



# Heat tolerance and evaporative cooling capacity in an arid-zone elephant shrew

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## Abstract

Endotherms vary widely in their capacity to defend sublethal body temperature ( $T_b$ ) during acute heat exposure. Interspecific variation in the upper thermal limits of small mammals remains poorly studied, particularly in taxa other than bats. We hypothesised that rupicolous elephant shrews (Macroscelidae), on account of their occupancy of above-ground rock crevices in hot habitats and rapid cursorial locomotion, have evolved pronounced heat tolerance capacities. To test this hypothesis, we quantified relationships between  $T_b$ , resting metabolic rate (RMR) and evaporative water loss (EWL) in western rock elephant shrews (*Elephantulus rupestris*) exposed to air temperature ( $T_{air}$ ) approaching or exceeding  $T_b$  under conditions of low humidity representative of the study population's arid, winter-rainfall habitat in western South Africa. Our data revealed a pronounced capacity to tolerate  $T_{air} > T_b$ , with *E. rupestris* tolerating  $T_{air}$  up to  $48.0 \pm 0.1$  °C while defending  $T_b > 7$  °C below  $T_{air}$  (maximum  $T_b = 41.64 \pm 0.16$  °C). Three behavioural pathways were employed to dissipate heat: open mouth panting, flattening their body posture, and nose-licking. At the highest experimental  $T_{air}$  values achieved, EWL increased 15.05-fold relative to normothermic levels and heat was dissipated evaporatively at rates equivalent to 174%–240% of metabolic heat production. The heat tolerance limit of  $T_{air} = 48$  °C in *E. rupestris* is one of the highest yet recorded in a non-volant small mammal, and our data support the notion that elephant shrews possess a pronounced capacity to avoid lethal hyperthermia during acute heat exposure.

**Keywords** Evaporation · Heat dissipation behaviour · Hyperthermia · Macroscelidae · Nose-licking · Panting

## Introduction

When the temperature of an endotherm's immediate environment exceeds its body temperature ( $T_b$ ), evaporative cooling becomes the sole heat dissipation avenue whereby  $T_b$  can be defended below lethal limits (Dawson 1954; Bartholomew and Cade 1963). Mammalian avenues of evaporative heat loss include sweating (Folk and Semken 1991; Withers et al. 2016), panting (Hales and Brown 1974; Robertshaw 2006)

and spreading saliva across body surfaces (Dawson 1973; Needham et al. 1974), with the relative importance of each avenue varying among taxa. Among small mammals, thermoregulation at high air temperature ( $T_{air}$ ) is best-understood among bats (Bartholomew et al. 1964; Licht and Leitner 1967; Czenze et al. 2022) and rodents (Hudson 1962; Downs and Perrin 1990; van Jaarsveld et al. 2021). The limited data for monotremes, small marsupials and other taxa with small body sizes suggest a more limited capacity for hyperthermia and evaporative cooling (reviewed by McKechnie and Wolf 2019).

One small mammal taxon under-represented in heat tolerance and evaporative cooling literature is the elephant shrews (superorder Afrotheria: Macroscelidea: Macroscelidae). Research on the thermal physiology of elephant shrews has primarily focussed on thermoregulation at lower  $T_{air}$ , particularly torpor and the use of exogenous heat sources during rewarming (Mzilikazi et al. 2002; Mzilikazi and Lovegrove 2004; Boyles et al. 2012). Rupicolous elephant shrews use daytime shelters among boulders and in rock

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cracks and crevices (Rathbun 2009), microhabitats that offer less thermal buffering from high daytime  $T_{\text{air}}$  compared to underground burrows. Their use of above-ground shelters, combined with the metabolic heat loads likely associated with their cursoriality characterized by fast running speeds (Lovegrove and Mowoe 2014), make rupicolous elephant shrews a good model for testing hypotheses concerning the evolution of evaporative cooling capacity and hyperthermia tolerance. Information on evaporative cooling among elephant shrews remains scant, with only a single study of thermoregulation at  $T_{\text{air}}$  approaching  $T_{\text{b}}$  in Cape elephant shrews (*Elephantulus edwardii*; Leon et al. 1983). These authors reported several avenues of heat dissipation, including open-mouth panting, nose-licking and flattened body posture, with the elephant shrews maintaining stable  $T_{\text{b}}$ , low EWL and metabolic rates (Leon et al. 1983).

We hypothesized that elephant shrews have evolved pronounced heat tolerance and evaporative cooling capacities on account of their occupancy of above-ground rock crevices and rapid cursorial locomotion. Specifically, we predicted that elephant shrews have a higher heat tolerance limit (the maximum  $T_{\text{air}}$  tolerated by a species before the onset of unregulated hyperthermia and loss of locomotor capacity), maximum  $T_{\text{b}}$  and evaporative cooling efficiency than most small, non-volant mammals. To test this prediction, we investigated the thermal physiology of the western rock elephant shrew (*Elephantulus rupestris* Smith 1831), a species confined to the arid western parts of southern Africa (Skinner and Chimimba 2005).

## Materials and methods

### Study site and species

Between 8 January and 2 February 2021 (austral summer) elephant shrews were trapped at the farm Verbe Noheep (30° 02' S, 17° 59' E) in the Kamiesberg mountains, Northern Cape province, South Africa. The study site is located in the arid Succulent Karoo biome, with predominantly winter rainfall. Summer conditions are characterised by maximum  $T_{\text{air}}$  regularly exceeding 30 °C, low productivity and limited surface water availability (Mucina and Rutherford 2006). The habitat at the study site consists of sparse vegetation on sandy soils between rocky outcrops. Mean  $\pm$  SD January daily maximum  $T_{\text{air}}$  at the study site is 28.5  $\pm$  0.14 °C [extracted from WorldClim 2 database (Fick and Hijmans 2017) at 1 km resolution], and dry conditions with mean  $\pm$  SD rainfall of 8.8  $\pm$  3.5 mm.

Western rock elephant shrews (*Elephantulus rupestris*; hereafter, elephant shrews) were captured ( $n = 10$  individuals; 4 males and 6 females) using Sherman traps baited with a combination of rolled oats, peanut butter and pilchards.

In-field identification was based on descriptions provided by Smit et al. (2008). The species is predominantly nocturnal in summer, and all individuals were trapped at night. The mean  $\pm$  SD body mass ( $M_{\text{b}}$ ) upon capture was 51.63  $\pm$  9.38 g (male  $M_{\text{b}} = 55.25 \pm 11.63$  g; female  $M_{\text{b}} = 49.22 \pm 7.72$  g). Following capture, elephant shrews were held in cages ( $\sim 0.3$  m<sup>3</sup>), with ad libitum food and water for at most 3 d. Following experiments, individuals were released at their site of capture.

### Air and body temperature measurements

Air temperature within metabolic chambers was measured using a thermistor probe (TC-100, Sable Systems, Las Vegas, NV, USA), inserted through the wall of each chamber and sealed using a 3-mm rubber grommet. Each elephant shrew's  $T_{\text{b}}$  was monitored using an intraperitoneally injected, passive integrated transponder (PIT) tag (BioTherm, Biomark, Boise ID, USA). The PIT tags were scanned every 5 s using a portable transceiver system (HPR+, Biomark, Boise, ID, USA), placed on top of the metabolic chamber. The PIT tags were calibrated in a circulating water bath (model F34; Julabo, Seelbach BW, Germany) over temperatures ranging from 35 to 50 °C against a Cu-Cn thermocouple connected to a reader (TC-100; Sable Systems, Las Vegas, NV, USA), which had been calibrated against a mercury-in-glass thermometer with NIST-traceable accuracy. Temperatures measured by PIT tags deviated 0.04  $\pm$  0.06 °C ( $n = 25$ ) from actual values.

### Gas exchange measurements

Rates of carbon dioxide production ( $\dot{V}_{\text{CO}_2}$ ; mL min<sup>-1</sup>) and EWL (g h<sup>-1</sup>) were quantified using open flow-through respirometry using the same approach as Whitfield et al. (2015) and Czenze et al. (2020). For measurements, elephant shrews were placed individually within a 3 L airtight chamber (20 cm high  $\times$  15 cm wide  $\times$  10 cm deep, Hobby Life, Istanbul, Turkey), previously shown by Whitfield et al. (2015) to not adsorb water vapour. Within the chamber, the elephant shrew rested on a layer of plastic mesh, above a 1 cm layer of mineral oil which trapped any excreta. The animal chamber was placed within a temperature-controlled chamber constructed from a  $\sim 100$  L ice chest modified by mounting a Peltier device (TC 720 OEM Thermoelectric Air Cooler, TE Technology, Traverse City MI, USA) in one wall of the ice chest, allowing  $T_{\text{air}}$  to be regulated using a digital controller (TC-720 Temperature Controller, TE Technology, Traverse City MI, USA).

Each animal chamber had an air inlet on one of the side walls near the top, with an elbow joint facing upwards, while the outlet was positioned beneath the plastic mesh, to maximise mixing of air within the chamber and reducing the

likelihood of an animal placing its face directly in front of the inlet. Atmospheric air supplied by an oil-free compressor was scrubbed of water vapour using a membrane dryer (CMD3 air dryer and filter, Champion Pneumatic, Quincy IL, USA). Dried air was then separated into baseline and experimental channels, with baseline flow rates regulated with a needle valve (Swagelok, Solon, OH, USA) and chamber incurrent flow rates using a mass flow controller (Alicat Scientific Inc., Tuscon AZ, USA). The mass flow controller was calibrated against a Gilibrator 2 (Sensidyne, St Petersburg, FL, USA). We used flow rates of 5–30 L min<sup>-1</sup>, adjusted to ensure chamber humidity remained low (dewpoint < -2.5 °C) and thereby avoid evaporative heat dissipation being impeded. During measurements, flow rates were increased if animals displayed signs of agitation. For each flow rate, we calculated the 99% equilibrium time following Lasiewski et al. (1966) and included only data collected after 99% equilibrium had been achieved.

Excurrent air from the experimental and baseline channels was sequentially subsampled using a respirometry multiplexer (model MUX3-1101-18 M, Sable Systems) in manual mode and SS-3 Sub-sampler (Sable Systems). These subsamples were then drawn through a CO<sub>2</sub>/H<sub>2</sub>O analyser (LI-840A, LI-COR, Lincoln, NE, USA), which was regularly zeroed with nitrogen and spanned with humidified air produced by a dewpoint generator (DG4, Sable Systems, Las Vegas, NV, USA). Voltage outputs from the CO<sub>2</sub>/H<sub>2</sub>O analyser and thermistor probes were digitized using an analogue–digital converter (model UI-3, Sable Systems, Las Vegas NV, USA) and then recorded with a sampling interval of 5 s using Expedata software (Sable Systems, Las Vegas, NV, USA).

## Experimental protocol

Body mass was recorded using an electronic balance (EJ-160, AD, Tokyo, Japan) before and after each set of measurements. Initially, an elephant shrew was placed within the metabolic chamber at a  $T_{\text{air}} = \sim 28$  °C for  $\sim 45$  min for habituation. To ensure post-absorptivity, prior to experimentation animals were deprived of food for at least 3 h. Measurements commenced at  $T_{\text{air}} = \sim 28$  °C, starting with a subsample of baseline air. Thereafter, animals experienced  $\sim 15$  min at each  $T_{\text{air}}$ , with stable H<sub>2</sub>O and CO<sub>2</sub> readings over a  $\sim 5$  min period obtained before  $T_{\text{air}}$  was increased to the next set-point. Increments of 4 °C were used at  $T_{\text{air}} \leq 40$  °C, with 2 °C increments then used at  $T_{\text{air}} > 40$  °C. Baseline readings lasting  $\sim 5$  min were regularly obtained during measurements. Total trial duration, including the initial habituation time, was 3–4 h. The stepped  $T_{\text{air}}$  protocol we used in this study yields very similar values of  $T_{\text{b}}$ , RMR and EWL steady-state measurements involving longer exposure to a single  $T_{\text{air}}$  set-point and is ethically preferable (Short et al. 2022).

During all measurements, behaviour was monitored using a surveillance camera with an infrared light source, which allowed us to record the onset of thermoregulatory behaviours (panting, saliva spreading and flattening of body posture) and facilitated monitoring animals and identifying thermal endpoints (Whitfield et al. 2015). We used the same thermal endpoints as Whitfield et al. (2015), with a run terminated and an animal removed from the chamber upon loss of coordination and/or balance, a sudden drop in RMR and EWL or a rapid, uncontrolled increase in  $T_{\text{b}}$ . Animals were also removed from the chamber if they showed agitation or sustained escape behaviour (for instance, scratching at the sides of the chamber) and these data were excluded from analyses. Upon removal from the chamber, ethanol-soaked cotton wool was dabbed on the elephant shrew's belly, aiding rapid heat dissipation and reestablishment of  $T_{\text{b}}$  at normothermic levels ( $\sim 34$ – $36$  °C). Elephant shrews were provided ad libitum food and water after each set of measurements.

## Data analysis

Data were analysed using Expedata Data Analysis Software (Sable Systems, Las Vegas, NV, USA), with analyser drift and lag correction using the relevant algorithms. Elephant shrews experienced a given  $T_{\text{air}}$  for  $\sim 15$  min, with the lowest and most stable 5 min periods of H<sub>2</sub>O and CO<sub>2</sub> being extracted for data analysis. Rates of  $\dot{V}_{\text{CO}_2}$  and EWL were estimated from these 5-min periods at a given  $T_{\text{air}}$  using Eqs. 9.5 and 9.6 from Lighton (2008), assuming 0.803 mg H<sub>2</sub>O mL<sup>-1</sup>. As animals were likely postabsorptive,  $\dot{V}_{\text{CO}_2}$  was converted to RMR (W) assuming a respiratory exchange ratio (RER) of 0.71 (i.e., lipid metabolism) and a thermal equivalence of 27.8 J mL<sup>-1</sup> CO<sub>2</sub> (Walsberg and Wolf 1995). We quantified the maximum error in evaporative heat loss (EHL) / metabolic heat production (MHP) potentially associated with an incorrect assumption of lipid metabolism by recalculating RMR assuming carbohydrate metabolism (i.e., RER = 1.00, thermal equivalence of 20.9 J mL<sup>-1</sup> CO<sub>2</sub>). Evaporative heat loss (EHL, W) was calculated from EWL assuming a latent heat of vaporisation of water of 2.406 J mg H<sub>2</sub>O<sup>-1</sup> at  $T_{\text{air}} = 40$  °C (Tracy et al. 2010). To estimate the potential contribution of metabolic water to water balance during acute heat exposure, we calculated metabolic water production (MWP) from RMR using values from Schmidt-Nielsen (1990).

Statistical analyses were performed using R (R Core Team 2021) implemented in RStudio. Inflection points for the response variables EWL, RMR and  $T_{\text{b}}$  as a function of  $T_{\text{air}}$  and EHL/MHP as a function to  $T_{\text{air}} - T_{\text{b}}$  were determined using the segmented.lme function (Mugge 2016) in the R package *segmented* (Mugge 2008). Subsets including data only above inflection points were created to estimate the slopes for the relationships of EWL, RMR,  $T_{\text{b}}$  and rate

of  $T_b$  increase as functions of  $T_{air}$  and EHL/MHP as a function of the  $T_{air} - T_b$  gradient. To determine the relationships between response variables and the predictor variable of  $T_{air}$ , linear mixed effects models (LMMs) were fitted to our data using the *nlme* package (Pinheiro et al. 2009). Significance was determined at  $\alpha=0.05$  and values were presented as mean  $\pm$  SD. We report marginal  $R^2$  ( $R^2_m$ ; considers variance of fixed effects but not random effects) for results of LMMs. To account for potential pseudoreplication (multiple measurements from the same individual) we included identity as a random factor in our models. For each response variable, the model with the best fit was determined using the package *MuMIn* (Bartoń 2013). Body mass and sex were initially included in the models, but subsequently removed as neither emerged as a significant predictor.

## Results

### Thermoregulatory behaviours

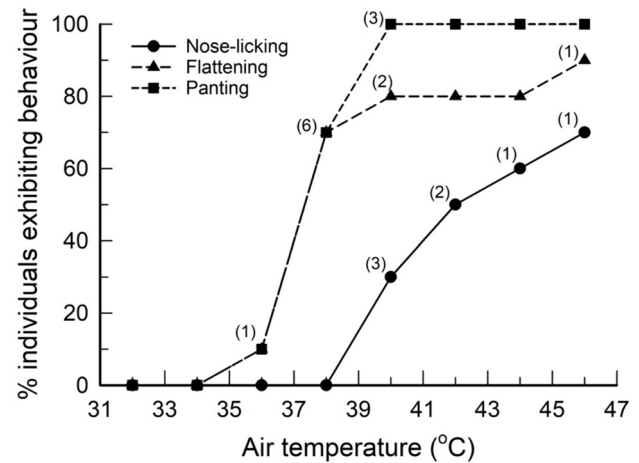
The elephant shrews showed three distinct thermoregulatory behaviours. Postural changes involving flattening the body against the mesh platform were closely associated with bouts of panting, with 3/10 individuals initiating these behaviours simultaneously. Open-mouthed panting, displayed by all 10 individuals, commenced at a  $T_{air} = 39.44 \pm 1.43$  °C and  $T_b = 38.52 \pm 0.65$  °C (Fig. 1). The  $T_{air}$  and  $T_b$  at the onset of flattened body posture ( $n=9$ ) were  $40.04 \pm 2.88$  °C and  $38.36 \pm 1.01$  °C, respectively (Fig. 1). Seven individuals displayed nose-licking following the onset of panting and body-flattening, at  $T_{air} = 42.41 \pm 1.66$  °C and  $T_b = 40.03 \pm 1.14$  °C (Figs. 1 and 2). These thermoregulatory behaviours were used intermittently, not continuously, following their commencement.

### Body temperature

The elephant shrews'  $T_b$  ranged from normothermic  $T_b = 35.7 \pm 0.58$  °C ( $n=10$ ) at  $T_{air} \sim 28$  °C to a maximum  $T_b = 41.64 \pm 0.16$  °C ( $n=3$ ) at  $T_{air} = 47.96 \pm 0.10$  °C (Table 1). Above an inflection at  $T_{air} = 35.61 \pm 2.04$  °C ( $n=10$ ),  $T_b$  values increased linearly and significantly with  $T_{air}$  (LMM; slope =  $0.46 \pm 0.02$  SE,  $R^2_m = 0.87$ ,  $P < 0.001$ ; Fig. 3). The single highest  $T_b$  recorded for an individual was  $T_b = 42.1$  °C at  $T_{air} \sim 46$  °C.

### Resting metabolic rate

An inflection in RMR at  $T_{air} = 37.56 \pm 0.01$  °C ( $n=10$ ) was interpreted as the upper critical limit of thermoneutrality ( $T_{uc}$ ) for *E. rupestris* (Fig. 3) and corresponded closely with the onset of panting and flattening of body



**Fig. 1** Percentage of western rock elephant shrews (*Elephantulus rupestris*) exhibiting one of three thermoregulatory behaviours over a range of air temperatures ( $T_{air}$  binned over 2-°C intervals). The number of new individuals exhibiting a behaviour at a given  $T_{air}$  is indicated within the brackets. Thermoregulatory behaviours: open-mouth panting ( $n=10$ , crosses), flattened body posture ( $n=9$ , triangles), and nose-licking ( $n=7$ , circles)

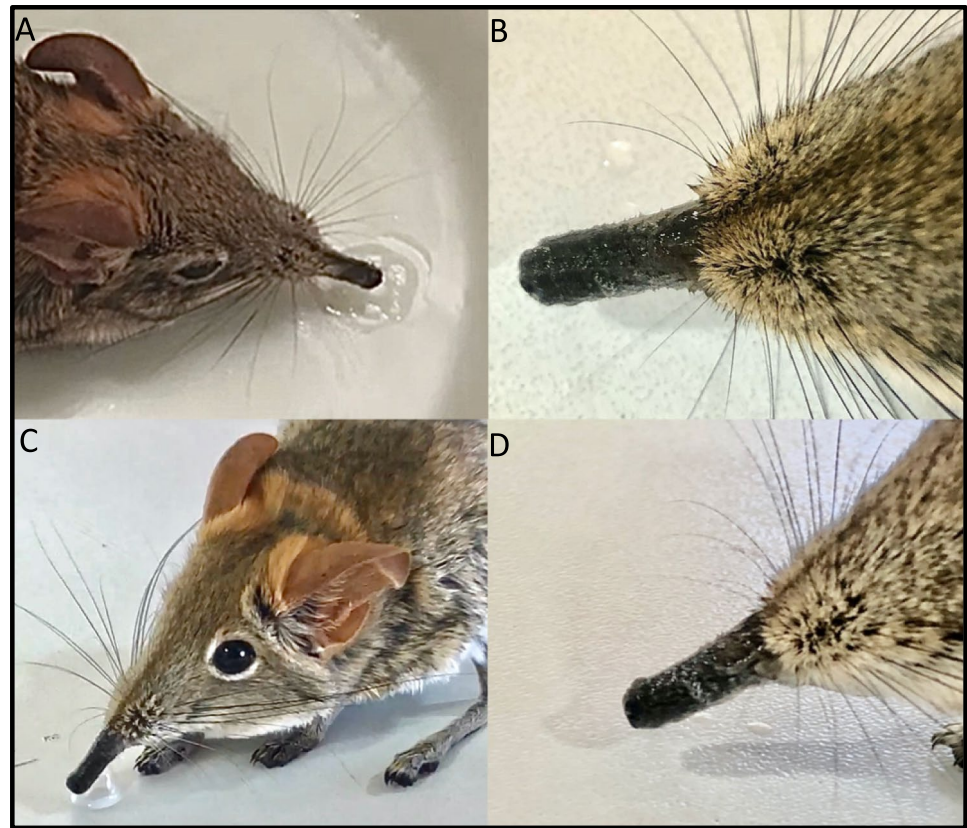
posture. The minimum active-phase RMR was  $0.40 \pm 0.07$  W ( $n=10$ ) at  $T_{air} \sim 32$  °C, which increased linearly and significantly (LMM: slope =  $43.29 \pm 4.25$  SE,  $R^2_m = 0.50$ ,  $P < 0.001$ ) above the  $T_{uc}$  to a maximum of  $0.82 \pm 0.10$  W ( $n=3$ ) at  $T_{air} \sim 48$  °C. Maximum RMR was equivalent to 2.03 X minimum RMR (Table 1).

### Evaporative water loss

Minimum EWL was  $0.14 \pm 0.04$  g h<sup>-1</sup> ( $n=10$ ) at  $T_{air} = 28$  °C. An inflection was evident at  $T_{air} = 38.86 \pm 0.67$  °C ( $n=10$ ), above which EWL increased linearly and significantly (LMM: slope =  $0.23 \pm 0.02$  SE,  $R^2_m = 0.67$ ,  $P < 0.001$ ) to a maximum of  $2.13 \pm 0.44$  g h<sup>-1</sup> ( $n=3$ ) at  $T_{air} \sim 48$  °C (Table 1, Fig. 3), equivalent to a 15.1-fold increase. The ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) calculated assuming RER = 0.71 was minimal at  $0.20 \pm 0.07$  ( $n=10$ ) at  $T_{air} \sim 28$  °C, with EHL/MHP = 0.58 when  $T_{air} = T_b$  (Fig. 3). Above an inflection at  $T_{air} - T_b = -0.47 \pm 0.64$  °C, EHL/MHP increased to a maximum of  $1.74 \pm 0.31$  ( $n=3$ ) at  $T_{air} \sim 48$  °C (Table 1). Values of EHL/MHP calculated assuming RER = 1.0 were higher, reaching a maximum of 2.40 at  $T_{air} \sim 48$  °C and EHL/MHP = 0.78 when  $T_{air} = T_b$  (Fig. 3). The fractional contribution of metabolic water production at high  $T_{air}$  decreased from 8.0% of EWL at  $T_{air} = 40$  °C to 3.6% at  $T_{air} = 48$  °C assuming lipid metabolism and from 6.0% to 2.7% assuming carbohydrate metabolism.



**Fig. 2** The nose of a western rock elephant shrew (*Elephantulus rupestris*) immediately after being removed from the metabolic chamber, following open flow-through respirometry. Individuals were placed on a dry surface and the fluid in the images is a result of their excessive production of saliva following acute heat exposure and use of saliva spreading on their elongated snouts



## Discussion

Our data support the hypothesis that an arid-zone elephant shrew possesses pronounced heat tolerance and evaporative cooling capacity. Under laboratory conditions, *E. rupestris* tolerated environmental temperatures up to 48 °C,  $T_b$  up to ~6 °C above normothermic levels, and dissipated heat evaporatively at maximum rates equivalent to 174–240% of metabolic heat production. These observations suggest the thermal physiology of *E. rupestris* is well-suited to high diurnal  $T_{air}$ , the use of above-ground rock crevices as refugia and the metabolic heat loads associated with cursoriality.

Thermoregulation in *E. rupestris* at  $T_{air}$  approaching or exceeding  $T_b$  differed from patterns previously reported for the congeneric *E. edwardii* (Leon et al. 1983), which also occurs at our study site. Over the range of  $T_{air}$  for which thermoregulation in both species has been quantified, the  $T_b$  of *E. rupestris* remained ~2 °C below that of *E. edwardii*, despite similar RMR and EWL (Leon et al. 1983). The difference in  $T_b$  between the two species could potentially arise from methodological differences between studies. Leon et al. (1983) measured  $T_b$  using a rectal thermocouple immediately after elephant shrews were removed from respirometry chambers, whereas we used injected PIT tags for continuous measurements. Moreover, the individuals studied by Leon et al. (1983) were held in captivity at constant  $T_{air} = 27$  °C

with ad libitum water and food for 21 days prior to measurements, raising the possibility that they had acclimatised to their mild, artificial environment (e.g., Nespolo et al. 1999). A third methodological difference concerns humidity in chambers during measurements; Leon et al. (1983) used flow rates of ~300 mL min<sup>-1</sup>, whereas in the present study flow rates were substantially higher and hence chamber humidities lower. High humidity reduces the efficiency of evaporative cooling under hot conditions (Lasiewski et al. 1966; Gerson et al. 2014). Whereas it is possible that the differences in  $T_b$  between these two species reflect physiological adaptation related to the arid-zone distribution of *E. rupestris* versus the fynbos-centred distribution of *E. edwardii* (Skinner and Chimimba 2005), we consider the methodological differences between the two studies the most likely explanation.

Consistent with Leon et al.'s (1983) observations for *E. edwardii*, behavioural changes were a major element of thermoregulation in *E. rupestris* during acute heat exposure. The body-flattening observed during measurements in both species presumably serves to increase conductive heat loss to cool rock substrates (Terrien et al. 2011), and resembles closely the posture adopted during sun-basking by other *Elephantulus* species (Mzilikazi et al. 2002). The saliva-spreading we observed in *E. rupestris* was not reported for *E. edwardii*, in which only occasional licking of the nose

**Table 1** Summary of the thermoregulatory performance of the western rock elephant shrew (*Elephantulus rupestris*) from the Succulent Karoo biome in Southern Africa

Variable	Mean $\pm$ SD (n)
Body mass (g)	51.63 $\pm$ 9.38 (10)
$T_b$	
Min. $T_b$ ( $^{\circ}$ C)	35.7 $\pm$ 0.58 (10)
Inflection $T_{air}$ ( $^{\circ}$ C)	35.61 $\pm$ 2.04 (10)
$T_b$ versus $T_{air}$ slope	0.46 $\pm$ 0.02 (SE)
Max $T_b$ ( $^{\circ}$ C)	41.64 $\pm$ 0.16 (3)
Max $T_{air}$ ( $^{\circ}$ C)	47.96 $\pm$ 0.10 (3)
RMR	
Min. RMR (W)	0.40 $\pm$ 0.07 (10)
$T_{ic}$ ( $^{\circ}$ C)	37.56 $\pm$ 0.01 (10)
RMR slope (mW $^{\circ}$ C $^{-1}$ )	43.29 $\pm$ 4.25 (SE)
Max. RMR (W)	0.82 $\pm$ 0.10 (3)
Max. RMR/min. RMR	2.03
EWL	
Min. EWL (g h $^{-1}$ )	0.14 $\pm$ 0.04 (10)
Inflection $T_{air}$ ( $^{\circ}$ C)	38.89 $\pm$ 0.67 (10)
EWL slope	0.23 $\pm$ 0.02 (SE)
Max. EWL (g h $^{-1}$ )	2.13 $\pm$ 0.44 (3)
Max. EWL/min. EWL	15.05
Min. EHL/MHP	0.20 $\pm$ 0.07 (10)
EHL/MHP inflection $T_{air}-T_b$ ( $^{\circ}$ C)	-0.47 $\pm$ 0.64 (10)
EHL/MHP slope	0.24 $\pm$ 0.03 (SE)
Max. EHL/MHP	1.74 $\pm$ 0.31 (3)

$T_b$  body temperature, RMR resting metabolic rate, EWL evaporative water loss, EHL evaporative heat loss, MHP metabolic heat production

Means, standard deviations (SD) or standard error (SE) and sample sizes (n) are reported

took place and no oral or nasal fluid loss was observed (Leon et al. 1983). Data on heat dissipation behaviours and their relationship to environmental temperature and activity are essential for understanding behavioural trade-offs that result in missed-opportunity costs and how those costs are likely increase with warming (Cunningham et al. 2021).

Other than Leon et al.'s (1983) data for *E. edwardii* and ours for *E. rupestris*, we are aware of only one other investigation of acute heat tolerance in an afrotherian mammal: (Bartholomew and Rainy 1971) study of the 4–5 kg yellow-spotted rock hyrax (*Heterohyrax brucei*) in Kenya. The hyraxes also exhibited pronounced hyperthermia, with  $T_b$  increasing from  $\sim 36$   $^{\circ}$ C at  $T_{air}=20$   $^{\circ}$ C to  $\sim 41$   $^{\circ}$ C at  $T_{air}=42.5$   $^{\circ}$ C (Bartholomew and Rainy 1971). These authors reported EHL/MHP = 1 at  $T_{air}=42.5$   $^{\circ}$ C, but these measurements took place under much higher humidity (11.4 g m $^{-3}$ , equivalent to relative humidity = 19.8% at  $T_{air}=42.5$   $^{\circ}$ C) than ours. Approximately 22% of EWL by the hyraxes occurred via sweating from the foot pads (Bartholomew

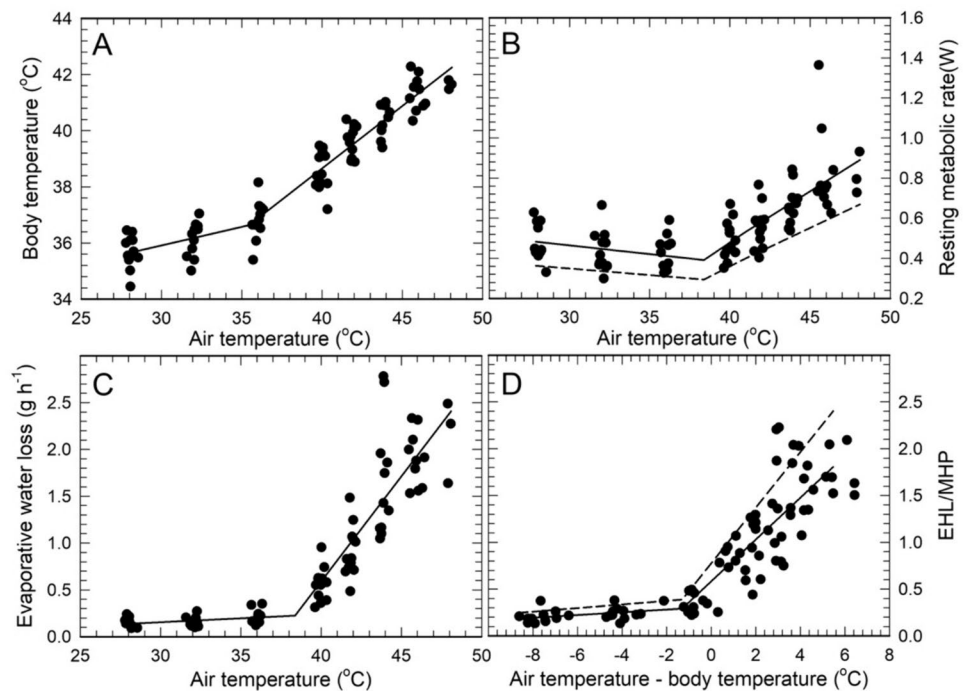
and Rainy 1971). More data on evaporative cooling capacity and heat tolerance among afrotherians will provide the basis for better understanding the vulnerability of these morphologically diverse group of mammals, many of which are threatened, to the increases in  $T_{air}$  and heat wave frequency associated with climate change (IPCC 2021).

The elephant shrews we investigated here showed a higher heat tolerance limit and greater evaporative cooling capacity compared to other southern African small mammals investigated using the same protocol for eliciting upper thermoregulatory limits, including rodents (van Jaarsveld et al. 2021) and mole-rats (Wallace et al. 2021). The heat tolerance limit of  $T_{air}=48$   $^{\circ}$ C for *E. rupestris* is higher than those reported for the rodents *Michaelamys namaquensis* ( $T_{air}=40.4$   $^{\circ}$ C), two populations of *Gerbillurus paeba* (40.5  $^{\circ}$ C and 41.5  $^{\circ}$ C), *Thallomys nigricauda* (44.6  $^{\circ}$ C; van Jaarsveld et al. 2021) or cricetids in the Mojave Desert (42–46  $^{\circ}$ C; Ramirez et al. 2022). Indeed, the only other non-volant small mammal with  $M_b \leq 100$  g reported to tolerate  $T_{air}$  as high as 48  $^{\circ}$ C is the antelope ground squirrel (*Ammospermophilus leucurus*; Hudson 1962). The maximum  $T_b$  of *E. rupestris* (41.6  $^{\circ}$ C) is similar to those observed in *M. namaquensis* and *T. nigricauda*, but lower than in Mojave cricetids, for which measurements were ended at  $T_b=43$   $^{\circ}$ C (Ramirez et al. 2022).

Among southern African arid-zone rodents investigated to date, only the arboreal black-tailed tree rat (*T. nigricauda*) possesses evaporative cooling efficiency (maximum EHL/MHP = 2.12) comparable to that of *E. rupestris*, probably on account of the former species' arboreality and use of roost microsites in which  $T_{air}$  regularly exceeds 40  $^{\circ}$ C (van Jaarsveld et al. 2021). Tree cavities and rock crevices are thought to expose small mammals to significantly higher maximum temperatures compared to subterranean burrows (Buffenstein 1984; van Jaarsveld et al. 2021), although crevice temperature profiles vary with structure and depth (Webb and Shine 1998; Croak et al. 2008). Moreover, the evaporative cooling capacity of *E. rupestris* is comparable to those of bats occupying hot diurnal roosts, for instance under building roofs (Maloney et al. 1999; Czenze et al. 2022).

Our findings for *E. rupestris* reiterate the need for investigating physiological constraints on heat tolerance likely to affect endotherm responses to rapid anthropogenic climate change and how the relevant thermal physiological traits have evolved. Whereas endotherm  $T_b$  was initially considered a non-adaptive constant (Scholander et al. 1950), there is increasing evidence for adaptation in maximum  $T_b$  and hyperthermia tolerance correlated with both micro- and macroclimate. This evidence includes significantly higher subcutaneous  $T_b$  maxima among bats occupying hot, less thermally-buffered roosts compared to those occupying cooler roosts (Czenze et al. 2022) and significantly higher maximum  $T_b$  and lower normothermic  $T_b$  among birds

**Fig. 3** Relationships between air temperature ( $T_{\text{air}}$ ) and body temperature (panel **A**), resting metabolic rate (panel **B**), and evaporative heat loss/metabolic heat production (EHL/MHP; panel **D**) in western rock elephant shrews (*Elephantulus rupestris*). In panels **A**, **B** and **C** the solid lines indicate linear mixed-effects regression models fitted to data above and below  $T_{\text{air}}$  inflections for each variable. In panel **D**, the solid line is for EHL/MHP calculated assuming lipid metabolism [i.e., respiratory exchange ratio (RER)=0.71] and the dashed line for EHL/MHP calculated assuming carbohydrate metabolism [i.e., RER=1.00]



inhabiting humid lowland environments compared to those from arid habitats (Freeman et al. 2022). Adaptive variation is also evident for other components of heat tolerance, including intra- and interspecific differences in evaporative cooling capacity and heat tolerance limits (Cory Toussaint and McKechnie 2012; Czenze et al. 2020, 2022; van Jaarsveld et al. 2021; Freeman et al. 2022).

Recent evidence suggests small terrestrial mammals inhabiting desert habitats are less vulnerable to climate change compared to arid-zone birds on account of the former's greater use of thermally buffered burrows and reduced evaporative cooling costs (Riddell et al. 2021). However, the same may not be true for crevice-dwelling taxa nor those that spend the day in arboreal cavities, reiterating the need for empirical data on heat tolerance and evaporative cooling capacity in a wider range of small mammal taxa and further tests of hypotheses concerning adaptative variation correlated with microclimate. Our data confirm that the acute heat tolerance of an arid-zone elephant shrew exceeds that of most non-volant small mammals investigated to date and reiterate the importance of species-specific thermal physiology data for predicting the direct impacts of increasing  $T_{\text{air}}$  on small mammals.

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**Author contribution** AEM and MTF designed and supervised the study, OJBC-M and MTF collected data, OJBC-M analysed the data and wrote the first draft of the manuscript, AEM and MTF edited the manuscript.

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**Data availability** Data is available from corresponding author on request.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Research involving human and/or animal participants** Work was conducted under authorisation from the Northern Cape government (permit number FAUNA 0010/2021). All experimental work was approved by the South African National Biodiversity Institute's Research Ethics and Scientific Committee (protocol P2020/24) and the Animal Ethics Committee of the University of Pretoria (NAS290/2020).

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