

Chapter 15

Summer Torpor and Sexual Segregation in the Subtropical Bat *Rhinopoma microphyllum*

Eran Levin, Amos Ar, Yoram Yom-Tov and Noga Kronfeld-Schor

Abstract During the past few years it has become clear that torpor and hibernation are not limited to high latitudes or cold climates. We studied summer roost selection and torpor patterns of a subtropical greater mouse-tailed bat, *Rhinopoma microphyllum*, on the edge of its distribution range. During summer, these bats exhibited complete sexual segregation, with males inhabiting a higher and cooler region. Both sexes inhabited warm and dry caves (28–32°C on average). Using radio telemetry, we measured body (skin) temperature and foraging patterns of both sexes during summer. Lactating females remained normothermic during the day and performed longer foraging bouts during the night, while both males and non-lactating females performed shallow torpor, and performed short foraging bouts during the night. We suggest that these differences result from the different energetic challenges of the two sexes during summer, which may contribute to sexual segregation in bats.

15.1 Introduction

During the past decade, it became evident that torpor is not limited to high latitudes, but also occurs in subtropical and tropical mammals, and in response to diverse environmental conditions including low ambient temperature, food and water availability, and ecological interactions (Carey et al. 2003; Cossins and Barnes 1996; Dausmann et al. 2004; Geiser and Stawski 2011; Levy et al. 2011a, b; Lovegrove and Génin 2008; Lovegrove and Raman 1998; Schmid et al. 2000; Schmid and Speakman 2000; Turbill et al. 2003). Here, we studied the summer roost

E. Levin (✉) · A. Ar · Y. Yom-Tov · N. Kronfeld-Schor
Department of Zoology, Tel Aviv University, 69978 Tel Aviv, Israel
e-mail: levinere@post.tau.ac.il

selection and thermal physiology of males and females of a subtropical insectivore bat, the greater mouse-tailed bat (*Rhinopoma microphyllum*) in northern Israel, which is the northern edge of its range. During summer, these bats exhibited complete sexual segregation, with males inhabiting a higher and cooler region.

Animal populations inhabiting the margins of the species distribution are interesting physiologically, since they may preserve important character combinations for adaptation to extreme environmental conditions (Hampe and Petit 2005; Lesica and Allendorf 1995). Thermal physiology and distribution constraints of these edge populations are expected to be of high importance for the response of species to climate change.

Greater mouse-tailed bats are medium-sized insectivore bats (25 g) inhabiting dry and warm regions of the “old world”—from North Africa, east to Thailand, and Sumatra (Altringham 1996). Greater mouse-tailed bats are well adapted to arid (Schlitter and Qumsiyeh 1996) or subtropical environments (Kulzer 1965). The tolerance of these bats to relatively low temperatures is limited, and it was assumed that they are unable to perform deep torpor or hibernation (Kulzer 1965). During summer, greater mouse-tailed bats have a specialist diet preference, based mainly on beetles and queens of carpenter ants (*Camponotus felah*). From July, greater mouse-tailed bats accumulate significant amounts of fat, sometimes reaching 50% of their body mass (Levin et al. 2009), which is similar (and even higher) to that reported during the pre-hibernatory period in temperate bats (Kronfeld-Schor et al. 2000; Kunz et al. 1998).

We studied the thermal physiology of both sexes of the greater mouse-tailed bats during summer, trying to understand the significance of the geographic segregation between sexes. Based on our results, we suggest that the sexual segregation in these bats is related to different thermal preferences between males and reproductively active females.

15.2 Methods

15.2.1 Study Area

The study was conducted in the northern Jordan valley, Israel (32° 46'N 35° 32'E). The climate in this area is subtropical, with a dry and hot summer (mean daily minimal and maximal temperatures in July: 22.8 and 37.5°C, respectively) and a moderate winter (mean daily minimal and maximal temperatures in February: 9.2 and 19.2°C, respectively; Israel Meteorological Service).

15.2.2 Radio Telemetry

During summer 2007 (23.7–10.8) and 2008 (26.6–1.8), a total of 38 greater mouse-tailed bats (19 females and 19 males) were tagged with radio-transmitters for

monitoring skin temperature and activity. During summer 2007 we tagged 10 males and 10 lactating females. During summer 2008 no reproductive females were observed in any of the greater mouse-tailed bat populations in Israel, so 9 non-lactating females and 9 males were tagged. We used BD2-CT radio transmitters (Holohil Systems, Canada) weighing 0.9 g for females and 1.1 g for males, within the accepted range of less than 5% of body weight (Aldridge and Brigham 1988; Bontadina et al. 2002). The hair between the shoulder blades was clipped and transmitters were attached using medical glue (Skin-Bond cement, Smith and Nephew United Inc., Largo, Florida, USA).

Two RX900 stationary receiver-data loggers (Televilt International, Sweden) were positioned near the entrance of the male and female roosts and a di-pole antenna was fixed inside each roost. Receivers were powered by external 12 V batteries that were charged during the day using solar panels (Shell Solar Industries, USA). The receivers were programmed to scan the relevant transmitter frequencies, allocating 45 s for each frequency (so each individual was scanned every ~ 15 min). An individual was considered to be foraging if no data were logged for more than 30 min. Skin temperature (T_{sk}) was obtained using the transmitter pulse rate, as measured and logged by the stationary receivers in the roosts. We used T_{sk} as an approximation of T_{b} based on studies showing that in small mammals T_{sk} is closely correlated to T_{b} (Audet and Thomas 1996; Daniel et al. 2010). The activity temperature of each individual (T_{ac}) was calculated from the last T_{sk} reading before bats emerged for their evening foraging bout (Kelly et al. 2007). Maximum skin temperature (T_{max}) was calculated from the average of 30 maximum T_{sk} measurements during the radio tracking period. In both colonies, ambient temperature (T_{a}) was recorded every 90 min using a temperature-data logger (HOBO, Onset, USA) positioned on the roost ceiling.

All procedures were carried out under permit no 25057/2006 from the Israel Nature Reserves and Park Authority (NPA).

15.3 Results

15.3.1 Summer Activity Rhythms and Body Temperature

As expected, the bats exhibited complete sexual segregation:

Males: Average daily T_{a} in the male colony during summer ranged between a minimum of $29.2 \pm 1^\circ\text{C}$ around 5:00 to $32.9 \pm 0.8^\circ\text{C}$ around 15:00 in summers 2007–2008 (Fig. 15.1a). A total of 138 full days of T_{sk} recordings were obtained from ten males (five in each season, Table 15.1). The other nine tagged individuals apparently moved to an unknown nearby colony after being caught and tagged, and were recorded foraging in the area. A single male remained in the males' roost every night after the evening foraging bout, but left the roost every morning before sunrise. The T_{sk} patterns of males in both summers were similar (Fig. 15.1c); after returning from a foraging bout T_{sk} fell almost immediately, and moderately rose at

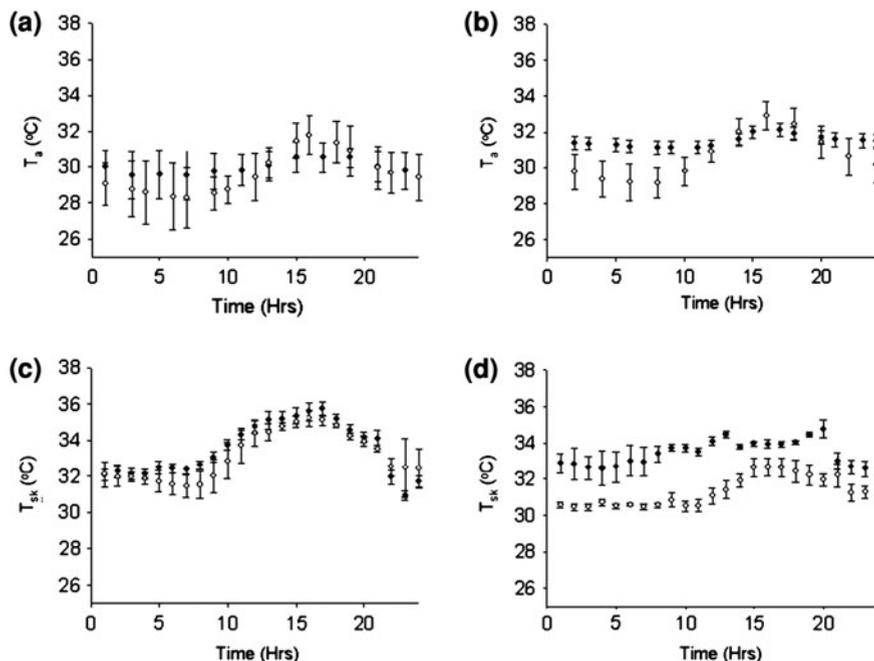


Fig. 15.1 Daily roost temperature cycles (\pm SD) of males (a) and females (b) and T_{sk} cycles (\pm SD) of males (c) and females (d) during summers 2007 (filled dots) and 2008 (empty dots)

Table 15.1 Foraging bout length (SD) and skin temperature (SD) of males and females greater mouse-tailed bats in summers 2007–2008 (t test, $*P < 0.05$)

Season	Sex	N	Min. foraging time (min)	Max. foraging time (min)	Av. foraging time (min)	T_{max}	T_{ac}
2007	M	5	41 (7)	272 (151)	117 (38)	38.1 (0.8)	34.4 (0.6)
	F	5	144 (138)*	457 (158)	306 (154)*	35.4 (0.5)*	35.3 (0.7)
2008	M	5	37 (8)	466 (148)	164 (70)	36.9 (0.8)	34.6 (0.7)
	F	4	240 (113)*	278 (103)	240 (113)	35.5 (0.9)*	34.5 (1)

noon (from 7:30 to 15:00), with a peak of T_{sk} above T_a around 15:30. After this peak, T_{sk} moderately decreased with T_a until bats actively re-warmed before leaving the cave to forage (Fig. 15.2).

Females: T_a in the female roost was similar to that of male roost, ranging between minimum of $29.6 \pm 1.3^\circ\text{C}$ around 5:00 to $30.5 \pm 0.8^\circ\text{C}$ around 15:00 (Fig. 15.1b). In response to trapping and transmitter attachment most females left the roost (carrying their pups with them during summer 2007) and were located using a directional antenna in another colony, 3.5 km northeast from the original maternity roost. We positioned the receiver-data logger in this roost for the two recording seasons. A total of 34 full days of T_{sk} recording were obtained from nine females (five individuals in 2007 and four in 2008, see Table 15.1). T_{sk} of lactating females (recorded during 2007) were significantly higher than recorded in the non-

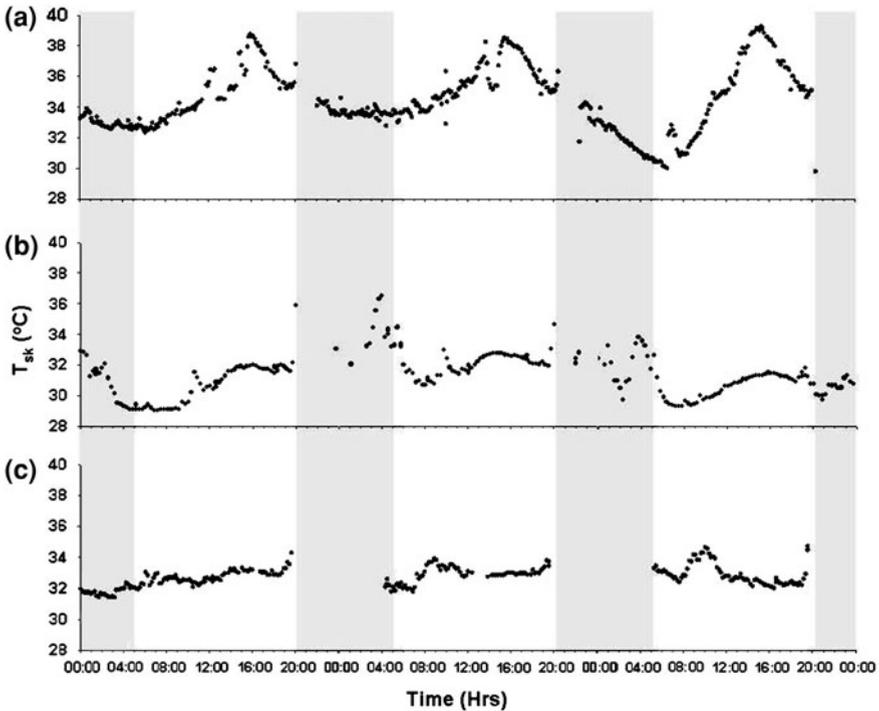


Fig. 15.2 T_{sk} cycles during 3 days in a male (a), a non-lactating female (b) and a lactating female (c) greater mouse-tailed bat. The empty parts are when bats left the cave to forage. Night time is gray shaded

lactating females (average $33.4 \pm 0.7^{\circ}\text{C}$, $n = 5$ vs. $31.2 \pm 0.8^{\circ}\text{C}$, $n = 4$), t test, $t = 9.4$, $P < 0.001$, Figs. 15.1d, 15.2b, c). In contrast to males, females tended to shift roosts, which resulted in a smaller sample size of T_{sk} recordings compared to males (34 vs. 138). When females left the roost to forage (lactating and non-lactating), they spent a significantly longer time outside the roost than males (Table 15.1). T_{ac} of females and males was not significantly different, but T_{max} was significantly higher in females during both summers (38.1 vs. 35.4°C on 2007 and 36.9 vs. 35.5°C on 2008, t test, $P < 0.05$, Table 15.1).

15.4 Discussion

We found that male and female greater mouse-tailed bats are “thermophile” bats that segregate throughout summer. During this time females are pregnant, give birth, and lactate, and both sexes accumulate pre-hibernatory body fat that is used as an energy source during winter hibernation, which they perform in relatively high T_a (Levin et al. 2009).

In northern Israel, both sexes of greater mouse-tailed bats inhabit subtropical habitats with high T_a and rich food sources. However, males roost at higher and cooler altitudes (average of 4°C difference in minimal daily temperature, [Israel meteorological service]). Nevertheless, we found no significant differences in summer roost T_a between males and females. Similar sexual segregation along an altitudinal gradient was observed in several temperate bat species (Senior et al. 2005). A common explanation for such segregation is that the bigger females exclude the smaller males to less productive regions. However, greater mouse-tailed bats males are at least 25% heavier than females (Levin et al. 2009) and therefore do not fit this pattern.

One possible variable differing between the male and female summer roost sites is the T_a outside the roost, which is about 4°C lower at the male roost area (18°C vs. 22°C). It is possible that some physiological or morphological differences, such as body mass or thermoregulatory abilities, differ between males and females, allowing males to be active during colder nights. In a recent paper, Humphries and Careau (2011) tested the hypothesis of activity-thermoregulatory heat substitution, which suggests that heat produced during activity in the cold reduces the energy expenditure for thermoregulation. They found that the scope for heat substitution increases with animals' body size and intensity of the activity (Humphries and Careau 2011). As T_a drops some of the heat produced by activity is used for thermoregulation, up to a point where heat produced by activity equals the amount needed for thermoregulation. Below this equilibrium point the animal has to start inverting energy in thermoregulation. Being larger than the females, it is expected that T_a at this equilibrium point, which is optimal in terms of energy usage efficiency, will be lower for greater mouse tail bat males. Moreover, it was suggested that in many mammalian species, including humans, there are thermoregulatory differences between males and females: females have lower T_{sk} , lower cooling rate, and reduced metabolic reaction to cold compared to males (McArdle et al. 1992; Vierck et al. 2008). These differences between sexes were shown to affect behavioral and physiological aspects such as aggregation in females (Terrien et al. 2010), or differences in geographic dispersal patterns between sexes (Cryan and Wolf 2003). Physiological, morphological, and behavioral differences between sexes (hormones, lactation, water balance, exercise capacity, adipose tissue to muscle ratio, body size, sociality, etc.) have the potential to contribute to these different ecological preferences (Kaciuba-Uscilko and Grucza 2001). These differences may exist also in greater mouse-tailed bats and contribute to the summer sexual segregation.

Acknowledgments This research was supported by THE ISRAEL SCIENCE FOUNDATION (grant No. 232/08). We are grateful to Dr. Amit Dolev of the Society for the Protection of Nature in Israel for good advice and help in the field.

References

- Aldridge HDJN, Brigham RM (1988) Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *J Mammal* 69:379–382
- Altringham JD (1996) *Bats biology and behavior*. Oxford University Press, London
- Audet D, Thomas DW (1996) Evaluation of the accuracy of body temperature measurements using external radio transmitters. *Can J Zool* 74:1778–1781
- Bontadina F, Schofield H, Naef-Daenzer B (2002) Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *J Zool* 258:281–290
- Carey HV, Andrews MT, Martin SL (2003) Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. *Physiol Rev* 83:1153–1181
- Cossins AR, Barnes B (1996) Hibernation—Southern discomfort. *Nature* 382:582–583
- Cryan PM, Wolf BO (2003) Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *J Exp Biol* 206:3381–3390
- Daniel S, Korine C, Pinshow B (2010) The use of torpor in reproductive female Hemprich’s long-eared bats (*Otonycteris hemprichii*). *Physiol Biochem Zool* 83:142–148
- Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Physiology: hibernation in a tropical primate. *Nature* 429:825–826
- Geiser F, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integr Comp Biol* 51(3):337–348
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8:461–467
- Humphries MM, Careau V (2011) Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. *Integr Comp Biol* 51:419–431
- Kaciuba-Uscilko H, Gruzca R (2001) Gender differences in thermoregulation. *Curr Opin Clin Nutr Metab Care* 4:533–536
- Kelly EJ, Mason M, Stoffberg S, Jacobs DS (2007) Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae). *Can J Zool* 85:883–890
- Kronfeld-Schor N, Richardson C, Silvia BA, Kunz TH, Widmaier EP (2000) Dissociation of leptin secretion and adiposity during prehibernatory fattening in little brown bats. *Am J Physiol* 279:R1277–R1281
- Kulzer E (1965) Temperaturregulation bei Fledermausen (*Chiroptera*) aus Verschiedenen Klimazonen. *Zeitschrift Fur Vergleichende Physiologie* 50:1–34
- Kunz TH, Wrazen JA, Burnett CD (1998) Changes in body mass and fat reserves in prehibernating little brown bats (*Myotis lucifugus*). *Ecoscience* 5:8–17
- Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? *Conserv Biol* 9:753–760
- Levin E, Yom-Tov Y, Barnea A (2009) Frequent summer nuptial flights of ants provide a primary food source for bats. *Naturwissenschaften* 96:477–483
- Levy O, Dayan T, Kronfeld-Schor N (2011a) Adaptive thermoregulation in golden spiny mice: the influence of season and food availability on body temperature. *Phys Biochem Zool* 84:175–184
- Levy O, Dayan T, Kronfeld-Schor N (2011b) Interspecific competition and torpor in golden spiny mice: two sides of the energy acquisition coin. *Integr Comp Biol* 51(3):441–448
- Lovegrove B, Génin F (2008) Torpor and hibernation in a basal placental mammal, the Lesser Hedgehog Tenrec (*Echinops telfairi*). *J Com Physiol B* 178:691–698
- Lovegrove BG, Raman J (1998) Torpor patterns in the pouched mouse (*Saccostomus campestris*; *Rodentia*): a model animal for unpredictable environments. *J Com Physiol B* 168:303–312
- McArdle W, Toner M, Magel J, Spinal R, Pandolf K (1992) Thermal responses of men and women during cold-water immersion: influence of exercise intensity. *Eur J Appl Physiol* 65:265–270
- Schliter A, Qumsiyeh M (1996) *Rhinopoma microphyllum*. *Mammal Sp* 542:1–5

- Schmid J, Ruf T, Heldmaier G (2000) Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. *J Com Physiol B* 170:59–68
- Schmid J, Speakman JR (2000) Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *J Com Physiol B* 170:633–641
- Senior P, Butlin RK, Altringham JD (2005) Sex and segregation in temperate bats. *Proc R Soc B* 272:2467–2473
- Terrien J, Perret M, Aujard F (2010) Gender markedly modulates behavioral thermoregulation in a non-human primate species, the mouse lemur (*Microcebus murinus*). *Physiol Behav* 101:469–473
- Turbill C, Kortner G, Geiser F (2003) Natural use of heterothermy by a small, tree roosting bat during summer. *Physiol Biochem Zool* 76:868–876
- Vierck CJ, Acosta-Rua AJ, Rossi HL, Neubert JK (2008) Sex differences in thermal pain sensitivity and sympathetic reactivity for two strains of rat. *J Pain* 9:739–749