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Body temperature patterns of a small endotherm in an extreme desert environment

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ABSTRACT

Most desert small mammals use mechanisms to avoid overheating or dehydration during summer (e.g. nocturnality or torpor), but some are apparently able to cope with higher body temperatures (T_b) than normally recorded for mammals (i.e. hyperthermia). In winter, some small desert mammals use torpor to conserve energy during cool periods. Still, surprisingly few studies have reported field body temperature patterns in small terrestrial mammals inhabiting deserts, so it is unclear how common hyperthermia and torpor are in desert mammals. We measured T_b of a murid rodent, the Libyan jird (*Meriones libycus*), during both summer and winter in Saudi Arabia. Modal, minimum, and maximum T_bs were higher in summer than in winter, with maximum T_bs near 42 °C during summer, among the highest T_bs ever recorded in wild mammals. Variation in T_b was significantly higher during summer than winter, which was mostly related to passive warming throughout the day as ambient temperatures regularly exceeded 45 °C during summer. Conversely, during winter, T_bs were highest during the nocturnal active period. While the summer T_bs we recorded are among the highest ever for either murids or small desert mammals, we suspect this represents a lack of data on free-ranging small mammals more than unique adaptations by this species.

1. Introduction

Maintenance of a high and constant body temperature (T_b) is one of the defining characteristics of endotherms. However, it is well known that endotherms, especially mammals, are often operating very close to their upper critical limit and that even small increases in T_b can cause decreases in performance (Angilletta et al., 2010) or death. While measurements of lethal T_bs are rare, they are thought to be below approximately 43 °C for most mammals (Adolph, 1947; Carpenter and Graham, 1967; Licht and Leitner, 1967) and loss of physiological performance likely occurs considerably below those temperatures in most mammals. Animals inhabiting deserts are especially interesting in this regard because they are often exposed to extremely hot temperatures during summer and cool temperatures during winter. Even in the shade, operative temperatures (a measure of environmental temperature accounting for solar radiation and wind) can be above the upper critical temperature during summer (Chappell and Bartholomew, 1981b), necessitating physiological or behavioural mechanisms to avoid hyperthermia (Walsberg, 2000). For example, relatively few small desert mammals are diurnal (Withers et al., 2004), some species aestivate (Withers et al., 1980), and some use shuttling or behavioural shading to lower T_b (Fick et al., 2009; Hainsworth, 1995). Still, these species must also be able to adjust seasonally to cope with temperatures approaching freezing in some deserts.

Given the plethora of laboratory studies on thermoregulation, metabolism, and water balance in small desert mammals (e.g. Grimpo et al., 2013; Gutman et al., 2006; Withers et al., 1980), and T_b patterns in larger desert mammals (e.g. Hetem et al., 2009; Hetem et al., 2010; Ostrowski and Williams, 2006), it is surprising how few studies have measured T_b patterns of small desert mammals in the wild, relative to their abundance. Further, nearly all of the papers reporting T_b patterns of small desert mammals have been done during winter (e.g. Körtner and Geiser, 2011; Pavey et al., 2009); almost no work has been done in the field during summer (Chappell and Bartholomew, 1981a; Elvert et al., 1999). Expanding the search to include papers on skin temperature of bats in deserts (e.g. Daniel et al., 2010), fossorial species (Jackson et al., 2009;

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Streicher et al., 2011), or small terrestrial mammals in hot environments other than deserts increases the number of papers somewhat, but small mammals in hot environments are still underrepresented in this literature. The few papers on small terrestrial mammals in deserts do report interesting aspects of T_b regulation. For example, during summer antelope ground squirrels in the North American Sonoran Desert exhibit extreme lability in T_b patterns, with maximum T_bs reaching 43.6 °C (Chappell and Bartholomew, 1981a). Activity patterns are also likely to affect T_b patterns, as evidenced by higher T_bs and more T_b lability in a diurnal spiny mouse (*Acomys russatus*) than a congeneric nocturnal species (*A. cahirinus*; Elvert et al., 1999). During winter, small desert mammals may use torpor to conserve energy and basking to lessen the costs of rewarming (Boyles et al., 2012; Warnecke and Geiser, 2009; Warnecke et al., 2008). While these observations are interesting, the lack of studies about both extremes in T_b and patterns of T_b displayed by small desert mammals preclude many generalizations.

The evolution of thermoregulatory patterns in mammals has long been of interest to researchers. In this context, there is clearly a need to collect T_b data of free-ranging mammals to fill geographic, ecological, and phylogenetic gaps. Here, we report T_b patterns in a small, nocturnal mammal species from a sandy desert in central Saudi Arabia. This study is among the first to report T_b characteristics of a small species during both summer and winter in the field, and helps fill an important gap in the availability of T_b data for mammals, which is currently skewed towards temperate and mesic species (Boyles et al., 2013).

2. Methods

2.1. Study species

The Libyan jird (*Meriones libycus*; Family Muridae) is considered a small mammal (50–215 g), but it is relatively large compared to many other murid rodents and other desert rodents in the same community (Scott and Dunstone, 2000). They inhabit desert regions from northwestern Africa to western China, but some taxonomic revisions may be in order to split this one widespread species into multiple species (Bray et al., 2014). They are gregarious, and therefore may be restricted to microhabitats with relatively high productivity, like dunes with perennial vegetation, to support the colonies (Daly and Daly, 1975; Scott and Dunstone, 2000). They are largely nocturnal (Alagaili et al., 2013), but are occasionally active during the day in winter (Ågren, 1979; Daly and Daly, 1975). Because they are often human commensals, most of the research on this species has focused on its role as a disease vector and its parasites (e.g. Yaghoobi-Ershadi et al., 1996).

2.2. Experimental design

We captured Libyan jirds in sandy habitats of the Unizah province, Saudi Arabia (26.136°N, 43.975°E) using locally built live traps. During summer 2013, we set traps shortly before sunset and collected them in early morning, while in winter 2013–2014 we set traps at approximately noon and checked them periodically throughout the night to ensure animals did not die from cold exposure. We trapped 20 animals in each season. Winter and summer body masses ranged between 90 and 213 g (mean: 126.3 g ± 30.28 SD) and 61–159 g (106.55 g ± 24.57 SD), respectively.

We transported jirds to an animal facility at the Zoology Department of King Saud University in Riyadh where we provided them with *ad libitum* food and water. We coated temperature-sensitive dataloggers (1 h recording intervals, 0.0625 °C resolution, iButtons, DS1922L, Maxim Semiconductors, Dallas, Texas) with biologically inert wax after comparing recorded temperatures to measured air temperatures to verify there were no outliers. A licensed veterinarian then implanted the dataloggers intraperitoneally following standard procedures. Animals were implanted while under isoflurane anesthesia by making a longitudinal incision in the abdominal side of the animal and at the linea alba; the incision was sutured using absorbable catgut. Animals were provided with a dose of long acting, broad spectrum antibiotic (Oxytetracycline, Pfizer) after surgery to minimize chances of post-surgery infection, and were held for 7–10 days to ensure recovery from surgeries. We released the animals in the same area where we captured them and attempted to recapture them after approximately two months during summer and five months during winter. We euthanized animals to retrieve dataloggers. Capture permits were issued by the Saudi Wildlife Authority. Experimental protocol was approved by the Animal Use and Care of the University of Pretoria, ethics clearance number EC029-16.

We calculated basic descriptive statistics for each individual (modal, minimum, and maximum T_b) as well as the Heterothermy Index (HI), which is essentially a biologically meaningful modification of a simple standard deviation that quantifies the amount of variation around the modal T_b instead of the mean T_b (Boyles et al., 2011) and allows for comparison of thermoregulatory patterns of species with diverse physiologies (Boyles et al., 2013). During summer, we recorded hourly air temperature (T_a) in the shade using an iButton. We recorded T_a in the same way during winter, but the data were misplaced, so we downloaded air temperature from a nearby weather station (Prince Nayef bin Abdulaziz Regional Airport). We compared modal, minimum, and maximum T_b, and HI values between seasons and genders using PROC GLM in SAS 9.3, after verifying the data met all assumptions of that test. We used PROC MIXED to evaluate the relationship between maximum T_a recorded and maximum T_b recorded on a day during summer accounting for individual as a random effect. For presentation purposes, we also conducted a simple regression (ignoring individual) between maximum T_a and maximum T_b.

3. Results

We recovered T_b data for 8 individuals in summer (5 males; 3 females) and 8 individuals in winter (5 males; 3 females). Body temperatures were generally representative of those displayed by other homeothermic mammals (Fig. 1). Modal T_b was significantly higher in summer than winter (38.20 ± 0.87 °C vs. 37.0 ± 0.22 °C; $F_{1,12} = 11.95$; $p = 0.005$), but did not vary between genders ($F_{1,12} = 0.05$; $p = 0.832$; Table 1). During winter, the daily maximum T_bs generally occurred at night, followed by a drop in T_b and maintenance of low T_bs throughout the day (Fig. 2). During summer, T_bs increased sharply throughout the day, peaked mid-afternoon, and dropped to an intermediate temperature throughout the night (Fig. 2). The daily maximum T_bs were almost always recorded in the afternoon and were strongly related to the maximum air temperature recorded that day ($F_{1,482} = 468.38$; $p < 0.0001$; Fig. 3), and there was significant variation among individuals ($F_{7,482} = 167.09$; $p < 0.0001$). The maximum T_b recorded during summer was 42.2 °C and the minimum T_b recorded during winter was 34.8 °C. During summer, the maximum T_b of every individual was recorded between 12:00 and 17:00 on 18 July 2013; the highest air temperature of the entire study (47.5 °C) was recorded at 14:00 that day. Maximum T_bs were significantly higher during summer (41.9 ± 0.29 °C vs. 39.8 ± 0.29 °C; $F_{1,12} = 167.09$; $p < 0.0001$) and minimum T_bs were significantly lower during winter (36.2 ± 0.53 °C vs. 35.1 ± 0.27 °C; $F_{1,12} = 33.00$; $p < 0.0001$). Neither minimum nor maximum T_bs were significantly different