Effect of torpor on the water economy of an arid-zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura*)

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Abstract

Metabolic rate and evaporative water loss (EWL) were measured for a small, arid-zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura*), when normothermic and torpid. Metabolic rate increased linearly with decreasing ambient temperature (T_a) for normothermic dunnarts, and calculated metabolic water production (MWP) ranged from 0.85 ± 0.05 (T_a = 30 °C) to 3.13 ± 0.22 mg H_2O g^{-1} h^{-1} (T_a = 11 °C). Torpor at T_a = 11 and 16 °C reduced metabolic water production to 24–36 % of normothermic values. EWL increased with decreasing T_a, and ranged from 1.81 ± 0.37 (T_a = 30°C) to 5.26 ± 0.86 mg H_2O g^{-1} h^{-1} (T_a = 11 °C). Torpor significantly reduced absolute EWL to 23.5- 42.3% of normothermic values, resulting in absolute water savings of 50-55 mg H_2O h^{-1}. The relative water economy (EWL/MWP) of the dunnarts was unfavourable, remaining >1 at all T_a investigated, and did not improve with torpor. Thus torpor in stripe-faced dunnarts results in absolute, but not relative, water savings.

Introduction

Torpor is an important mechanism for reducing energy and water use in small mammals and birds (McNab 2002). During torpor, body temperature (T_b) falls by up to 35°C below normothermic resting T_b, and metabolic rate (MR) may be as little as 1 % of basal MR (BMR), reducing energy expenditure by as much as 99% (Withers *et al*. 1980; Geiser and Ruf 1995). Torpor is particularly important for small species, which have high mass-specific MRs and high surface area to volume ratios that augment heat and water loss. Generally, reducing energy expenditure is considered to be the major role of torpor (Geiser 2004), but it may also be important for water conservation, especially for arid-zone species (MacMillen 1965; Schmid and Speakman 2000; Cryan and Wolf 2003). Reductions in MR, T_b, food requirements and activity, and the associated reductions in evaporative, faecal and urinary water loss mean that torpor may potentially lead to substantial water savings. Gerbils (*Gerbillus pusillus*) enter torpor in response to water as well as food deprivation (Buffenstein 1985) and mouse-lemurs (*Microcebus murinus*) using torpor have lower field water turnover rates than individuals remaining normothermic (Schmid and Speakman 2000). Evaporative water loss (EWL) is a commonly-measured component of the water budget, and may account for up to 70 % of total water loss (MacMillen 1990). EWL during torpor has been measured in placental mammals and birds (Carpenter 1964; Lasiewski 1964; McMillen 1965; Buffenstein 1985; Hosken and Withers 1997, 1999) however, no data are available for marsupials.

Here we examine the effect of torpor on the EWL of the stripe-faced dunnart (*Sminthopsis macroura*), a small 15-25 g marsupial (family Dasyuridae). It feeds on invertebrates and, like most dasyurids, routinely uses torpor (Morton 1991). Torpor may be either spontaneous (food available) or induced (food restricted) and is especially frequent when dry food is provided and water is withheld (Song and Geiser 1997). Torpor bouts are always less than 24 hours in duration, and T_b is maintained at or above 14 °C (Geiser and Baudinette 1987). *Sminthopsis macroura* inhabits shrublands and grasslands and is distributed throughout the arid and semi-arid areas of central and northern Australia and therefore is well suited for investigating the effect of torpor on water loss and water economy.

Methods

Metabolic and EWL measurements were made for a total of 17 individual (11 female and 6 male) adult, non-reproductive *S. macroura* obtained from a breeding colony at the University of New England. Dunnarts in the colony were maintained under a natural photoperiod for Armidale, NSW (30° 30’ S 151° 39’ E) at 22°C on a mixture of moistened cat chow and canned dog food, with water *ad libitum*. Experiments were conducted from April to June (autumn/winter) 2004.

Rates of oxygen consumption (VO_2), carbon dioxide production (VCO_2) and EWL of the dunnarts was measured by open flow-through respirometry over 24 hours, at ambient temperatures (T_a) of 11, 16, 21 and 30°C. Dunnarts were placed on a mesh grid (to allow faeces and urine to fall through to the bottom of the chamber where they were quickly desiccated by the dry airflow) in a metabolic chamber (1.1 L), which in turn was situated in a temperature control cabinet. Dunnarts were placed in the metabolic system in the early evening and left in the system until the following evening. Airflow, provided by a Schego M2KS pump, was dried with silica gel, then divided, with air going to the chamber passing through an Omega FMA5698 mass flow meter and the remainder going directly to a 2 way solenoid valve to give a reference air sample. Flow rates to the chamber of between 200 and 400 mL min^{-1} maintained % $O_2 > 19.95$ and % $CO_2 < 0.5$. Air exiting the chamber passed through a Vaisala HMP35B humidity probe, through a column of Drierite ($CaSO_4$) to remove water vapour, and then to the solenoid valve. The valve switched from animal to reference air every two hours for 15 minutes (controlled by a PC) and background levels of O_2 and CO_2 were set to 0.2096 and 0.000 respectively, to account for any drift resulting in changes in ambient temperature or pressure. The O_2 and CO_2 content of a 50 ml min^{-1} sub-sample of air from the solenoid (either animal or reference) was measured with a David Bishop 280 Combo O_2 and CO_2 analyser. Outputs from the mass flow meter, relative humidity (RH) probe and gas analyser were connected to a 16 bit analogue to digital converter, and the resulting voltages were saved by a PC every 60 sec. At the conclusion of the experiment, the dunnart was removed from the chamber and a rectal T_b measured immediately to the nearest 0.1 °C using a plastic-tipped, calibrated thermocouple with a Omega HH-71T thermocouple meter.

Experiments were terminated and the dunnarts removed from the chamber if the chamber air became saturated (due to excessive urine or faeces) and was not dried by the dry air stream after 60 min (if this occurred it was generally soon after the commencement of the experiment). Increased EWL due to urine and faeces could be identified by a characteristic pattern in the continuous EWL trace and we are confident that our EWL values do not include urinary or faecal water. Generally the dry air flow rapidly desiccated any urine or faeces produced. Sections of at least 20 min of the continuous traces of VO_2, VCO_2 and EWL were selected and averaged when MR and EWL had become stable and minimal. VO_2, VCO_2 and EWL were calculated after Withers (2001) and were used to calculate resting MR (RMR; at $T_a < 30°C$), BMR (at $T_a = 30°C$) and torpor MR (TMR; where MR<75% RMR). Not all 17 individuals were available for measurement at each T_a and not all dunnarts would enter torpor, even at the lowest T_a. Therefore normothermic and torpid measurements are not necessarily from the same individuals. A total of 6 measurements were obtained for normothermic dunnarts at T_as of

11 and 21 °C, 9 measurements at 16 °C and 10 measurements at 30 °C, with 5 measurements of torpid dunnarts at 11 °C and 6 at 16 °C. Dunnarts did not enter torpor at 20 or 30 °C. Individual dunnarts were measured at each T_a randomly.

The mass flow meter was calibrated by timing the replacement of water with air in a volumetric flask (corrected to STPD). The RH probe was two-point calibrated (0 and 100 % RH) prior to every experiment. The O_2 and CO_2 analysers, and the RH probe were calibrated weekly after Withers (2001), and in addition the O_2 and CO_2 calibration was checked with a precision gas mix (BOC Gases).

Metabolic water production (MWP) was calculated from VO_2 for each dunnart where mg H_2O produced per mL O_2 consumed was determined from its measured respiratory exchange ratio (RER; VO_2/VCO_2) after Withers (1992). T_a = 30°C was assumed to be within the thermoneutral zone for *S. macroura* (Geiser and Baudinette 1987; Hinds *et al.* 1993). Values are presented as mean ± standard error where N = number of individuals and n = number of measurements. ANOVA with Student–Newman-Keuls post hoc tests were used to determine differences between T_as and between normothermic and torpid dunnarts, using *Statisti*XL V1.4.

Results

The mean body mass of all dunnarts over all temperatures was 20.0 ± 0.5 g (range 13.7 – 25.6 g; N = 17, n = 42). Mean T_b of normothermic dunnarts was 34.2 ± 0.7°C at T_a = 11°C, 33.5 ± 0.8 °C at T_a = 16°C, 35.1 ± 0.6 °C at T_a = 21°C and 35.7 ± 0.3°C at T_a =

30°C. Dunnarts generally entered torpor in the early morning (~6.00 am) and remained torpid until late morning (~11.30am), when they would arouse and remain normothermic until removed from the chamber until the early evening. Of the dunnarts remaining in the chamber for the full 24 hours, 43 % entered torpor at 16°C and 71% at 11°C.

RMR of normothermic dunnarts was significantly affected by T_a ($F_{3,25} = 50.33$, $p < 0.001$), with RMR at each T_a being significantly different to all other T_as (4.79 ± 0.28 mL O_2 g^{-1} h^{-1} at 11°C, 3.79 ± 0.19 mL O_2 g^{-1} h^{-1} at 16°C, 3.09 ± 0.27 mL O_2 g^{-1} h^{-1} at 20°C and 1.40 ± 0.09 mL O_2 g^{-1} h^{-1} at 30°C; SNK $p \leq 0.022$). RMR decreased linearly with increasing T_a ($RMR = -0.18T_a + 6.7$; $F_{1,28} = 170.5$, $p < 0.001$, $R^2 = 0.86$; Figure 1A). BMR ($T_a = 30°C$) was 1.40 ± 0.09 mL O_2 g^{-1} h^{-1}. TMR (1.77 ± 0.25 mL O_2 g^{-1} h^{-1} at 11°C and 0.908 ± 0.14 mL O_2 g^{-1} h^{-1} at 16°C) was significantly lower than RMR ($F_{1,22} = 176.98$, $p < 0.001$; Figure 1A) and values were 36.5 % and 24.1 % of RMR at 11 and 16°C respectively. TMR was 126 % (at 11°C) and 64.8 % (at 16°C) of BMR. VCO_2 showed the same pattern as VO_2, and therefore VCO_2 data are not presented separately here. Mean normothermic RER ranged from 0.74 ± 0.021 (11°C) to 0.90 ± 0.053 (20°C), and was affected by T_a ($F_{3,25} = 3.606$, $p = 0.027$), with the RER at 16 °C (0.75 ± 0.019) being significantly lower than that at 20°C. Basal RER was 0.83 ± 0.81. Torpor did not affect the RER ($F_{1,22} = 0.516$, $p = 0.489$). Calculated MWP for normothermic dunnarts was 0.85 ± 0.05 mg H_2O g^{-1} h^{-1} at $T_a = 30°C$, 1.86 ± 0.01 at $T_a = 20°C$, 2.44 ± 0.12 at $T_a = 16 °C$ and 3.13 ± 0.22 mg H_2O g^{-1} h^{-1} at $T_a = 11°C$. For torpid dunnarts MWP was 0.59 ± 0.09 mg H_2O g^{-1} h^{-1} at 11°C and 1.13 ± 0.18 mg H_2O g^{-1} h^{-1} at 16°C.

EWL of normothermic dunnarts was significantly affected by T_a ($F_{3,24} = 8.04$, $p = 0.001$; Figure 1B). EWL at 11°C (5.26 ± 0.86 mg H_2O g^{-1} h^{-1}) was significantly higher than that at 16°C (3.54 ± 0.47 mg H_2O g^{-1} h^{-1}), 20°C (2.60 ± 0.22 mg H_2O g^{-1} h^{-1}) and 30°C (1.81 ± 0.37 mg H_2O g^{-1} h^{-1}). Torpor significantly reduced EWL at both T_as ($F_{1,22} = 33.49$, $p < 0.001$). EWL during torpor (EWL_{torpor}) was 42.3% (2.23 ± 0.31 mg H_2O g^{-1} h^{-1}) of normothermic values at 11°C, 23.5% (0.83 ± 0.25 mg H_2O g^{-1} h^{-1}) at 16°C, and was 123.2% (11°C) and 46.0 % (16°C) of that at thermoneutrality (30°C).

Discussion

Our study provides the first information on water loss and water economy during torpor for a marsupial. It shows that torpor is not only important in the conservation of energy, but may also play an important role in reducing water loss in arid zone marsupials. The use of torpor and its associated energy and water conservation may partly explain why dasyurid marsupials are so successful in the Australian arid zone.

RMR of normothermic dunnarts responded as expected for an endotherm, increasing significantly with decreasing T_a below thermoneutrality (Figure 1A). Accordingly, calculated MWP also increased with decreasing T_a. BMR, measured at the thermoneutral T_a of 30°C (Geiser and Baudinette 1987; Hinds *et al*. 1993) and a T_b of 35.7 °C, was 1.40 ± 0.082 mL O_2 g^{-1} h^{-1} and (after correcting all values to a common T_b of 35 °C assuming an Q_{10} of 2.5, Withers *et al*. 2000; Guppy and Withers 1999) was comparable to values measured previously for this species (1.55 mL O_2 g^{-1} h^{-1} Hinds *et al*. 1993; 1.15 mL O_2 g^{-1} h^{-1} Geiser and Baudinette 1987; 1.31 ± 0.096 mL O_2 g^{-1} h^{-1} present study). The BMR of *S.*

macroura was 109% (after T_b correction) to 123 % (no T_b correction) of that predicted for a marsupial of similar mass (Withers *et al*. 2000) and fell well within the 95% prediction limits for the allometric regression of BMR for marsupials (Cooper *et al*. submitted).

TMR was approximately 30 % of RMR (at the equivalent T_a) at both 11 and 16 °C, indicating substantial energy savings. A T_a of 11 °C is below the minimum defended T_b for dunnarts (~14 °C; Geiser and Baudinette, 1987) and TMR>BMR (126 %), reflecting thermoregulatory costs during torpor at low T_a. In contrast T_a = 16 °C is above the minimum defended T_b and accordingly TMR<BMR (64.8 %), as there is no thermoregulatory component to TMR and T_b is low. The reduction in MR during torpor substantially reduced calculated MWP to 24.1% (11°C) and 36.5 % (16°C) of normothermic values. The RER of normothermic as well as torpid dunnarts was in the theoretical range of 0.7-1 (Withers 1992), indicating that measurements of TMR were taken during steady state torpor.

EWL of normothermic *S. macroura* did not begin to increase at T_a = 30°C in comparison to those measured at lower T_a (Figure 1B), suggesting that this is close to its lower critical temperature. EWL of dunnarts at thermoneutrality was only 42 % of that predicted for all marsupials, and 47 % of that predicted for dasyurids (Hinds and MacMillen 1985). However, comparisons of EWL between studies are complicated methodological differences, resulting in varying relative humidities in the metabolic chamber, directly affecting EWL. Moreover, the time required to wash water through the metabolic system requires long experimental periods to obtain standardised measures of EWL (see Cooper 2004). The very low RH at which EWL was measured at T_a = 30 °C (8.8 ± 1.78 %) suggests that the standard EWL of the dunnarts was not inhibited by chamber RH, and that their EWL was indeed low. However, these measurements of EWL were made using a flow-through humidity probe, over long periods, to ensure that initially high levels of water had been washed through the system and thus only minimal, constant rates of EWL were used. This is not possible to determine using the gravimetric method of MacMillen and Hinds (1986), which was used to generate the comparative equations. This may account for higher predicted rates of EWL based on these equations than our measurements. Thus it remains equivocal if the EWL of normothermic *S. macroura* is indeed low for a marsupial of its size, although a low EWL is not surprising considering the comparatively low EWL measured for some other arid-zone mammals and birds (Withers *et al*. 1980; Hinds and MacMillan 1985; Tieleman and Williams 1999; Cooper and Withers 2003). In addition, the renal indices of *S. macroura* are large (Brooker and Withers 1994; McAllan *et al*. 1996). Increasing renal size relative to body mass, together with morphological characteristics are correlated with increasing habitat aridity (Brooker and Withers 1994; McAllan *et al*. 1996) and coupled with low EWL indicate significant potential to conserve water in an arid environment.

For normothermic dunnarts, EWL was higher at low T_a than all other T_as, presumably because of increased respiratory water loss resulting from increased respiratory ventilation. Patterns of EWL below thermoneutrality for endotherms are variable: EWL may increase with T_a, remain constant, or decrease with T_a (Withers 1992), dependant on the relative importance of cutaneous or respiratory avenues of water loss.

The effect of torpor on EWL has not been quantified previously for marsupials. In the only other study, EWL in torpid honey possums *Tarsipes rostratus* was too low to measure with a flow-through metabolic system (Withers *et al*. 1990). However, in placental mammals and birds torpor use results in a substantial reduction in EWL. In torpid bats EWL is 14–50 % of normothermic values (Carpenter 1964; Morris *et al*. 1994; Hosken and Withers 1997, 1999), gerbils (*Gerbillus pusillus*) reduced daily EWL to 27 % of normothermic values (Buffenstein 1985), and the absolute reduction in EWL during torpor in the cactus mouse (*Peromyscus eremicus*) is around 37 % of normothermic values (MacMillen 1965). Lasiewski (1964) measured a three- to six-fold difference in EWL between torpid and normothermic hummingbirds. In our study torpor results in absolute water savings of 50 - 55 mg H_2O h^{-1} in comparison to normothermic dunnarts. The benefits of torpor use for EWL are proportionally greater at T_as above the minimum defended T_b (~14°C; Geiser and Baudinette 1987) as respiratory water loss is low because ventilation is reduced (e.g. EWL_{torpor} is 23.5 % at $T_a = 16°C$ and 42.3 % at $T_a = 11°C$ of normothermic values). At T_as below 14°C the thermoregulatory increase in TMR is associated with an increase in EWL, a relationship that to our knowledge has not been previously determined. However, the absolute reduction in EWL with torpor is similar above and below the minimum defended T_b (50 mg H_2O h^{-1} at $T_a = 11$ °C and 55 mg H_2O h^{-1} at $T_a = 16$ °C).

MWP and EWL are major avenues of water gain and loss for mammals and birds, and in some species (e.g. granivores) can account for up to 70 % of water flux (MacMillen 1990). For insectivorous animals, such as *S. macroura*, a combination of a high preformed water content and intermediate to low digestibility of the diet means that metabolic water production is a less important avenue for water intake, as to remain in energy balance sufficient food is ingested to maintain a relatively high water intake (Nagy and Peterson 1988; Cooper and Withers 2004). However, in arid environments when food as well as free water are scarce or unpredictable, MWP may be an important avenue of water gain, even for insectivorous species. The relative water economy of an animal is calculated as the ratio between EWL and metabolic water production. When this ratio is <1, water production through food oxidation exceeds water loss via evaporation, and the animal is in more favourable water balance than when the ratio EWL/MWP is >1 (MacMillen 1990).

Generally, for endotherms the EWL/MWP is dependant on body mass and T_a. Smaller species have lower ratios, due to greater thermal conductance and greater increases in MR with decreasing T_a. If MR decreases and EWL remains constant or increases with T_a, then EWL/MWP increases at higher T_a. The T_a where EWL = MWP, the point of relative water economy (PRWE), is an indication of the species' overall water economy (assuming MWP and EWL are both significant components of the water budget). Arid-adapted species generally have a higher PRWE than mesic species (Hinds and MacMillen 1985; MacMillen and Hinds 1998; MacMillen 1990; MacMillen and Baudinette 1993).

The ratio EWL/MWP for normothermic *S. macroura* at all T_as investigated was >1 (1.42 ± 0.13 at 16°C to 1.98 ± 0.40 at 30°C; Figure 2). There was no PRWE and T_a did not affect EWL/MWP ($F_{3,27} = 0.664$, $p = 0.581$), in contrast to granivorous birds and rodents. The relatively constant EWL/MWP in *S. macroura* is a consequence of increasing EWL and MWP with decreasing T_a. It is somewhat surprising that *S. macroura* did not have a more favourable ratio of EWL/MWP, considering their arid-zone distribution. Thermoneutral ratios of EWL/VO_2 as low as 0.5-0.59 (at T_a = 28°C) have been recorded for desert rodents, while even white laboratory rats and mice with high ratios of 0.94 and 0.85 (Hudson 1962) are more economical than *S. macroura* (1.28 ± 0.25). However, granivorous/insectivorous arid-zone *P. eremicus* also have a higher-than-expected thermoneutral ratio of EWL/VO_2 of 1.2 (McMillen 1965). Thus a favourable water economy is not always associated with an arid-zone distribution (although for *P. eremicus* the ratio improves dramatically to 0.5 at low T_a). Renal modifications for increased urine concentrating capacity in both *S. macroura* and *P. eremicus* (Altschuler *et* al. 1979; Brooker and Withers 1994; McAllan *et al.* 1996), a diet relatively high in preformed water (Bell 1990), a semi-fossorial habit and nocturnal foraging may all counteract this unfavourable ratio.

Torpor did not affect EWL/MWP in *S. macroura* ($F_{1,22} = 0.851$, $p = 0.366$). This suggests that although torpor reduces absolute water flux, the relative water economy is not altered. Torpor reduces both EWL and MWP, and therefore the ratio of the two variables remains unchanged. The significant absolute reduction in EWL appears to be a direct result of the low TMR. Absolute rather than relative water savings resulting from torpor have also been measured in gerbils, which had a similar ratio of EWL/RMR when normothermic and torpid (Buffenstein 1985). However, in cactus mice, the ratio of EWL/RMR was much higher (1.74-3.18) in torpid than in resting (0.51-0.93) individuals, suggesting that in this species, relative water economy decreases with torpor, presumably due to cutaneous EWL contributing more substantially to total EWL than respiratory EWL (MacMillen 1965). Thus, while low TMR and associated low MWP limits the possible advantage of torpor for water economy in dunnarts, torpor is efficient in substantially reducing absolute EWL.

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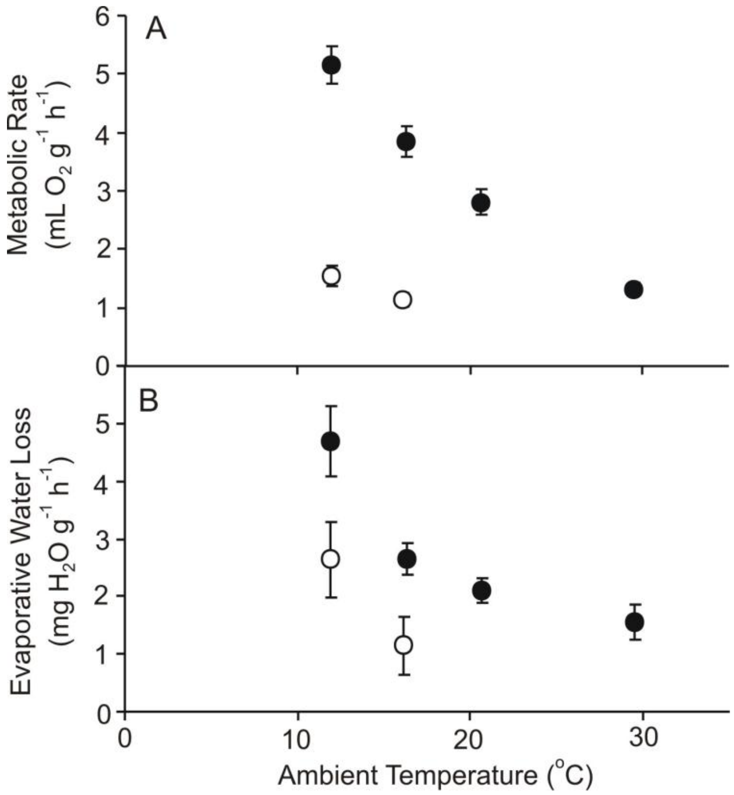

Figure 1:

Metabolic rate and evaporative water loss of normothermic (dots) and torpid (circles) stripe-faced dunnarts (*Sminthopsis macroura*) at various ambient temperatures. Values are mean ± S.E. and n = N. For normothermic dunnarts, n = 6 at T_a = 11-20 °C and 10 at T_a = 30°C; for torpid dunnarts, n = 6 at T_a = 11 and 10 at T_a =16 °C.

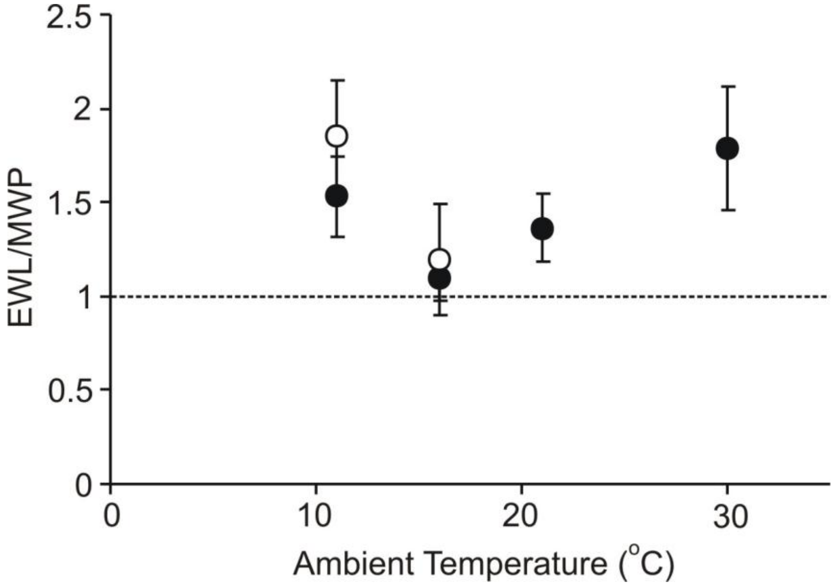

Figure 2:

Ratio of evaporative water loss (EWL) to metabolic water production (MWP) of stripe-faced dunnarts (*Sminthopsis macroura*) when normothermic (dots) and torpid (circles) at various ambient temperatures. The dashed line indicates EWL = MWP. Values are mean ± S.E, n as for Figure 1.