Interspecific variation in thermoregulation among three sympatric bats inhabiting a hot, semi-arid environment

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Abstract

Bats in hot roosts experience some of the most thermally challenging environments of any endotherms, but little is known about how heat tolerance and evaporative cooling capacity varies among species. We investigated thermoregulation in three sympatric species (*Nycteris thebaica, Taphozous mauritianus*, and *Sauromys petrophilus*) in a hot, semi-arid environment by measuring body temperature (T_b), metabolic rate and evaporative water loss (EWL) at air temperatures (T_a) of 10 - 42 °C. *S. petrophilus* was highly heterothermic with no clear thermoneutral zone, and exhibited rapid increases in EWL at high T_a to a maximum of 23.7 ± 7.4 mg g^{-1} hr^{-1} at $T_a \approx 42$ °C, with a concomitant maximum T_b of 43.7±1.0 °C. *T. mauritianus* remained largely normothermic at T_as below thermoneutrality, and increased EWL to 14.7 ± 1.3 mg g^{-1}

hr^{-1} at $T_a \approx 42$ °C, with a maximum T_b of 42.9 ± 1.6 °C. In *N. thebaica*, EWL began increasing at lower T_a than in either of the other species, and reached a maximum of 18.6±2.1 mg g^{-1} hr^{-1} at T_a = 39.4 °C, with comparatively high maximum T_b values of 45.0±0.9°C. Under the conditions of our study, *N. thebaica* was considerably less heat tolerant than the other two species. Among seven species of bats for which data on T_b as well as roost temperatures in comparison to outside T_a are available, we found limited evidence for a correlation between overall heat tolerance and the extent to which roosts are buffered from high T_a.

Key words

body temperature, evaporative water loss, heat tolerance, hyperthermia, basal metabolic rate

Introduction

Life originated in aquatic environments, and terrestrial habitats, particularly those that are hot and arid, pose significant physiological challenges related to the avoidance of hyperthermia and desiccation (Gordon and Olson 1995). Many endotherms regularly encounter environmental temperatures that exceed body temperature (T_b), and under these conditions T_b can be maintained below environmental temperature only through evaporative heat dissipation (Dawson and Whittow 2000; King and Farner 1961). Evaporative water loss (EWL) via cutaneous and/or respiratory pathways thus represents a crucial thermoregulatory mechanism in hot environments, and rates of EWL rapidly increase when environmental temperature exceeds T_b (King and Farner 1961; Licht and Leitner 1967b). Thermoregulation under very hot conditions is also strongly dependent on body mass, as rates of heat exchange between an organism and its environment are proportional to surface area/volume (Calder 1996; Schmidt-

Nielsen 1984).

Many small mammals avoid very high environmental temperatures by using thermally-buffered microsites such as burrows during the day, but one taxon that represents a notable exception is the Chiroptera. In tropical and subtropical latitudes, bats often occupy roost sites where they are potentially exposed to very high roost temperatures (T_{roost}) for long periods each day, making these roosts among the most thermally challenging environments encountered by endotherms. Bats either tolerate high T_{roost}, or behaviourally avoid them by moving to cooler microsites (Bronner et al. 1999; Herreid 1967; Licht and Leitner 1967b). Species such *Myotis yumanensis, Antrozous pallidus* and *Tadarida brasiliensis* are frequently exposed to T_{roost} = 40-50˚C (Herreid 1967; Licht and Leitner 1967a), and the southern African molossid *Mops condylurus* regularly roosts at T_{roost} > 40°C and actively selects microsites with T_{roost} = 35 - 42°C (Bronner et al. 1999).

Although the use of hot roosts by bats is well documented, considerably less is known about their thermoregulation at high T_{roost}. Like other small endotherms, bats rapidly increase EWL under hot conditions (Herreid and Schmidt-Nielsen 1966; Maloney et al. 1999; Marom et al. 2006). In one of the few detailed examinations of how bats cope with very high T_{roost}, *M. condylurus* roosting under a corrugated iron roof in eastern South Africa were found to dissipate up to 132 % of metabolic heat production via EWL (Maloney et al. 1999). In the latter species, an increase in air temperature (T_a) from 25 to 45 °C was associated with a 12-fold increase in EWL, and observed rates of EWL at T_a = 45 °C represented water loss equivalent to approximately 2% of body mass per hour (Maloney et al. 1999). Maximum T_b during heat exposure in *M. condylurus* was 43 °C (Maloney et al. 1999), and to the best of our knowledge this remains the highest T_b recorded to date in a bat. In contrast, T_b in

two species sympatric in the Negev Desert never exceeded 40 °C, even at $T_a \approx 40$ °C (Marom et al. 2006).

Roosting bats may lose substantial fractions of their body mass via evaporative cooling on a daily basis. Studier et al. (1970) examined dehydration tolerance in several *Myotis* species, and found that diurnal mass loss ranged from 6.4-21.9% of body mass in warm, dry roosts. Body mass losses equivalent to 23-32% were associated with 50 % mortality in most species (Studier et al. 1970). However, the latter values are based on bats roosting in relative mild thermal conditions, and dehydration rates are likely to be far higher in very hot roosts. In *M. condylurus*, for instance, total EWL on a very hot day estimated from a T_{roost} profile was equivalent to 44 % of body mass, leading Maloney et al. (1999) to conclude that the bats must have selected cooler microsites within the roost and/or reduced heat gain by clustering together. Data on acute dehydration tolerance limits for bats experiencing very high roost temperatures are lacking.

The aim of this study was to investigate thermoregulation at high T_a in three southern African bat species that occur sympatrically in a hot semi-arid environment. The Limpopo River valley, where we conducted our study, is one of the hottest parts of southern Africa, with T_a sometimes exceeding 43 ˚C in mid-summer (South African Weather Service). However, common bat species in this area use a variety of roosts that differ in thermal properties, particularly in terms of buffering them from maximum T_a (D. Cory Toussaint, *pers. ob.*), providing a model system for addressing questions related to interspecific variation in heat tolerance and thermoregulatory capacity at high environmental temperatures. We hypothesised that interspecific variation in heat tolerance and evaporative cooling capacity is correlated with roost thermal properties, and varies among sympatric species that roost in microsites that

differ in the extent to which they are thermally buffered from high outside T_a. Specifically, we predicted that species using comparatively hotter microsites as diurnal roosts should have a greater capacity to maintain T_b below environmental temperature compared with species that use comparatively cooler microsites.

Materials and Methods

Study site

The study took place in the private game reserve Makulu Makete (S 22˚ 35 09' E 28˚ 52') near the town of Alldays in the Limpopo River valley, Limpopo Province of South Africa. The reserve is 3703 ha in extent and characterised by hot summers and cool winters, and a mean annual rainfall of 388 mm. The topography of the area is predominantly flat, with vegetation consisting mainly of mopane (*Colophospermum mopane*) woodland with scattered baobab trees (*Adansonia digitata*).

Study species and roost sites

Evaporative water loss (EWL), metabolic rate (MR) and body temperature (T_b) was measured during the austral summer of 2010-2011 in *Nycteris thebaica* (Egyptian slit-faced bat; Nycteridae)*, Taphozous mauritianus* (Mauritian tomb bat; Emballonuridae) and *Sauromys petrophilus* (Roberts' flat-headed bat; Molossidae) in a field laboratory set up in a bungalow at Makulu Makete. All bats used in the study were adults. The mean body masses (M_b) of *N. thebaica* (28 males, 4 females)*, T. mauritianus* (9 males, 6 females) and *S. petrophilus* (29 males, 9 females) used in the study were 11.65 ± 0.97 g (n=32), 26.17 ± 2.70 g (n=15) and 10.98 ± 1.38 g (n=38) respectively.

Individuals of each species were caught using different strategies based on

their ecology and roosting habits. *N. thebaica* were actively captured with a hand net from their night roost (an old hunters' hut) between 02:30 and 03:00, before they returned to their day roost in a large cavity in a baobab tree. *T. mauritianus* were captured at two day roost sites on buildings using a mist net placed in front of each roost. *S. petrophilus* roosted in rock crevices during the day and were captured the night before measurements in a mistnet extended over a waterhole near the roost sites. Bats of all three species were held in cloth bags until measurements commenced at approximately 06:00 each day. Bats were fed mealworms and provided with water in captivity, but all measurements took place at least 2 hr after feeding. Each individual was used for measurements at a maximum of three T_a values, and time in captivity did not exceed 24 hours.

Roost, air and body temperature measurements

Air temperatures within roost sites (T_{roost}) were recorded during late summer using miniature data loggers (resolution = 0.0625 °C, iButton Thermochron DS1922L, Dallas Semiconductor, Dallas, TX, USA) suspended so as to measure air rather than surface temperature. The roosts used by *N. thebaica* and *S. petrophilus* were completely shaded from solar radiation, and did not allow for much air movement, and so we are confident that these measurements provide a reasonable approximation of the operative temperatures (Bakken 1992) experienced by the bats. Outside air temperature (T_a) was recorded using an iButton suspended in a ventilated white polystyrene cup placed in the shade on the side of a building that was also used by *T. mauritianus* as a day roost. Although the operative temperatures experienced by this species were potentially influenced more by wind and radiation than was the case for the other two species, there was little discernable wind on most days during the study,

other than during occasional afternoon thunderstorms, and individuals typically roosted deep in the eaves of thatched roofs, where they would have been exposed to little reflected radiation.

Body temperatures (T_b) above 25 °C were measured using temperature sensitive passive integrated transponder (PIT) tags (Destron Fearing, St. Paul MN, USA) injected subcutaneously between the scapulae of each bat. These PIT-tags cannot read temperatures below 25 °C, and thus we have no T_b data below this value. Body temperature data were recorded using a handheld reader (Pocket Reader EX, Destron Fearing, St. Paul MN, USA) modified to energise and receive signals from PIT tags via external antennae. An external antenna, housed in a rectangular plastic box, was attached to one side of each metabolism chamber. In bats, subcutaneous temperature provides an accurate measure of core T_b (Gorman et al. 1991).

All iButtons and a representative sample of ten PIT tags were calibrated before use in a circulating waterbath over temperatures from 15-45 °C and 25-47.5 °C respectively (measurement precision = 0.2 °C), using a mercury-in-glass thermometer with accuracy traceable to the US National Bureau of Standards. The resulting calibration equation for the PIT tags, determined using a linear regression fitted to data for all ten, was $y = 1.0384x + 0.1055$ ($r^2 = 0.9995$), where y is actual temperature and x is measured temperature. Our decision to calibrate just a subset of the PIT tags was based on the very small variance in measured temperatures: SD values for the ten calibrated tags decreased with increasing water temperature from 0.148 °C at 26 °C to 0.067 °C at 47 °C.

Gas exchange measurements

Respiratory gas exchange [oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production

($\dot{V}_{CO_2}$)] and EWL were measured at T_as of approximately 10 – 42 °C using an open flow-through respirometry system. Bats were placed individually in 1.3 L metabolic chambers constructed from Lock-tight™ storage containers. A small rectangle of shade cloth was secured to the inside of the chamber lid and the vertical wall of the chamber nearest the PIT tag antenna, in order to encourage bats to cling within reception range. A 1-cm layer of mineral oil was placed in the bottom of each chamber to prevent evaporation from urine and faeces, with a plastic mesh platform (large enough mesh to allow faeces to fall through) positioned approximately 10 cm above the oil layer. The chambers were placed in a controlled-environment cabinet (PTC-1, Sable Systems, Las Vegas NV, USA) which controlled air temperature via a Peltier device.

Atmospheric air supplied by a pump (model DOA-P13-BN, Gast Air Pumps, Benton Harbour, Michigan, USA) passed through a filter (model F3000-8G, CKD Corporation, Shanghai, China), before being partially dried using two silica gel columns connected in series. The airstream was then split and passed through needle valves (Swagelok, Solon OH, USA), which regulated the flow rate to each chamber (maximum of three chambers used simultaneously). Flow rates were measured before and after each run using the mass flow meter of an SS-3 Subsampler (Sable Systems, Las Vegas NV, USA), regularly calibrated using a 1-L soap bubble flow meter (Baker and Pouchot 1983) in order to verify that flow rates had not changed during an experimental run. Flow rates of 500-700 ml min^{-1} were used, which ensured that O_2 concentrations within the chambers remained above 20.4 %, and water vapour pressure remained low, with a maximum chamber water vapour partial pressure of 1.7 kPa, equivalent to a dewpoint of 15 °C. The 99 % equilibrium times (Lasiewski et al. 1966) for the chambers ranged from 8.5 – 11.9 min. To enhance mixing of air within

the chambers, the air inlet was positioned near the bottom of the chamber and the outlet near the top. Chamber T_a was measured using calibrated Cu-Cn thermocouples (Physitemp, Clifton, NJ, USA) inserted into the chambers through small holes in the lids and secured in place, and a TC-1000 Thermocouple Meter (Sable Systems).

Excurrent air from each chamber and a baseline channel of incurrent air were sequentially subsampled using a TR-RM8 Respirometry Multiplexer and SS-3 Subsampler (Sable Systems). At the start of each run, baseline air was first subsampled for 3 min, then air from each chamber was subsampled for 15 min, followed by another 3-min baseline. Subsampled air was first pulled through a RH-300 water vapour analyser (Sable Systems), regularly zeroed using nitrogen and spanned by calculating the water vapour pressure of saturated air at a known temperature, generated by bubbling atmospheric air through water at room temperature and then through water 3-4 °C cooler than room temperature. Subsampled air then passed through a CO_2 analyser (CA-10a, Sable Systems) and O_2 analyser (FC-10a, Sable Systems) to determine fractional CO_2 and O_2 concentrations respectively. The CO_2 analyser was regularly zeroed using nitrogen and spanned against an analytically certified gas with a known CO_2 concentration of 2002 ppm (AFROX, Johannesburg, South Africa). The O_2 analyser was regularly spanned to a fractional O_2 concentration of 20.95% using dry CO_2-free air that was generated by passing atmospheric air through soda lime and then magnesium perchlorate (Merck Chemicals, Wadeville, South Africa). All tubing used in the system was Bev-A-Line tubing (Thermoplastic Processes Inc., Warren, NJ, USA). Voltage outputs from all analysers were digitised using a Universal Interface II (Sable Systems), and recorded with a sampling interval of 1 s using a personal computer with Expedata software (Sable Systems).

Experimental protocol

All gas exchange and T_b measurements took place during the day, i.e, in the rest-phase of the bats' circadian cycles. Bats were exposed to T_as of 10-42°C in increments of 5°C, except at T_a > 40 °C. At T_a between 10 and 25°C, each individual was exposed to three T_a values selected randomly on each day of experiments for 3-4 hr per T_a value. At T_as between 30 and 40°C, however, only two T_a values were used per run, and bats were exposed to each T_a for a maximum of 3 hr. Incremental or decremental changes in T_a occurred rapidly, and it typically took < 20 min for T_a within the chamber to stabilise at a new level. At the highest T_a of approximately 42°C, individuals were only exposed to constant T_a for 45 - 60 min and removed immediately thereafter and given water to drink. If T_b spiked to levels suggestive of uncontrolled hyperthermia, the bats were immediately removed from the environmental chamber, given water to drink and placed in a cloth bag in a cool room. Sample sizes for RMR, EWL and T_b at each T_a were typically 6-7 individuals, with the exception of *N. thebaica* at $T_a \approx 40$°C (n = 3), and *S. petrophilus* T_b data at $T_a <$ 25°C on account of the inability of the PIT tags to measure temperatures below 25°C. During all measurements, T_b was continuously monitored, and reported values were associated with periods of approximately stable metabolic rate and EWL. At no time did we detect rapid decreases in T_b as would be expected during entry into torpor, or increases as would be expected during rewarming following a torpor bout.

Data analyses

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were calculated using equations 9.4 and 9.5 respectively, the rate of water vapour production ($\dot{V}_{H_2O}$) was calculated using equation 9.6, and excurrent

flow rate was calculated using equation 9.3 in Lighton (2008). Resting metabolic rates and EWL rates were calculated from steady-state traces of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ in ExpeData, with the lowest 1-min mean values considered to be representative of resting values. Respiratory exchange ratios (RER) were determined as $\dot{V}_{CO_2} / \dot{V}_{O_2}$. RER values averaged 0.77 ± 0.17. On several occasions, bats exhibited RER values outside the range of 0.71-1.00. Although the latter range is considered typical for animals metabolising carbohydrates and lipids, values less than 0.71 and greater than 1.00 have been reported in birds (Walsberg and Wolf 1995) and are not necessarily a product of experimental error. Values below 0.71 may be due to the incomplete oxidation of fat and loss of CO_2 by non-pulmonary routes, such as bicarbonate ion excretion and storage, whereas values > 1.00 are generally associated with fat synthesis (Walsberg and Wolf 1995). We are not aware of reliable thermal equivalence data for RER values beyond the 0.71-1.00 range; thus, we assumed RER = 0.71 for lower values and RER = 1.00 for higher values. Metabolic rates were determined by converting the gas exchange measurements using the thermal equivalence data in Table 4.2 in Withers (1992). Using this approach within the 0.71-1.00 range involves the assumption that only carbohydrates and lipids are metabolized, and a maximum error of 6% is associated with protein catabolism (Walsberg and Wolf 1995). All metabolic rates were expressed in Watts (W).

The thermoneutral zone of each species was determined using the Broken Stick procedure in R (R 2.13.0, R Development Core Team) to identify the lower critical limit of thermoneutrality (T_{LC}). The upper critical limit of thermoneutrality (T_{UC}) was determined by calculating the intercept of two regressions fitted to the most level part of the metabolic rate data and through the increase in metabolic rate thereafter, as there were usually too few data points above the T_{UC} to use the Broken

Stick procedure. Dry heat transfer coefficients (mW $°C^{-1}$ cm^{-2}) were calculated following (Dawson and Schmidt-Nielsen 1966). Surface area (A_b) was not measured in the bats used for experiments, but was instead subsequently estimated from museum specimens [four *T. mauritianus* (A_b = 44.98 ± 3.44 cm^2), seven *S. petrophilus* (A_b = 24.56 ± 0.95 cm^2) and ten *N. thebaica* (A_b = 22.90 ± 2.32 cm^2)] using the same approach as Marom et al. (2006). Because dry heat transfer coefficients were estimated using a single mean A_b value per species, we calculated a single dry heat transfer coefficient value per T_a per species and do not report variances.

For interspecific BMR comparisons, we obtained published BMR data for 39 species (Electronic Supplementary Material), mainly from the sources in Marom et al. (2006). Body mass and BMR data were $\log_{10}$ transformed prior to analyses. To compare the BMR of our study species to those of other bats, we first tested for phylogenetic signals in M_b and BMR using randomization tests for the mean-squared error and by calculating the *K*-statistic (Blomberg et al. 2003), MatLab program PHYSIG_LL.m). We constructed a tree for the 42 species (39 from literature plus three from present study) based on the (Bininda-Emonds et al. 2007) supertree using the program Mesquite (Maddison and Maddison 2011). Since M_b (K = 0.689, $P < 0.001$) and BMR (K = 0.577, $P < 0.001$) both exhibited significant phylogenetic signals, we fitted conventional ordinary least squares (OLS) and phylogenetically informed least squares (PGLS) regressions to $\log_{10}$BMR (W) and $\log_{10}M_b$ (g) data using the MatLab program REGRESSIONv2.m (Lavin et al. 2008). In order to determine the model that provided the best fit to the data, we applied the various branch length transformations available in REGRESSIONv2.m, namely Brownian motion (no transformation), Ornstein–Uhlenbeck (OU), Grafen's ρ, and Pagel's λ, and

then compared original Akaike Information Criterion (AIC) and corrected AIC (AICc) values to identify the model that provided the best fit (Lavin et al. 2008; Swanson and Garland 2009). Our regression analysis indicated that a phylogenetically informed regression using Grafen's ρ-transformation provided the best fit to the data (Table 2). Thus, in order to compare the observed BMRs of *N. thebaica*, *T. mauritianus* and *S. petrophilus* to allometrically expected values, we calculated phylogenetically independent 95 % prediction intervals for each species, following Garland and Ives (2000). After branch lengths were transformed using Grafen's ρ-transformation, each species was sequentially pruned from the phylogeny, the tree re-rooted, and prediction intervals calculated from independent contrasts in the MS-DOS program PDTREE (Garland and Ives 2000). We also calculated a phylogenetically independent regression for the overall data set (Garland and Ives 2000).

As an exploratory analysis of the possibility of a correlation between the roost thermal properties and the thermoregulatory capacity at high T_a among bats in general, we surveyed the literature for studies that reported information on physiological responses to high T_a as well as roost site thermal properties. As an index of the capacity to defend T_b under very hot conditions, we used the change in T_b associated with an increase in T_a from 35°C (i.e., just below typical normothermic T_b) to 40°C (i.e., just above typical normothermic T_b) as an index of heat tolerance. We then examined whether this index of heat tolerance is correlated with the extent to which roosts are buffered from high outside T_a, using the difference between maximum T_{roost} and maximum T_a as an indication of the thermal buffering of a specific roost site. We used data for *Mops condylurus* (Bronner et al. 1999; Maloney et al. 1999), *Myotis yumanensis*, *Antrozous pallidus* and *Tadarida brasiliensis* (Licht and Leitner 1967a; Licht and Leitner 1967b), and the three species examined in the

present study. We recognize that these indices are overly simplistic quantifications of variables that are in reality determined by a host of complex interactions between abiotic and physiological variables, and intend this merely as a preliminary analysis aimed at developing a hypothesis to be tested in future studies. Moreover, the small size of the data set (seven species - see below) precludes the possibility of reliably testing for a phylogenetic signal using the *K*-statistic (Blomberg et al. 2003). We analysed the relationship between the heat tolerance index and roost thermal properties using the same model-fitting approach as outlined above.

Results

Thermoregulation at moderate air temperatures

Patterns of thermoregulation at moderate T_a varied considerably among species (Figure 1), with corresponding variation in parameters such as EWL and BMR (Table 1). Most *N. thebaica* and all but one *T. mauritianus* remained normothermic during measurements at T_a below thermoneutrality, i.e., T_b remained within the ranges characteristic of thermoneutral conditions (Figure 1). The T_b of several *N. thebaica* decreased below 35 °C at T_as of 10-20°C, with one individual exhibiting T_b = 26.8 °C at T_a = 9.9 °C (Figure 1). One *T. mauritianus* male reduced T_b to a minimum of 32.2°C at T_a=10.3 °C. In contrast to these two species, *S. petrophilus* were highly heterothermic at T_as between 10 and 30°C, with many T_b values falling below 25°C, and thus not measurable by the PIT tags we used (Figure 1). Moreover, *S. petrophilus* did not show a clear thermoneutral zone. Although metabolic rate in this species remained stable at T_a values of approximately 30 - 35 °C (Figure 2), T_b did not, and was significantly lower at $T_a \approx 30$ °C compared with $T_a \approx 35$ °C (Holm-Sidak Post-

hoc Test, t= 5.933, P < 0.001). Mass-specific EWL in *N. thebaica* at T_a = 25 °C was approximately 4-fold higher than in the other species (Table 1). Mass-specific rates of EWL at thermoneutral T_as were similar in *T. mauritianus* and *S. petrophilus*, despite the much larger M_b of the former species (Table 1).

Interspecific basal metabolic rate comparison

There was an overall significant relationship between log BMR and log body mass ($p<0.001$) best described by the phylogenetically independent regression $\log BMR = -1.824+0.764M_b$ (Figure 4). The BMR values for *T. mauritianus* and *N. thebaica* fell within the 95% prediction intervals, and are both virtually identical to the allometrically expected values (Figure 4). In contrast, the minimum resting metabolic rate of *S. petrophilus* fell below the phylogenetically corrected lower 95 % prediction interval (Figure 4), and is thus significantly lower than the BMR expected based on the phylogenetic position of this species.

Thermoregulation at high air temperatures

The three species varied substantially in their responses to T_a approaching or exceeding normothermic T_b (Figure 1,3). EWL increased rapidly in *T. mauritianus*, with a maximum rate of 14.7 ± 1.3 mg g^{-1} hr^{-1} at $T_a \approx 42$ °C, equivalent to 12 X EWL at $T_a \approx 25$ °C. Body temperature increased from normothermic levels of 38.7±3.4 to a maximum of 42.9 ± 1.6 °C at $T_a \approx$ 40-42 °C (Table 2, Figure 1), with one individual exhibiting T_b = 44.9 °C at T_a = 41.8 °C. Dry heat transfer coefficient values increased from a minimum of 0.35 mW $°C^{-1}$ cm^{-2} at $T_a \approx 20$ °C to 1.24 mW $°C^{-1}$ cm^{-2} at $T_a \approx 42$ °C.

S. petrophilus also exhibited rapid increases in EWL with increasing T_a

(Figure 3), with a maximum EWL = 23.7 ± 7.4 mg g^{-1} hr^{-1} at $T_a \approx 42$ °C, equivalent to 21 X EWL at $T_a \approx 25$ °C, although this number is inflated by this species' pronounced heterothermy. Mean T_b increased from normothermic values of 37.6±0.4 °C (n = 7) to 43.7±1.0 °C (n = 6) at $T_a \approx 42$ °C (Table 2, Figure 1), with one individual exhibiting $T_b = 46.5$°C at $T_a = 41.7$ °C. Unlike *T. mauritianus, S. petrophilus* showed an approximately two-fold increase in metabolic rate between $T_a \approx 40$ °C and $T_a \approx 42$ °C (Figure 2). Dry heat transfer coefficient was minimal at $T_a \approx 30$ °C (0.19 mW $°C^{-1}$ cm^{-2}), and increased to 1.28 mW $°C^{-1}$ cm^{-2} at $T_a \approx 42$ °C.

Evaporative water loss in *N. thebaica* increased much more gradually with increasing T_a than in the other two species, and began increasing at T_a = 25-30 °C (Figure 3). The maximum EWL was 18.6±2.1 mg g^{-1} hr^{-1} (n = 3) at $T_a = 39.4 \pm 0.0$ °C, equivalent to approximately 4 X EWL at $T_a \approx 25$ °C, a much lower fractional increase than in the other species. The maximum T_b observed in this species was 45.0±0.9°C (n = 3) at $T_a = 39.4 \pm 0.0$ °C, although one individual exhibited $T_b = 46.5$°C without any apparent ill-effects. Dry heat transfer coefficient values increased from a minimum of 0.26 mW $°C^{-1}$ cm^{-2} at $T_a \approx 30$ °C to 0.83 mW $°C^{-1}$ cm^{-2} at $T_a \approx 39$ °C. Overall, *N. thebaica* was the least heat tolerant of the three species, with several individuals dying at $T_a = 39.4 \pm 0.0$ °C, hence the low sample size and absence of data for this species at $T_a \approx 42$ °C.

Roost temperatures and interspecific variation in heat tolerance

The baobab tree cavity used by all *N. thebaica* individuals involved in this study was well buffered against daily T_a fluctuations, maintaining an average $T_{roost} = 27.6 \pm 0.6$ °C and never exceeding 30 °C even when outside $T_a > 35$ °C. The *T. mauritianus* individuals roosted in shaded sites below overhanging thatch roofs, and experienced

T_{roost} very similar to outside T_a. The rock crevice used by *S. petrophilus* was the hottest of the three roost sites, with T_{roost} routinely exceeding T_a by > 2 °C.

In our analysis of a possible correlation between an index of heat tolerance (IHT, change in T_b as T_a increases from 35 °C to 40 °C) and roost thermal buffering ($T_{roost\_max} - T_{a\_max}$), an OLS regression provided a significant fit [$IHT = 4.438 - 0.070(T_{roost\_max} - T_{a\_max})$, $F_{slope} = 8.572$, $P = 0.033$, Figure 5] whereas none of the PGLS regressions did, but the latter result most likely reflects the small sample size involved.

Discussion

Our data reveal considerable variation in thermoregulatory responses to high T_a and heat tolerance among three sympatric bat species inhabiting a hot, semi-arid habitat in northern South Africa. Although all three species exhibited increases in T_b and EWL qualitatively typical of endotherms experiencing environmental temperatures approaching or exceeding normothermic T_b, the shapes of relationships between EWL, T_b and T_a varied markedly.

Interspecific variation in basal metabolic rate and thermoregulation at moderate T_a

The BMRs of *N. thebaica* and *T. mauritianus* were very close to allometrically predicted values (Figure 4). The relationship between T_a, RMR and T_b in *S. petrophilus* did not follow the pattern typical of endotherms, and consequently we do not consider the minimum RMR observed in this species to represent a true BMR. This conclusion is reinforced by the observation that the minimum RMR of *S. petrophilus* was equivalent to just only 44% of the predicted BMR value, and relative to M_b, is considerably lower than any BMR so far measured in a bat species (Figure

4). Our data for *S. petrophilus* confirm that not all bats follow the classic model of endotherm thermoregulation (Scholander et al. 1950), and parameters such as BMR and TNZ may not be applicable to all species.

At lower T_a values, the RMRs of *Nycteris thebaica, Taphozous mauritianus* and *Sauromys petrophilus* generally increased with decreasing temperature, a pattern typical of endotherms (Scholander et al. 1950; Wimsatt 1970). *T. mauritianus* was the least heterothermic of the three species, whereas *S. petrophilus* was the most heterothermic. However, thermoregulation in *S. petrophilus* differed in that T_b decreased with decreasing T_a between 10 and 25 °C (Figure 1). It did not closely track T_a as typically occurs during torpor and hibernation (e.g., Geiser and Brigham 2000; Willis et al. 2005), although the relatively short period (3-4 hr) for which bats were exposed to each T_a value makes this conclusion difficult to verify. Our lack of T_b measurements below 25 °C, together with the possibility of non-steady-state metabolic rates raised by the large variances for *S. petrophilus* RMR (Figure 2), mean that heterothermy in this species requires further investigation.

Mass-specific rates of EWL scale allometrically with M_b in bats, decreasing with increasing M_b (Studier 1970). Our observation that mass-specific EWL at thermoneutral T_a is similar among species that vary more two-fold in M_b, but differs approximately 4-fold among species of similar M_b, reiterates the importance of M_b-independent interspecific variation in bats and other animals. One factor potentially contributing to the higher resting EWL in *N. thebaica* concerns wing morphology; gleaners such *Nycteris* spp. tend to have lower wing-loading (and thus greater wing surface area per unit M_b) than *Taphzous* spp. and molossids (Norberg and Rayner 1987). A second factor driving the higher EWL of *N. thebaica* may be the much larger ears of this species compared to *T. mauritianus* and *S. petrophilus*.

Interspecific variation in responses to high air temperatures

The hyperthermic T_b values we observed are among the highest reported so far for bats, including during flight (Kurta 1986; Thomas and Suthers 1972). However, very few studies have examined hyperthermic T_bs in bats in response to acute heat exposure. *Myotis lucifugus* tolerated $T_b \approx 42$ °C, and *M. sodalis* survived, although stressed, at $T_b = 41$-42 °C (Henshaw and Folk 1966). *Mops condylurus* exhibited $T_b \approx 43$ °C at $T_a \approx 45$ °C (Maloney et al. 1999). The maximum T_bs of our species were also considerably higher than those of *Tadarida teniotis* and *Otonycteris hemprichii* at $T_a = 40$ °C (Marom et al. 2006) and *Pipistrellus pipistrellus* at $T_a \approx 38$ °C (Genoud and Christe 2011).

There are two potential sources of uncertainty regarding our T_b measurements. First, PIT tags were injected subcutaneously and it is possible that the measured temperature represents a value between core T_b and the temperature of the animal's environment; gradients of 2-3 °C between skin and core temperature are common in studies of heterothermy in free-ranging mammals and birds (Willis and Brigham 2003). However, since bats always maintained $T_b > T_a$ during our study, any gradient between subcutaneous and core temperature would have caused the PIT tags to underestimate rather than overestimate T_b, reinforcing the validity of these high values. Second, the PIT tags were located near where thermogenic brown adipose tissue (BAT), the site of non-shivering thermogenesis (NST), is most likely to occur (Cannon and Nedergaard 2004; Rothwell and Stock 1985). NST in bats is primarily used during rewarming from torpor and/or hibernation (Cannon and Nedergaard 2004), and it is highly unlikely these species would have been producing excess heat via NST and thus elevating interscapular subcutaneous T_b when exposed to high T_a in

our study. We cannot, however, exclude the possibility of T_b values observed at lower T_a being influenced by NST.

In all three species, EWL increased rapidly at T_as above the TNZ, but pronounced interspecific variation was evident in EWL-T_a relationships (Figure 3). Whereas EWL in *T. mauritianus* and *S. petrophilus* increased very rapidly at higher T_a, a pattern similar to that observed in *Mops condylurus* (Maloney et al. 1999) and a number of other species (e.g.,Marom et al. 2006), EWL in *N. thebaica* began increasing at lower T_a, increased more gradually, and reached a maximum value far lower than those of *M. condylurus* or *T. mauritianus* (Figure 3). These differences in EWL patterns are mirrored by interspecific variation in T_b; whereas *M. condylurus*, *T. mauritianus* and *S. petrophilus* all maintained $T_b < 44$ °C at $T_a \approx 42$ °C, the T_b of *N. thebaica* increased rapidly, and reached 45 °C at $T_a \approx 39$ °C, with several individuals dying at this T_a. These data reveal the variation in heat tolerance that can exist within sympatric species occurring at a single site, and reiterate the importance of factors other than climate in determining a taxon's thermoregulatory capacity. One such variable may be phylogeny; several authors have noted pronounced heat tolerance in members of the Molossidae (Licht and Leitner 1967a; Maloney et al. 1999), and the greater heat tolerance of *S. petrophilus* is qualitatively consistent with this idea.

Interspecific variation in heat tolerance, roost thermal properties and implications for predicting climate change impacts

Our exploratory analysis of interspecific variation in heat tolerance supports the hypothesis that species occupying hotter (relative to outside air temperature) roosts have a better capacity to regulate T_b via evaporative heat loss, manifested as smaller increases in T_b associated with T_a exceeding normothermic T_b (Figure 5). This

analysis is severely constrained by a) the fact in all these studies, just one roost site per species was examined, b) a small sample size, which precludes reliably testing for a phylogenetic signal (Blomberg et al. 2003), and c) our index of roost thermal buffering that does not account for the complexity of thermal microclimates and physiological factors determining heat tolerance. Nevertheless, on the basis of this exploratory analysis, we suggest that the hypothesis that there is a linkage between roost thermal properties and interspecific variation in thermoregulatory capacity at high environmental temperatures should be more carefully investigated by combining laboratory data with careful measurements of the thermal conditions in roosts. Should such studies confirm a pattern of greater heat tolerance and evaporative cooling in species using hotter roosts, the next step would be to establish the extent to which this pattern represents "hard-wired" genotypic interspecific variation versus phenotypic plasticity via experiments in which the ability of bats to increase their capacity to thermoregulate in very hot conditions is explored via thermal acclimation experiments.

Finally, the interspecific variation in heat tolerance and capacity for evaporative cooling that exists in the three sympatric species we investigated here has implications for predicting the impacts of climate change on bats roosting in hot microsites. A recent report indicates that heat wave conditions that currently represent a 1-in-20 year occurrence are likely to become 1-in-5 year to 1-in-2 year events by the end of the 21st Century, and extreme daily maximum T_a will increase by 2-5 °C over the same period (IPCC 2011). The recent mass die-offs observed in Australian flying-foxes reveal that, like birds, bats are vulnerable to direct mortality during very hot weather (McKechnie and Wolf 2010; Welbergen et al. 2008). Our data highlight several issues that need to be taken into account when predicting climate change

impacts on bat communities in hot environments. Microsite availability, and the presence of landscape elements that provide thermally-buffered roost sites, will be critical elements of models for climate change impacts. Comparatively cool microsites such as the baobab tree cavity in which our study population roosted would appear to be critical for the presence of *N. thebaica* at our study site, and may buffer this species from future increases in extreme maximum T_a. The rapid increases in EWL at high T_a in *S. petrophilus* may mean that, despite being comparatively heat tolerant, this species may also be the most vulnerable to lethal dehydration during future heat waves. Alternatively, rising temperatures may increase competition for cool microsites, with species currently using hotter sites becoming increasingly reliant on sites such as those currently used by *N. thebaica*.

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Table 1. Body mass, body temperature (T_b), lower and upper critical limits of thermoneutrality (T_{LC} and T_{UC}, respectively), mass-specific basal metabolic rate (BMR) and evaporative water loss (EWL) in three species of bats, namely *Nycteris thebaica, Taphozous mauritianus* and *Sauromys petrophilus*, in the Limpopo River valley, South Africa. Sample sizes are given in parentheses.

Species	Body Mass (g)	T_{LC}[a] (°C)	T_{UC}[a] (°C)	T_b (°C)	BMR (mW g^{-1})	EWL at 25°C (mg g^{-1} hr^{-1})
N. thebaica	11.7±1.0 (32)	26.2	33.6	38.6±1.4 (19)	8.9±2.7 (12)	4.7±1.5 (9)
T. mauritianus	26.2±2.7 (15)	29.0	34.2	38.7±3.4 (11)	6.6±2.2 (7)	1.2±0.5 (8)
S. petrophilus	11.0±1.4 (37)	----	----	37.6±0.4 (7)	3.4±0.6 (9)[b]	1.1±0.6 (10)

[a] Value calculated from complete data set for each species

[b] Minimum resting metabolic rate; cannot be considered BMR for reasons discussed in text

Table 2. Regression models fitted to $\log_{10}M_b$ (g) and $\log_{10}$BMR (W) data for 42 bat species (see Electronic Supplementary Material) using either conventional ordinary least squares (OLS) or phylogenetically informed approaches. For phylogenetically informed regressions, we applied various branch length transformations available in the MatLab program REGRESSIONv2.m, namely PGLS (Brownian motion, i.e., no transformation), Ornstein–Uhlenbeck (Reg OU), Grafen's ρ (Reg ρ), and Pagel's λ (Reg λ) (Lavin et al. 2008). The model with the lowest Akaike Information Criterion (AIC) and corrected AIC (AICc) values, indicating best fit, is indicated in bold. Akaike weights (w_i) are also provided.

Model	**Intercept**	**SE**	**Slope**	**SE**	**Ln maximum likelihood**	**Transform parameter**	**R^{2*}**	**AIC**	**AICc**	w_i
OLS	-1.833	0.037	0.767	0.026	59.090	----	0.910	-112.179	-111.904	< 0.001
PGLS	-1.928	0.087	0. 829	0.033	60.291	----	0.874	-114.581	-114.305	< 0.001
Reg OU	-1.899	0.047	0. 799	0.033	68.091	d = 0.385	0.868	-128.183	-127.718	0.349
Reg ρ	**-1.882**	**0.059**	**0.790**	**0.035**	**68.329**	**ρ = 0.428**	**0.850**	**-128.659**	**-128.194**	0.443
Reg λ	-1.880	0.070	0. 790	0.036	67.575	λ = 0.827	0.843	-127.150	-126.685	0.208

*Not comparable between conventional and phylogenetically informed regressions (Lavin et al. 2008).

Figure legends

Figure 1. Body temperature (T_b) in *Nycteris thebaica, Taphozous mauritianus* and *Sauromys petrophilus* experimentally exposed to air temperature (T_a) ranging from approximately 10°C to 42°C. For *N. thebaica*, data from heterothermic individuals are indicated with open symbols, with sample sizes indicated in parentheses. Error bars indicate standard deviation. The lower right panel shows comparative patterns of T_b in four southern African bats: *Nycteris thebaica* (orange), *Taphozous mauritianus* (blue), *Sauromys petrophilus* (green) and *Mops condylurus* (black). Data for *M. condylurus* are from Maloney et al. (1999).

Figure 2. Resting metabolic rate (RMR) in *Nycteris thebaica, Taphozous mauritianus* and *Sauromys petrophilus* experimentally exposed to air temperature (T_a) ranging from approximately 10°C to 42°C. For *N. thebaica*, data from heterothermic individuals are indicated with open symbols. Error bars indicate standard deviation. The lower right panel shows comparative patterns of RMR in four southern African bats: *Nycteris thebaica* (orange), *Taphozous mauritianus* (blue), *Sauromys petrophilus* (green) and *Mops condylurus* (black). Data for *M. condylurus* are from Maloney et al. (1999).

Figure 3. Evaporative water loss (EWL) in *Nycteris thebaica, Taphozous mauritianus* and *Sauromys petrophilus* experimentally exposed to air temperature (T_a) ranging from approximately 10°C to 42°C. For *N. thebaica*, data from heterothermic individuals are indicated with open symbols. Error bars indicate standard deviation.

The lower right panel shows comparative patterns of EWL in four southern African bats: *Nycteris thebaica* (orange), *Taphozous mauritianus* (blue), *Sauromys petrophilus* (green) and *Mops condylurus* (black). Data for *M. condylurus* are from Maloney et al. (1999).

Figure 4. Allometric scaling of basal metabolic rates (BMR; see Electronic Supplementary Material) in bats with a phylogenetically informed regression (solid line, Grafen's ρ-transformation of branch lengths). The BMRs of *Nycteris thebaica* and *Taphozous mauritianus*, and the minimum resting metabolic rate of *Sauromys petrophilus* (which, for reasons discussed in the text, we do not consider BMR) are represented by the open triangle symbols. The dashed lines are the 95% prediction intervals for the BMR of *S. petrophilus*, calculated following Garland and Ives (2000).

Figure 5. Relationship between index of heat tolerance [change in body temperature associated with increase in air temperature (T_a) from 35 to 40 °C] and the difference between roost temperature (T_{roost}) and outside (T_a) in seven bat species. An ordinary least squares regression that provided a significant fit is indicated by the solid line.

Figure 1

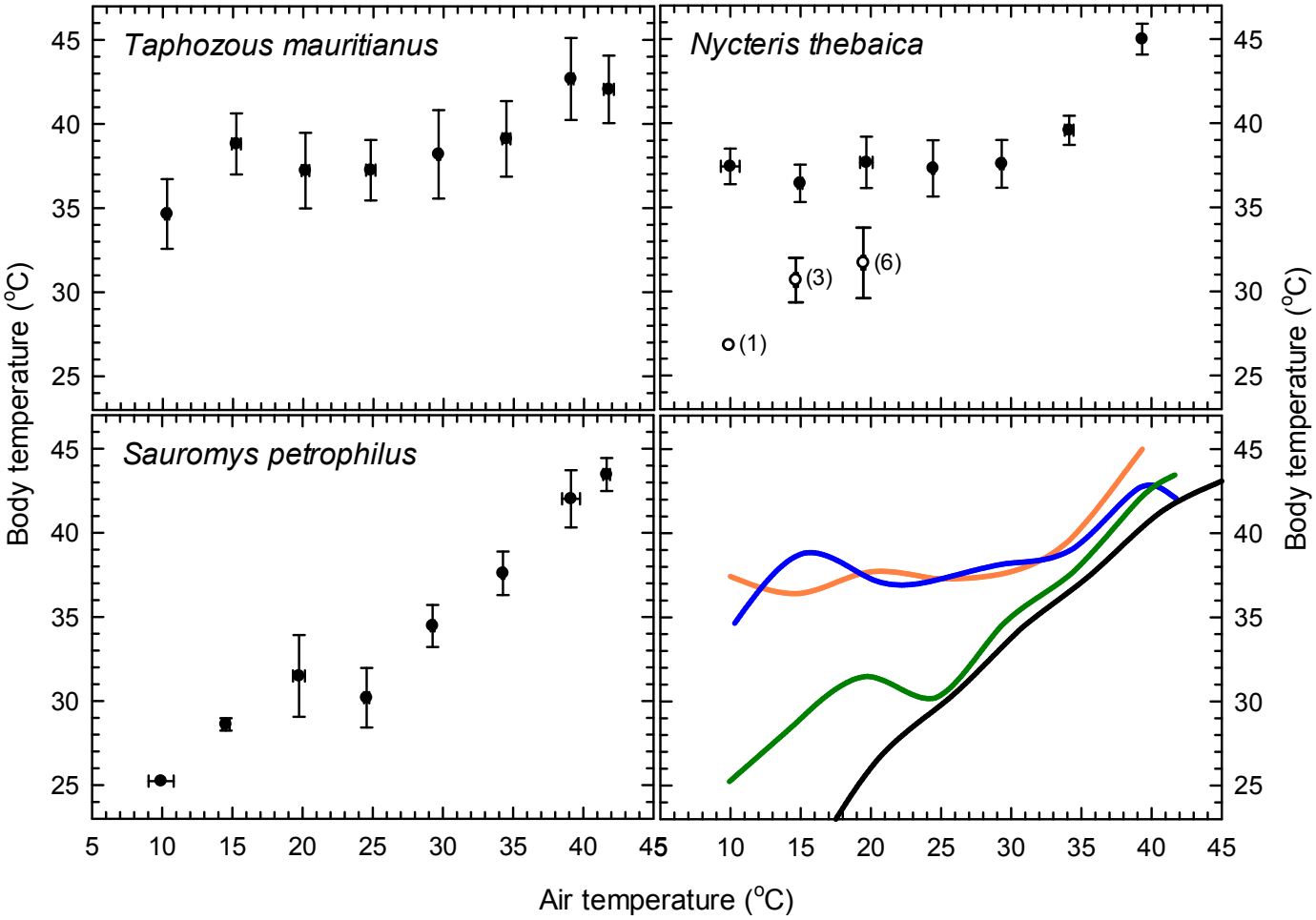
Taphozous mauritianus
Nycteris thebaica
Sauromys petrophilus
(1)
(3)
(6)
Body temperature (°C)
Air temperature (°C)

Figure 2

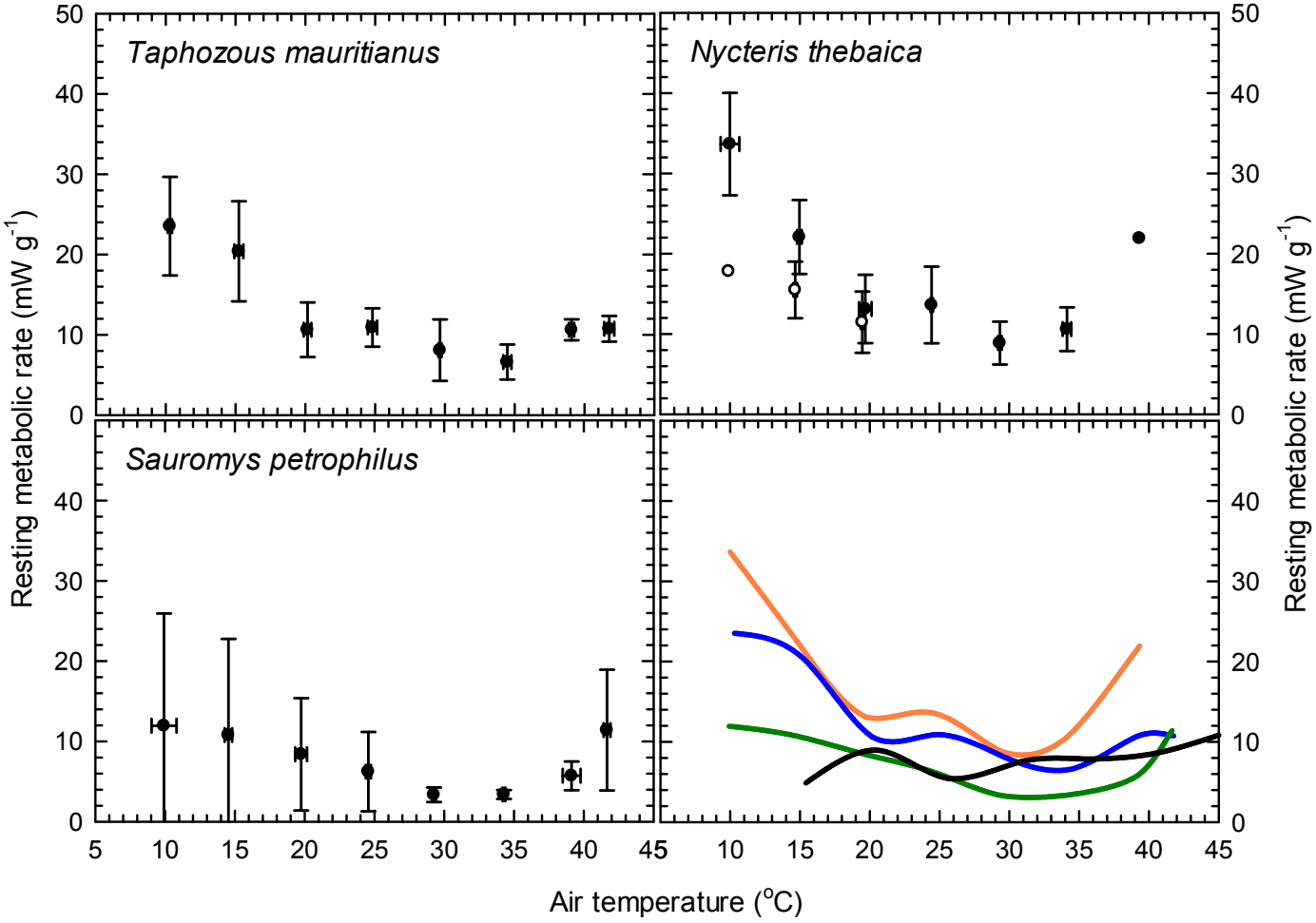
Taphozous mauritianus
Nycteris thebaica
Sauromys petrophilus
Resting metabolic rate (mW g-1)
Air temperature (°C)
0
10
20
30
40
50
5
10
15
20
25
30
35
40
45

Figure 3

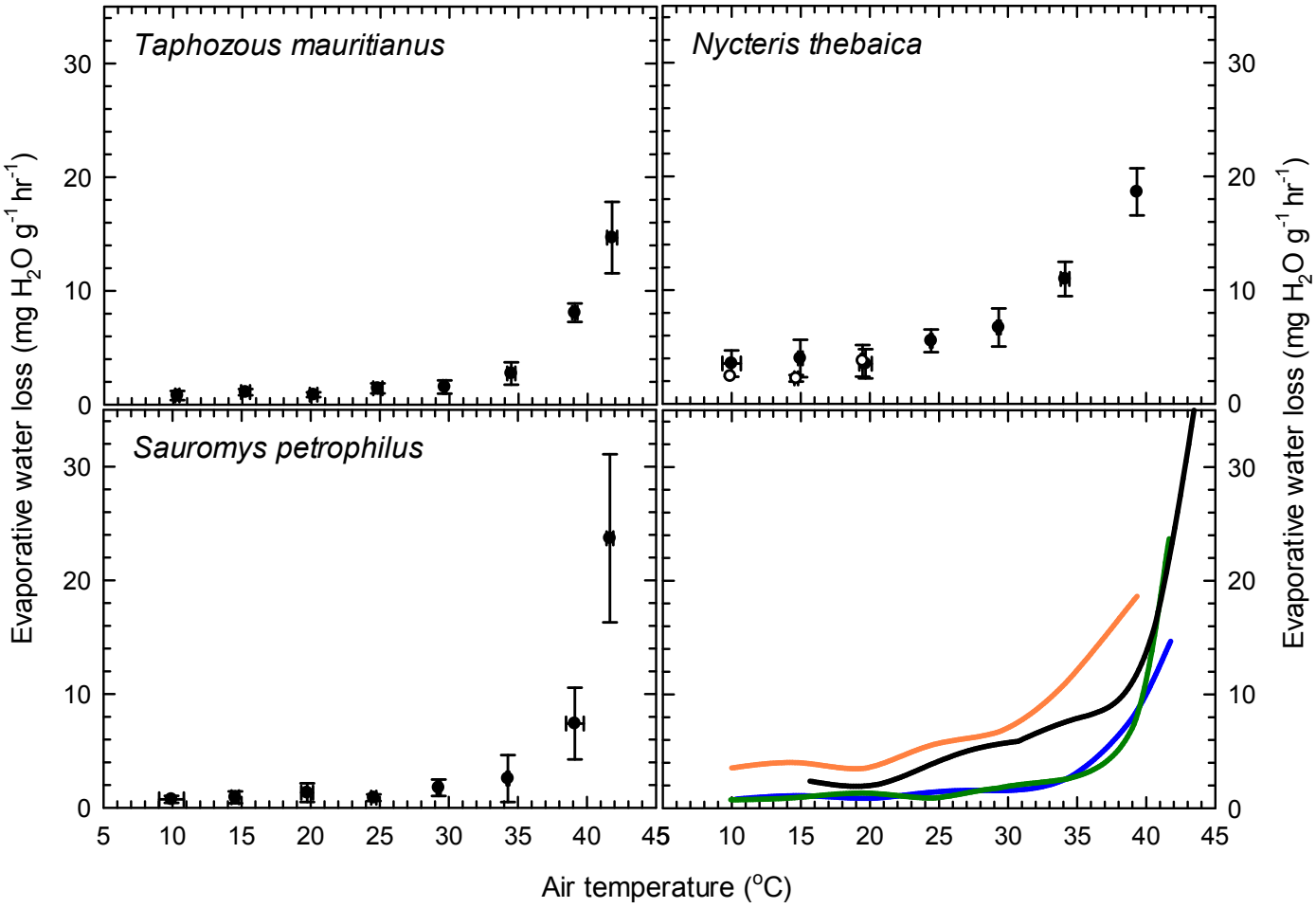
Taphozous mauritianus
Nycteris thebaica
Sauromys petrophilus
Evaporative water loss (mg H2O g-1 hr-1)
Air temperature (°C)
0
10
20
30
5
10
15
20
25
30
35
40
45

Figure 4

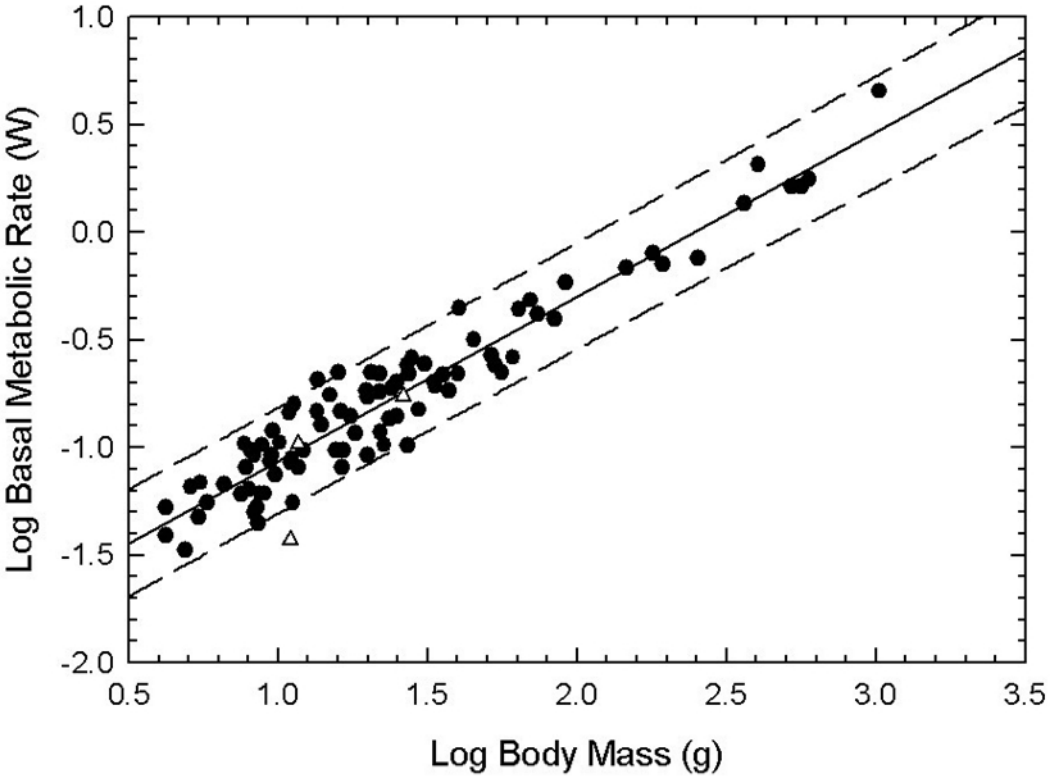
Log Basal Metabolic Rate (W)
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Log Body Mass (g)

Figure 5