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Research Article

Heat tolerance of female Yuma Myotis (*Myotis yumanensis*) in the hottest part of their Canadian range

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Abstract

High ambient temperatures (T_a) pose a significant challenge to small endotherms that rely on limited water reserves to thermoregulate via evaporative cooling and are exacerbated for species inhabiting poorly insulated microsites. We used flow-through respirometry to investigate the thermoregulatory strategies and capacities of nonreproductive female Yuma Myotis (*Myotis yumanensis*) from one of the hottest areas of their range. Based on our physiological data and the NicheMapR biophysical model, we also calculated the evaporative cooling requirements and dehydration risk of these females when roosting in artificial structures during a heatwave in 2021 (modeled results) and during the warmest day of our study (measured results). Our results indicated that non-reproductive female *M. yumanensis* can tolerate a maximum T_a of 44 °C in dry air, adopting a thermoconforming strategy, possibly due to evaporative cooling restrictions imposed by their low water reserves. Our results allude to *M. yumanensis* using thermal gradients within roosts to avoid high roost temperatures and demonstrate that bats roosting in a South-facing artificial roost exposed to high solar radiation would have faced lethal dehydration during the 2021 heatwave. Our results underscore the importance of natural roosts in the landscape and highlight designing artificial roosts that offer a wide thermal gradient to allow the persistence of this species during current extreme climatic events.

Keywords bats, conservation, evaporative cooling, heat tolerance, heat waves, *Myotis yumanensis*, roosts, thermoregulation

Tolerancia a las altas temperaturas de las hembras de Yuma Myotis (*Myotis yumanensis*) en la zonas más cálidas de su rango de dispersión en Canadá

Resumen

Las altas temperaturas ambientales (Ta) representan un desafío significativo para los animales pequeños endotérmicos que dependen de reservas limitadas de agua para su termorregulación mediante el enfriamiento por evaporación, problema agravado en especies que habitan microhábitats con pobre aislamiento térmico. En este estudio, utilizamos respirometría de flujo continuo para investigar las estrategias y capacidades termorreguladoras de las hembras en estado no reproductivo del murciélago Myotis de Yuma (*Myotis yumanensis*) provenientes de una de las zonas más cálidas de su rango espacial en Canadá. También calculamos los requerimientos de enfriamiento evaporativo y el riesgo de deshidratación de estas hembras cuando se refugiaron en estructuras artificiales durante la ola de calor en 2021 (resultados modelados) y durante el día más cálido de nuestro estudio (resultados medidos), a partir de datos fisiológicos y del modelo biofísico NicheMapR. Nuestros resultados indican que las hembras no reproductivas de *M. yumanensis* pueden tolerar una Ta máxima de hasta 44 °C en aire seco. Para ello y por medio de una estrategia de termoconformidad, regulan su temperatura corporal con la del medio ambiente, probablemente por las restricciones al enfriamiento evaporativo que les impone sus bajas reservas de agua. Nuestros hallazgos sugieren que *M. yumanensis* utiliza gradientes térmicos dentro de los refugios para evitar temperaturas excesivamente

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altas, y demuestran que los murciélagos que se refugiaron en un lugares artificiales orientados al sur, y por lo tanto expuesto a una elevada radiación solar, habrían enfrentado deshidratación letal durante la ola de calor de 2021. Nuestros resultados subrayan la importancia de los refugios naturales en el paisaje y destacan la necesidad de diseñar refugios artificiales que ofrezcan un amplio gradiente térmico, con el fin de permitir la persistencia de esta especie ante los actuales eventos climáticos extremos

Palabras clave conservación de la especie *Myotis yumanensis*, enfriamiento por evaporación, murciélagos, olas de calor, refugios, termorregulación, tolerancia al calor

For small endotherms living in hot environments, heat dissipation presents a challenge that can be mitigated using convective, conductive, radiative, and evaporative heat loss until ambient temperatures (T_a) increase above body temperature (T_b), at which point evaporative cooling becomes the only means available (Tattersall et al. 2012). Some species display a remarkably high evaporative cooling capacity [the ratio of maximum evaporative heat loss/metabolic heat production (EHL/MHP)] allowing them to tolerate extreme T_as. For example, Namaqua sandgrouse (*Pterocles namaqua;* ~170 g) and rufous-cheeked nightjars (*Caprimulgus rufigena;* ~52 g) inhabiting arid environments can achieve maximum evaporative cooling capacity (EHL/MHP) > 5, meaning their evaporative water loss is sufficient to dissipate 500% of their metabolic heat production (O'Connor et al. 2017; Czenze et al. 2021a). A contrasting strategy is employed by some very small arid-adapted endotherms where, rather than dissipate the heat evaporatively, they allow skin temperature (which can differ from T_b) to increase up to 45.8 °C (Bondarenco et al. 2014). Tolerating elevated T_b (hyperthermia), *in lieu* of evaporative cooling, allows arid-adapted species to conserve limited water reserves. However, even within a species, differences between habitats and reproductive ecologies can lead to differences in thermoregulatory capacities (Noakes et al. 2016; de Mel et al. 2024, 2025a).

Many bats exhibit sex differences in their roost temperature preferences with reproductive females often selecting warmer roosts to facilitate offspring development (Kerth et al. 2001; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Rensel et al. 2023), but warmer maternity roosts are more vulnerable to overheating (Flaquer et al. 2014; Bideguren et al. 2019; Pruvot et al. 2019; Crawford and O'Keefe 2021; Griffiths 2022). The threat of overheating in these inherently warm roosts is exacerbated during adverse weather events like heatwaves (Flaquer et al. 2014; Griffiths 2022). Climate change is increasing the frequency and intensity of heatwaves (Viceto et al. 2019; IPCC 2021) that can push bats beyond their lethal thresholds, with mortality most often reported from the Southern hemisphere but also from some temperate Northern hemisphere areas (Welbergen et al. 2008; Ratnayake et al. 2019; Crawford et al. 2022; Griffiths 2022). For example, several observations in British Columbia, Canada suggest that *Myotis* bats are threatened by mass mortality events during high temperatures (Lausen et al. 2022). Additionally, in Spain *Pipistrelle* bats were incapacitated during high temperatures (Flaquer et al. 2014). Despite the urgency to better understand the responses of animals in temperate regions to changing climates, there are limited data quantifying their vulnerability to high T_a in these regions (e.g., Noakes et al. 2021; Czenze et al. 2022; de Mel et al. 2025b).

The Fraser Canyon in southern British Columbia supports a high diversity of bats for Canada, but this area experiences frequent forest fires and summer temperatures >40 °C. In western Canada, female Yuma Myotis (*Myotis yumanensis)* choose maternity roosts with a larger temperature gradient in a variety of natural and anthropogenic structures, whereas males typically roost solitarily in cooler roosts (Lausen et al. 2022). Yuma Myotis are not currently a species of conservation concern, but they represent a good model species to evaluate the potential impacts of climate change because they are similar in size and ecology to endangered *M. lucifugus*, *M. sodalis*, and *M. septentrionalis*. The Fraser Canyon population experiences some of the highest maximum summer T_a in the country (Environment and Climate Change Canada 2025) and may be exposed to substantial selection pressure for efficient thermoregulatory performance. There are currently no data on heat tolerance for *Myotis* species from this region. Amongst North American *Myotis*, only *M. lucifugus* has been studied from a heat tolerance context and that work was in a considerably cooler location (Noakes et al. 2021). Gaining a greater understanding of the heat tolerance limits (HTL; the highest T_a tolerable before the onset of severe hyperthermia and/or dehydration) of *M. yumanensis* in this location would allow for focused and effective conservation measures for a variety of temperate bat species.

We used flow-through respirometry to quantify the thermal physiology of a population of female *M. yumanensis* from the Fraser Canyon to investigate their vulnerability to heat waves. Given their propensity to roost in poorly insulated artificial roosts exposed to regular high summer temperatures combined with their low body mass (~6 g) and consequent low body water reserves, we predicted that female *M. yumanensis* would adopt a more thermoconforming strategy as opposed to relying on high rates of evaporative cooling.

Methods

Ethics approval

This work was approved by the animal ethics committees of the University of New England (ARA22-051) and University of Regina (AUP23-03). Fieldwork was conducted 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

Our study was conducted in and around Lillooet, British Columbia (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 BC, consists of mountainous valleys containing woodlands dominated by a variety of pine (*Pinus* spp.) and fir (*Pseudotsuga* spp.) trees (Brayshaw 1996). Our study area was adjacent to the Fraser River and numerous other standing water sources including lakes and artificial reservoirs. This region of the Fraser Canyon is characterized by steep rock/mudstone canyon walls, with the surrounding area varying widely in elevation; our sites were mostly within ~200 m of the Fraser River in mixed grassland and pine habitat.

Summer temperatures in the study area are among the highest in Canada (Environment and Climate Change Canada 2025), having reached a Canadian record maximum of 49 °C on 29 June, 2021 during a heatwave (Eberle et al. 2022; Abbasi 2024). The projected number of heatwaves (3 or more consecutive days with temperatures > 30 °C) in Lillooet has increased from 2.0 to 3.5 per year since 2005 (Climate Atlas of Canada 2025). In addition to the increase in frequency of heatwaves, this region has also experienced increased drought conditions in the past 2 decades (Government of Canada 2025).

Bat capture and handling

From 27 July 2023 to 28 August 2023, we captured *M. yumanensis* (7 females) for respirometry experiments using mist nets and harp traps. Bats were aged, and only non-reproductive adult females were kept for use in experiments. We transported bats in individual cloth bags to the field laboratory and held them in a quiet, temperature-controlled, darkened room for < 24 h. Bats were offered water using a pipette and fed mealworm larvae (*Tenebrio molitor*) until they gained ≥ 10% body mass. To measure subcutaneous temperature (T_{sub}), individuals had a temperature-sensitive PIT-tag (Biotherm, Biomark, Boise, Idaho, United States, accuracy ± 0.5 °C) implanted subcutaneously between the scapulae on the night of capture after being fed. Gas exchange measurements began the morning after initial capture > 9 h since capture, during their normal rest phase period.

Gas exchange measurements

We used a flow-through respirometry system to measure carbon dioxide production ($\dot{V}CO_2$) and evaporative water loss (EWL). Airtight respirometry chambers were constructed from 0.5 L glass jars and included a wire mesh platform elevated ~2 cm above a ~1 cm layer of mineral oil. The mineral oil trapped any excreta during the experiment. The walls and top of the chamber were covered in mesh to allow bats to crawl, hang, and assume natural roosting postures. The respirometry chamber was placed in a modified warming/cooling environmental chamber (14 liters; WAECO mobile refrigeration unit, 14 L, TC-14FL, VIC, Australia), the T_a of which could be controlled manually. The T_{sub} readings from PIT-tags were recorded every 10 sec during respirometry using a reader system attached to a racket antenna placed adjacent to the respirometry chamber (HPR+, Biomark, Boise, Idaho, United States).

Air was supplied using a pump (Simple deluxe, Model: GPUMPAIR65, California, United States) with a maximum capacity of 65 L min^{-1}. Atmospheric air was passed through a column of silica to scrub water before being split into a baseline (fed directly into the analyzer) and a chamber channel, which was fed into the jar containing the individual. Aalborg rotameters (Aalborg Instruments & Controls, Inc., Orangeburg, New York, United States) were used to regulate both baseline and chamber airflow, which were then measured using a mass flow meter (0.5 to 5 SLPM, Alicat Scientific Inc., Tucson, Arizona, United States). The air inlet was connected to a piece of Bev-A-Line IV tubing (Thermoplastic Processes Inc., Georgetown, Delaware, United States) that supplied air below the wire mesh platform, while the air outlet was placed on the lid of the jar to maximize air mixing. The flow rate was adjusted as necessary depending on the behavior of the bat at each T_a. Flow rates ranged from 1.3 to 2.5 L min^{-1} to ensure that humidity was regulated below 8 ppt. $\dot{V}CO_2$ and H_2O were measured from the baseline and chamber excurrent air pulled through a Field Metabolic System (FMS, Sable Systems, North Las Vegas, Nevada, United States). The CO_2 sensor of the FMS was zeroed using nitrogen and spanned using a known CO_2 concentration (2,000 ppm). The H_2O sensor of the FMS was spanned using air saturated with H_2O at 2 dew point temperatures and zeroed using nitrogen following the protocol of Marom et al. (2006). All gas measurements were recorded at 5 s intervals using Expedata software (Sable Systems, North Las Vegas, Nevada, United States).

Experimental protocol

Experimental runs, lasting 3 to 5 h, were conducted between 07:00 and 18:00 following Czenze et al. (2022) and Freeman et al. (2022). Bats were exposed to incrementally higher experimental T_a in a stepped profile. We used this method as it allows for the collection of data indistinguishable from steady-state measurements, without exposing individuals to prolonged periods of potentially dangerously high temperatures (Short et al. 2022).

Individuals were acclimated for 1 h at T_a = 28 °C before we recorded any physiological values. The T_a from 28 °C was increased in 4 °C increments until 40 °C. After 40 °C, experimental T_a was increased in 2 °C increments. Individuals spent a minimum of 20 min at each experimental T_a before measurements were obtained. We waited for T_{sub}, $\dot{V}CO_2$, and EWL to stabilize at constant values before we sampled $\dot{V}CO_2$ and H_2O for 5 min. Individuals were continuously monitored using an infra-red video camera and trials were terminated immediately when an individual displayed restless behavior (e.g., chewing on the mesh) indicating that it had reached its HTL. Bats were weighed and offered water immediately after removal from the chamber, placed back in cloth bags in the darkened room, and allowed to rest at room temperature. Mealworms and water were offered 1 h later, and then again before the bat was released at the site of capture that night. All experimental bats were successfully released. This same protocol has been used to measure heat tolerance and evaporative cooling in other bat species (Czenze et al. 2021b, 2022; Noakes et al. 2021; de Mel et al. 2024), birds (Czenze et al. 2020, 2021a), and rodents (van Jaarsveld et al. 2021), resulting in no significant loss of M_b in recaptured individuals (Czenze et al. 2021b).

Statistical analysis

Analyzer drift and lag were corrected using Expedata software. The lowest stable 5 min measures of CO_2 and water vapor at each T_a were used to calculate $\dot{V}CO_2$ and EWL, assuming 0.803 mg H_2O ml^{-1} vapor using equations 9.5 and 9.6 (Lighton 2008). Since the gut passage times of most insectivorous bats are < 5 h (Grant 1988; Roswag et al. 2012) we considered individuals to be post-absorptive; thus, resting metabolic rate (RMR) was calculated from $\dot{V}CO_2$ assuming a respiratory exchange ratio (RER) = 0.71 (Walsberg and Wolf 1995) and $\dot{V}CO_2$ was converted to metabolic rate (W) assuming 27.8 J CO_2 ml^{-1} (Withers 1992). Resting metabolic rate was calculated for each individual. Rates of EWL were converted to evaporative heat loss (EHL; W) assuming a latent heat of vaporization of water of 2.406 J/mg at 40 °C (Tracy et al. 2010). We used a metric of evaporative cooling capacity by dividing EHL by metabolic heat production (MHP; W; EHL/MHP). We also calculated evaporative scope (maximum EWL/minimum EWL) to allow for comparison with other published data.

All statistical analyses were performed in R 4.2.3 (R Core Team 2021). Inflection points were identified for each physiological response in T_{sub}, RMR, EWL, and EHL/MHP in relation to experimental T_a (package: segmented.lme; Muggeo 2016). The segmented regressions were compared to simple linear regressions using ANOVA. The physiological response of T_{sub}, RMR, EWL, and EHL/MHP to experimental T_a above inflection points, was tested using linear mixed effect models (package "NLME"; Pinheiro et al. 2009). Bat ID was included as a random effect in the models to account for repeated measurements from individuals. We compared the global models to reduced models and, based on null hypothesis testing, selected the most appropriate predictor variables to retain in the final model. We chose the model with the lowest AIC value, and if the AIC values did not differ by >2 we chose the most parsimonious model (Supplementary Data SD2; Tredennick et al. 2021; Beilke and O'Keefe 2023). In all analyses, significance was assigned at $\alpha = 0.05$ or, in case of inflection points, where 95% confidence intervals did not overlap.

Roost temperature recordings and evaporative water requirement calculations

From 29 July 2023 to 20 September 2023, we recorded the roost temperatures (T_{roost}) of 3 *M. yumanensis* roosts using iButtons (Thermochron iButton, Maxim Integrated, San Jose, California, United States, logging interval = 60 min). Two roosts were in the opposite walls of an abandoned barn at Kwotlenemo Lake (KL North-facing and KL South-facing; ~920 m asl), while the third was in Lillooet (LI) 6 km away at a lower elevation (~550 m asl) in the wall of a gas station. At each site, T_a was also recorded using an iButton deployed in the shade at a height of 2 m, within 50 m of the roost. At all 3 roosts, we deployed the iButtons > 25 cm from where most of the bats were roosting (determined by accumulation of guano on the floor beneath) to avoid the T_b of the bats influencing the iButton readings.

We predicted the temperature of each roost during the 2021 heatwave using the linear regression equation of the respective T_{roost} and T_a of the site. Given that Kwotlenemo Lake is outside the coverage of the Lillooet Environment Canada weather station, we estimated the T_a for the relevant time period with the ERA5 dataset via the "NicheMapR" package (Klinges et al. 2022). For the evaporative water requirement calculations, we used the hottest day recorded during our study period (site-specific, 14 August for Kwotlenemo Lake and 16 August for Lillooet) and for 29 June 2021 (at both sites), coinciding with the heatwave of 2021.

We used 2 methods to calculate the evaporative water requirements for female *M. yumanensis*. The first method used the regressions of the relationship between T_a and waEWL obtained from our respirometry experiments and the mean body mass of the females in the experiment. We used these data in conjunction with T_{roost} to calculate evaporative water requirements. We present the results as the mass of H_2O as a percentage of body mass required for bats to maintain thermal balance while roosting, following Czenze et al. (2022) and de Mel et al. (2024).

The second method used was the endotherm model in the "NicheMapR" biophysical modelling package (Supplementary Data SD1; Kearney et al. 2021). The suite of subroutines of the endotherm model uses species-specific morphological and physiological inputs to solve coupled energy and water budget equations. To parameterize the model, we measured hair properties of museum specimens using a dissecting microscope (Olympus SZX7, Olympus Corp., Tokyo, Japan). We measured the length and diameter (at the base) of 10 hairs on the dorsal (intrascapular; length = 8.1 ± 1.8 E-03 m, diameter ~ 5E-06 m) and ventral (abdominal, length = 6.8 ± 1.6 E-03 m, diameter ~ 5E-06 m) surface of 5 individuals and calculated the density of hairs on both surfaces (dorsal = 1.1 ± 0.1 E + 09/m^2, ventral = 1.34 ± 0.4 E + 09/m^2) for each individual. Due to the unavailability of *M. yumanensis* specimens, we used specimens of *M. lucifugus* as a proxy. These 2 species share similar physical characteristics such as mass (*M. yumanensis* = 5.5 g, *M. lucifugus* = 6.7 g), total length (*M. yumanensis* = 82 mm, *M. lucifugus* = 86 mm), and forearm length (*M. yumanensis* = 34.7 mm, *M. lucifugus* = 36.5 mm; Lausen et al. 2022), and occupy similar niches—thus we assumed that the hair properties of *M. yumanensis* and *M. lucifugus* would be similar. We used the average of these calculations in the final model. All parameters used in the endotherm model calculations are given in Supplementary Data SD2. By using Pearson correlation, Root mean square deviation (RMSD) and R^2 tests, we formally compared the correlation between the results of the regression models and endotherm models for T_b, waRMR and waEWL following de Mel et al. (2025b; Supplementary Data SD3).

Results

The majority of female *M. yumanensis* measured (5 of 7) tolerated a maximum T_a of 44 °C with a single individual tolerating T_a = 46 °C, and 1 only at T_a = 42 °C. Only the physiological relationship between T_b and T_a exhibited a distinct inflection point (28.6 °C; Table 1) while all other physiological variables were best fit with a simple linear regression (Fig. 1). The final reduced mixed effect model for all physiological variables only included T_a as a significant predictor variable (Supplementary Data SD4).

The highest mean T_b achieved was 44.0 °C with a single individual reaching 44.7 °C at T_a = 44 °C (Fig. 2a). The highest RMR achieved was 0.14 W with a single individual achieving an absolute maximum RMR of 0.19 W at T_a = 44 °C (Fig. 2b). The EWL of *M. yumanensis* increased linearly with increasing T_a. The EWL rate at T_a = 40 °C was ~0.10 g h^{-1}, with the maximum EWL being 0.13 g h^{-1}. The absolute maximum EWL achieved was 0.18 g h^{-1} by a single individual exposed to 44 °C (Fig. 1c). There was no discernible inflection point for EHL/MHP ~ T_a, and the maximum value calculated was 0.63 (Table 1), indicating that the bats we studied did not dissipate > 100% of MHP at high T_a (Fig. 2d).

Table 1 Summary of thermoregulatory performance variables as a function of air temperature (T_a; °C) in 7 non-reproductive female *Myotis yumanensis* from Lillooet, BC, Canada (27 July 2023 to 28 August 2023).

		Mean
	Mass (g)	5.8 ± 0.7
T_a (°C)	Max bin T_a	46 (1)
		44 (5)
T_b (°C)	Min T_b	35.4 ± 0.9
	Inflection T_a	28.6
	95% Conf int	27.9, 29.4
	Max T_b	44.7 (1)
		44.0 (5)
waRMR (W)	Min waRMR	0.08 ± 0.03
	Inflection T_a	na
	Max waRMR	0.19 (1)
		0.14 ± 0.03 (5)
	Max waRMR/Min waRMR	1.75
waEWL (g/h)	Min waEWL	0.03 ± 0.01 (7)
	Inflection T_a	na
	Max EWL	0.18 (1)
		0.13 ± 0.03 (5)
	Max waEWL/Min waEWL	4.3
EHL/MHP	Min EHL/MHP	0.28 ± 0.10 (7)
	Inflection T_a	na
	Max EHL/MHP	0.97 (1)
		0.63 ± 0.09 (5)

Thermoregulatory variables include subcutaneous temperature (T_{sub}; °C), resting metabolic rate (RMR; W), evaporative water loss (EWL; g h^{-1}), and evaporative heat loss/metabolic heat production (EHL/MHP). "Max" and "Min" indicate maximum and minimum values for each variable, respectively. Mean values are reported ± SD with sample sizes in parentheses. Max, bin T_a (°C) = maximum 1 °C-width bin of T_a at which we recorded stable measurements. Inflection point of T_b reported with 95% confidence intervals.

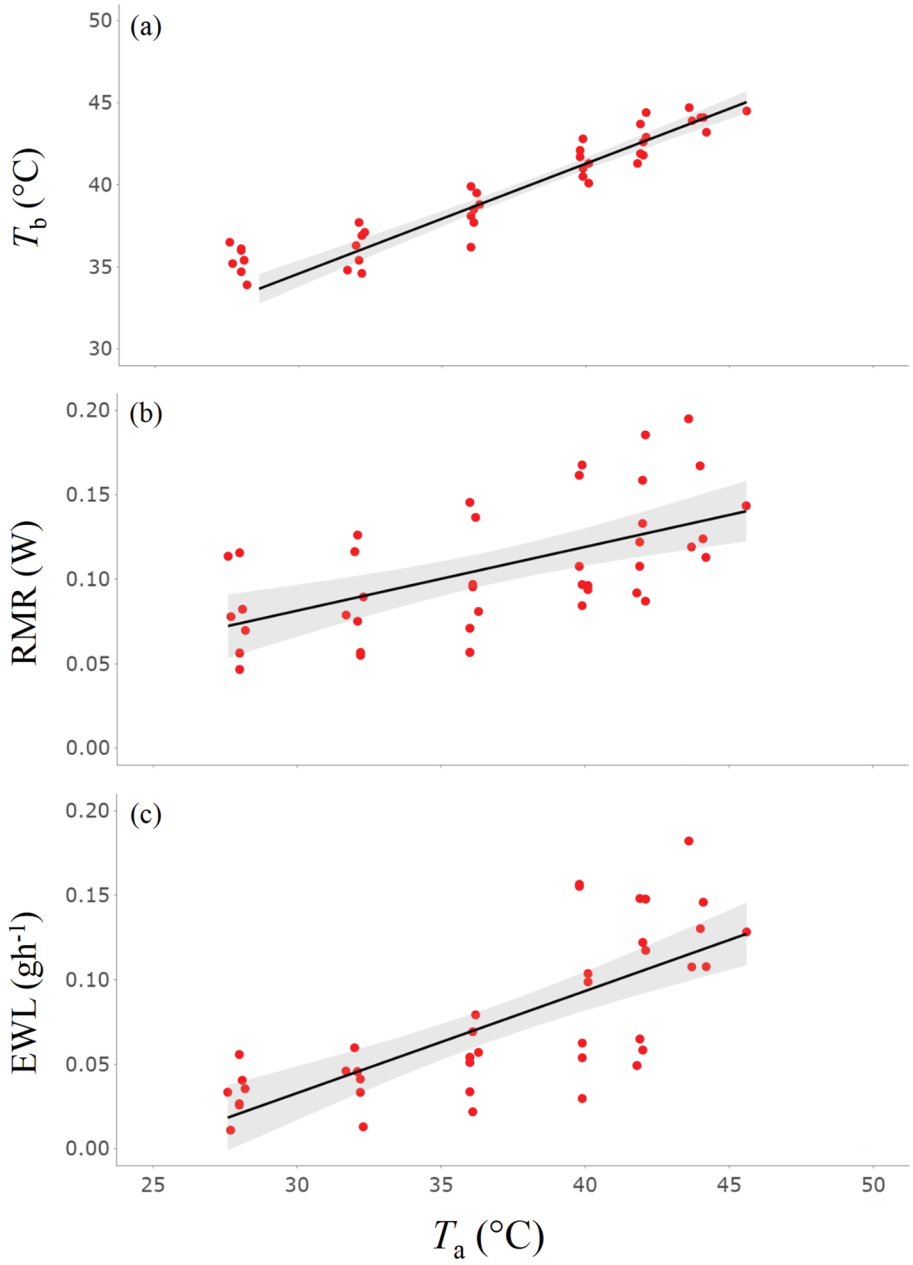

Fig. 1 (a) Subcutaneous body temperature (T_b), (b) resting metabolic rate (RMR), and (c) evaporative water loss (EWL at high air temperatures (T_a) for 7 non-reproductive female Yuma Myotis (*Myotis yumanensis*) from Lillooet BC, Canada. Solid lines and shaded grey area represent regressions and 95% confidence intervals respectively (in the case of $T_b \sim T_a$ regression line fitted to data above inflection points; Table 1).

Evaporative water requirement calculations

The waEWL ~ T_a results from our respirometry experiments and endotherm model were highly correlated (Pearson correlation coefficient: $r(36) = 0.79$, $P < 0.001$; RMSD = 0.03; $R^2 = 0.63$; Fig. 2). During 14 August 2023 at the Kwotlenemo lake site, we recorded the highest T_a of the study period (37 °C; T_a range = 14.5 to 37.0 °C). This maximum T_a coincided with KL North-facing T_{roost} = 41.5 °C, and KL South-facing T_{roost} = 50.0 °C. In the KL South-facing roost, T_{roost} remained > 40 °C for 3 h in late afternoon when bats were present. The evaporative water requirement for a female roosting in the KL North-facing roost was 0.56 g (9.62% of M_b) H_2O and 0.76 g (12.97% of M_b) for the KL South-facing roost. The endotherm model predicted similar results where a female roosting in the KL North-facing roost would have required 0.36 g (6.19% of M_b) H_2O for evaporative cooling, while a female roosting in the KL South-facing roost would have required 0.89 g (15.45% of M_b) H_2O for evaporative cooling.

At the Lillooet site, the highest T_a (39.3 °C) was recorded on 16 August (T_a range = 22.7 to 39.3 °C), with the LI T_{roost} = 46.0 °C. The T_{roost} remained > 40 °C for 5 h in the afternoon and the evaporative water requirement for a female roosting in LI roost was 1.05 g (18.03% of M_b) H_2O. The endotherm model predicted similar results where a female roosting in the LI roost would have required 0.99 g (17.0% of M_b) H_2O for evaporative cooling.

Evaporative water requirements during the heatwave of 2021

During 29 June 2021, the highest T_a recorded at the Kwotlenemo Lake site was 39.4 °C (T_a range = 18.5 to 39.4 °C). Under these conditions the

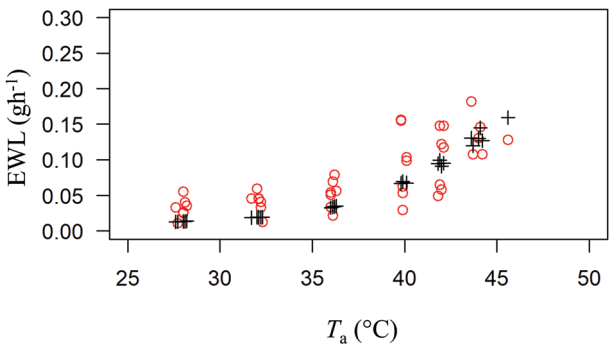

Fig. 2 Experimental measurements of evaporative water loss (EWL; H_2O g h^{-1}; circles) and results from endotherm model predictions (black crosses) for 7 non-reproductive female Yuma Myotis (*Myotis yumanensis*) at high ambient temperatures T_a.

KL North-facing roost would have reached T_{roost} = 38.0 °C while the KL South-facing roost reached T_{roost} = 42.0 °C and remained > 40 °C for approximately 5 h in the afternoon. The evaporative water requirement for a female roosting in the KL North-facing roost would have been 0.61 g (10.43% of M_b) and 0.81 g (13.93% of M_b) for a female in the South-facing roost. The endotherm model predicted that a female roosting in the KL North-facing roost would have required 0.34 g (5.85% of M_b) H_2O for evaporative cooling while a female roosting in the KL South-facing roost would have required 0.59 g (10.33% of M_b) of H_2O.

At the Lillooet site, the highest T_a recorded was 42.6 °C (T_a range = 21.5 to 42.6 °C). The LI roost would have reached a T_{roost} = 47.7 °C (T_a range = 24.3–47.7 °C) and the T_{roost} would have remained > 40 °C for approximately 10 h. The evaporative water requirement for a female roosting in the LI roost would have been 1.47 g (25.21% of M_b) H_2O. The endotherm model predicted that a female roosting in the LI roost would have required 1.73 g (29.79% of M_b) H_2O for evaporative cooling.

Discussion

Understanding the complex dynamic between the T_a, T_{roost}, and the thermoregulatory patterns of endotherms is critical for devising effective conservation strategies. Our results indicate that female *M. yumanensis* adopt a thermoconforming strategy that allows for an increase in T_b while maximizing the conservation of water. As hypothesized, this trade-off appears to reflect physiological constraints imposed by limited water turnover and low body mass, rather than an adaptive enhancement of heat tolerance per se. The absence of inflection points in evaporative water loss and a low EHL/MHP ratio further reinforces the notion that these bats are unable to sustain high rates of evaporative cooling, even when exposed to potentially lethal roost temperatures.

There were no detectable inflection points for any of the physiological variables in *M. yumanensis* except for T_b (Table 1; Fig. 2). However, even this inflection point was only 0.6 °C above the lowest experimental T_a. Therefore, it appears that the *M. yumanensis* we studied allowed T_b to increase undefended. For instance, by the time T_a reached 40 °C, *M. yumanensis* allowed its T_b to rise to ~41 °C, while the ecologically similar *M. lucifugus* (M_b = 6.7 g; Lausen et al. 2022) defends a T_b ~38 °C (Noakes et al. 2021). At their respective heat tolerance limits, *M. yumanensis* allowed a T_b of 44 °C while *M. lucifugus* defends T_b below 42 °C (Noakes et al. 2021). One possible reason for this linear increase of T_b is that *M. yumanensis* is slightly smaller than the *M. lucifugus*. Thus, *M. yumanensis* has a higher surface area/volume ratio and likely experiences a high influx of exogenous heat when T_a is greater than T_b compared to *M. lucifugus* (Schmidt-Nielsen 1997; McNab 2002; Geiser 2021). Furthermore, the ecosystem in Saskatchewan where *M. lucifugus* was studied by Noakes et al. (2021) does not experience a T_a as high as at our study site (Environment and Climate Change Canada 2025), likely reducing selection pressure to conserve water and allowing higher rates of evaporative cooling and consequently lower T_b. Similar variation in thermoregulation along an aridity gradient has previously been documented in small endotherms including bats and rodents (Glanville et al. 2012; Mussñoz-Garcia et al. 2016).

One method of maintaining a low T_b in the face of high T_a is to increase evaporative cooling (McKechnie and Wolf 2019), as observed in the larger, sympatric big brown bats (*Eptesicus fuscus*, M_b ~ 20 g; de Mel et al. 2025b). However, the early onset of evaporative cooling (~7 °C below normothermic T_b; Fig. 1c) in *M. yumanensis* possibly prevents it from sustaining high EWL rates unlike comparable species. For example, *M. lucifugus*, *Pipistrellus pipistrellus* (M_b = 5.7 g), *P. pygmaeus* (M_b = 5.2 g), and *P. hesperidus* (M_b = 5.9 g) achieve at least ~3-fold greater maximum EWL rates (0.36 g h^{-1}, 0.40 g h^{-1}, 0.30 g h^{-1}, 0.36 g h^{-1} respectively; Czenze et al. 2021b; Noakes et al. 2021; Czenze et al. 2022) compared to *M. yumanensis* (0.13 g h^{-1}). These species achieve this by delaying the inflection of EWL and then rapidly using conserved water for evaporative cooling as opposed to an early onset and gradual increase of EWL. Evaporative cooling in *M. yumanensis* is potentially further hindered by the allometric relationship between their low M_b and low water reserves (Nagy and Peterson 1987; Song and Beissinger 2020). This relationship may necessitate the production of metabolic water to augment evaporative cooling; an assumption supported by the linear increase of RMR with increasing T_a (Fig. 2b). As a consequence of a steady increase in RMR and concomitant low rates of EWL, the *M. yumanensis* that we studied can only dissipate a maximum of 63% of their MHP (Table 1; Fig. 2d). In fact, the absolute maximum EHL/MHP achieved by an individual was 0.97 indicating that this species may not have the capacity to dissipate all the heat it produces.

Low EHL/MHP ratios are characteristic of species not acclimatized to high T_a (Czenze et al. 2021b; O'Connor et al. 2021). For example, 3 southern African bat species inhabiting cool caves exhibited EHL/MHP values 0.78 to 0.98 (Czenze et al. 2021b) while the cold-adapted snow bunting (*Plectrophenax nivalis*) achieved an EHL/MHP < 1 (O'Connor et al. 2021). However, because the population of *M. yumanensis* that we studied regularly experiences high summer T_a and drought events, the low evaporative cooling capacity is possibly due to the need to conserve limited water reserves. The need to conserve water and energy reserves would be even more pronounced in pregnant and lactating females (Kurta et al. 1989, 1990; Adams and Hayes 2008) leading to less water and energy being available for thermoregulation. Thus, pregnant and lactating females could experience greater heat stress and consequent mortality compared to the non-reproductive adults that we studied. We add the caveat that our respirometry temperature treatments were of short duration (<1 h per treatment) but under natural conditions the high T_{roost} would have lasted for much longer (e.g., modelled LI T_{roost} during the 2021 heat wave was > 40 °C for > 10 h). It is important to consider respirometry-based observations in tandem with natural T_{roost} conditions.

The NicheMapR endotherm model has previously been successfully used to model the EWL of small endotherms (Conradie et al. 2023). We found that model estimates and our physiological

Table 2 Estimated daytime evaporative cooling requirements (Evaporative water loss (EWL) g H_2O, % body mass) calculated using linear regressions and the endotherm model of female *Myotis yumanensis* using 3 roosts (KL North-facing, KL South-facing, and LI) in Lillooet, BC, Canada.

Roost	Year	Highest T_{roost} (°C)	Linear regressions		Endotherm model	
			EWL (g)	EWL (% M_b)	EWL (g)	EWL (% M_b)
KL North	2021	38.0	0.61	10.43	0.34	5.85
	2023	41.5	0.56	9.62	0.36	6.19
KL South	2021	42.0	0.81	13.93	0.59	10.33
	2023	50.0	0.76	12.97	0.89	15.45
LI	2021	47.7	1.47	25.21	1.73	29.79
	2023	46.0	1.05	18.03	0.99	17.00

Evaporative cooling requirements calculated for the heatwave in 2021 (29 June), and warmest day of the study period (Site specific: 14 August 2023; KL North-facing, KL South-facing, 16 August 2023; LI).

measurements of EWL were highly comparable (Supplementary Data SD2). According to both methods, assuming a lethal dehydration threshold of 25% body mass (Studier et al. 1970), *M. yumanensis* in the LI roost during the heatwave of 2021 would have succumbed to lethal dehydration (25.2% M_b [linear regression], 29.8% M_b [endotherm model]; Table 2). However, no other roost had the conditions necessary for lethal dehydration during the 2021 heatwave or during our 2023 study period. In fact, during the 2021 heatwave, the KL North-facing roost would have only necessitated an EWL requirement of 10.4% M_b (linear regression) and 5.85% M_b (endotherm model; Table 2), because it had less exposure to solar radiation. This phenomenon has previously been reported for North and East-facing bat boxes (Mering and Chambers 2012; Flaquer et al. 2014), emphasizing the need for artificial roosts with minimal solar exposure, enhanced insulation, or other means of thermal buffering capacity to ensure the persistence of this species in human-dominated landscapes.

Yuma Myotis roost in the largest maternity colonies (thousands of individuals) of any bat species in BC (Lausen et al. 2022). Roosts with many individuals often have elevated temperature and water vapor pressure, which affects ability of an individual to dissipate heat (Bartonička and Řehák 2007), but may play an important role in reducing water loss. For example, in high humidity trials, trumpeter hornbills (*Bycanistes bucinator*) exhibited ~70% lower EWL rates, which reduced their ability to dissipate heat corresponding to lower heat tolerance limits by up to 7.5 °C (Coulson et al. 2025). Therefore, when measuring or modelling the effects of water vapor pressure in the roosts, future studies need to consider humidity as a key roost microclimate trait to fully understand overheating potential from heat stress. Adaptation to reduce water loss probably is most important for lactating female *M. yumanensis* in arid environments, as their heat flux is naturally higher than larger bodied bats. While formation of colonies of adult female bats has evolutionarily been adaptive, heat waves may put large maternity colonies at risk of overheating. As our data were collected under dry air conditions, bats were exposed to the conditions to allow for the most effective evaporative cooling and still could not dissipate 100% of their heat produced. Therefore, the limits of *M. yumanensis* occupying artificial roosts with high humidity in our study area could be lower than what we recorded, and we urge conservation managers to consider our results conservatively.

Given their reduced cooling capacities, *M. yumanensis* near Lillooet must rely on selecting cooler roosts and other forms of behavioral thermoregulation, similar to Angolan free-tailed bats (*Mops condylurus*) that move to cooler microsites within their roost during high T_{roost} (Bronner et al. 1999). Similar behavioral thermoregulation within large roosts has been observed in other populations of *M. yumanensis* (Licht and Leitner 1967). In the absence of thermal gradients within the roost, *M. yumanensis* is prone to switching roosts in favor of those that are cooler (Rensel et al. 2023). Thus, the 2 roosts in buildings may have been structurally complex enough to offer varying T_{roost} within them for *M. yumanensis* to persist during high T_a. However, as illustrated by our results for the LI roost during the 2021 heatwave, prolonged high T_a and resultant T_{roost} could overwhelm the thermoregulatory capacities of *M. yumanensis*, exposing them to increased risk of both dehydration and hyperthermia. Our results further emphasize the need for well-placed and thermally buffered artificial roosts.

Our results indicate that *M. yumanensis* prioritize the conservation of water while adopting a thermoconforming pattern when contending with high T_a. Thus, the availability of well insulated roosts that are structurally complex enough to provide thermal gradients are likely important for the persistence of small bats in the hottest parts of their range. These findings are applicable to other small endotherms. As temperatures increase due to climate change conservation management strategies that incorporate artificial roosts will need to ensure structural design and placement that keeps thermal tolerances of the target fauna in mind.

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Author contributions

Ruvinda K. de Mel (Formal analysis, Investigation, Writing—original draft, Writing—review & editing), Mark Brigham (Conceptualization, Funding acquisition, Investigation, Project administration, Writing—original draft, Writing—review & editing), Dylan E. Baloun (Formal analysis, Investigation, Writing—review & editing), Cori Lausen (Investigation,

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Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Explanation of endotherm model.

Supplementary Data SD2. Table showing variables used in the endotherm model to calculate evaporative water loss.

Supplementary Data SD3. Table showing results of correlation tests between respirometry results and endotherm model predictions.

Supplementary Data SD4. Table showing linear mixed effect model outputs.

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Conflict of interest

None declared.

Data availability

Data included in the manuscript will be available on zendono or from the senior author.

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