintaining elevated T_b. Remaining homeothermic entails substantial energetic costs which are exacerbated during adverse weather conditions (Speakman & Rowland 1999, White & Seymour 2003, Clarke & Rothery 2008). Many small mammals and birds can reduce energy expenditure through reduction of T_b and metabolic activity during torpor (Geiser 2004, Heldmaier et al. 2004, Speakman 2007). For example, insectivorous bats from temperate regions hibernate during the cold winter season when food is typically not available and commonly use torpor during the active season from spring to autumn (Turbill et al. 2003a, Willis et al. 2005). Although the extent of heterothermy and hypometabolism is usually less pronounced during short bouts of torpor than in hibernation (Geiser & Ruf 1995, Wojciechowski et al. 2007), the short-term decrease in metabolism in summer also leads to profound energy savings (Geiser 2004, Heldmaier et al. 2004). Entering torpor may lead to considerable physiological and ecological costs (Wojciechowski et al. 2007). Possibly, the greatest potential cost of employing torpor in summer is suppression of reproductive processes, in particular fetal development, milk production and body heat transfer from mother to offspring (Racey & Swift 1981, Wilde et al. 1999). In temperate latitudes, late birth and late weaning reduce the time necessary for females and young to acquire fat to fuel hibernation. The lack of sufficient fat deposition may result in higher mortality of young bats, particularly over winter (Thomas et al. 1990). Furthermore, prolonged use of torpor by pregnant females might lead to resorption or abortion of offspring (Roer 1973, Grindal et al. 1992). Male bats using torpor have to cope with costs including reduced testicular growth and maintenance, suppressed accessory gland activity and diminished spermatogenesis and copulation activity (Jolly & Blackshaw 1988, Hamilton & Barclay 1994, Grinevitch et al. 1995, Entwistle et al. 1998, Dietz & Kalko 2006). In temperate zone bats, reproductive stages are asynchronous between sexes (Racey 1974, Entwistle et al. 1998, Dietz & Kalko 2006). While females are pregnant in spring, lactating in mid-summer and post-lactating in late summer, males are sexually inactive in early spring. They exhibit increasing spermatogenetic activity from early to late summer when mating season begins (Racey 1974, Entwistle et al. 1998, Encarnação et al. 2004).

Sex-differences in reproductive activity should result in differences in thermoregulatory strategies by males and females during summer (Dietz & Kalko 2006). Most studies about thermoregulation of bats focus on only one sex (e.g. Audet & Fenton 1988, Entwistle et al. 1998, Lausen & Barclay 2003, Turbill et al. 2003a, b, Willis et al. 2005, Solick & Barclay 2006), encompass only one reproductive period (e.g. Cryan & Wolf 2003, Turbill 2006a, b) or were conducted in the laboratory (Kurta 1986, Kurta & Kunz 1987, Geiser et al. 2000, e.g., Geiser 2004). Results of the field studies about sex-differences in thermoregulation of Nearctic bats show that males use torpor more frequently than reproductive females (Hamilton & Barclay 1994, Grinevitch et al. 1995). However, given that the data are mostly limited to studies of bats living in anthropogenic structures, information on bats roosting in trees are lacking even though trees are the most common natural roost sites (Kunz & Lumsden 2003).

The goal of our study was to investigate thermoregulation during the entire breeding season by Palaearctic, tree roosting Bechstein's bat (*Myotis bechsteinii*) and Daubenton's bat (*M. daubentonii*). For both European bat species, old growth deciduous forests are important habitats because they provide many tree species in multiple stages of growth and decay for roosting (Schlapp 1990). *M. bechsteinii* differs from the trawling *M. daubentonii* mainly in the manner it forages, specifically in that they mostly glean arthropods e.g., Lepidoptera and Coleoptera from vegetation and the ground (Wolz 2002, Siemers & Kerth 2006, Siemers & Swift 2006). *M. daubentonii* is mainly adapted to hunt for insects above water surfaces where it feeds mostly on swarming or emerging Chironomidae (Swift & Racey 1983, Kalko & Schnitzler 1989). However, in contrast to aerial hawking bats that forage on flying prey in strong dependence of T_a conditions, gleaning and hawking bats like *M. bechsteinii* and *M. daubentonii* also forage successfully during periods with low T_a (Barclay 1991, Chruszcz & Barclay 2003, Dietz & Kalko 2007). For both bat species, we expected to find comparable sex-differences in thermoregulation. We expected T_a would affect thermoregulation of reproductive active bats less than actual reproductive condition. We hypothesised that in order to maximise fetal development and milk production, females should maintain high T_b during pregnancy and lactation period while torpor would be used predominantly in the post-lactation period. In contrast, adult males are expected to reduce T_b more often especially at low T_a during the energetically costly period for females (pregnancy and parturition), because they are not involved in the development and rearing of the young. However, as sperm production commences, thermoregulatory behaviour of the males should change accordingly.

Methods

Study sites

Our study of thermoregulation of Daubenton's bats took place in Philosophenwald, a deciduous forest near the city of Giessen (highest elevation: 274 m a.s.l.) in central Germany (50.35 N; 8.40 E). Mean annual precipitation and temperature of Giessen are 590 mm and 9.1°C respectively. Several ponds and the River Lahn are the most important feeding sites of Daubenton's bats that catch emerging and swarming prey over water surfaces. Philosophenwald is dominated by *Fagus sylvatica* which contain the woodpecker cavities, brunch breaks and crevices which *M. daubentonii* use as roosts. Thermoregulation of Bechstein's bats was investigated in a deciduous forest ("Friemholz") in Luxembourg

Table 1. *Summary of radio-tracking data of* Myotis bechsteinii *and* M. daubentonii *sampled in Luxembourg and in Germany, respectively. Reproductive periods (RP) of males are pre-spermatogenesis (PS), early spermatogenesis (ES), main spermatogenesis (MS) and advanced spermatogenesis (AS). RPs of females are early pregnancy (EP), late pregnancy (LP), lactation (Lac) and post-lactation (Post-Lac).*

Tracking Period	Species	RP	Sex	Individual	Mass	Recorded bat days	Hourly recordings
I	Bechstein's bats	EP	F	F1	8.9	5	70
		PS	M	M1	9.0	20	280
II	Bechstein's bats	LP	F	F2	12.5	4	63
		LP	F	F3	12.1	3	46
		LP	F	F4	12	8	116
		ES	M	M2	9.0	5	75
	Daubenton's bats	LP	F	F1	10.7	5	70
		LP	F	F2	11.3	5	70
		LP	F	F3	10.0	4,5	65
		ES	M	M1	7.1	5	70
		ES	M	M2	8.0	3	42
III	Bechstein's bats	Lac	F	F5	10.2	14	210
		Lac	F	F6	11.1	9	130
	Daubenton's bats	Lac	F	F4	9.5	4	60
		MS	M	M3	8.0	5	75
IV	Bechstein's bats	Post-Lac	F	F7	11	8	112
		Post-Lac	F	F8	9.8	8	112
		Post-Lac	F	F9	9.5	5	70
		AS	M	M3	9.0	10	139
	Daubenton's bats	Post-Lac	F	F5	9.1	3	42
		Post-Lac	F	F6	9.4	4	56
		AS	M	M4	9.5	4	56
		AS	M	M5	8.5	3	42
	Total recordings					144	2062

near the city of Echternach (49.80 N; 6.43 E). The forest is located at 350 m a.s.l. on a montane plateau in the "Little Switzerland" region of Luxembourg. Average annual precipitation and temperature of Echternach are 750 mm and 8.5°C. Friemholz is dominated by *Quercus robur*, *Carpinus betulus* and *Fagus sylvatica*. These tree species offer *M. bechsteinii* day and night roosts in form of woodpecker cavities and crevices.

Radio telemetry

With reference to studies on *M. bechsteinii* (Kerth et al. 2001, Dietz & Pir 2009), *M. daubentonii* (Encarnação et al. 2004) and other European *Myotis* species (Racey 1974) we divided the reproductive cycle of the bats into four periods. For females, we differentiated between early pregnancy (Tracking period I), late pregnancy (Tracking period II), lactation (Tracking period III) and post-lactation (Tracking period IV). Reproductive periods of males were delineated as pre-spermatogenesis (Tracking period I), early spermatogenesis (Tracking period II), main spermatogenesis (Tracking period III) and advanced spermatogenesis (Tracking period IV). For determination of reproductive status we caught bats in mist nets set near and around known roost trees and used the methods described by Racey (1974). Pregnant bats were determined by gently palpating the abdomen. Lactating bats were identified by a bare patch around their swollen nipples. Size and form of the nipples and growth of hair served as indicator for post-lactation. The reproductive status of males was determined by assessing the size of the testes, distension of the epididymis and coloration of the tunica vaginalis (Racey 1974, Encarnação et al. 2004). The bats were weighed to the nearest 0.1 g using a digital scale (Kern digital scale CM 60-2N, Kern and Sohn GmbH, Balingen-Frommern, Germany). Forearm length was measured with dial callipers (accuracy: 0.1 mm). The age of the bats was determined by evaluating the closure of the epiphysis (Anthony 1988), length of wrists, abrasion of teeth and evaluation of a chin spot (Richardson 1994).

We tagged Bechstein's bats and Daubenton's bats (Table 1) with LB-2T temperature-sensitive radio-transmitters (Holohil Systems Ltd., Carp., Ontario, Canada) to measure T_{sk} and to locate day roosts. The usefulness of temperature-sensitive transmitters for investigations of thermoregulatory behaviour of bats in the field was first demonstrated by Audet & Thomas (1996) and Barclay et al. (1996). They found that externally measured T_{sk} accurately reflects T_b and T_{sk} values are only slightly affected by T_a. Their study revealed T_{sk} to be within 2.0°C of rectal temperature with a maximum deviation of only 3.3°C. Willis & Brigham (2003) also showed that T_b is only slightly higher than T_{sk}. Transmitter mass represented 3.4–6.8% of the bat's body mass, well below and in a few cases slightly above the 5% suggested for radio-tracking studies (see Aldridge & Brigham 1988, ASM guidelines 1998). We glued the transmitters onto the skin between the shoulder blades of the bats using Skinbond surgical adhesive (Smith & Nephew United, Inc., Largo, Florida, USA). Roosting bats were tracked using Yaesu receivers (VR-500, modified by Wagener, Cologne, Germany) with 2-element Yagi antennae (HB9CV) and T_{sk} measured manually. To record T_{sk}, we timed the pulse rate of the transmitter through pulse counting in three successive 1-minute-sessions using a stop watch. The measurements were taken 2-3 times per hour on all days a transmitter remained on a bat (3-20 days). Pulse rates were translated into T_{sk} using transmitter-specific calibration curves provided by the manufacturer. Hourly measurements of T_{sk} were averaged leading to a total sample of 2062 hourly skin temperature recordings from 144 bat-days (one bat measured on one day). In addition, we recorded hourly T_a during 24 hours at all bat days using Thermochron iButtons® (Dallas Semiconductor Corp., Dallas, Texas, USA, resolution ± 0.5°C) placed 2 m above the ground on a shaded tree trunk in the centre of the study forest.

Data analysis

For comparisons of thermoregulatory patterns between sexes and periods we defined the time of our measurements of T_{sk} as bat day. A bat day depended upon emergence and return time to the day roost and excluded all hours during which bats were foraging out of the roost. Bat days lasted 14 hours (6:00 am–8:00 pm) in May and in August and 15 hours (6:00 am–9:00 pm) in June and in July, respectively. For all temperatures (mean, min and max T_{sk}, differences between T_{sk} and T_a) and environmental conditions ($T_{a,}$ humidity) we calculated individual mean daily values and standard deviations (± SD) during the time an individual roosted. Subsequently, we averaged the mean values for each reproductive stage (early pregnancy, late pregnancy, lactation and post-lactation versus pre-spermatogenesis, early spermatogenesis, main spermatogenesis and advanced spermatogenesis). We tested the data for normality using Kolmogorov-Smirnov tests. The influence of gender, reproductive period and environmental conditions on individual T_{sk} was tested using General Linear Model analysis (GLM). All data were non-normal, thus we applied Kruskal-Wallis nonparametric one-way ANOVAs to test for significant differences between reproductive periods of females and males and a Mann-Whitney U-test to test for significant differences between the thermoregulation of two groups (either between different reproductive periods of one sex or between both sexes during one tracking period). We calculated Spearman rank correlations to assess the relationship between T_{sk} and T_a. Probability level determining significance was set to $p < 0.05$. All statistical analyses were performed using Statistica 6.0 (SigmaStat).

Results

Influence of reproduction period on thermoregulation

General linear model analyses (GLMs) revealed that min T_{sk}, mean T_{sk} and max T_{sk} as well as T_{sk} - T_a each varied significantly within the whole data of 2062 hourly T_{sk} recordings from 144 census days. Reproductive period and especially the interaction between reproductive period and sex and the interaction between reproductive period and T_a explained most of the variation in our data set (Table 2). In contrast, environmental conditions like air humidity influenced thermoregulation either very weakly or not at all. Kruskal-Wallis ANOVAs further confirmed reproductive condition as major factor influencing thermoregulation of both sexes (Table 3). Species-specific comparisons showed that females of both species reached very similar daily min, mean

Table 2. *Results of GLM analysis to test the dependence of daily minimum, mean and maximum T_{sk} and daily T_{sk} - T_a differences of tree-dwelling* Myotis *bat species (*Myotis bechsteinii *and* M. daubentonii*) regarding species, gender, reproductive period and environmental conditions (daily mean T_a, humidity, wind speed). Tracking days are listed in Table 1. n.s. = not significant. Note: F = Fit, * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

explaining variable / depending variable	Overall model	species	sex	period	T_a	humidity	species & period	sex & period	species & sex	T_a & species	T_a & sex	T_a & period
Daily mean T_{sk}	F = 78.92***	15.45***	n.s.	16.76***	30.90***	n.s.	n.s.	4.12*	13.16***	10.12**	22.86***	10.64***
Daily min T_{sk}	F = 80.23***	n.s.	18.20***	55.26***	62.82***	5.91*	n.s.	10.52**	25.26***	n.s.	n.s.	39.16***
Daily max T_{sk}	F = 44.12***	3.90*	6.80*	5.55*	n.s.	n.s.	5.87***	5.02*	n.s.	7.07***	n.s.	7.03**
Daily mean T_{sk} - daily mean T_a	F = 41.33***	n.s.	n.s.	23.52***	n.s.	n.s.	13.19***	4.07*	15.86***	23.79***	14.70***	31.92***

Table 3. *Kruskal-Wallis-ANOVA-based comparisons of daily minimum (min), mean and maximum (max) skin temperature (T_{sk}) and T_{sk} - T_a differences between all investigated reproductive periods of male and of female Bechstein's bats (*Myotis bechsteinii*) and Daubenton's bats (*M. daubentonii*). For each tested thermoregulation describing variable, H-values with significance levels of the inter-periodical differences are given. df = degrees of freedom. * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

Species	Sex	df	mean T_{sk}	max T_{sk}	min T_{sk}	T_{sk} - T_a
M. bechsteinii	F	3	39.517***		36.523***	25.102***
	M	2	25.796***	21.296***	25.013***	25.826***
M. daubentonii	F	3	14.973***	6.513*	14.844***	15.107***
	M	2	11.654**	1.978	13.545***	11.777**

and max T_{sk} in every investigated reproductive period. In females of both bat species, daily mean, min and max T_{sk} were highest and the values remained nearly equally stable during late pregnancy and lactation (Fig. 1 and 2). During early pregnancy and post-lactation period daily mean, min and max T_{sk} dropped to significantly lower levels (Mann-Whitney-U-tests, $p < 0.05$). For instance, for Bechstein's bats and Daubenton's bats, in post-lactation, daily min T_{sk} was 23.4 ± 0.9°C and 22.5 ± 0.9°C respectively. In contrast, late pregnant and lactating females of both bat species reached daily min T_{sk} between 31.8 ± 2.7°C and 33.0 ± 2.5°C. Compared to females, mean, min and max T_{sk} of male Bechstein's bats and Daubenton's bats in the same reproductive period were not that synchronous. However, in case of male Daubenton's bats, daily min T_{sk} increased continuously from early spermatogenesis (17.7 ± 0.8°C) over main spermatogenesis (21.1 ± 6.6°C) to advanced spermatogenesis (30.3 ± 4.9°C). Min T_{sk} of male Bechstein's bats similarly increased continuously from spring (13.0 ± 2.1°C) over summer (18.9 ± 2.0°C) to autumn (20.3 ± 1.5°C).

Influence of gender on thermoregulation

Sex-specific comparisons showed that mean, min and max T_{sk} differed significantly between female and male bats of both *Myotis* species especially during tracking periods I, II and III (Fig. 1 and 2, Mann-Whitney-U-tests comparing sexes: $p < 0.05$). In tracking period I, mean T_{sk} of female Bechstein's bat in early pregnancy exceeded those of the male in pre-spermatogenesis on average about 9°C. In tracking period II, female Bechstein's bats in late pregnancy on average had an 8°C higher daily mean T_{sk} of the males in early spermatogenesis. Similarly, daily mean T_{sk} of female Daubenton's bats in late pregnancy and in lactation exceeded those of male Daubenton's bats in early and in main spermatogenesis on average about 12.5°C and 7.7°C, respectively. For both species, sex-based differences in daily mean, min and max T_{sk} reversed or at least declined to a non-significant level during tracking period IV. For example, daily mean T_{sk} of post-lactating females of both *Myotis* species (Bechstein's bats: 26.5°C ± 1.9, Daubenton's bats: 26.7°C ± 0.5) exceeded those of males in advanced spermatogenesis only about 3°C (male Bechstein's bats: 23.5°C ± 0.7) or fell 6°C below daily mean T_{sk} of males (male Daubenton's bats: 32.8°C ± 2.5).

Influence of ambient temperature on thermoregulation

GLM analyses revealed T_a as the environmental condition with the most influence on thermoregulation of the investigated bats. Differences between daily mean T_{sk} and daily mean T_a (T_{sk} - T_a) varied significantly between reproductive periods of females as well as between reproductive periods of males of both *Myotis* species (Kruskal-Wallis ANOVAs, Table 3). T_{sk} - T_a of females in late pregnancy and in lactation (Bechstein's bats 16.6°C ± 0.7 and 14.9 ± 1.5°C, Daubenton's bats 18.5 ± 1.4°C and 15.2 ± 3.0°C) were similar and significantly higher (Mann-Whitney-U-tests, $p < 0.05$) than those of early pregnant (Bechstein's bats 9.2°C ± 5.2) and post-lactating bats (Bechstein's bats 11.0 ± 1.8°C, Daubenton's bats 11.0 ± 1.1°C).

Species-specific comparisons confirmed that within the same reproductive periods, T_{sk} - T_a of females and males were similar between the two investigated *Myotis*-species with the exception of advanced spermatogenesis during which T_{sk} - T_a of male Daubenton's bats were significantly higher (about 4–5°C) than T_{sk} - T_a of male Bechstein's bats (Mann-Whitney-U-tests, Table 4). In males, T_{sk} - T_a of Bechstein's bats increased significantly from pre-spermatogenesis (2.0 ± 4.4°C) over early spermatogenesis (8.2 ± 0.8°C) to advanced spermatogenesis (9.5 ± 1.1°C) and T_{sk} - T_a of

Table 4. *Mann-Whitney U-test-based species-specific comparisons of daily minimum (min), mean and maximum (max) skin temperature (T_{sk}) and differences of mean daily T_{sk} and T_a (T_{sk} - T_a) of male and female Bechstein's bats (*Myotis bechsteinii*) and Daubenton's bats (*M. daubentonii*) during different tracking periods. For each variable U-values with significance levels of species-specific differences are given. * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

Tracking Period	Sex	mean T_{sk}	max T_{sk}	min T_{sk}	mean T_a	T_{sk} - T_a
II	F	581.25	579.69	579.31	579.69	581.25
	M	102.92*	102.60	100.58	102.00	102.92
III	F	214.60	212.50*	211.13	214.08	214.67
IV	F	355.25	354.28*	105.89	354.76	355.25
	M	105.00***	103.46**	105.00**	105.00**	105.00**

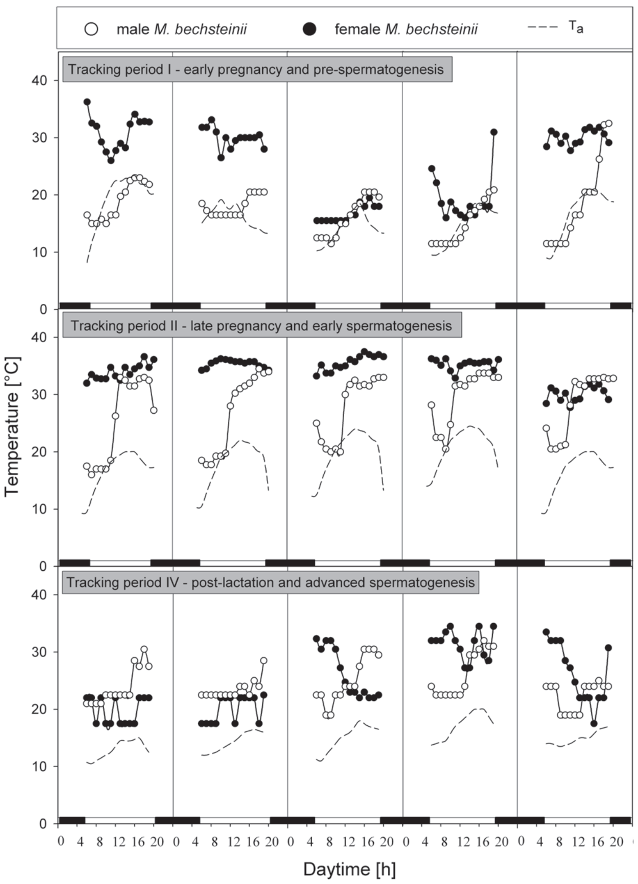

Fig. 1. *Hourly T_{sk} of simultaneously radio-tracked male and female* Myotis bechsteinii *in different tracking periods of their life cycle. Dark bars indicate scotophase.*

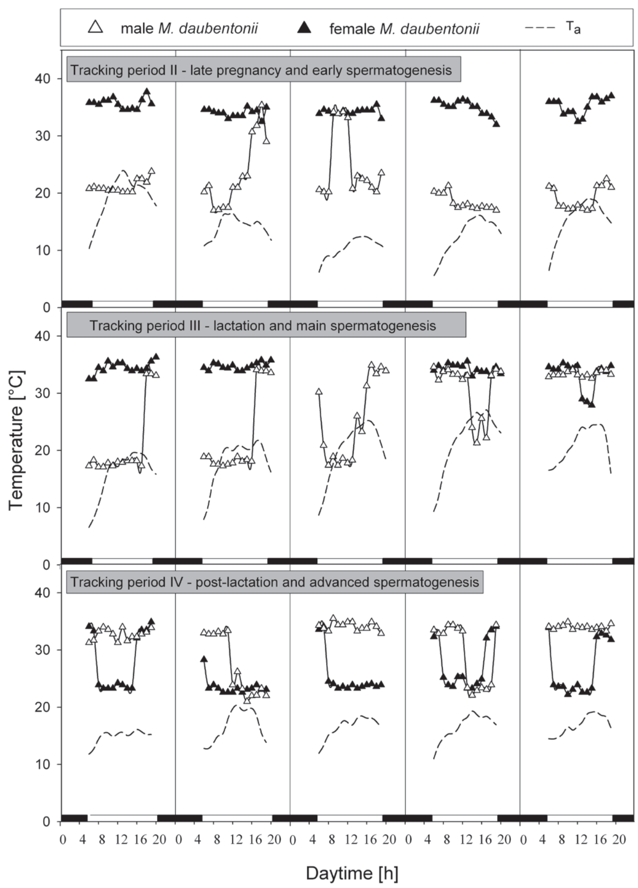

Fig. 2. *Hourly T_{sk} of simultaneously radio-tracked male and female* Myotis daubentonii *in different tracking periods of their life cycle. Dark bars indicate scotophase.*

Daubenton's bats increased from early spermatogenesis (5.5 ± 0.9°C) over main spermatogenesis (7.2 ± 3.6°C) to advanced spermatogenesis (14.1 ± 1.0°C) (Mann-Whitney-U-tests, $p < 0.05$).

T_{sk} of males and females of both bat species usually exceeded T_a to the highest extent during evening and morning hours when T_a was lowest and bats were active after returning from foraging to their roosts or prior of leaving roosts for foraging (Fig. 3). During midday hours, T_{sk} - T_a differences were lowest because of highest T_a and lowest T_{sk} at this time of the day (Fig. 3). In case of Bechstein's bats, Spearman rank correlation analysis between hourly T_{sk} and T_a showed that hourly T_{sk} - T_a correlations of females in early pregnancy ($r_s = 0.330$, $p = 0.005$, $n = 70$), in late pregnancy ($r_s = 0.199$, $p = 0.003$, $n = 225$), in lactation ($r_s = -0.043$, $p = 0.428$, $n = 330$) and in post-lactation ($r_s = 0.330$, $p < 0.001$, $n = 294$) were clearly weaker than hourly T_{sk} - T_a correlations of the simultaneously tracked males although these decreased continuously from pre-spermatogenesis ($r_s = 0.787$, $p < 0.001$, $n = 280$) over early spermatogenesis ($r_s = 0.708$, $p < 0.001$, $n = 75$) to advanced spermatogenesis ($r_s = 0.555$, $p < 0.001$, $n = 139$). Hourly T_{sk} - T_a correlations of male Daubenton's bats increased slightly from early spermatogenesis ($r_s = -0.109$, $p = 0.253$, $n = 162$) over main spermatogenesis ($r_s = 0.268$, $p = 0.021$, $n = 75$) to advanced spermatogenesis ($r_s = 0.363$, $p < 0.001$, $n = 98$) and were similarly weak as the hourly T_{sk} - T_a correlations of female Daubenton's bats in late pregnancy ($r_s = 0.107$, $p = 0.117$, $n = 197$), in lactation ($r_s = -0.256$, $p = 0.048$, $n = 60$) and in post-lactation ($r_s = -0.262$, $p = 0.009$, $n = 98$).

Discussion

The study revealed that both tree-roosting *Myotis* species showed a very similar thermoregulatory behaviour that varied between sexes and reproductive periods. As postulated, females maintained constantly high T_b during late pregnancy and lactation period whereas early pregnant and post-lactating females reduced T_b to conserve energy significantly more often. Males allowed T_b to decrease less frequently, to a smaller extent and for shorter duration per day during advanced spermatogenesis compared to earlier in the year, when there was less sexual activity. It is obvious that both sexes adapted thermoregulation primarily to reproductive activity as it was shown for Nearctic bats roosting in buildings (Hamilton & Barclay 1994, e.g. Grinevitch et al. 1995, Cryan & Wolf 2003). Environmental conditions barely explained the observed T_{sk} fluctuations of the bats in our study

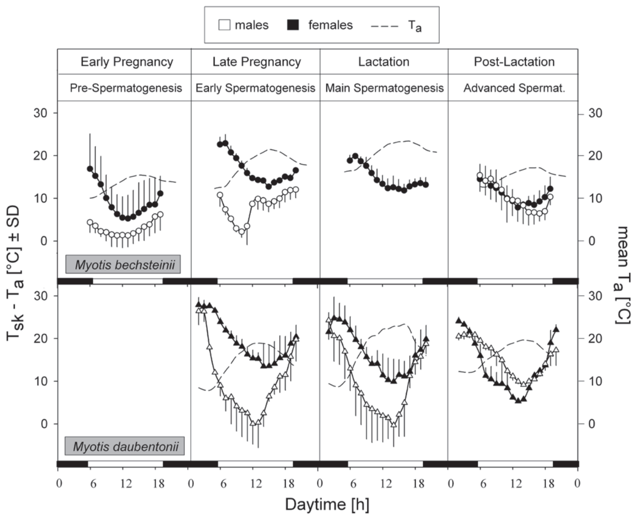

Fig. 3. *Differences of mean daily T_{sk} and T_a (T_{sk} - T_a) of male and female Bechstein's bats (*Myotis bechsteinii*) and Daubenton's bats (*M. daubentonii*) during different reproduction periods compared to ambient temperature (T_a).*

especially because T_{sk} significantly varied between females and males which were simultaneously radio-tracked under similar environmental conditions.

In contrast to our findings, studies on the thermoregulation of other temperate bat species suggest that the individuals' thermoregulatory behaviour depends to a much higher extent on environmental conditions (e.g. Audet & Fenton 1988, Hamilton & Barclay 1994, Grinevitch et al. 1995, Lausen & Barclay 2003, Turbill et al. 2003a, b, Turbill & Geiser 2006, Willis et al. 2006). This may possibly be related to the primarily aerial hawking foraging strategy of those bats (Barclay 1991, Chruszscz & Barclay 2003). Food intake by aerial hawking during night hours with low T_a is likely to be low as flight activity of winged prey is limited under these conditions (Racey & Swift 1985, Hickey & Fenton 1996). Therefore, aerial hawkers forage mainly during warm night hours during dusk and dawn (e.g. Rydell 1993, Swift 1997). Trawling and gleaning bats which we investigated here can forage successfully all night long, even when T_a is low (Chruszscz & Barclay 2003). Foraging behaviour of Bechstein's bats and Daubenton's bats was not significantly correlated with environmental conditions throughout the night (Dietz & Kalko 2007, Dietz & Pir 2009) suggesting a mostly T_a independent foraging activity as it was found for gleaning *Myotis evotis* (Chruszscz & Barclay 2003). *M. daubentonii* mainly feeds on swarming chironomids, capturing them close to water surfaces (Kalko & Schnitzler 1989). Insect density over water surfaces is less affected by short-term low-T_a because of the heat saving capacity of water (Dietz & Kalko 2007). *M. bechsteinii* is able to hawk and glean non-volant prey from vegetation and the ground and may catch sitting arthropods e.g., Lepidoptera-larvae and Coleoptera that are characterized by lower T_a-dependent activity than flying insects (Wolz 2002, Siemers & Kerth 2006, Siemers & Swift 2006).

In addition to energy intake by foraging, roosting habits may also influence thermoregulation (Solick & Barclay 2006, Boyles 2007, Willis & Brigham 2007). For example, roosting solitary and in exposed roosts incurs much higher costs for maintenance of homeothermy compared to roosting in maternity colonies in well isolated roosts (Willis & Brigham 2007). This probably explains why bats roosting in rock crevices or in foliage and why solitary roosting pregnant and lactating temperate bats (Lausen & Barclay 2003, Solick & Barclay 2006, Willis et al. 2006) reduce body temperature much more frequently than reproducing female Bechstein's bats and Daubenton's bats that communally roost in tree cavities (Dietz & Kalko 2006). For instance, rock-roosting *Eptesicus fuscus* usually become torpid on at least 40% of bat days, independently from reproductive condition (Lausen & Barclay 2003).

During our study, female *M. bechsteinii* and *M. daubentonii* formed maternity colonies in cavities made by woodpeckers in oaks and beeches. Males roosted solitary in natural crevices of hornbeams and beeches. These sex-differences in roosting habits are also directly related to differences in thermoregulation (Hamilton & Barclay 1994, Grinevitch et al. 1995, Kerth & Morf 2004). Roosting solitary in crevices with high temperature fluctuations might be advantageous for the solitary males as lower temperatures improve conditions for cooling down and going into torpor and higher temperature fluctuations during day roosting foster passive rewarming (Hamilton & Barclay 1994, Grinevitch et al. 1995, Turbill et al. 2003a, 2006a). Compared to the beech and hornbeam crevices with large entrances, well isolated woodpecker-made cavities with small openings have a much more stable microclimate (Sedgeley & O´Donnell 1999, Ruczynski & Bogdanowicz 2005). Hence, in addition to social thermoregulation through clustering, roosting in woodpecker-made cavities may markedly reduce the females' costs for maintaining high T_b during reproduction (Solick & Barclay 2006, Boyles 2007, Willis & Brigham 2007).

However, our findings for female bats suggest that the need for avoiding T_b reduction is lower during early pregnancy, when embryo mass is relatively small, and during post-lactation, when juveniles have been weaned, than during late pregnancy and lactation when the embryo and the neonate reach the high body mass that is typical for bats (Kurta & Kunz 1987, Cretekos et al. 2005). Females of other bat species similarly decreased T_b reduction from early pregnancy to late pregnancy (Audet & Fenton 1988, Hoying & Kunz 1998) and lactation (Audet & Fenton 1988, Hamilton & Barclay 1994, Grinevitch et al. 1995, Chruszcz & Barclay 2002, Lausen & Barclay 2003, Solick & Barclay 2006). We assume that to overcome the energetically demanding periods of late pregnancy and lactation, an adequate amount of fat reserves saved through regular T_b reduction in early pregnancy might be very advantageous (Geiser & Masters 1994). Female and juvenile temperate bats profit from regular strong T_b reduction during post-lactation because autumnal energy-saving and conservation of fat stores significantly decrease winter mortality (Audet & Fenton 1988, Barclay 1991). Moreover, the quantity of autumnal deposited fat that remains after hibernation is linked to successful ovulation in spring and hence contributes to successful fertilization and beginning of pregnancy in the following year (Kunz et al. 1998).

In case of male *Myotis* bats, we assume that high T_b are most important during the spermatogenic period in summer and autumn. Testicular recrudescence and sperm production are inhibited by use of torpor in small mammals (Meistrich et al. 1973, Barnes et al. 1988, Fietz et al. 2004). The same may be true for bats. Supporting this, low T_b markedly diminished the number of spermatozoa that male sharp-nosed tomb bats (*Taphozous georgianus*) produce per day (Jolly & Blackshaw 1988). Moreover, sperm supply may limit reproductive success of male bats (e.g. Shapiro & Giraldeau 1996), especially under conditions of sperm competition. These are likely to occur in Bechstein's bats and Daubenton's bats where one female potentially mates with several males (Kerth & Morf 2004).

Males compensated the energetic costs of maintaining homeothermy through increased foraging activity, hence increased intake of food (Dietz & Kalko 2007) and through T_b reduction in the morning hours, when temperatures in natural tree roost were lowest (own unpublished data). During periods of elevated reproductive activity, bats were observed to remarkably lose body mass if not increasing foraging or torpor use (Entwistle et al. 1998). As our data indicate, to prepare for the energy demanding spermatogenic period, male *Myotis* bats exhibit energy saving and fat conservation through regular strong T_b reductions during pre-spermatogenesis in spring. Consistent with this, short bouts of deep torpor not only seem to be ubiquitous amongst aspermatogenic male bats in temperate climate zones but also in regions where milder, subtropical climates guarantee favourable T_a for foraging in spring (Turbill et al. 2003a, 2006a, b). T_b was regularly reduced by male Bechstein's bats in August, too, indicating that the use of torpor might also outweigh the benefit of whole-day normothermy during advanced spermatogenesis when most sperms and gonadal tissue have already been produced (Racey & Tam 1974). We found males with filled epididymes in tree roost at the end of July. Becoming torpid during this time would reduce copulation frequencies, especially in case of Daubenton's bats because females of this species that have gained enough weight for hibernation already leave their breeding areas at the beginning of September to settle in the hibernation site (Harrje 1994). In addition, the minimized extent of T_b reduction by males during advanced spermatogenesis may reflect a reduced ability to lower T_b when testosterone levels are high (Entwistle et al. 1998). However, even small temperature reductions as in shallow torpor can already result in substantial energy savings for bats (Webb et al. 1993) and during late summer might especially contribute to saving fat in preparation for hibernation (Grinevitch et al. 1995).

Overall we conclude that female and male Bechstein's bat and Daubenton's bats as well as other bats in the temperate climate zone actively adapt their thermoregulatory behaviour to optimize their reproductive success. Furthermore, the feeding strategy of "gleaning" and "trawling" contributes to the observed plasticity of thermoregulation because gleaning and trawling bats are likely to be much less influenced by environmental conditions than aerial hawking bats.

Acknowledgements

We are very grateful to Prof. Dr. Elisabeth K.V. Kalko for suggestions and discussions about the ecological function of thermoregulation in temperate bats. We are also grateful to Dr. Justin Boyles and a second reviewer for very helpful comments to the manuscript.

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Appendix. *Abbreviations used.*

AS	advanced spermatogenesis
ES	early spermatogenesis
EP	early pregnancy
Lac	lactation
LP	late pregnancy
Post-Lac	post-lactation
PS	pre-spermatogenesis
T_a	ambient temperature
T_b	body temperature
T_{sk}	skin temperature