Metabolic, hygric and ventilatory physiology of a hypermetabolic marsupial, the honey possum (*Tarsipes rostratus*).

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Keywords: Basal metabolic rate, body temperature, evaporative water loss, marsupial, ventilation, water economy

Abstract

The honey possum is the only non-volant mammal to feed exclusively on a diet of nectar and pollen. Like other mammalian and avian nectarivores, previous studies indicated that the honey possum's basal metabolic rate was higher than predicted for a marsupial of equivalent body mass. However, these early measurements have been questioned. We re-examined the basal metabolic rate (2.52 ± 0.222 ml O_2 g^{-1} h^{-1}) of the honey possum and confirm that it is indeed higher (162%) than predicted for other marsupials both before and after accounting for phylogenetic history. This, together with its small body mass (5.4 ± 0.14 g; 1.3 % of that predicted by phylogeny) may be attributed to its nectarivorous diet and mesic distribution. Its high basal metabolic rate is associated with a high standard body temperature (36.6 ± 0.48 °C) and oxygen extraction (19.4%), but interestingly the honey possum has a high point of relative water economy (17.0°C) and its standard evaporative water loss (4.33± 0.394 mg H_2O g^{-1} h^{-1}) is not elevated above that of other marsupials, despite its mesic habitat and high dietary water intake.

Introduction

The honey possum (*Tarsipes rostratus*) is a small (5-15g) marsupial belonging to the monospecific family Tarsipedoidae. Honey possums are restricted to the coastal sand plain heathlands of south-west Western Australia (Renfree 1998) where an abundance of Protoaceae and Myrtaceae plant species ensures year round availability of flowers that enables the honey possum to survive entirely on a diet of nectar and pollen (Russell and Renfree 1989). Honey possums have a number of morphological adaptations associated with their specialised diet, including a long, brush-tipped tongue, ridged palate, elongated snout, vestigial teeth, reduced masticatory muscles

and stomach diverticulum for nectar storage (Richardson *et al*. 1986; Russell and Renfree 1989).

A nectarivorous diet has been associated with a high basal metabolic rate (BMR; McNab 1980; 1986; 1988; 2003) and high rates of water turnover (Nicolson and Fleming 2003) in placental mammals and birds. Withers *et al*. (1990) measured the BMR, body temperature (T_b) and evaporative water loss (EWL) of the honey possum. They found it to have a high BMR compared to that predicted for a marsupial of equivalent body mass and attributed this to physiological adaptation to a nectarivorous diet. Withers *et al*. (2006) found that the honey possum was the only marsupial to have a statistically higher than predicted BMR both before and after correction for phylogenetic history, and again attributed this to its nectarivorous diet. However, McNab (2005) queried the existing data for the honey possum, as its BMR was higher than for any other marsupial, and excluded it from his analysis of the effects of diet on BMR of marsupials. He stated that "I should like to see a re-examination of the honey 'possum with special attention paid to the zone of thermoneutrality…".

We therefore re-examine the metabolic physiology of euthermic honey possums, presenting new BMR, T_b and EWL data, and provide additional ventilatory and water economy data for this unique nectarivorous marsupial. We compare these data to other marsupials to determine if the honey possum does indeed have a higher than predicted BMR, and to examine if other related physiological variables are likewise elevated.

Methods

Seven adult honey possums (three females and four males) were captured in pit traps at Cataby, 170 km north of Perth, Western Australia (30°C 44'S, 115°C 32' E) during February and August 2008. They were housed indoors at Curtin University in large plastic crates at an ambient temperature of approximately 22°C with a 12/12 light dark cycle. Fresh drinking water and a mixture of honey, water and baby cereal was provided *ad lib.* Cardboard boxes, toilet rolls, vegetation and a wood-shaving substrate were provided for environmental enrichment. At the conclusion of the study, the animals were returned to their place of capture.

Standard open-flow respirometry was used to measure the oxygen consumption (VO_2), carbon dioxide production (VCO_2) and evaporative water loss (EWL) of the honey possums at ambient temperatures (T_a) of 14.5, 19.4, 24.8, 27, 29.4, 32 and 34°C. Individuals were measured at each T_a in random order, with N = 6 at T_a = 25°C and N = 7 at all other T_a. Although the honey possums would sometimes enter torpor during experiments at low T_a, the frequency, depth and duration of torpor was variable and therefore we present only data for euthermic individuals.

The respirometry system consisted of an Aalborg mass flow controller that regulated the flow of compressed air (dried with column of drieirte) through a tubular perspex metabolic chamber situated in a controlled temperature cabinet, at a rate of 200 to 300 ml min^{-1}. Excurrent air passed over a thin film capacitance relative humidity (RH) and T_a probe (Vaisala MNP 45A) with a sub-sample passing through a column of drierite to remove water vapour, a carbon dioxide analyser (Qubit S153) and finally an oxygen analyser (Servomex OA184). The gas analysers were interfaced to a PC via a RS232 serial port using Brymen multimeters (BM202 for RH, CO_2 and T_a; TBM859CF for O_2). Custom-written Visual Basic data acquisition software (VB

v6) was used to record O_2, CO_2, RH and T_a every 20 seconds throughout the experimental period.

Oxygen analysers were two-point calibrated using compressed nitrogen (0% O_2) and dry ambient air (20.95% O_2); CO_2 analysers were calibrated with compressed N_2 (0% CO_2) and a certified gas mix (0.53% CO_2; BOCS). The calibration of the RH probes was confirmed using two points, 1 % (dried with Drierite to 0.005 mg. L^{-1}) and 100 % (saturated; generated by breathing on the probe) RH. Flow meters were calibrated using a Bubble-O-Meter bubble flow meter.

Ventilatory data were measured using whole-body plethysmography, with the metabolic chamber acting as a plethysmograph (Malan 1973; Withers 1977; Dawson et al. 2000; Larcombe 2002; Cooper and Withers 2004). Pressure changes due to the warming and humidifying of inspired air were detected with a custom-made pressure transducer (Motorola MPX2010 sensor). Analog voltage outputs from the pressure transducer were converted to a digital signal using a Pico Technology ADC 11 data logger, and were recorded on a PC every 15 ms for approximately 20 sec using PicoScope. Between two and six sets of ventilatory data were obtained for an individual honey possum at each T_a, so a single mean was calculated for each ventilatory variable for each individual at each T_a.

Honey possums were fasted by removing food from their cages in the afternoon of the day preceding the commencement of experiments. They were measured in the metabolic system for 6 to 9 hours (see Cooper and Withers 2009) at each T_a, during their inactive phase (day) until VO_2, VCO_2 and EWL had become stable and minimal. Honey possums were observed in the metabolism chamber during experiments with a Swann Max-IP-cam camera under infrared light. VO_2, VCO_2, and EWL at each T_a were calculated from the average of each variable over the 20 minute

period where they were stable and minimal. Calculations were after Withers (2001) and were accomplished using a custom written VB data analysis program. Respiratory exchange ratio (RER) was calculated as VCO_2/VO_2. Metabolic water production (MWP; mg g^{-1} h^{-1}) was calculated using the measured RER for that experiment after Withers (1992) and the relative water economy (RWE) was calculated as MWP/EWL. The point of relative water economy (PRWE) was calculated from the regression of RWE and T_a, for all individual data points, as the T_a at which RWE = 1.

Ventilatory measurements were made when a low and stable metabolic rate and digital footage of the animal confirmed it was quiet and resting, preferably at the end of the experimental period. Resting ventilatory measurements could not be made for all individuals at all T_a, so N = 4 at 14.5 and 19.4°C, N = 6 at 32 and 34°C and N = 7 at all other T_a. The honey possum was removed from the chamber at the conclusion of the experiment and its T_b immediately measured using a plastic-tipped thermocouple (connected to a Digi-Sense 91100-20 thermocouple meter) inserted into the cloaca. Ventilatory variables (respiratory frequency, f_R; tidal volume, V_T; minute volume, V_I; oxygen extraction, EO_2) were calculated after Malan (1973) and Cooper and Withers (2004). We used the calibration technique of Szewczak and Powell (2003) to mathematically convert the open plethysmograph system to a closed system to account for the time course of calibration injections and breathing pressure pulses. A custom-written VB data analysis program was used for ventilatory calculations. EO_2 was calculated using the VO_2 at the time of ventilatory measurements.

All values are presented as mean ± S.E., where N = number of individuals and n = number of measurements. Ventilatory values are presented at body temperature and pressure saturated (BTPS), although standard temperature and pressure dry (STPD) was used to calculate EO_2. Effects of T_a on physiological variables were

examined using ANOVA with Student Newman-Keuls *post hoc* tests (SNK), and generalised least squares regression. These statistical analyses were conducted using statisti*XL* (v1.6). Values of physiological variables for the honey possum were compared to standard (thermoneutral) values of other marsupials using the data summary of Withers et al. (2006; where N = 61 for BMR, 59 for T_b, 55 for C_{wet} and 24 for EWL) and for ventilatory variables data of Hallam and Dawson (1993), Chappell and Dawson (1994), Dawson et al. (2000), Larcombe (2002), Cooper and Withers (2004), Larcombe et al. (2006), Larcombe and Withers (2006) and Cooper et al. (2009). These comparisons were made by examining the position of the honey possum relative to the 95% prediction limits for the $\log_{10}$-transformed allometric regression (T_b values were not log-transformed) after Cooper and Withers (2006). The magnitude of the difference between observed and predicted values was calculated using the minimum variance unbiased estimator (MVUE) of Hayes and Shonkwiler (2006, 2007). Phylogenetically-predicted mass was calculated using autocorrelation (Cheverud and Dow 1985; Rohlf 2001; using the marsupial trait values and phylogeny for 61 marsupial species of Withers et al. 2006) as the product of the trait (mass) and a weighting matrix (calculated from the distance matrix of phylogenetic distances between each pair of marsupial species), that was fitted as closely as possible to the actual trait values by iteration with a varying constant of proportionality (ρ). Honey possums were also compared to the 95% prediction limits of a phylogenetically independent allometric relationship for each physiological variable, where variables were rendered independent of phylogeny by autocorrelation, again using the dataset and phylogeny of Withers *et al.* (2006) where N is as for the conventional analysis.

Results

Mean body mass of all honey possums over all experiments (N = 7, n = 48) was 5.4 ± 0.14 g. This body mass was only 1.3 % of the 406 g phylogenetically predicted body mass. Observations of the honey possums within the metabolic chamber indicated that they rested quietly for most of the experimental period, with occasional brief periods of activity. Active periods could be clearly identified by elevated VO_2, VCO_2 and EWL and were excluded from the analysis.

The honey possums' T_b was independent of T_a ($F_{6,38}$ = 1.53, P = 0.193; Figure 1A). Mean T_b at thermoneutrality (T_a = 32°C) was 36.6 ± 0.48 °C, and was significantly higher than predicted (34.3°C) from the conventional allometric relationship for marsupials (Figure 2A). After accounting for phylogenetic history, there was no longer a significant allometric relationship for marsupial T_b to compare the honey possum to. However, a normal deviate test indicated that the honey possums's T_b did not differ statistically from the phylogenetically independent T_b values for other marsupials (P = 0.159).

There was a significant effect of T_a on VO_2 ($F_{6,41}$= 39.01, P<0.001), which was higher at T_a = 14.5 °C (9.84 ± 0.731 ml O_2 g^{-1} h^{-1}) and T_a = 19.4°C (7.33 ± 0.404 ml O_2 g^{-1} h^{-1}) than at all other T_a (SNK P < 0.001) and higher at T_a = 25°C than all T_a ≥ 29.4°C (SNK ≤ 0.011). We define the lowest metabolic rate at T_a = 32°C of 2.52 ± 0.222 ml O_2 g^{-1} h^{-1} as BMR. VCO_2 values mirrored VO_2 values and so are not presented separately here. There was no effect of T_a on RER ($F_{6,41}$ = 0.222, P = 0.967), with the average RER of all honey possums over all experiments (N = 7, n = 48) being 0.73 ± 0.024. There was a significant negative linear regression (VO_2 = -0.450 (± 0.040)T_a + 16.45 (±0.953); $F_{1,32}$ = 129.1, P < 0.001, R^2 = 0.80) between VO_2 and T_a ≤ 29.4 °C, extrapolating to a predicted thermoneutral T_b (i.e. T_a where VO_2 = 0) of 36.6°C. The honey possums' BMR was 162 % of that predicted for an

equivalently sized marsupial (Figure 2B). This was significantly higher than predicted, falling outside the 95% prediction limits for the allometric regression of BMR for marsupials both before and after accounting for phylogenetic history.

There were significant effects of T_a on all ventilatory variables ($P \leq 0.041$; Figure 3). f_R ranged from 75 ± 4 breaths min^{-1} at T_a = 32°C to 285 ± 36 at T_a = 14.5°C and was related to T_a at $T_a \leq 32$°C with a significant negative linear relationship (R^2 = 0.72, $F_{1,34}$ = 87.3, $P < 0.001$). f_R was higher at T_a = 14.5 °C and T_a = 19.4°C (210 ± 21 breaths min^{-1}) than at all other T_a (SNK $P \leq 0.007$). V_T ranged from 0.066 ± 0.005 ml at T_a = 25°C to 0.120 ± 0.009 ml at T_a = 10.4°C. V_T at T_a = 19.4°C was greater than at 24.8°C, 27°C and 29.4°C, and greater at T_a = 32°C than 28°C (SNK $P \leq 0.032$). However, there was no significant linear relationship with T_a ($F_{1,34}$ = 2.1, P = 0.160). There was a significant negative linear relationship for V_I at $T_a \leq 32$°C (R^2 = 0.54, $F_{1,34}$ = 38.8, $P < 0.001$), with V_I at 14.5° C (26.4 ± 2.7 ml min^{-1}) and 19.4°C (21.9 ± 4.1 ml min^{-1}) being higher than at all $T_a \geq 24.8$°C (SNK $P < 0.001$). EO_2 ranged from 17.5% at T_a = 20°C to 30.8% at T_a = 30°C, but there was no significant linear relationship with T_a ($F_{1,34}$ = 0.698, P = 0.404). Ventilatory variables at thermoneutrality (T_a = 32°C) were 101 % (f_R; 75 ± 4 breaths min^{-1}), 85% (V_T; 0.106 ± 0.007 ml), 90% (V_I; 7.9 ± 0.62 ml min^{-1}) and 163% (EO_2; 19.4%,) of those predicted for an equivalently sized marsupial.

EWL of honey possums ranged from 4.33± 0.394 mg H_2O g^{-1} h^{-1} at T_a = 29.4 °C to 9.83 ± 1.36 mg H_2O g^{-1} h^{-1} at T_a = 34°C. There was a significant effect of T_a on EWL ($F_{6,41}$ = 5.48, $P < 0.001$) with EWL at T_a = 35°C being significantly higher (SNK $P \leq 0.002$) than at all other T_a (Figure 1C). We define the minimal EWL of 4.33± 0.394 mg H_2O g^{-1} h^{-1} as their standard EWL for comparison with other species; this was 102 % of predicted, conforming to the marsupial allometric EWL

relationship both before and after accounting for phylogenetic history (Figure 2C). There was a highly significant negative linear relationship between T_a and RWE for honey possums (RWE = -0.049 (±0.004)T_a + 1.835(±0.095); $F_{1,46}$ = 189, P < 0.001; R^2 = 0.80), with the PRWE (the T_a where RWE = 1) occurring at 17.0°C (Figure 4).

Discussion

We confirm that the honey possum does indeed have a higher BMR (162% of predicted) than other marsupials, as suggested by Withers et al. (1990). This high BMR is associated with a high T_b and EO_2, but interestingly the honey possum has a high PRWE and its EWL is not elevated above that of other marsupials, despite its mesic habitat and high dietary water intake.

The tight correlation between any directly observed activity and elevated rates of VO_2, VCO_2 and EWL, along with long measurement durations (Cooper and Withers 2009) means that we are confident our data are for resting honey possums. Following the suggestion of McNab (2005), we paid especially close attention to the thermoneutral zone, measuring at approximately 2.5°C increments between 25 and 35°C to ensure that we obtained data at thermoneutrality. Our estimate of BMR is unequivocally measured at thermoneutrality as it occurred at a T_a after which EWL had already started to increase sharply and therefore would not occur at a T_a > 32°C, and the linearity of VO_2 against T_a at $T_a \leq$ 32°C indicates that MR would not be lower at a T_a < 32°C. Consequently, we are confident that our measurements of BMR, standard EWL and standard ventilatory parameters conform to the standardised criteria (see McNab 1997; Cooper and Withers 2009) for measurement of these comparative variables.

Our T_b of 36.6 ± 0.48 °C for thermoneutral honey possums is consistent with the 36.6 ± 0.2 °C measured by Withers et al. (1990). The honey possums were able to

regulate T_b against a temperature differential of up to 21.6 °C when euthermic. T_b was not influenced by T_a, and honey possums conformed to the Scholander-Irving model of heat balance; the relationship between VO_2 and T_a extrapolated to a predicted T_b the same as that measured. The honey possums measured by Withers et al. (1990) did not conform as well to the Scholander-Irving model, but this species is heterothermic, and so it can be difficult to measure truly euthermic animals at low T_a. The thermoneutral T_b of the honey possum was higher than predicted for an equivalently-sized marsupial, which is not surprising considering its higher-than-predicted BMR and the interrelationship between T_b and MR.

Although queried by McNab (2005), the hypermetabolic data of Withers et al. (1990) are supported by our study, and we have confirmed the findings of Withers et al. (2006) that honey possum is the only marsupial to have a significantly elevated BMR (Figure 2B). Our estimate of BMR (2.52 ± 0.222 ml O_2 g^{-1} h^{-1}) was not significantly different from the previously measured BMR (2.9 ± 0.3; T_{10} = 1.04, P = 0.314). The small difference observed may be accounted for by Withers et al. (1990) only measuring two animals (of the five used to estimate BMR) at the T_a at which we determined MR to be minimal. As suggested by McNab (2005), determining the narrow thermoneutral zone of a small species can be difficult.

The honey possum has many morphological specialisations associated with its strictly nectarivorous diet (Richardson et al. 1986). We found that it is also much smaller than expected based on its position in the marsupial phylgenetic tree, only 1.3% of its predicted body mass. This may be considered an additional morphological adaptation, as nectarivorous species are generally smaller than non-nectarivorous species (Brown et al. 1978; Pyke 1980; Nicolson and Fleming 2003). The morphological adaptations of the honey possum suggest a long evolutionary history of

feeding on nectar and pollen. It may therefore be predicted that this species has evolved physiological as well as anatomical adaptation to its diet. Even after taking into account its phylogenetic position amongst the marsupials, the honey possum's BMR remained significantly higher than predicted for a marsupial of equivalent body mass. This indicates that its high BMR is independent of evolutionary inertia, and may be considered adaptive without the confounding effect of phylogenetic affiliation.

The food-habit hypothesis posits that animals feeding on diets with a high energy content, that are easily digestible, free of chemical deterrents and which are readily available can afford to have high metabolic rates (Cruz-Neto & Bozinovic 2004). The honey possum's high BMR may be attributed to its easily digestible, high-energy food, or to the increased costs of locomotion required to visit sufficient plants to meet the daily energy requirement (Voigt *et al.* 2006). Withers *et al.* (2006) found that climate influences BMR of marsupials, with habitat aridity, temperature and intra-annual rainfall variability all significant determinates of marsupial BMR. The honey possum's mesic Mediterranean habitat is consistent with a higher BMR than for marsupials from arid habitats. However, the honey possum is the only species to be hypermetabolic; no other marsupial, even considering those from very mesic environments with lower T_a and/or lower rainfall variability, has been shown to statistically exceed their allometrically predicted BMR. Combined with previous findings that nectarivory is related to a high BMR in both birds and placental mammals (McNab 1980; 1986; 1988; 2003; 2008; 2009), a high BMR for the only exclusively nectarivorous member of a third taxonomic group, the marsupials, is consistent with the hypothesis that a nectarivorous diet is indeed associated with a high BMR.

It has long been accepted that marsupials have a BMR that is about 70% of that of placental mammals (Dawson and Hulbert 1969). Although a number of placental mammals have a BMR as low or lower than marsupials, no marsupials have a BMR approaching the high rates of some placental grazers or carnivores (McNab 1986; 2005). The honey possum, with a high BMR by marsupial standards, has a BMR that is 98 % to 124 % of that predicted for a generalised mammal (Table 1 and 2 of White and Seymour 2005 for studies since 1985; McNab 2008) and 114 % of that predicted for a placental mammal (McNab 2008). Thus despite being a marsupial, the honey possum achieves a BMR equivalent to that of generalised placental mammal.

Cooper et al. (2003) found a strong correlation between BMR and FMR for marsupials, with a predicted FMR of 28.5 kJ day^{-1} for the honey possum. This value is comparable to the 25.1 and 28.6 kJ day^{-1} measured by Bradshaw and Bradshaw (1999; 2007; accounting for isotopic fractionation), and a little lower than the mean FMR of Nagy et al. (1995) and Bradshaw and Bradshaw (1999) of 35.4 (uncorrected for isotopic fractionation). The FMR/BMR ratio for the honey possum is high (4.5 to 5.5), as is predicted for a very small marsupial (Cooper et al. 2003) and for a nectarivorous mammal (Speakman 2000). Nagy et al. (1995) and Bradshaw and Bradshaw (1999) found that the FMR of the honey possum was 73 to 100% of predicted compared to that of other marsupials. This low to moderate FMR is surprising, considering its high BMR and high-energy diet. However, compared to a more recent allometric relationship for FMR of marsupials (Cooper et al. 2003), the honey possum has an FMR that is 133% of predicted. This falls within the 95% prediction limits for the relationship, but it is difficult to show statistical significance for FMR as the relationship is more variable and thus the prediction limits wider than for BMR, especially for a small species towards the lower limit of the regression (see

Cooper and Withers 2006). Thus it remains equivocal if the honey possum has an elevated FMR.

The honey possums accommodated their increased VO_2 at low T_a with an increased V_I, which resulted from an increase in f_R rather than any systematic increase in V_T. This is typical of small mammals, while larger species increase V_T rather than f_R, presumably due to size-dependant differences in the mechanics and energetics of ventilation (Larcombe 2002; Cooper and Withers 2004). Despite its high BMR, V_I was 90% of predicted for a similar-sized marsupial, but EO_2 was 163%. Thus, compared to other small marsupials, the honey possum seems to have increased EO_2 rather than V_I to account for its increased BMR. This may however be an artefact of ensuring that we measured completely calm and resting animals as resting individuals are likely to have a higher EO_2 and lower V_I than active individuals (Larcombe 2002; Cooper and Withers 2004).

We expected honey possums to have a high EWL and poor RWE, due to their mesic distribution, high dietary water intake (nectar is 50-90% water; Slaven and Richardson 1988) and other physiological adaptations to high rates of water flux. Honey possums have a high mean field water turnover of 9.6 ml H_2O day^{-1} (Nagy et al. 1995; Bradshaw and Bradshaw 1999), 189% of that predicted for a marsupial by the allometric equation of Cooper et al. (2003). Their kidneys show specialisation for production of copious, dilute urine, with an undivided medulla and small relative medullary area (Slaven and Richardson 1988), presumably to enable them to maintain ion and water balance with a very high dietary water intake. However, the EWL of the honey possum confirmed closely to the marsupial allometric relationship, and they had a surprisingly high PRWE of 17.0°C. Comparison of EWL data is complicated, due to methodological effects such as measurement technique, chamber humidity and

experimental duration (Cooper and Withers 2008, 2009; Cooper et al. 2009) which make the existing dataset for marsupial EWL variable (Withers et al. 2006). We suspect that many of the existing standard EWL values for small marsupials are overestimates (see Cooper and Withers 2009) and therefore it is equivocal if the honey possum has an EWL that conforms to other marsupials.

Data concerning the PRWE is presently available for only 4 other marsupial species; the arid-zone little red kaluta (*Dasykaluta rosamondae*; PRWE = 16.1°C; Withers and Cooper 2009), sandhill dunnart (*Sminthopsis psammophila*; PRWE = 18.0°C; Withers and Cooper in press) and striped faced dunnart (which does not reach a PRWE; Cooper et al. 2005), and the Neotropical gracile mouse opossum (*Gracilinanus agilis*; PRWE = 11.5°C; Cooper et al. 2009). Despite the abundance of water in its diet and its mesic habitat, the honey possum's PRWE is the second-highest measured so far for a marsupial, and is equivalent to arid-zone marsupials. This is unexpected, as the PRWE should provide an index to a species' adaptation to water restriction, and has been found to be higher for arid than mesic mammals and birds (MacMillen 1983; MacMillen 1990; MacMillen and Baudinette 1993). The high PRWE for the honey possum results from a high MR, and thus high MWP (as may be expected for a mesic, nectarivorous species), rather than from a reduced EWL (as might be expected for species from arid habitats). Clearly more EWL and especially RWE data are required for marsupials to enable comparative analyses and determine environmental correlates.

Acknowledgements

We thank Daniel Jordan and Ti West for providing accommodation and meals during field work. Jason Fraser originally set up the pit trapping grid used to catch the honey

possums. Funding for this project was provided by an Australian Research Council Discovery grant and a Curtin University Centre for Ecosystem Diversity and Dynamics grant to CEC. APCN would like to thank Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) for a scholarship while at the University of Western Australia and Curtin University. This is manuscript number CEDD45-2009 of the Centre for Ecosystem Diversity and Dynamics, Curtin University.

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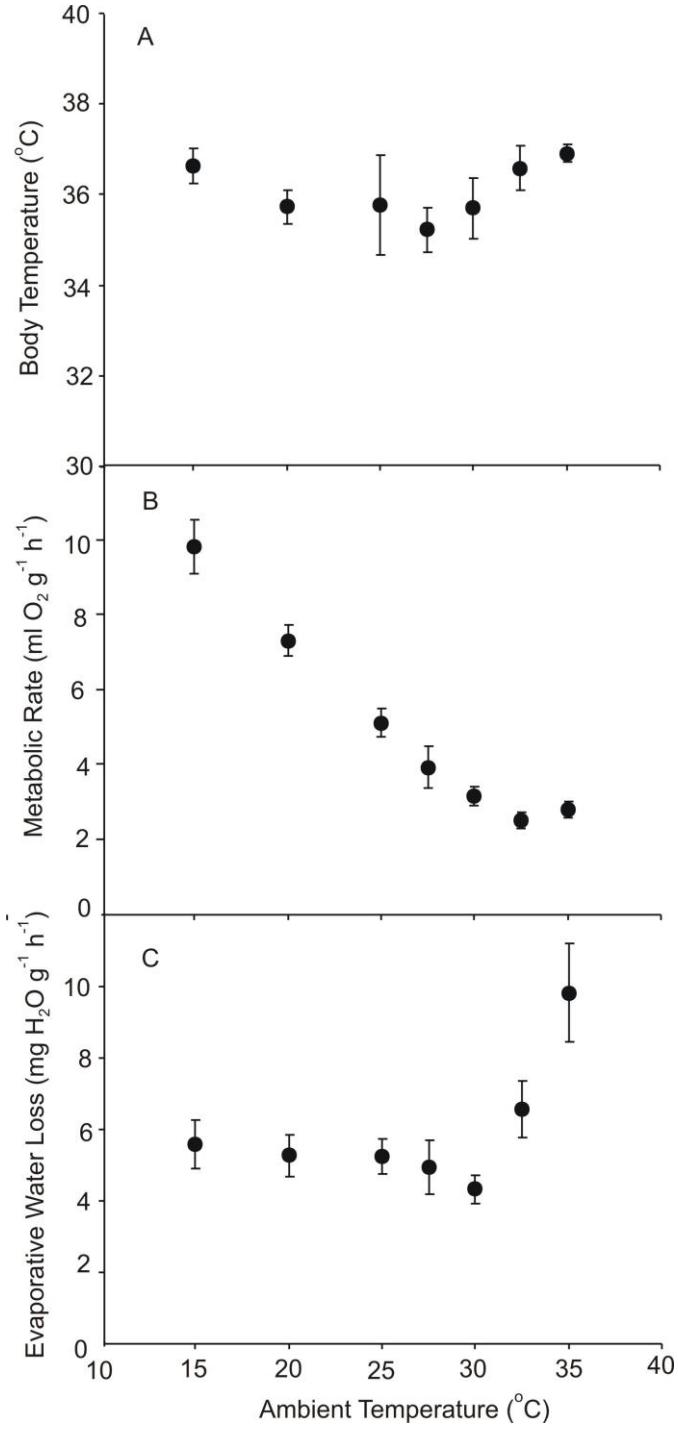

Figure one: Body temperature (A), metabolic rate (B) and evaporative water loss (C) of honey possums at ambient temperatures of 14.5 to 34°C (mean ± SE; N = 6 at 24.5°C and N = 7 at all other ambient temperatures)

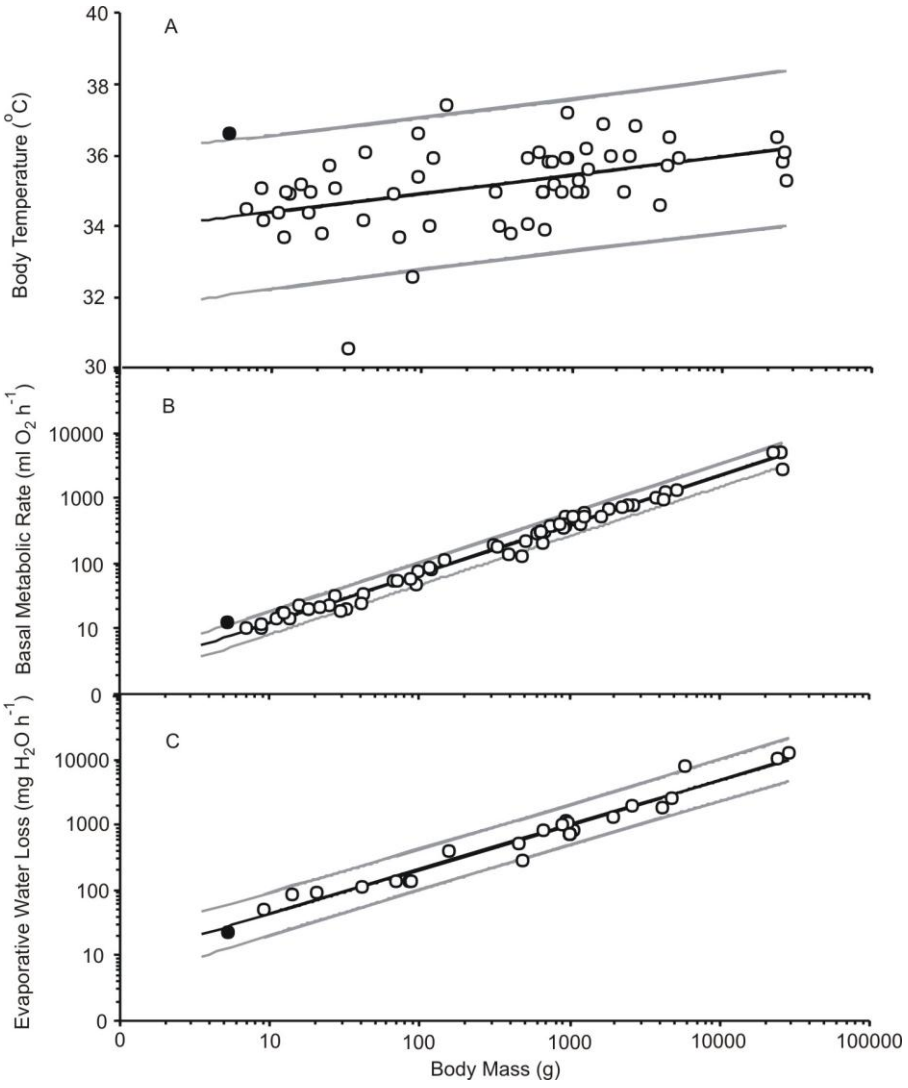

Figure two: The honey possum (black circle) compared to the marsupial allometric relationships for body temperature (A), metabolic rate (B) and evaporative water loss (C; white circles; data from Withers et al. 2006). The dark line is the regression line, and the grey lines the 95% prediction limits for an additional species.

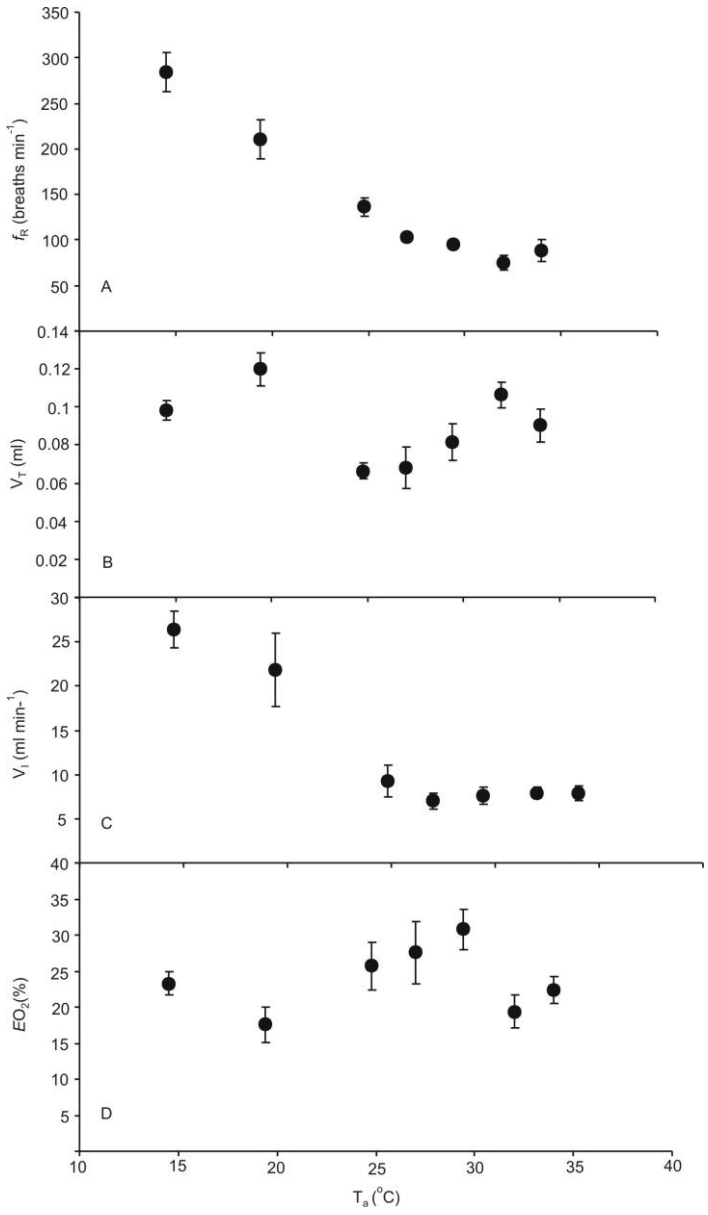

Figure three: Respiratory rate (f_R; A), tidal volume (V_T; B), minute volume (V_I; C) and oxygen extraction (EO2; D) for honey possums (*Tarsipes rostratus*) at a range of ambient temperatures (T_a). Values are mean ± S.E., N = 4 at T_a = 14.5 and 19.4°C, N = 6 at 32 and 34°C and N = 7 at all other T_a).

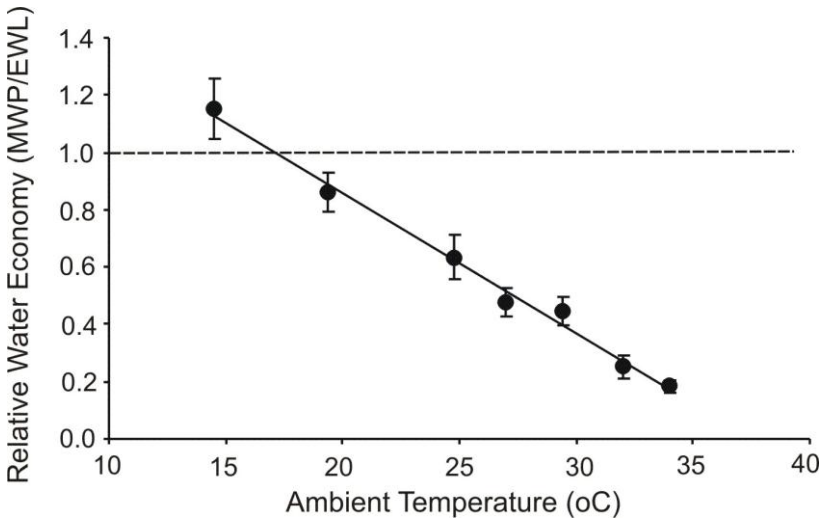

Figure four: Relative water economy, calculated as metabolic water production (mg H_2O g^{-1} h^{-1})/evaporative water loss (mg H_2O g^{-1} h^{-1}) as a function of ambient temperature for the honey possum (mean ± SE; N = 6 at 24.5°C and N = 7 at all other ambient temperatures). The solid line is the regression line, the dashed line indicates relative water economy = 1, where the evaporative water loss is balanced by metabolic water production.