

RESEARCH ARTICLE

Home is where the heat is: Thermoregulation of European bats inhabiting artificial roosts and the threat of heat waves

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Handling Editor: Annabel Smith**Abstract**

1. Anthropogenic land use changes, such as deforestation and commercial forestry, have substantially reduced natural roost sites for European bats. A common conservation solution is to provide artificial roosts (i.e. bat boxes), but there are concerns that these can become hotter than natural roosts in summer and could be death traps during heat waves. Nevertheless, females of several bat species form maternity colonies in these boxes, thus occupying hotter and more humid microclimates than solitarily roosting males. We tested if cooling efficiency and heat tolerance differ between sexes in European bats, and estimated the evaporative water requirements for bats living in bat boxes during hot summer days.
2. We used indirect calorimetry and thermometry to quantify thermoregulation at high air temperatures (T_a) in four species of vespertilionid bats that regularly occupy artificial roosts. We measured resting metabolic heat production, evaporative water loss rates (EWL) and body temperature (T_b) at T_a between 28°C and 48°C during summer. We predicted that females have higher evaporative cooling efficiency (evaporative heat loss/metabolic heat production) than males, allowing them to reach their heat tolerance limit at higher T_a .
3. We found no sex differences in maximum evaporative cooling efficiency, maximum T_b , and maximum T_a tolerated. However, the patterns of increasing EWL with T_a differed between sexes. Females tolerated higher T_a before increasing EWL than males and then rapidly increased EWL to higher values than males at the maximum T_a tolerated. These sex differences in heat dissipation strategies may reflect varying ecological and physiological constraints associated with different summer roosting habits.
4. *Synthesis and applications.* Our study revealed that some small European bat species are already at risk of succumbing to lethal dehydration during present-day heat waves, with daytime evaporative water requirements equivalent to ~30% of body mass in sun-exposed boxes. For conservation managers working with common European bat species, particularly those in monoculture forests with woodcrete bat-boxes, our physiologically informed

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recommendations include positioning boxes in diverse locations varying in aspect and sun exposure. This will ensure thermal heterogeneity of roost sites and provide a wide gradient of microclimate conditions, allowing for roost switching when necessary.

KEYWORDS

bats, body temperature, evaporative water loss, heat tolerance, heat waves, resting metabolic heat production, roost microclimate

1 | INTRODUCTION

High summer temperatures can be physiologically demanding for endothermic animals due to the energy and water costs required for evaporative cooling (Schmidt-Nielsen, 1997). When air temperature (T_a) rises above body temperature (T_b), mammals and birds increase respiratory evaporative water loss (EWL) to dissipate heat, which involves a concurrent increase in metabolic heat production (Bartholomew, 1972; McKechnie & Wolf, 2019). Many endothermic species breed during summer, and reproduction results in additional energy costs and heat loads that are disparate between sexes (Gittleman & Thompson, 1988; Racey & Entwistle, 2000). Sex differences in heat dissipation strategies have recently been reported in a bird during summer, with female southern yellow-billed hornbills *Tockus leucomelas* using less energy and water than males at high T_a , likely to cope with their hotter and more humid roost microclimates during the reproductive season (van Jaarsveld, Bennett, Czenze, et al., 2021). As far as we are aware, no studies have investigated sex differences in the heat dissipation capacities of mammals at high T_a , although pregnancy and lactation are associated with increased water requirements, T_b , metabolic demands and heat stress for females (e.g. small rodents: Gamo et al., 2013; Zhao et al., 2020). Thus, similar to *T. leucomelas*, we may expect that female mammals have more efficient heat dissipation than males.

Among some bats and birds, there is a positive correlation between T_a and the proportion of females-to-males at a geographical scale, suggesting that females prefer higher T_a (Magory Cohen et al., 2021). At a microenvironmental scale, in the summertime, many bat species use relatively hot roosts and some exhibit sex differences in roosting habits (Kerth et al., 2001; Lourenço & Palmeirim, 2004; Maloney et al., 1999). Reproductive and post-reproductive females typically form maternity colonies including the young-of-the-year, whereas adult males more frequently occupy solitary roosts (Gerell & Lundberg, 1985; Kasprzyk & Ruczyński, 2001; Lourenço & Palmeirim, 2004). Although elevated temperatures in communal roosts can be conducive to offspring development (Simons et al., 2011), exceedingly high temperatures may lead to dehydration, deleterious hyperthermia and impaired milk production (Adams, 2010; Zhao et al., 2020). Some bat species experiencing hotter roost temperatures (T_{roost}) have higher heat tolerance limits and evaporative cooling efficiency than those occupying cooler roosts (Cory Toussaint & McKechnie, 2012; Czenze,

Smit, et al., 2022; Czenze, Naidoo, et al., 2020; Marom et al., 2006; Noakes et al., 2021). However, these are interspecific comparisons and it is possible that a similar pattern exists between sexes within bat species.

The urgency to understand the ability of bats to cope with high T_a s highlighted by the predicted increase in global temperatures and the frequency intensity of heat waves due to anthropogenic climate change (IPCC, 2021). There have been several reports of heat-related mortality of pteropodid bats in the southern hemisphere, which are predicted to increase due to climate change (McKechnie et al., 2021; Ratnayake et al., 2019; Welbergen et al., 2008). Although less common, there are reports of heat-related mortality of vespertilionid bats using artificial roosts in South-Western Europe (Alcalde et al., 2017; Flaquer et al., 2014). These bats are also threatened by anthropogenic land-use changes, including deforestation, habitat fragmentation and plantation forests (Kunz & Parsons, 2009).

Intensive forestry practices have resulted in a substantial loss of natural roost sites for tree-roosting species (López-Baucells et al., 2017; Patriquin & Barclay, 2003; Ruczyński & Bogdanowicz, 2005). Many European bat species are now largely dependent on artificial roosts (henceforth 'bat boxes'), which are hung to mitigate the loss of natural roosts (Flaquer et al., 2006; Kasprzyk & Ruczyński, 2001; López-Baucells et al., 2017). However, bat boxes can become hotter than natural roosts, sometimes exceeding normothermic T_b (Bideguren et al., 2019; Crawford & O'Keefe, 2021; Flaquer et al., 2014; Lourenço & Palmeirim, 2004), and individuals have been observed abandoning boxes at $T_{\text{roost}} > 40^\circ\text{C}$ (Flaquer et al., 2014; Lourenço & Palmeirim, 2004). Several recent studies warn that bat boxes are at risk of overheating and that this conservation practice may be an ecological trap for bats (Crawford & O'Keefe, 2021; Crawford et al., 2022; Flaquer et al., 2014; Fontaine et al., 2021; Griffiths, 2021); however, none have measured the heat tolerance or evaporative water requirements of their occupants to quantify that risk.

We investigated the thermoregulatory strategies in the heat of four species of north-temperate vespertilionid bats that inhabit bat boxes by measuring resting metabolic heat production, evaporative water loss and T_b at progressively higher T_a . We tested the hypothesis that the ability of bats to cope with high T_a s varies between males and post-reproductive females in relation to sex differences in summer roosting habits. Both sexes use bat boxes during summer, but roosts occupied by maternity colonies can be significantly

hotter than unoccupied roosts (Kerth et al., 2001; Ruczyński, 2006). Thus, we predicted that females would tolerate higher maximum T_a s and have greater evaporative cooling efficiency than males. Using these data and T_{roost} recordings, we estimated the evaporative water requirements of bats during hot, mid-summer days and present-day heatwaves in Europe to understand their vulnerability to rapidly changing climates.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

All experiments were approved by the Local Committee for Ethics in Animal Research in Bydgoszcz, Poland (decisions # 24/2021, 37/2021, 38/2021) and Regional Directorate of Environmental Protection (decisions # WOP.6401.4.38.2021.MO, WOP.6401.4.38.2021.MO.2 and WOP.6205.62.2021.KLD).

Bats were collected from sawdust concrete (woodcrete) bat boxes during summer (26 July–22 August 2021). Bat boxes were located in monoculture Scots pine (*Pinus sylvestris*; 60–85 years old) plantations near Solec Kujawski (53.06°N, 18.23°E), the field station of Nicolaus Copernicus University in Sobiny (53.66°N, 18.40°E), and city parks in Toruń (53.02°N, 18.57°E), Poland. In Sobiny, ~30% of bat boxes are occupied as early as 3 weeks after hanging (personal observation). We captured non-reproductive *Nyctalus noctula* (10 females, 10 males), *Pipistrellus nathusii* (13 females, 12 males), *P. pygmaeus* (11 females, 10 males) and *P. pipistrellus* (10 females, 7 males), and checked that females were not lactating by gently squeezing their nipples to ensure they did not expel milk. Females were mainly collected from colonies of ~6–30 individuals, whereas males roosted solitarily or in small groups of ≤4 individuals.

After capture, bats were transported in cloth bags to Nicolaus Copernicus University in Toruń, where they were housed in a polyester mesh cage in a dark, temperature-controlled room ($T_a = 20 \pm 2^\circ\text{C}$). Every evening in captivity, individuals were provided with water from a pipette and hand fed mealworm *Tenebrio molitor* larvae until satiated or until they had gained ≥10% body mass. After feeding on the day of capture, a temperature-sensitive PIT tag (Biotherm, Biomark, Boise ID, USA) was injected subcutaneously between the shoulder blades of each individual for T_b measurements.

To determine the thermal profiles of bat boxes during mid-summer (Figure 1), we fixed iButtons (1922L, Maxim Integrated) to the inside walls of four bat boxes in Sobiny and recorded T_{roost} at 15-min intervals from 10 to 26 July 2021. We selected boxes varying in aspect and sun exposure, with two east-facing boxes in full-shade and sun-exposed positions respectively, and two west-facing boxes similarly varying in exposure. These boxes were used by bats before and after T_{roost} measurements, but we cannot confirm they were occupied during T_{roost} recordings. We also recorded the T_a about 2 m from each bat box, using iButtons placed in full shade and ~3 m above the ground.

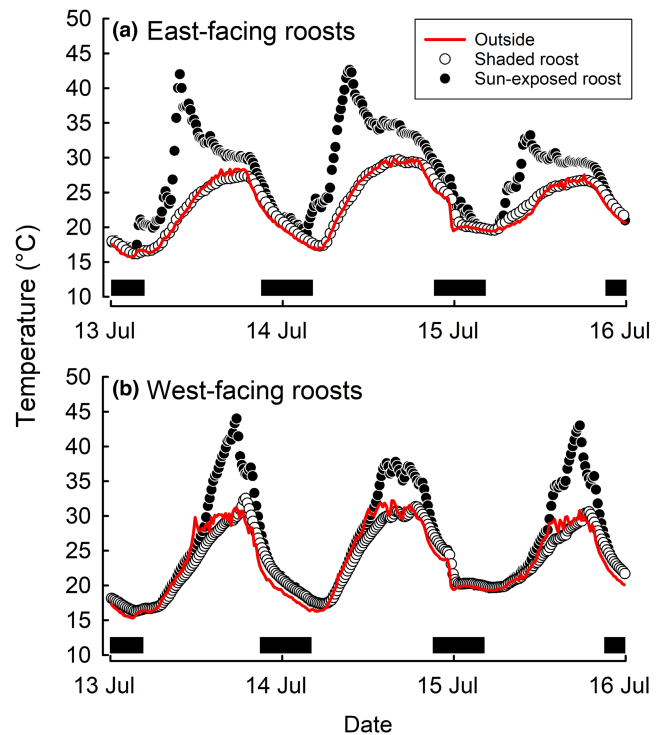


FIGURE 1 Comparison of ambient temperature (red line), and roost temperatures of sun-exposed (black circles) and fully shaded (white circles) bat boxes during 13–15 July 2021 in Sobiny, Poland. (a) East-facing boxes, (b) West-facing boxes; black bars at the bottom indicate night-time hours.

2.2 | Gas exchange and body temperature measurements

We measured the rate of carbon dioxide production (\dot{V}_{CO_2}) and EWL of bats using two positive-pressure flow-through respirometry systems (see Supporting Information for details). Respirometry chambers were constructed from air-tight glass pickle jars (0.5-L for *Pipistrellus* sp., 0.85-L for *N. noctula*). Each chamber was outfitted with a cylindrical metal cage to elevate individuals >1.5 cm above a ~1 cm layer of mineral oil, which prevented the evaporation of water from excreta influencing EWL values (Figure S1). This metal cage allowed bats to move freely within the chamber and adopt a natural, head-down roosting posture. We measured T_b of individuals every 10 s throughout respirometry trials, by placing a racket antenna (Biotherm, Biomark, Boise ID) next to the chamber to detect temperature readings from the PIT tags.

Values of resting \dot{V}_{CO_2} and EWL were calculated from the lowest stable 3-min periods of CO_2 and H_2O for each individual at each T_a . We calculated metabolic heat production (W) from \dot{V}_{CO_2} assuming a respiratory exchange ratio of 0.7 (Walsberg & Wolf, 1995) and a joule equivalence value of 27.8 J/ml CO_2 (Withers, 1992). To convert the volume of water into mass, we assumed 0.803 mg/ml H_2O (Lighton, 2008). Rates of EWL were converted to evaporative heat loss (W) assuming a latent heat of vaporization of 2.406 J/mg H_2O at 40°C (Tracy et al., 2010).

2.3 | Experimental protocol

To quantify the thermoregulatory responses of bats to high T_a , we measured \dot{V}_{CO_2} , EWL, and T_b of individuals over progressively higher T_a s during the daytime. Measurements for each individual were conducted within 72 h of capture, but typically within 24 h. Prior to measurements, we recorded body mass of individuals using an electronic balance (Ohaus Traveller, TA501, accuracy: 0.1 g). We then placed bats inside the respirometry chamber at a moderate T_a (either 28 or 30°C, selected randomly) for ~1 h to habituate them to the experimental setup. We started measurements when bats were calm and had stable readings of T_b , \dot{V}_{CO_2} , and EWL.

Individuals were kept at each set-point T_a for at least 20 min, after which we obtained stable recordings of T_b , \dot{V}_{CO_2} , and EWL for ≥ 3 -min. We then increased T_a to the next set-point value, increasing in 4°C increments until $T_a = 40^\circ\text{C}$, and in 2°C increments at $T_a > 40^\circ\text{C}$ until bats reached their heat tolerance limit. We define the heat tolerance limit as the T_a at which an individual showed clear signs of behavioural or physiological distress (e.g. a rapid increase in T_b , EWL or \dot{V}_{CO_2} , loss of coordination or balance, or prolonged escape behaviour). We continuously monitored the behaviour of bats throughout measurements using an infrared video camera, and trials were ended immediately when individuals reached their heat tolerance limit. The measurement period for each individual was ~3–5 h, including the 1-h habituation time. Our methods reflect the danger of maintaining endotherms at high T_a for long periods, and this protocol is similar to recent studies measuring the heat tolerance and evaporative cooling capacities of bats (Czenze, Naidoo, et al., 2020; Noakes et al., 2021), rodents (van Jaarsveld, Bennett, Kemp, et al., 2021) and birds (Czenze, Kemp, et al., 2020; Whitfield et al., 2015).

After removal from the chamber, we measured the mass of individuals and immediately offered them water until satiated. Bats were then placed in a cloth bag to rest, hand-fed with mealworms ~30 min later and released at dusk. We recaptured 12 individuals between 5 and 21 days after measurements, and all had body mass similar to initial capture mass, suggesting there were no long-term negative effects of our protocol (see also: (Czenze, Smit, et al., 2022)).

2.4 | Data analysis

2.4.1 | Thermoregulation at high T_a

For each individual, we took the lowest stable 3-min trace of \dot{V}_{CO_2} at each set-point T_a as representative of resting bats, and calculated the average metabolic heat production, EWL and T_b . The sex-specific mean values $\pm SD$ of these variables were calculated using data from individuals at each T_a for each species respectively. Thus, the maximum and minimum values (Table S1) represent a subset of individuals in some cases (e.g. only three male *P. nathusii* tolerated $T_a = 46^\circ\text{C}$). If the maximum value of a physiological variable was represented by one individual, we also report the mean value at the second

highest T_a . We calculated the maximum fractional increase in EWL (i.e. evaporative scope = maximum EWL/minimum EWL), maximum evaporative cooling efficiency (evaporative heat loss/metabolic heat production), and the T_a and T_b at the heat tolerance limit for each individual.

All statistical analyses were performed in R 4.0.5 (R Core Team, 2021), fitting models to analyse variation in physiological response variables in each species separately. To compare the relationships of T_b , EWL and metabolic heat production with T_a between sexes, we first used the package SEGMENTED.LME (Muggeo, 2016) to identify inflection points in these relationships for males and females respectively. We then fitted linear mixed effect models above sex-specific inflection points using the NLME package (v3.1–149; Pinheiro et al., 2009). To account for repeated measurements in individuals, we included individual identity as a random factor in these models. The initial models included T_a , sex and the interaction between T_a and sex as predictor variables. As we were testing a hypothesis and thus modelling for inference, we selected which predictor variables to retain in the final models based on null hypothesis testing (Tredennick et al., 2021). We calculated the estimated marginal means of evaporative scope, evaporative cooling efficiency and the T_a and T_b at the heat tolerance limit for each sex in each species, using the EMMEAN package (v1.4.6; Lenth, 2021). In all analyses we assigned the significance level at $\alpha = 0.05$.

2.4.2 | Estimated evaporative water requirements in artificial roosts

We define the evaporative water requirements as the mass of H_2O necessary for bats to maintain thermal balance while resting. For each species, we used the sex-specific relationship between EWL and T_a , and T_{roost} recorded in Sobiny to estimate the daytime evaporative water requirements for males and females roosting in each of the four bat boxes. The T_{roost} of the sun-exposed west-facing box in Sobiny was highly correlated with outside T_a ($r^2 = 0.93$), and we used this relationship to predict the T_{roost} of individuals in Sobiny during the heatwave of 2019. As we were not collecting data in Sobiny during 2019, we used T_a data collected from Chojnice (~55 km W of Sobiny, same latitude: 53.7°N) during the hottest day of the heat wave (daily maximum $T_a = 34.6^\circ\text{C}$).

3 | RESULTS

3.1 | Bat thermoregulation in the heat

The heat tolerance limits of individuals of all species typically ranged between $T_a = 44^\circ\text{C}$ and 46°C , with only three individuals (*N. noctula*: one male, two females) reaching $T_a = 48^\circ\text{C}$. The T_b , metabolic heat production and EWL of males and females of each species typically increased with increasing T_a above respective inflection points (Figures 2 and 3; Table S1). The only exception to this was that T_b

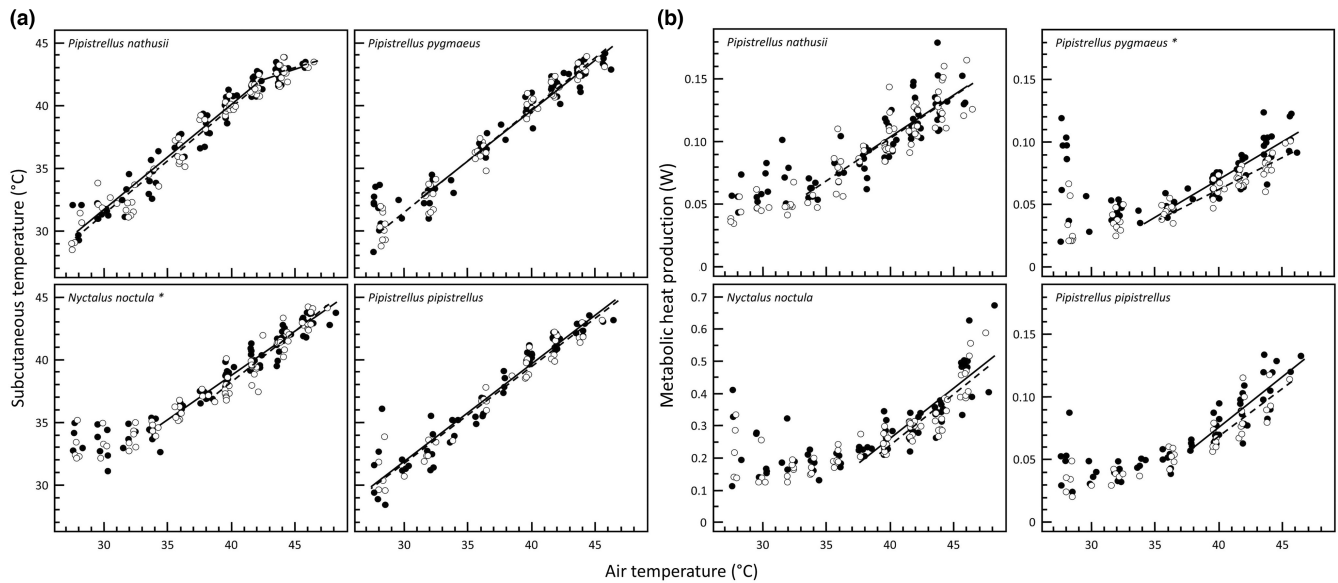
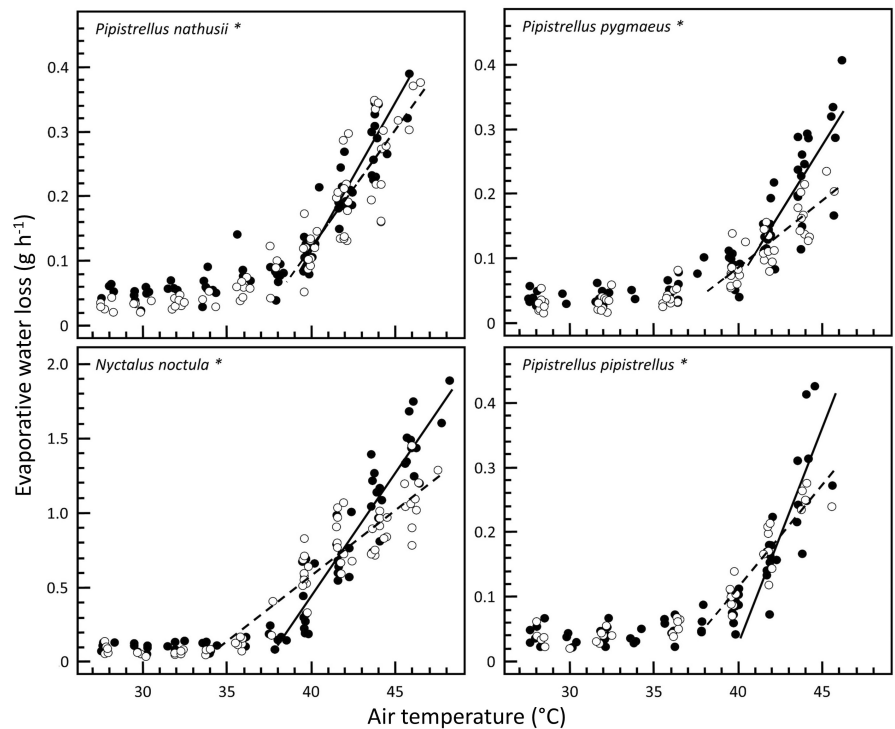


FIGURE 2 (a) Subcutaneous temperature (T_{sub}) and (b) metabolic heat production (MHP) at high air temperatures (T_a) in four European bat species during summer. Black circles represent females and white circles represent males. In each panel *represents a significant interaction term between sex and T_a in the linear models fitted to T_{sub} above T_a inflection points. The solid and dashed lines indicate significant linear regressions for females and males respectively. Note the difference in MHP y-axis scale for *Nyctalus noctula*.

FIGURE 3 Evaporative water loss (EWL) at high air temperatures (T_a) in four European bat species during summer. Black circles represent females and white circles represent males. In each panel *represents a significant interaction term between sex and T_a in the linear models fitted to EWL above T_a inflection points. The solid and dashed lines indicate significant linear regressions for females and males respectively. Note the difference in y-axis scale for *Nyctalus noctula*.



increased over the entire T_a range in both sexes of *P. nathusii* and *P. pipistrellus*, and male *P. pygmaeus*.

For each species, the final models fitted to each physiological variable described a large portion of variance in the data (range of r^2 of models: 0.75–0.97; Table S2). The final models of increasing T_b for the three *Pipistrellus* species excluded $T_a \times \text{sex}$ and sex as predictor variables, indicating no T_b difference between males and females at high T_a (Table S2). Conversely, $T_a \times \text{sex}$ was included in the final T_b model for *N. noctula*, with females exhibiting a shallower slope in

the relationship between increasing T_b and T_a compared to males (Figure 2a). For increasing metabolic heat production, $T_a \times \text{sex}$ and sex were excluded from the final models, except for *P. pygmaeus* in which females had a steeper slope of increasing metabolic heat production with T_a relative to males (Figure 2b). In contrast, the EWL model for all four species included $T_a \times \text{sex}$ with females consistently exhibiting a steeper slope in increasing EWL compared to males (Figure 3). In all species except *P. nathusii*, this resulted in significantly higher maximum EWL (i.e. at the highest T_a) for females than for males (no overlap

of confidence intervals; Table S4). Furthermore, for *N. noctula*, *P. pipistrellus* and *P. pygmaeus* the inflection T_a at which bats increased evaporative cooling was significantly higher for females than for males (by 2.4–4°C; Figure 3; Table S1). However, for all species, the mean of individual maximum values of evaporative scope, evaporative cooling efficiency, heat tolerance limit and T_b at this limit did not differ significantly between females and males (Table S3).

3.2 | Evaporative water requirements in a hot bat box

Between 10 and 26 July 2021, T_a in Sobiny ranged from 10.5 to 32.2°C. The T_{roost} of bat boxes in sun-exposed positions were substantially hotter than outside T_a (Figure 1), with maximum T_{roost} occurring in the morning for east-facing boxes (~9:00) and afternoon for west-facing boxes (~17:00). Despite this temporal difference, daily maximum T_{roost} were similar for east- (37.0 ± 4.1°C) and west-facing (35.1 ± 5.1°C) boxes. We recorded $T_{roost} > 40^\circ\text{C}$ on 3 and 2 days in sun-exposed east- and west-facing boxes respectively, with the highest T_{roost} of 44.0°C recorded in a west-facing box when $T_a = 31.2^\circ\text{C}$ (13 July). In contrast, T_{roost} in shaded boxes closely tracked T_a (temperature difference <6°C), and had lower daily maximum values (highest $T_{roost} = 29.7^\circ\text{C}$) and amplitudes (east-facing: 11.0 ± 2.7°C, west-facing: 12.3 ± 2.9°C) compared to sun-exposed boxes (east-facing: 22.0 ± 4.8°C, west-facing 19.9 ± 4.4°C).

We estimated the evaporative water requirements of individuals during daylight hours on the three hottest days during T_{roost} recordings (13–15 July). Water requirements were highest on 14 July (maximum $T_a = 29.5^\circ\text{C}$; Table 1), and were consistently higher in sun-exposed compared to shaded roosts. Among sun-exposed roosts, water costs were higher in the east-facing box (maximum $T_{roost} = 41.9^\circ\text{C}$) than the west-facing box (maximum $T_{roost} = 37.8^\circ\text{C}$). As a percentage of average body mass, the daytime evaporative water requirements for male and female bats of each species was similar and ranged from ~10% of body mass for female *N. noctula* to 19% for female *P. pygmaeus* (Table 1).

TABLE 1 Estimated daytime evaporative water requirements (g H₂O; % body mass) of four species of European bats inhabiting artificial roost boxes varying in aspect and sun exposure. Species-specific water requirements were estimated using the sex-specific relationships between evaporative water loss and air temperature (range: ~28 to 48°C) derived from segmented linear mixed effect models. We substituted air temperature with roost temperature in these equations, using values measured in bat boxes during the hottest day of recordings (14 July 2021)

Bat box position	Daytime evaporative water requirements (g H ₂ O, % body mass)							
	<i>Nyctalus noctula</i>		<i>Pipistrellus nathusii</i>		<i>P. pygmaeus</i>		<i>P. pipistrellus</i>	
	Male	Female	Male	Female	Male	Female	Male	Female
East-facing, sun-exposed	3.12 (10.6%)	2.96 (9.7%)	0.99 (13.8%)	1.25 (16.5%)	0.73 (16.2%)	0.99 (19.1%)	0.91 (17.5%)	0.87 (15.2%)
East-facing, shaded	1.34 (4.6%)	1.63 (5.3%)	0.43 (5.9%)	0.77 (10.1%)	0.42 (9.4%)	0.55 (10.7%)	0.56 (10.7%)	0.54 (9.5%)
West-facing, sun-exposed	2.33 (7.9%)	1.96 (6.4%)	0.69 (9.6%)	0.98 (12.9%)	0.56 (12.4%)	0.77 (14.8%)	0.68 (13.0%)	0.74 (12.9%)
West-facing, shaded	1.33 (4.5%)	1.66 (5.4%)	0.46 (6.4%)	0.79 (10.4%)	0.47 (10.6%)	0.58 (11.2%)	0.58 (11.1%)	0.57 (9.9%)
Mean ± SD body mass (g)	29.4 ± 1.9	30.6 ± 1.2	7.2 ± 0.5	7.6 ± 0.4	4.5 ± 0.4	5.2 ± 0.4	5.2 ± 0.4	5.7 ± 0.3

4 | DISCUSSION

We report the first recorded sex differences in bat thermoregulation in the heat, with the onset of evaporative cooling occurring at a higher T_a in females than males in all species (Figure 3). However, there were no sex differences in the maximum evaporative cooling efficiencies or highest T_a tolerated, likely due to a steeper slope of increasing EWL with T_a after the delayed increase in EWL in females. Nevertheless, at the highest T_a s, females of all species except *P. nathusii* had significantly higher EWL than males while maintaining similar T_b . This suggests that females are better at tolerating moderately high T_a (i.e. ≤40°C), which are likely typical of T_{roost} during European summers. However, both sexes have a similar tolerance of extremely high T_a , despite significant sex differences in maximum EWL. Our physiologically informed estimates of daytime evaporative water requirements indicate that temperate-zone bats using artificial roosts in sun-exposed positions are vulnerable to current and future heatwaves, and we urge conservation managers to consider this while planning and installing artificial bat roosts.

The heat tolerance limits (~44–48°C), T_b s at these limits (~43.5–44.5°C), evaporative scopes (7.9–20.2), and maximum evaporative cooling efficiencies (1.5–2.8) we recorded are similar to those reported for other bat species (Czenze, Smit, et al., 2022; Czenze, Naidoo, et al., 2020; Licht & Leitner, 1967; Maloney et al., 1999; Noakes et al., 2021). In contrast to our predictions, these variables did not vary between sexes in any species, suggesting that females do not possess higher overall heat tolerance.

Maximum physiological values do not necessarily reflect variation in thermoregulatory strategies in response to increasing T_a (e.g. van Jaarsveld, Bennett, Czenze, et al., 2021). For all four bat species at $T_a = 40^\circ\text{C}$, females consistently had lower EWL than males (51%–83% of males; Figure 3), despite similar metabolic heat production (93%–116% of males; Figure 2). This pattern changed with increasing T_a , and females at $T_a = 46^\circ\text{C}$ had higher EWL than males in all species (111%–130% of males) with little change in metabolic heat production (100%–121% of males). Collectively, these patterns lead to lower evaporative cooling efficiency at $T_a = 40^\circ\text{C}$, but higher at

$T_a = 46^\circ\text{C}$, in females compared to males (Figure S2; Tables S4–S6), despite ultimately no sex differences in maximum cooling efficiency. The thermal conditions within maternity colonies or communal roosts (e.g. heat gain from the roost and conspecifics, and high humidity) present challenges for females to thermoregulate effectively when T_a exceeds T_b . However, if the water vapour pressure deficit in the roost permits evaporative heat loss, female bats may still effectively dissipate this excess heat at the cost of increased dehydration risk. To the best of our knowledge, only one study exists on sex differences in dehydration tolerance and thermoregulation in mammals (Thwaites et al., 1990). At T_a of 34 and 36°C, water-deprived female rabbits maintained lower T_b despite smaller changes in respiration rate than water-deprived males (Thwaites et al., 1990), suggesting a better dehydration tolerance. Clearly, at $T_{\text{roost}} > 40^\circ\text{C}$ female bats are able to dissipate more heat evaporatively than males, and achieve this by delaying and then rapidly increasing EWL. Thus, the patterns we recorded may reflect different roosting habits and heat loads of females and males suggesting that female bats face stronger selection pressures for effective thermoregulation at high T_a .

For bats in the wild, roost microclimates can vary with the position in the environment, particularly with cardinal orientation and exposure to solar radiation (Figure 1). To estimate the consequences of changes in T_{roost} for water and thermal balance of bats, we combined our physiological measurements with T_{roost} data collected from bat boxes in a pine monoculture forest in Sobiny during mid-summer. On the hottest day of T_{roost} recordings, our evaporative water requirement estimates, as a percentage of body mass, suggest individuals occupying a sun-exposed, east-facing box range from ~10% in *N. noctula* to ~19% in *P. pygmaeus*. However, these water requirements are approximately halved in most species if a box in full shade is selected (Table 1). The lethal dehydration limits of bats are largely unknown, but range from 23% to 32% of body mass loss for four *Myotis* species (Studier et al., 1970). This indicates that water loss on the hottest day during our study period was likely tolerable for bats, but approach the lethal range in the smaller *Pipistrellus* species. This suggests that smaller European bat species could be particularly at risk of lethal dehydration during heat waves.

During the summer of 2019, an extreme heat event in continental Europe caused some of the highest temperatures recorded in Poland for June (<http://danepubliczne.imgw.pl>). We estimate that species roosting in the sun-exposed west-facing box during this heat wave would require water loss equivalent to between ~23% (*N. noctula*) and 34% (*P. pipistrellus*) of body mass for cooling. We also estimate that the maximum T_{roost} in this box reached ~43°C, a T_a most individuals tolerated during physiological measurements; however, the T_{roost} would exceed 40°C for more than 7 h compared to only 1 h on the hottest day of the present study. Some European bat species abandon roosts when $T_{\text{roost}} > 40\text{--}45^\circ\text{C}$ (Lourenço & Palmeirim, 2004). The highest T_{roost} we recorded (44.0°C) occurred when $T_a = 31.2^\circ\text{C}$, and the T_a at Chojnice exceeded 31.2°C on 12 days from 2018 to 2021. Considering that high summer T_a and heat waves are predicted to increase in

frequency and intensity (IPCC, 2021), sustained high T_{roost} may threaten the viability of smaller bat species dependent on bat boxes.

The species studied here are common across Europe, with Sobiny being near the centre of their distributions, and our evaporative water requirement estimates have direct conservation value as bat boxes are a common conservation solution for the loss of natural roosts (Flaquer et al., 2014; Kasprzyk & Ruczyński, 2001). These estimates are specific for bats roosting in single-chamber, woodcrete bat boxes in monoculture forests. Woodcrete boxes are common in Europe and are occupied by several bat species (Dodds & Bilston, 2013; Kasprzyk & Ruczyński, 2001), which highlights the risk of placing them in direct sunlight. We recommend placing bat boxes in positions varying in sun exposure and orientation, thus mimicking the thermal heterogeneity of natural roost sites. This will allow for active roost selection by bats (Kerth et al., 2001; Ruczyński, 2006) and roost switching when necessary (Ellison et al., 2007; Patriquin et al., 2016). This variation is critical to ensure there are suitable microclimates for individuals during post-hibernation or migration, for maternity colonies, and to prevent them from becoming death traps during heat waves (Bideguren et al., 2019; Flaquer et al., 2014; Fontaine et al., 2021; Griffiths, 2021). These recommendations are of particular importance to conservation managers in the hotter and dryer regions of these species' range where heat-related mortality is already being observed (Alcalde et al., 2017; Flaquer et al., 2014).

Although our study is the first to link the thermoregulatory responses of bats at high T_a with summer T_{roost} of bat boxes, we acknowledge three important limitations. (a) Our T_{roost} recordings may not represent the operative temperature bats experience. However, bat boxes are enclosed spaces without direct solar radiation and convection acting upon individuals, and thus T_{roost} is likely a good approximation of operative temperature. (b) Our daytime evaporative water requirements estimates are based on a relationship between EWL and T_a from data collected under dry air conditions. In the wild, particularly in communal roosts, bats can experience high humidity, which reduces evaporative cooling efficiency and elevates heat stress (Licht & Leitner, 1967). Therefore, our values may represent an underestimate of daytime evaporative water requirements. (c) The dehydration tolerance of bats in the wild will vary with overnight water gain. To address this, we used published data on prey consumption and water content of prey and estimate that bats gain 0.84 g H₂O per 1 g of insects consumed (see Supporting Information for details), and that on a good foraging night bats could gain water equivalent to ~21% of body mass. For all species, this would meet cooling requirements during the hottest day of T_{roost} recordings (Table 1), but would only provide 62%–90% of daytime cooling requirements in the sun-exposed west-facing box during the 2019 heat wave.

In conclusion, our work reveals that simply quantifying maximum values of thermoregulatory traits may not be sufficient to accurately capture intraspecific variation in thermoregulation at high T_a . Our physiologically informed estimates are the first to use the

occupants of bat boxes to determine their suitability and validates the concerns of recent literature that improperly placed bat boxes can lead to conservation pitfalls due to overheating (e.g. Crawford & O'Keefe, 2021; Crawford et al., 2022). Understanding thermoregulatory strategies at high T_a is vital for predicting how endothermic animals will respond to increasing temperatures and heat waves, and such information needs to be incorporated into mechanistic models predicting the responses of species to anthropogenic climate change (Ratnayake et al., 2019; Welbergen et al., 2008).

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas, designed the methodology and captured bats. Z.J.C. and M.J.N. collected and analysed the data. All authors led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study brings together authors from three continents. M.S.W. is a scientist based in the country where the study was carried out. When relevant, literature published by scientists from the region was cited.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3tx95x6jk> (Czenze, Noakes, et al., 2022).

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