Comparative Biochemistry and Physiology, Part A 191 (2016) 156–165

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Metabolic rate, evaporative water loss and thermoregulatory state in four species of bats in the Negev desert

Agustí Muñoz-Garcia [a,b,*], Paloma Larraín [a], Miriam Ben-Hamo [a], Ariovaldo Cruz-Neto [c], Joseph B. Williams [b], Berry Pinshow [a], Carmi Korine [a]

[a] *Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, 8499000 Midreshet Ben-Gurion, Israel*
[b] *Department of Evolution, Ecology and Organismal Biology, Ohio State University at Mansfield, Aronoff Lab, 318 W 12th Ave., Columbus, OH 43210, United States*
[c] *Departamento de Zoologia, IB, Universidade Estadual Paulista, Caixa Postal 199, 13506-900 Rio Claro, São Paulo, Brazil*

ARTICLE INFO

Article history:
Received 16 June 2015
Received in revised form 7 October 2015
Accepted 7 October 2015
Available online 13 October 2015

Keywords:
Bats
Respiratory water loss
Cutaneous evaporative water loss
Metabolic rate
Torpor
Desert

ABSTRACT

Life in deserts is challenging for bats because of their relatively high energy and water requirements; nevertheless bats thrive in desert environments. We postulated that bats from desert environments have lower metabolic rates (MR) and total evaporative water loss (TEWL) than their mesic counterparts. To test this idea, we measured MR and TEWL of four species of bats, which inhabit the Negev desert in Israel, one species mainly restricted to hyper-arid deserts (*Otonycteris hemprichii*), two species from semi-desert areas (*Eptesicus bottae* and *Plecotus christii*), and one widespread species (*Pipistrellus kuhlii*). We also measured separately, in the same individuals, the two components of TEWL, respiratory water loss (RWL) and cutaneous evaporative water loss (CEWL), using a mask. In all the species, MR and TEWL were significantly reduced during torpor, the latter being a consequence of reductions in both RWL and CEWL. Then, we evaluated whether MR and TEWL in bats differ according to their geographic distributions, and whether those rates change with T_a and the use of torpor. We did not find significant differences in MR among species, but we found that TEWL was lowest in the species restricted to desert habitats, intermediate in the semi-desert dwelling species, and highest in the widespread species, perhaps a consequence of adaptation to life in deserts. Our results were supported by a subsequent analysis of data collected from the literature on rates of TEWL for 35 bat species from desert and mesic habitats.

1. Introduction

Mid-latitude deserts are characterized by high daytime ambient temperatures (T_a), intense solar radiation, low humidity, desiccating winds, scarce and unpredictable food supplies, and free-water availability (Noy-Meir, 1973), conditions that potentially exert strong selective pressures on biota. Some endothermic animals that live in deserts have morphological and behavioral adaptations, which include different degrees of fossoriality, nocturnality, or both, thus avoiding high heat loads and low air humidity during the day (Schmidt-Nielsen, 1964). Desert-dwelling birds and mammals are also physiologically adapted to cope with these environmental conditions; they have generally lower metabolic rates (MR) and lower rates of evaporative water loss (EWL) than their mesic counterparts (Schmidt-Nielsen and Schmidt-Nielsen, 1950; Lovegrove, 2000, 2003; Williams and Tieleman, 2005; Van Sant et al., 2012).

The only order of volant mammals, bats number over 1300 species, which occupy a variety of habitats on all continents, except Antarctica (Fenton and Simmons, 2014). Although bats expend some 15 times as much energy during flight than at rest (Speakman and Thomas, 2003), they have lower basal metabolic rates (BMR) than that of other mammals of the same body mass (m_b) (McNab, 1982; Speakman and Thomas, 2003; Marom et al., 2006). Bats have significantly larger surface to volume ratios than terrestrial mammals of similar m_b due to their membranous wings, which are vascularized and not insulated by fur (Hill and Smith, 1984), leading to the idea that cutaneous evaporative water loss should be significant in bats (Licht and Leitner, 1967; Thomas et al., 1991; Minnaar et al., 2014)

Total evaporative water loss (TEWL), the sum of respiratory water loss (RWL) and cutaneous evaporative water loss (CEWL), is the main avenue of water loss in small mammals, representing up to 80–85% of their total water loss (Studier, 1970). Some bats apparently lose twice as much water through evaporation than terrestrial mammals of the same body mass because of their relatively large surface areas (Studier, 1970; Webb, 1995), but these conclusions are based on studies

---

[*] Corresponding author at: Department of Evolution, Ecology and Organismal Biology, Ohio State University, Aronoff Lab, 318 W 12th Ave., Columbus, OH 43210, United States.
E-mail address: munozgarcia.1@osu.edu (A. Muñoz-Garcia).

http://dx.doi.org/10.1016/j.cbpa.2015.10.010
1095-6433/

with small samples sizes. Therefore, it is intriguing that bats live in many desert environments, since they harbor traits that potentially increase energy consumption and water loss.

Many species of bats can enter torpor, a state wherein bats allow their body temperature (T_b) to drop below normal by 5–15 °C, but as much as 20 °C, with a concomitant decrease in MR and possibly water loss (Herreid and Schmidt-Nielsen, 1966; Webb, 1995; Schmidt-Nielsen, 1997; Ruf and Geiser, 2014). Torpor may be a key feature that allows mammals to colonize and survive in a wide variety of habitats (Bozinovic and Marquet, 1991; Lovegrove and Raman, 1998; Rambaldini and Brigham, 2008). Bats may enter shallow torpor on a daily basis, reducing T_b by just a few degrees for several hours, or they may endure longer and deeper torpor bouts that can last from weeks to months. Prolonged bouts of deep torpor are used by species of bats from diverse environments and may occur at low T_a, hibernation in winter, for example, or when prey are scarce (Brack and Twente, 1985; Turbill et al., 2003; Geiser, 2004; Zubaid et al., 2006).

Of the 32 species of bats that occur in Israel, 12 species are found in the Negev Desert (Yom-Tov and Kadmon, 1998; Korine and Pinshow, 2004). Consequently it seems likely that these species have adaptations to conserve energy and prevent excessive rates of evaporative water loss (Kunz, 1982; Geiser, 2004; Marom et al., 2006; Muñoz-Garcia et al., 2012a). Nonetheless, some studies report that desert-dwelling bat species do not have significantly lower MR or water loss than those of mesic species (Marom et al., 2006; Muñoz-Garcia et al., 2012a,b), suggesting that desert bats might not show specific adaptations to live in these environments. However, few desert species have been examined. Also, measurements of TEWL available in the literature were mostly made on normothermic animals, i.e., animals defending high T_b, with few measurements on torpid bats, making it difficult to evaluate differences in energy expenditure and water fluxes between desert and mesic species.

Since metabolic rates and TEWL are reduced by 50–90% during torpor (Carpenter, 1969; Morris et al., 1994), the use of torpor by desert species of bats is of adaptive significance. Bats are not known to defecate or urinate during torpor (Webb, 1995), and therefore it is commonly assumed that all water losses during torpor are evaporative. Marom et al. (2006) measured the rates of TEWL in two species of bat that inhabit the Negev Desert: one that lives only in deserts, *Otonycteris hemprichii*, and another that is found throughout Israel, *Tadarida teniotis*. Bats entered torpor at low T_as during the day, as determined by their significantly reduced T_b, compared to T_b in normothermic bats measured at night. The lower MR that ensues during torpor should lead to reduced RWL and, therefore, reduced TEWL. However, the authors did not find significant differences in TEWL between torpid and normothermic bats. These data suggest that during torpor, CEWL might be similar to or even increase over that during normothermy, a counterintuitive result. To test this idea, Muñoz-Garcia et al. (2012a) measured CEWL and RWL in Kuhl's pipistrelle (*Pipistrellus kuhlii*) a widespread species but one that also inhabits the Negev Desert. The authors found that, when in deep torpor, CEWL of bats was similar or even higher than that of bats in shallow torpor, leading Muñoz-Garcia et al. (2012a) to hypothesize that bats exert less physiological control over CEWL when torpid.

In the present study, we evaluated whether rates of metabolism and water loss in bats differ according to their geographic distributions, and whether those rates change with T_a and the use of torpor. We measured MR and TEWL of four sympatric species of bats in the Negev Desert: one species whose range is restricted mainly to hyper-arid deserts (*O. hemprichii*), two hyper-arid and semi-desert species (*Eptesicus bottae* and *Plecotus christii*), and one widespread species (*P. kuhlii*) (Yom-Tov and Kadmon, 1998; Nowak, 1999). We hypothesized that species of bat found only in deserts have adaptations to reduce energy expenditure and water loss, in contrast to bats that live in mesic environments. We predicted that, while euthermic, MR and TEWL of bats at rest would be lowest in the desert species (*O. hemprichii*), intermediate in the semi-desert dwelling species (*E. bottae* and *P. christii*), and highest in the widespread species (*P. kuhlii*). To further test the hypothesis that there is a relationship between TEWL and habitat, we compared rates of TEWL for 35 bat species from desert and mesic habitats. We predicted that desert species have lower rates of TEWL than mesic species. Moreover, we predicted that bats in torpor have reduced MR and rates of TEWL, which result from reductions in both RWL and CEWL, and that these reductions are greater in desert species than in mesic species.

2. Materials and methods

2.1. Experimental animals

We captured non-reproductive adult bats in the central Negev Highlands. Experiments were done on the Sede-Boqer Campus of Ben-Gurion University of the Negev. Bats were kept in separate, large, covered outdoor cages (2 × 2 × 4 m) and fed daily with sufficient *Tenebrio* larvae to enable them to maintain m_b. Water with vitamins (RIBOS, Biopet, Maabarot, Israel) was provided ad libitum. Bats were exposed to semi-natural weather and light conditions during captivity. The cage was shaded and provided with a bat box for roosting. Once measurements were completed, animals were released at their place of capture.

2.2. Measurements of resting metabolic rate and total evaporative water loss

We calculated MR, TEWL, CEWL and RWL in postabsorptive individuals using a multi-channel, open-flow respirometry system to measure O_2 consumption ($\dot{V}O_2$), CO_2 production ($\dot{V}CO_2$) and water loss. Measurements were made at four different ambient temperatures (T_a): 10 °C, 15 °C, 30 °C and 35 °C. Bats were weighed before and after measurements to $\pm$0.01 g on a digital balance (Scout SP202, Ohaus, NJ, USA). We recorded rectal temperature as a proxy for T_b before and after respirometry measurements using a sheathed, 36-gauge type-T thermocouple, read with a microprocessor thermometer (OMEGA, model HH23, Stanford, CT, USA). We also measured T_a continuously with a thermocouple (same type as above) located inside a controlled temperature cabinet (Thermo Scientific, model Precision 815, OH, USA) where metabolic chambers were placed.

To measure MR and TEWL, we placed each bat in a plastic metabolic chamber (Lock&Lock model HPL93, 0.35 L). For the smallest species, *P. kuhlii*, we built chambers using plastic containers (50 cm^3) that were covered with dark tape to minimize stress to the animals during measurements. Each chamber was lined with 0.25 cm plastic-dipped hardware cloth from which the bats could hang upside down. Paraffin oil at the bottom of the chambers trapped feces and urine that could add water vapor to the air sample. Air was pumped into the metabolic chambers from outside the building through a purged gas generator (Purge Gas model #PCDA-1-12-m-32-C, Broomfield, CO, USA) providing dry, CO_2-free air. Flow rates ranged from 160 to 180 mL/min for the medium-sized chambers and ~100 mL/min for the small chambers. From every chamber, a subsample of air was pumped through an eight-channel multiplexer (G244 gas switcher, Qubit Systems Inc.) that routed the sample of air from each chamber to the gas analyzers, enabling the sequential monitoring of up to six animals. The multiplexer was programmed to automatically select channels, alternating between a chamber containing an animal and the reference channel that had an empty chamber and served to generate a baseline for each cycle. Each cycle started with 300 s of reference chamber air, followed by 300 s from each of the chambers containing an animal. We separated the 300 s intervals with 60 s switches to the reference chamber. Air coming from the multiplexer was then routed through a dew point meter (RH-