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RESEARCH ARTICLE

Using physiology to unravel the implications of heatwaves for big brown bats (*Eptesicus fuscus*)

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ABSTRACT

Nocturnal endotherms are vulnerable to high ambient temperatures (T_a) during the day when sequestered in retreat sites. Artificial roost design must therefore account for the thermal sensitivity of target species and the potential roost temperatures during heatwave conditions at installation sites. We recorded physiological responses of big brown bats (*Eptesicus fuscus*) under naturally observed roost temperatures using flow-through respirometry. We used the resulting data to parameterise a biophysical model with which we calculated the evaporative cooling requirements as percent body mass during the hottest day of 2023 and a heatwave during 2021. Our data revealed that the evaporative cooling requirements of bats roosting in certain artificial roosts would have exceeded the lethal dehydration threshold for both females and males during the 2021 heatwave (>22.1% body mass). Regardless of the availability of freestanding water in the environment, bats roosting in artificial roosts prone to overheating are at risk of lethal dehydration during heatwaves, even in high latitude habitats. Therefore, conservation management of small nocturnal endotherms should incorporate both physiological data and roost microclimate data when designing and deploying artificial roosts.

KEY WORDS: Endotherms, Conservation, Biophysical models, Thermoregulation, Climate change, Artificial roosts

INTRODUCTION

An animal's physiological capabilities fundamentally shape its habitat selection (Anderson et al., 1979; van Beest et al., 2012). Climate change is increasing the frequency and intensity of heat waves (IPCC, 2021; Viceto et al., 2019) and, in a warming world, the physiological consequences of habitat selection and thus the microclimate an animal experiences will directly influence their persistence.

In 1991, Huey posed the question 'How and to what extent do the physical environment and physiology jointly influence behaviour…?' (Huey, 1991). There are three critical steps to answering this question: (1) the microclimates available in a habitat must be mapped; (2) the physiological variables must be quantified; and (3) the physiological suitability of habitats can then be predicted by integrating both the environmental and physiological data (Huey, 1991). This integration reveals how habitats shape behaviour through microclimates, affecting physiology, ecological performance and ultimately influencing population-level processes (Briscoe et al., 2016, 2023). Biophysical modelling techniques can explicitly quantify the link between physiology and ecology and are increasingly applied in ecology and conservation to inform decisions in the face of climate change (Briscoe et al., 2023; Ma et al., 2023; Wild et al., 2025).

For small endotherms (i.e. small mammals and birds), thermal homeostasis is increasingly difficult to mitigate behaviourally (e.g. postural changes or microhabitat selection) as air temperatures increase beyond body temperature (T_b), at which point evaporative cooling usually becomes the primary means available to regulate T_b (Studier et al., 1970; Tattersall et al., 2012). The use and effectiveness of evaporative cooling are influenced by microclimate conditions and behavioural ecology, as species inhabiting warmer microsites possess greater evaporative cooling capacities and heat tolerance (Czenze et al., 2021; Freeman et al., 2022). Diurnal species with reliable access to drinking water often exhibit higher rates of evaporative water loss compared with species that rely on thermal refugia (i.e. burrows or tree hollows; Czenze et al., 2020; Hoole et al., 2019; van Jaarsveld et al., 2021). Nocturnal animals are more restricted in terms of behaviour and microclimate availability and are consequently more reliant on physiological mechanisms to achieve thermal homeostasis.

The rest phase of nocturnal endotherms coincides with the hottest part of the day, which limits access to refugia with varied microclimates and freestanding water in the landscape. Species that roost or den in confined spaces (i.e. hollows, burrows and artificial habitats) have a limited capacity to thermoregulate behaviourally through postural changes but are exposed to less solar radiation and lower windspeed, making them interesting and tractable cases for calculating daily energy and water balance during heatwaves. For many nocturnal species, the threat of climate change is exacerbated by habitat destruction (Laurance et al., 2008). Although artificial roosts are a common conservation tool used to counteract the loss of habitat, they vary in their designs, construction and efficacy (Griffiths et al., 2018, 2022), and there has been limited guidance available for effective use, especially regarding thermoregulation (Kearney et al., 2011).

Bats are a highly diverse group of nocturnal endotherms, with >1400 species that thrive in many climates (Simmons and Cirranello, 2023). In the Southern Hemisphere, some species tolerate roost temperatures >50°C (Bronner et al., 1999; Maloney et al., 1999) and

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skin temperatures >45°C (Bondarenco et al., 2014). However, during extreme heat, bats may face lethal hyperthermia (Griffiths, 2022; Lausen et al., 2022a); therefore, individuals face a trade-off between potential sources of mortality such as abandoning a roost, which is accompanied by a significant metabolic cost and predation risk (Lima and O'Keefe, 2013). Temperate latitude species also face threats of heat-induced mass mortality (Lausen et al., 2022b), yet there are limited data about the vulnerability of these species to high temperatures (e.g. Czenze et al., 2022; Noakes et al., 2021).

There is an urgency to quantify the effects of high roost temperatures on bats, given some females typically choose relatively warm roosts that facilitate offspring development (Chruszcz and Barclay, 2002; Kerth et al., 2001; Lausen and Barclay, 2003). However, warm maternity roosts are vulnerable to overheating during heatwaves and, unlike adults, young-of-year cannot abandon an overheating roost and could face mortality (Bartonička and Řehák, 2007; Flaquer et al., 2014; Griffiths, 2022). With global temperatures and the occurrence of heatwaves predicted to increase (IPCC, 2021), poorly constructed and/or placed artificial habitats may serve as death traps even with accessible freestanding water nearby. By understanding the physiological limits of the target fauna, mitigation plans using artificial roosts can be more focused and effective conservation measures in the face of global climate change.

Here, we first assessed the thermoregulatory strategies of a small endotherm, the big brown bat (*Eptesicus fuscus*). We hypothesised that given their high body mass (M_b) compared with smaller bat species, *E. fuscus* would adopt a thermoregulatory strategy favouring efficient evaporative cooling as opposed to facultative hyperthermia. We also hypothesised that females would be more conservative than males in their water economy owing to their habit of forming maternity colonies in inherently warmer roosts, which exposes them to consistently higher roost temperatures (T_{roost}). We then evaluated the physiological consequences of roost temperatures via the integration of flow-through respirometry and biophysical modelling to quantify vulnerability of *E. fuscus* to heatwaves. Specifically, we (1) recorded microclimates available in the habitat *in situ*; (2) quantified physiological variables in the heat using respirometry and investigated differences in thermal physiology between males and females; and (3) predicted the physiological suitability of artificial habitats by integrating environmental and physiological data using the endotherm model of NicheMapR (Kearney et al., 2021). We then used this knowledge to estimate the daily water requirements for big brown bats in the Fraser Valley, British Columbia, Canada, during current heatwaves. This species roosts and forms maternity colonies in a variety of natural and anthropogenic structures (Lausen and Barclay, 2003; Lausen et al., 2022b), and this population experiences some of the highest maximum summer ambient temperature (T_a) values in the country (>45°C; Canadian Environment and Natural Resources, 2024). Our results are relevant to conservation managers working on small nocturnal endotherms and can be used by local authorities to help inform the decision-making process regarding artificial habitat creation.

MATERIALS AND METHODS

Ethics statement

This work was approved by the animal ethics committees of the University of New England (ARA22-051) and University of Regina (AUP23-03). The work was carried out under a Government of British Columbia general wildlife permit (KA23-792033) and a Government of Canada species at risk permit (SARA-PYR-2023-0749).

Study site

The study was conducted in and around Lillooet, BC, Canada (50° 41′34.55″N, 121°56′12.88″W), on the unceded territory of the St'át'imc Nation. Lillooet, and the surrounding interior of British Columbia, is comprised of semi-arid mountains with woodlands dominated by a variety of pine (*Pinus* spp.) and fir (*Pseudotsuga* spp.) trees. The area is situated adjacent to the Fraser River and has numerous standing water sources in the form of glacial waterways and artificial reservoirs. This region of the Fraser River (Lytton-Lillooet) is characterised by steep rock/mudstone canyon walls, and the surrounding areas vary widely in elevation; our sites ranged from ∼200 m (close to Fraser River) mixed grassland pine habitat to ∼900 m in forested mountain terrain (near Kwotlenemo Lake, 50°42′49.5″N, 121°49′14.3″W). In the lowest elevations of this area, summer temperatures are typically some of the highest in Canada (Canadian Environment and Natural Resources, 2024), having reached a Canadian record maximum of 49°C on 29 June 2021 during a heatwave (Abbasi, 2024; Eberle et al., 2022).

Bat capture and handling

During 27 July–28 August 2023, we captured 11 female and 11 male *Eptesicus fuscus* (Beauvois 1796) to use in respirometry experiments. Bats were aged, sexed and weighed immediately post capture. Only non-reproductive adults were used in the experiments. Bats were transported in cloth bags to the field laboratory within 30 min and were held in a quiet, temperature-controlled, darkened room for <24 h. Bats were fed superworm (*Zophobas atratus*) larvae until their M_b increased ≥10% and were also offered water using a sterile plastic pipette. Subcutaneous temperature (T_{sub}) was measured by subcutaneously implanted temperature-sensitive PIT tag (Biotherm, Biomark, Boise, ID, USA, accuracy ±0.5°C) between the scapulae. Gas exchange measurements were performed the morning after initial capture during the bat's rest phase.

Gas exchange measurements

We used an experimental protocol identical to Czenze et al. (2022) (see Supplementary Materials and Methods) comprising a flow-through respirometry system to measure oxygen ($\dot{V}_{O_2}$), whole-animal evaporative water loss (waEWL) and carbon dioxide ($\dot{V}_{CO_2}$). Respirometry chambers were placed in a modified mobile refrigerator (14 litres; WAECO mobile refrigeration unit), of which the temperature was controlled manually. Every 10 s, the subcutaneous temperature (T_{sub}) readings from PIT tags were recorded using a reader system attached to a racket antenna placed within the refrigerator next to the chamber (HPR+, Biomark).

Air was supplied using an oil free pump (model GPUMPAIR65, Simple Deluxe, Duarte, CA, USA) after passing through a column of silica to scrub water before being split into baseline and chamber channels. Aalborg rotameters (Aalborg Instruments & Controls, Inc., Orangeburg, NY, USA) were used to regulate both baseline and chamber airflow, which were then measured using a mass flow meter (0.5–5 SLPM, Alicat Scientific Inc., Tucson, AZ, USA). Flow rates ranged from 0.86 to 3.0 l min^{-1} depending on the mass and behaviour of each individual. $\dot{V}_{CO_2}$, $\dot{V}_{O_2}$ and H_2O were measured from the baseline and chamber excurrent air that was pulled through a Field Metabolic System (FMS, Sable Systems, North Las Vegas, NV, USA). All gas measurements were recorded at 5 s intervals using ExpeData software (Sable Systems).

Experimental protocol

Experimental runs, lasting 3–5 h, were conducted between 07:00 and 18:00 h following established methods (Czenze et al., 2022;

Freeman et al., 2022). Bats were incrementally exposed to higher experimental T_a values in a stepped profile. Individuals were acclimated for 1 h at experimental T_a=28°C before recording physiological data. Data collection began at an experimental T_a=28°C, which was increased by 4°C until 40°C. After 40°C, experimental T_a was increased in 2°C increments. Before measurements were obtained, individuals were allowed a minimum of 20–30 min at each experimental T_a. We waited for T_{sub}, $\dot{V}_{CO_2}$ and waEWL to stabilise before sampling gas for 5 min. Individuals were monitored using an infrared video camera throughout the experimental trials, which were immediately aborted if the individual began biting the chamber mesh or became restless while moving about the chamber. Bats were immediately removed from the chamber, weighed and then offered water. Bats were allowed to rest at room temperature in the dark in clean cloth bags. Food and water were offered 1 h later, and again before individuals were released at the capture site that same evening.

Statistical analysis

All statistical analyses were performed in R 4.2.3 (https://www.r-project.org/). Inflection points were identified for each physiological response of T_{sub}, whole-animal resting metabolic rate (waRMR), waEWL and evaporative cooling capacity [evaporative heat loss/metabolic heat production (EHL/MHP)] in relation to experimental T_a (R package segmented.lme; Muggeo et al., 2014). The segmented regressions were compared with simple linear regressions using ANOVA, which indicated segmented regression models to be the best fit for all physiological variables for females. For males, only waEWL~T_a was better fit by a segmented regression.

The physiological response of T_{sub}, waRMR, waEWL and EHL/MHP to experimental T_a, above the sex-specific inflection points, were tested using linear mixed-effect models (R package nlme; https://cran.r-project.org/package=nlme). T_a, body mass (M_b), sex, and the interaction between experimental T_a and sex were included as fixed effects in the global models. To account for repeated measurements from individuals, the individual ID of bats was included as a random effect in the models. We then compared the global models to the reduced models by backwards step elimination and selected the predictor variables to retain in the final model (Beilke and O'Keefe, 2023; Tredennick et al., 2021).

To compare differences between the physiological responses of each sex at each experimental T_a, we calculated the estimated marginal means for T_{sub}, waRMR, waEWL and EHL/MHP (R package emmeans; https://cran.r-project.org/package=emmeans). The maximum and minimum values (Table 1) in some cases represent a subset of individuals (e.g. only two males tolerated T_a=48°C). If only one individual represented the maximum value of a physiological variable, we also report the mean value at the second highest experimental T_a. In all analyses, α=0.05 was used to assign significance or, in the case of inflection points, where the 95% confidence intervals did not overlap.

Roost microclimate measurements and evaporative water requirement calculations

In the summer of 2023 (30 July–27 August 2023), using iButtons (Thermochron iButton, Maxim Integrated, San Jose, CA, USA; logging interval=60 min), we recorded T_{roost} for four *E. fuscus* roosts at two sites: two roosts in a building at a nearby (6 km) higher elevation (Δ550 m) site (Kwotlenemo Lake) and two bat boxes near the Fraser River at Lillooet. We also recorded T_a for each site by placing an iButton in a shaded location adjacent to the roosts.

Table 1. Summary of thermoregulatory performance variables as a function of ambient temperature (T_a; °C) in *Eptesicus fuscus* from Lillooet, BC, Canada (27 July–28 August 2023)

	Female	Male
Mass (g)	20.7±2.6 (11)	19.6±2.8 (11)
Subcutaneous temperature (T_{sub})		
Min. T_{sub} (°C)	34.9±1.4	32.9±2.2
Inflection T_a (°C)	29.6 (27.3–31.7)	n.a.
T_{sub} at max. bin T_a (°C)	43.9 (1)	44.1 (1)
	42.9±0.6 (6)	43.3±0.6 (2)
T_{sub} slope (°C °C^{-1})	0.53	0.6
Max. bin T_a (°C)	48 (6)	48 (2)
	46 (11)	46 (7)
Whole-animal resting metabolic rate (waRMR)		
Min. waRMR (W)	0.11±0.02 (10)	0.08±0.02
Inflection T_a (°C)	33.2 (32.2–34.3)	n.a.
Max. waRMR (W)	0.40 (1)	0.29 (1)
	0.27±0.07 (6)	0.21±0.03 (11)
waRMR slope (mW °C^{-1})	12.2	8.2
Max. waRMR/Min. waRMR	2.45	2.62
Whole-animal evaporative water loss (waEWL)		
Min. waEWL (g h^{-1})	0.03±0.02 (11)	0.03±0.02 (8)
Inflection T_a (°C)	37.8 (36.9–38.6)*	35.3 (33.6–36.8)*
Max. EWL (g h^{-1})	0.99 (1)	0.75 (1)
	0.79±0.14 (6)	0.72±0.03 (2)
waEWL slope (g h^{-1} °C^{-1})	0.07	0.04
Evaporative scope	26	24
Min. EHL/MHP	0.14±0.09 (11)	0.25±0.12 (8)
Inflection T_a (°C)	35.2 (33.1–37.3)	n.a.
Max. EHL/MHP	2.75 (1)	2.92 (1)
	2.05±0.50 (6)	2.42 (2)

Thermoregulatory variables include subcutaneous temperature (T_{sub}; °C), whole-animal resting metabolic rate (waRMR; W), whole-animal evaporative water loss (waEWL; g h^{-1}) and evaporative heat loss/metabolic heat production (EHL/MHP). 'Max.' and 'Min.' indicate maximum and minimum values, respectively, for each physiological variable. Means±s.d. are reported with sample sizes within parentheses. Max. bin T_a (°C) is the maximum 1°C-width bin of T_a at which we recorded stable measurements. Inflection points are reported with 95% confidence intervals in parentheses. *Significantly different inflection points between sexes (P<0.05).

At the Kwotlenemo site, the two roosts were on opposite ends of the building located where the roof peaked (KL east-facing roost, KL west-facing roost, hereafter). The east-facing roost received direct sunlight in the morning, whereas the west-facing roost received dappled sunlight in the afternoon. The two roosts at Lillooet were wooden bat boxes mounted 3 m above ground on a pole in direct sunlight (LI north-facing box, LI south-facing box).

To estimate the T_{roost} experienced by bats during a heatwave in 2021, we used the linear regression equation for each roost based on the relationship between T_{roost} and T_a we collected in 2023 (correlation values between all *E. fuscus* roosts ranged from R^2=0.82 to 0.97). Owing to the separating mountain topography and differences in elevations, roosts at Kwotlenemo Lake were considered outside of the immediate coverage of the Lillooet Environment Canada weather station. Therefore, we estimated T_a of this location for the relevant periods using the ERA5 dataset via the NicheMapR package (Klinges et al., 2022).

For each *E. fuscus* roost, we calculated the time T_{roost} was above the waEWL inflection point of females and males. Estimated daily evaporative cooling requirements were defined as the mass of H_2O as a percentage of M_b needed for bats to achieve thermal balance while roosting (Czenze et al., 2022; de Mel et al., 2024). We estimated daily evaporative cooling requirements for both female and male *E. fuscus* using the mean M_b of each sex and sex-specific relationships between T_a and waEWL. We performed these calculations for the hottest day during our study (15 and 16 August 2023; site-specific), and the hottest day recorded the study area (29 June 2021; Canada Environment and Natural Resources, 2024).

Finally, we used the endotherm model of the NicheMapR biophysical modelling package (Kearney et al., 2021) to model the EWL for each sex for the above conditions. The endotherm model consists of a suite of subroutines to solve coupled energy and water budgets according to physiological and morphological traits that can be customised to match species-specific behavioural thermoregulatory sequences (Conradie et al., 2023; Kearney et al., 2021; Rogers et al., 2021). We parameterised and tested the model following published methods (Conradie et al., 2024; Rogers et al., 2021), assessing the goodness-of-fit of the sex-specific regression models (described above) and endotherm models for T_b, waRMR and waEWL using Pearson correlation, root mean square deviation (RMSD) and R^2 tests. To parameterise the model, we measured hair properties using a dissecting microscope (Olympus SZX7) of museum specimens of *E. fuscus* (five males and five females). We measured the length and diameter of 10 hairs per dorsal and ventral surface for each individual. We also calculated the density of hairs on both surfaces for each individual. We used the average of these calculations for each sex and the average mass of each sex from our study samples in the final model (Table S3).

RESULTS

Respirometry in the heat

There was no significant difference in the M_b between males and females (ANOVA, $F_{1,20}$=0.87, P=0.36). Both males and females could tolerate T_a=48°C; however, this T_a was tolerated by 54.5% (n=6/11) of females and only 18% (n=2/11) of males (Table 1). Both sexes maintained similar T_{sub} throughout all experimental T_a values (Table S1, Fig. S1A), similar T_{sub} at their respective heat tolerance limit (females=42.9±0.6°C, males=43.3±0.6°C; Table 1), and similar absolute maximum T_{sub} (females=43.9°C, males=44.1°C; Table 1).

The final reduced mixed-effect model for waRMR~T_a retained the interaction term T_a×sex, indicating that at high T_a values, females increased their waRMR more rapidly than males (Table S2, Fig. S1B). Both sexes maintained similar waRMR across all experimental temperatures (Table S1), but females achieved a maximum waRMR (0.27±0.07 W) that was 28.5% greater than that of males (0.21±0.03 W). The absolute maximum waRMR of females (0.40 W) was 37.9% greater than the respective value for males (0.29 W).

The final reduced mixed-effect models for waEWL~T_a retained the interaction term T_a×sex, indicating that females increase their waEWL at a higher rate than males at the high T_a values (Table S2, Fig. S1C). At T_a=40°C, females maintained significantly lower waEWL rates compared with males (Table S1) but achieved similar waEWL rates to males at higher experimental T_a values (42–48°C; Table S1). The absolute maximum waEWL for females (0.99 g h^{-1}) was greater than for males (0.75 g h^{-1}) by ∼25%. The inflection point of waEWL with increasing T_a for females (37.8°C, CI=36.9–38.6°C) was significantly higher than that of the males (35.3°C, CI=33.6–36.8°C).

2023 evaporative cooling requirements

The results from the respirometry experiments and endotherm model for waEWL~T_a were highly correlated (female waEWL: Pearson correlation coefficient r_{77}=0.964, P<0.001, RMSD=0.079 g h^{-1}, R^2=0.93; male waEWL: Pearson correlation coefficient r_{70}=0.868, P<0.001, RMSD=0.144 g h^{-1}, R^2=0.75; Fig. 1).

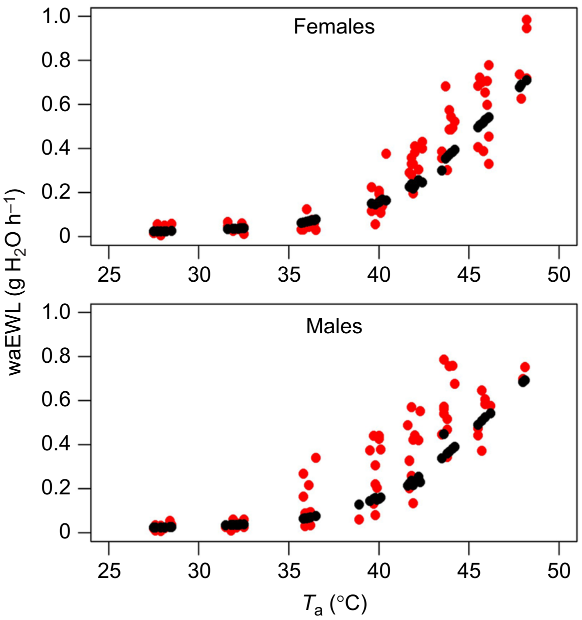

Fig. 1. Experimental data for evaporative water loss (g H_2O h^{-1}; red circles) and results from endotherm model predictions (black circles) for female (n=11) and male (n=11) big brown bats (*Eptesicus fuscus*) at high air temperatures. waEWL, whole-animal evaporative water loss; T_a, ambient temperature.

We estimated the evaporative cooling requirements of individuals during daylight hours on 16 August for both Kwotlenemo Lake roosts and 15 August for both Lillooet boxes. In Kwotlenemo Lake, 16 August coincided with the absolute maximum T_a of 35.5°C and absolute maximum daily range=21.5°C. The absolute maximum T_{roost} of the east-facing roost was 38.5°C (16 August) and 32°C for the west-facing roost (16 August). We used data for 15 August in Lillooet as it coincided with the absolute maximum T_a of 39.5°C and absolute maximum daily range=20.5°C. The absolute maximum T_{roost} of the north-facing box was 40.5°C (16 August) and 44.5°C for the south-facing box (16 August).

Using the respirometry data for the Kwotlenemo Lake roosts, the daytime evaporative cooling requirements, as a percentage of average M_b, for females and males were low (east-facing: female 2.9%, male 6.2%; west-facing: females 2.5%, males 4.0%; Table 2). The endotherm model predicted similar evaporative cooling requirements (east-facing: females 3.5%, and males 3.5% M_b; west-facing: females 2.1%, males 2.2% M_b; Table 2).

Using the respirometry data for the Lillooet roosts, the daytime evaporative cooling requirements, as a percentage of average M_b, in both bat-boxes were higher for both sexes than Kwotlenemo Lake (north-facing: females 7.7%, males 10.0%; south-facing: females 10.8%, males 15.3%). Again, the endotherm model predicted similar evaporative cooling requirements (north-facing: females 5.3%, males 5.4%; south-facing: females 9.1%, males 9.2%; Table 2).

2021 heatwave evaporative cooling requirements

Using the site-specific regressions of T_{roost}~T_a, we estimated the T_{roost} for KL east-facing, KL west-facing, LI north-facing and LI south-facing roosts for 29 June 2021. The absolute maximum T_{roost} for the Kwotlenemo Lake east-facing roost was 55.5°C and T_{roost} was >50°C for 6 h and above 40°C for 11 h, whereas the absolute maximum T_{roost} of the west-facing roost was 42.3°C. In the LI north-facing roost,

Table 2. Estimated daytime evaporative cooling requirements (g H_2O, % body mass) calculated using linear regressions and the endotherm model of female and male *Eptesicus fuscus* using four roosts in BC, Canada

		Linear regression				Endotherm model			
		Female		Male		Female		Male	
Roost ID	Highest T_{roost} (°C)	EWL (g)	EWL (% M_b)	EWL (g)	EWL (% M_b)	EWL (g)	EWL (% M_b)	EWL (g)	EWL (% M_b)
KL east-facing 2021	55.5	10.5	50.7	9.9	50.3	10.3	49.7	9.7	49.7
KL west-facing 2021	42.3	1.9	9.4	3.0	15.6	1.7	8.0	1.6	8.1
LI north-facing 2021	48.1	5.3	25.5	5.9	29.9	4.7	22.5	4.3	22.1
LI south-facing 2021	50.8	7.0	33.8	7.2	36.7	6.4	30.8	6.1	30.9
KL east-facing 2023	38.5	0.6	2.9	1.2	6.2	0.7	3.5	0.7	3.5
KL west-facing 2023	32.0	0.5	2.5	0.8	4.0	0.4	2.1	0.4	2.2
LI north-facing 2023	40.5	1.6	7.7	1.9	10.0	1.1	5.3	1.1	5.4
LI south-facing 2023	44.4	2.2	10.8	3.0	15.3	1.9	9.1	1.8	9.2

The four roosts comprised two buildings [Kwotlenemo Lake (KL) east-facing and west-facing] and two bat-boxes [Lillooet (LI) north-facing and south-facing]. Evaporative cooling requirements were calculated for the heatwave in 2021 (29 June: KL east-facing, KL west-facing, LI north-facing, LI south-facing), and the warmest day of the study period (15 August 2023: LI north-facing, LI south-facing; 16 August 2023: KL east-facing, KL west-facing). EWL, evaporative water loss.

maximum T_{roost} was 48.1°C and T_{roost} was above 40°C for 10 h. For the LI south-facing roost, the maximum T_{roost}=50.8°C, whereas T_{roost} was >50°C for 1 h and above 40°C for 10 h.

Using the respirometry data for the Kwotlenemo Lake roosts, the daytime evaporative cooling requirements, as a percentage of average M_b, were significantly higher than for the hottest day in 2023 (east-facing: female 50.7%, male 50.3%; west-facing: female 9.4%, male 15.6%). The endotherm model predicted similar values (east-facing: female 49.7%, male 49.7%; west-facing: female 8.0%, male 8.1%; Table 2).

Based on the respirometry data for the Lillooet roosts, the daytime evaporative cooling requirements, as a percentage of M_b, were also considerably higher compared with those for the warmest day in 2023 (north-facing: female 25.5%, male 29.9%; south-facing: female 33.8%, male 36.7%). The endotherm model again predicted similar requirements (north-facing: female 22.5%, male 22.1%; south-facing: female 30.8%, male 30.9%; Table 2).

DISCUSSION

Understanding how temperate animals cope with extreme heat events is critical for the conservation of those populations in the face of global climate change, yet it remains an understudied aspect of their ecology. In one of the hottest areas of their Canadian range, *E. fuscus* occupy anthropogenic roosts that may exceed 48°C, which is similar to their experimental heat tolerance limits as demonstrated in the present study. We found that individuals tolerate T_b values exceeding 43°C, they can dissipate >200% of their MHP evaporatively, and females were more tolerant of the heat and significantly delayed the onset of evaporative cooling until higher temperatures compared with males, suggesting intra-specific differences in reproductive pressures during summer.

Although both sexes tolerated T_a=48°C, more individual females consistently tolerated the highest T_a values when compared with males (T_a=48°C: females n=6, males n=2 Table 1). Female *E. fuscus* prefer warmer roost sites when forming maternity colonies, a phenomenon that has been reported for many species (Kerth et al., 2001; Lausen and Barclay, 2003; Rensel et al., 2022). Furthermore, multiple individuals clustering in a maternity roost also increases T_{roost} (Willis and Brigham, 2007). Therefore, there should be selection pressure on females to possess higher heat tolerance limits than males. Females delaying active thermoregulation and the consequent increase in endogenous heat until 33.2°C (males displayed no inflection point in waRMR; Table 1) may be achieved by maintaining lower heart rates (Keicher et al., 2022). This would allow females to delay the use of evaporative cooling, and indeed females began increasing their waEWL at significantly higher T_a (37.8°C) than males (35.3°C; Table 1), implying that females prioritise the conservation of water reserves until relatively higher T_a.

The adaptation of delaying the onset of evaporative cooling and then rapidly using water to cool allows females to effectively conserve water, but still minimise the risk of lethal hyperthermia, and has been observed in other female bats (Czenze et al., 2022; de Mel et al., 2024; Noakes et al., 2021). By conserving their water reserves, females can allocate more water towards lactation while occupying warmer maternity colonies. The high waEWL rates we recorded in *E. fuscus* are comparable to those of the much larger common noctule (*Nyctalus noctula* ∼30 g M_b; Czenze et al., 2022). This allows *E. fuscus* to dissipate >200% of their metabolic heat production at their respective heat tolerance limits (Table S1, Fig. S1D). The abundance of standing water in the study area presumably allows *E. fuscus* to predictably replenish the water lost during the day and thereby sustain these high waEWL rates. Considering that these individuals were caught at water sources early in the evening, this suggests that close proximity to readily and predictably available water is critical for their survival.

Many artificial roosts are designed to maximise heat gain based on the observation that species select warmer roosts for increased growth rate of pups (Kerth et al., 2001; Lausen and Barclay, 2003). However, warm roosts, whether anthropogenic (e.g. Flaquer et al., 2014) or natural (e.g. Lausen et al., 2022a), may become unsuitably hot during high summer temperatures and heatwaves, such that individuals continuing to use them succumb to hyperthermia and/or dehydration (Bideguren et al., 2019; Flaquer et al., 2014). Aside from direct mortality, small endotherms exposed to chronic high T_a can experience sublethal effects (Catry et al., 2015; Kemp et al., 2020). These sublethal effects may manifest as diminished juvenile growth due to reduced milk production given its substantial water costs (Adams and Hayes, 2021; Huang et al., 2020; Kunz et al., 1983; Kurta et al., 1989). Therefore, owing to their altricial nature, juveniles face an increased risk of the deleterious effects of sustained high temperatures compared with adults (Alcalde et al., 2017; Griffiths, 2022). Further, the physiological costs of lactation on adult females during high T_a would increase risk of dehydration, leading to significant mass loss and potential pup abandonment (Mo et al., 2022; Zhao et al., 2020). Together, these sub-lethal effects may threaten long-term population viability even if adults can tolerate current heatwaves.

The biophysical endotherm model of NicheMapR has previously been used to estimate waEWL in southern yellow-billed hornbills (*Tokus leucomelas*) and the results mirrored those obtained from physiological measurements (R^2=0.86; Conradie et al., 2023). Our results from respirometry and the endotherm model were also similar (Table S4): the greatest discrepancy of waEWL between the methods was 7.8% M_b (males, LI north-facing box; 2021) and the smallest was 0.4% M_b (males, KL west-facing roost 2023). Although data on lethal dehydration limits of bats are scarce, Studier et al. (1970) reported that a loss of 22.8–32.3% M_b was lethal to half the study sample in five *Myotis* species. Both models indicate that during the 2023 study period, the evaporative cooling requirements in any roost would not have exceeded 16% M_b [females=2.5–10.8% M_b (respirometry), 2.1–9.1% M_b (endotherm model); males=4.0–15.3% M_b (respirometry), 2.2–9.2% M_b (endotherm model); Table 1]. However, during the 2021 heatwave, both methods indicate lethal dehydration risk in all roosts [females=25.5–50.7% M_b loss (respirometry), 22.5–49.7% M_b loss (endotherm model); males=29.9–50.3% M_b loss (respirometry), 22.1–49.7% M_b loss (endotherm model); Table 2], except for the shaded west-facing roost, which remained below 15.6%. The values here exceed those estimated for bats using identical methods for local heatwaves in Poland (23–34% M_b; Czenze et al., 2022) and Australia (females=36.5% M_b, males=47.3% M_b; de Mel et al., 2024). It is also important to note that our calculations were performed under dry air conditions and that higher humidity in natural air conditions will further increase heat stress by diminishing the evaporative cooling capacity of these bats (Coulson et al., 2025). Together, these results create a sobering image of the effects of an extreme heat event for bats occupying anthropogenic roosts, and underscore the urgency to understand species’ responses to heat for effective adaptive management.

Our results suggest that although temperatures may only briefly exceed the experimental heat tolerance, the prolonged exposure to temperatures >40°C (e.g. 11 h in the KL east-facing roost during the 2021 heatwave) is likely to be the direct source of mortality in this population during future. The cardinal direction of an artificial roost heavily influences its microclimate and consequently the evaporative cooling requirements of the individuals inside (Bideguren et al., 2019; Czenze et al., 2022; Mering and Chambers, 2014). The pattern we recorded of east- and south-facing roosts exhibiting higher temperature fluctuations has been recorded previously (Flaquer et al., 2014; Mering and Chambers, 2012). However, as we demonstrate, the cardinal direction makes little difference to the inhabitants of artificial roosts in full sun during heatwaves, and we suggest conservation managers to be purposeful in the construction of artificial roosts that provide a wide range of microclimate options (e.g. bat condos; Holroyd et al., 2023) or multiple roost structures that range from fully exposed to solar radiation, to full shade in a relatively small roosting area when possible. We also recommend using a variety of construction materials, with some structures built with low thermal conductance for stable microclimates in high heat, and other structures that heat and cool quickly. The latter structures are likely to be most suitable in the cool spring, when female bats benefit from roosts that warm quickly in the day and facilitate gestation (Lausen and Barclay, 2003). Creating multiple structures of varying microclimates is likely to most closely mimic roosts comprising a natural roosting area (Bideguren et al., 2019; Crawford and O’Keefe, 2021; Doty et al., 2016; Griffiths et al., 2022).

Conclusions

Our results demonstrate how efficient evaporative cooling in *E. fuscus* allows them to tolerate high T_a values and to persist in the hottest region of Canada while roosting in artificial roosts poorly insulated from heat. We also show intra-specific variation in the thermoregulatory strategies of *E. fuscus*, with females exhibiting higher tolerance and conservative use of water for evaporative cooling. These differences may be a result of disparate pressures pertaining to the reproductive ecologies of females and males. We show that biophysical models can accurately predict physiological responses to the heat and can be broadly applied to other endotherm taxa to help predict how species will respond to heatwaves in given areas or across their range. Finally, these results reiterate how inappropriately placed artificial roosts function as death-traps owing to overheating, and highlight the importance of managing habitat for sufficient variation in roost microclimates, including provision of safe and effective artificial roosts or roosting areas. Overheating of bat roosts is likely to increase in frequency with a changing climate, and bats will increasingly depend on cooler roost options. Thus, we urge future conservation plans to take advantage of ecophysiology and mechanistic modelling when designing adaptive management for target fauna.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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Data and resource availability

Data are available from Mendeley (doi:10.17632/nd72vx7ct3.1).

ECR Spotlight

This article has an associated ECR Spotlight interview with Ruvinda de Mel.

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Table S1. Estimated marginal means (emmeans) model output comparing means for each sex (F: female, M: male) within each treatment ambient temperature (T_a) for body temperature (Tb), whole animal resting metabolic rate (waRMR), whole animal evaporative water loss (waEWL), and the ratio of evaporative heat loss/metabolic heat production (EHL/MHP) for *E. fuscus*. Standard error (SE), degrees of freedom (df), lower critical limit (lower.CL), and upper critical limit (upper.CL), were reported, with significant differences being determined when critical limits do not overlap between the sex categories. Significant sex differences within each T_a are in bold.

T_b						
T_a	Sex	emmean	SE	df	lower.CL	upper.CL
32	F	34.9	0.222	138	34.5	35.4
	M	34.8	0.191	138	34.4	35.2
	Sex	emmean	SE	df	lower.CL	upper.CL
36	F	37.2	0.173	138	36.9	37.6
	M	37.1	0.153	138	36.8	37.4
	Sex	emmean	SE	df	lower.CL	upper.CL
40	F	39.5	0.148	138	39.2	39.8
	M	39.4	0.148	138	39.1	39.7
	Sex	emmean	SE	df	lower.CL	upper.CL
42	F	40.7	0.149	138	40.4	41
	M	40.5	0.16	138	40.2	40.8

	Sex	emmean	SE	df	lower.CL	upper.CL
44	F	41.8	0.16	138	41.5	42.1
	M	41.7	0.18	138	41.3	42
	Sex	emmean	SE	df	lower.CL	upper.CL
46	F	43.0	0.178	138	42.6	43.3
	M	42.8	0.204	138	42.4	43.2
	Sex	emmean	SE	df	lower.CL	upper.CL
48	F	44.1	0.202	138	43.7	44.5
	M	44.0	0.233	138	43.5	44.4

waRMR

T_a	Sex	emmean	SE	df	lower.CL	upper.CL
36	F	0.131	0.007	128	0.118	0.145
	M	0.121	0.005	128	0.111	0.131
	Sex	emmean	SE	df	lower.CL	upper.CL
40	F	0.168	0.005	128	0.158	0.179
	M	0.158	0.005	128	0.149	0.167
	Sex	emmean	SE	df	lower.CL	upper.CL
42	F	0.187	0.005	128	0.177	0.197
	M	0.177	0.005	128	0.166	0.187
	Sex	emmean	SE	df	lower.CL	upper.CL
44	F	0.205	0.005	128	0.195	0.216
	M	0.195	0.006	128	0.183	0.207
	Sex	emmean	SE	df	lower.CL	upper.CL
46	F	0.224	0.006	128	0.213	0.235
	M	0.214	0.007	128	0.200	0.227

	Sex	emmean	SE	df	lower.CL	upper.CL
48	F	0.242	0.007	128	0.23-	0.255
	M	0.232	0.008	128	0.216	0.248

waEWL

T_a	Sex	emmean	SE	df	lower.CL	upper.CL
36	F	0.003	0.034	98	-0.065	0.070
	M	0.082	0.027	98	0.028	0.135
	Sex	emmean	SE	df	lower.CL	upper.CL
40	**F**	**0.232**	**0.022**	**98**	**0.189**	**0.276**
	M	**0.312**	**0.018**	**98**	**0.276**	**0.346**
	Sex	emmean	SE	df	lower.CL	upper.CL
42	**F**	**0.346**	**0.019**	**98**	**0.310**	**0.383**
	M	**0.425**	**0.017**	**98**	**0.392**	**0.459**
	Sex	emmean	SE	df	lower.CL	upper.CL
44	F	0.461	0.018	98	0.426	0.496
	M	0.550	0.020	98	0.501	0.579
	Sex	emmean	SE	df	lower.CL	upper.CL
46	F	0.575	0.020	98	0.536	0.615
	M	0.654	0.025	98	0.606	0.703
	Sex	emmean	SE	df	lower.CL	upper.CL
48	F	0.690	0.025	98	0.640	0.739
	M	0.769	0.031	98	0.708	0.830

EHL/MHP

T_a	Sex	emmean	SE	df	lower.CL	upper.CL
36	**F**	**0.460**	**0.079**	**128**	**0.304**	**0.617**
	M	**0.922**	**0.059**	**128**	**0.805**	**1.039**

	Sex	emmean	SE	df	lower.CL	upper.CL
40	**F**	**0.930**	**0.063**	**128**	**0.804**	**1.055**
	M	**1.391**	**0.057**	**128**	**1.279**	**1.504**
	Sex	emmean	SE	df	lower.CL	upper.CL
42	**F**	**1.164**	**0.061**	**128**	**1.044**	**1.285**
	M	**1.626**	**0.063**	**128**	**1.502**	**1.750**
	Sex	emmean	SE	df	lower.CL	upper.CL
44	**F**	**1.399**	**0.063**	**128**	**1.275**	**1.523**
	M	**1.861**	**0.072**	**128**	**1.719**	**2.002**
	Sex	emmean	SE	df	lower.CL	upper.CL
46	**F**	**1.634**	**0.068**	**128**	**1.498**	**1.769**
	M	**2.096**	**0.083**	**128**	**1.932**	**2.260**
	Sex	emmean	SE	df	lower.CL	upper.CL
48	**F**	**1.868**	**0.077**	**128**	**1.715**	**2.022**
	M	**2.330**	**0.096**	**128**	**2.141**	**2.520**

Table S2. Linear mixed effect model output for body temperature (T_b; °C), whole animal resting metabolic rate (waRMR; W), whole animal evaporative water loss (waEWL; g/h), and the ratio of evaporative heat loss/metabolic heat production (EHL/MHP) of *E. fuscus* with respect to experimentally increasing ambient temperature (T_a; °C), sex, and body mass (mass; g). The reference category for sex was male. Bold indicates significance at α = 0.05.

Dependent Variable	Fixed Effect	Estimate	Degrees of Freedom	t	P
T_b	Intercept	16.54	134.07	23.27	<0.0001
	T_a	0.57	125.95	32.66	<0.0001
waRMR	Intercept	-0.33	114.53	-7.02	<0.0001
	T_a	0.01	109.22	11.15	<0.0001
	Sex (Male)	0.16	117.45	2.91	0.004
	T_a *Sex (Male)	-0.004	109.69	-3.16	0.002
waEWL	Intercept	-2.63	81.92	-12.56	<0.0001
	T_a	0.07	79.11	14.76	<0.0001
	Sex (Male)	0.87	82.85	3.39	0.001
	T_a *Sex (Male)	-0.02	79.16	-3.11	0.003
EHL/MHP	Intercept	-5.03	116.13	-9.35	<0.0001
	T_a	0.15	108.98	11.77	<0.0001
	Sex (Male)	1.81	119.58	2.92	0.004
	T_a *Sex (Male)	-0.03	109.32	-2.25	0.030

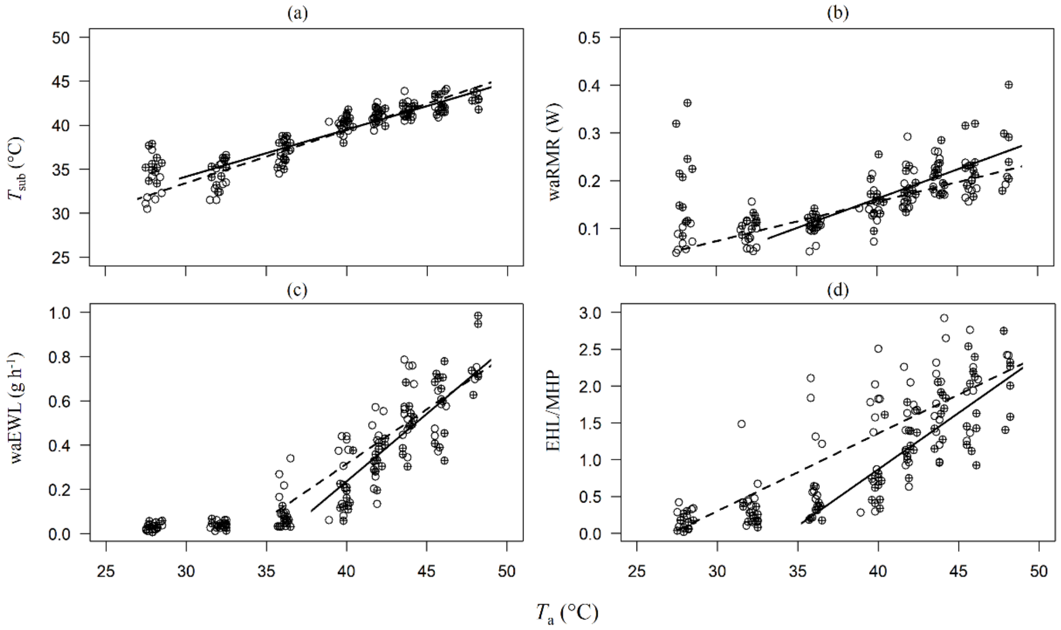

Fig. S1. (a) Subcutaneous body temperature (T_{sub}), (b) whole animal resting metabolic rate (waRMR), (c) whole animal evaporative water loss (waEWL) and (d) evaporative heat loss (EHL)/metabolic heat production (MHP) at high air temperatures (T_a (°C)) of male ($n = 11$) and female ($n = 11$) big brown bats (*Eptesicus fuscus*) from Lillooet B.C., Canada. Dashed and solid lines represent regressions for males and females respectively above inflection points (Table 1). Open circles indicate males and filled circles indicate females. Note absence of an inflection point in T_{sub}, waRMR and EHL/MHP in males.

Supplementary Materials and Methods

Endotherm model

We set wind speed (VEL) and relative humidity (RH) to match the conditions of the respirometry chamber. The core temperature (TC), minimum core temperature (TC_MIN) and maximum core temperature (TC_MAX) was set using the T_b values measured during the respirometry trials. The SHAPE, SHAPE_B and SHAPE_B_MAX values were set to fit *E. fuscus*. The base skin wetness (PCTWET) was set assuming only the nose region of the bat was wet initially. Maximum skin wetness (PCTWET_MAX) was set for the bat licking its arms while intervals by which skin wetness is increased (%) (PCTWET_INC) was set to match our respirometry data. Increment by which panting is increased (PANT_INC), maximum panting rate (PANT_MAX) and multiplier on basal metabolic rate at maximum panting level (PANT_MULT) was adjusted to fit our respirometry data. Thermoregulation mode (TREGMODE) was adjusted to reflect the thermoregulatory patterns of bats and TORPOR was set to 1 as most individuals entered or was beginning to enter torpor at 28 °C. All other values were set to default. We compared the endotherm model output for each individual bat for its experimental T_as and compared with the respirometry data using R2, Pearson correlation and Root mean square deviation tests (Table S4).

Table S3. Variables used in the endotherm model to calculate evaporative water loss for *Eptesicus fuscus* (females and males).

Variable	*Eptesicus fuscus* (female)	*Eptesicus fuscus (male)*
VEL: Wind speed (m/s)	0.5	0.5
RH: Relative humidity (%)	3	3
TC: Core temperature (°C)	36	36
TC_MAX: Maximum core temp (°C)	43	43

TC_INC: Increment by which TC is elevated (°C)	0.1	0.1
AMASS: Body mass (g)	20.7	19.6
SHAPE_B	1.1	1.1
SHAPE_B_MAX: maximum ratio of length to width/depth	5	5
UNCURL	0.1	0.1
SHAPE	4	4
SAMODE	2	2
DHAIRD: Hair diameter, dorsal (m)	1.2E-05	1.2E-05
DHAIRV: Hair diameter, ventral (m)	8E-06	8E-06
LHAIRD: Hair length, dorsal (m)	7.7E-03	8.3E-03
LHAIRDV: Hair length, ventral (m)	7.5E-03	7.3E-03
RHOD: Hair density, dorsal (1/m2)	1.83E+09	1.5E+09
RHOV: Hair density, ventral (1/m2)	1.52E+09	1.81E+09
: Fur reflectivity, dorsal	0.248	0.248
: Fur reflectivity, ventral	0.351	0.351
ZFURD: Fur depth, dorsal (m)	4E-03	4E-03
ZFURV: Fur depth, ventral (m)	4E-03	4E-03
PCTWET: base skin wetness (%)	0.5	0.5
PCTWET_MAX: Maximum skin wetness (%)	10	10
PCTWET_INC: intervals by which skin wetness is increased (%)	0.05	0.05
PCTBAREVAP: surface area for evaporation that is skin	10	10
Q10	2.5	2.5
QBASAL: Basal heat generation (W)	(70 * AMASS ^ 0.75) * (4.185 / (24 * 3.6)) / 2	(70 * AMASS ^ 0.75) * (4.185 / (24 * 3.6)) / 2
DELTAR: offset between air temperature and breath (°C)	5	5
EXTREF: O_2 extraction efficiency	25	25
PANT_INC: increment by which panting is increased	0.05	0.0.5
PANT_MAX: Maximum panting rate	7	7
PANT_MULT: multiplier on basal metabolic rate at maximum panting level	1	1
AK1: initial thermal conductivity of flesh	0.412	0.412
AK1_INC: increment by which AK1 is increased per iteration	0.1	0.1
TREGMODE	2	2
TORPOR	1	1
AK1_MAX: maximum flesh conductivity (W/mK)	2.8	2.8
TC_MIN: Minimum core temperature (°C)	8	8

Table S4. Results of the correlation tests between respirometry results and endotherm model predictions for female and male big brown bats (*Eptesicus fuscus*). Tests included R^2, Pearson correlation and Root mean square deviation (RMSD).

Sex	Variable	R^2	Pearson's Correlation					RMSD
			r	t	df	p	CI	
Female	T_b (°C)	0.845	0.919	20.643	78	< 2.2e-16	0.877 0.948	1.958
Female	waRMR (W)	0.636	0.797	11.594	77	< 2.2e-16	0.699 0.865	0.042
Female	waEWL (H_2O g/h)	0.931	0.965	32.274	77	< 2.2e-16	0.945 0.977	0.079
Male	T_b (°C)	0.887	0.942	23.386	70	< 2.2e-16	0.908 0.963	1.693
Male	waRMR (W)	0.574	0.757	9.6367	69	2.097e-14	0.637 0.842	0.044
Male	waEWL (H_2O g/h)	0.754	0.868	14.651	70	< 2.2e-16	0.797 0.916	0.145