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Environmental physiology of a small marsupial inhabiting arid floodplains

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ABSTRACT

Giles' planigale (*Planigale gilesi*) is among the smallest extant marsupials and inhabits deep soil cracks in arid floodplains. We examined whether its physiology shows specific adaptations to its extreme habitat. Metabolic rate, body temperature, evaporative water loss and thermal conductance were measured for eight planigales (average mass 9 g) exposed to four different ambient temperatures ranging from 10 °C to 32 °C. Water economy and respiratory variables were measured for the first time in this species. All of these standard physiological variables conformed to allometrically-predicted values for a marsupial. All variables were significantly affected by ambient temperature, except tidal volume and dry thermal conductance. Metabolic rate increased substantially at low ambient temperatures, as required to maintain a relatively constant body temperature of about 32–34 °C. This increased oxygen demand was accommodated by increased ventilation rather than increased oxygen extraction. Planigales had a comparatively high point of relative water economy of 19.1 °C, consistent with their small body size and arid habitat. Torpor reduced energy expenditure by 79% and evaporative water loss by 62%. Our study suggests that torpor use, along with behavioural adaptations, suffice for *P. gilesi* to live underground in arid habitats without further physiological adaptations.

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1. Introduction

Mammals living in arid habitats are often characterised by specific physiological, morphological and behavioural adaptations to their environment both at an inter-specific and intra-specific level (Degen, 1997). For example, basal metabolic rate (BMR) is lower for placental mammals from arid habitats than for those from mesic habitats (McNab and Morrison, 1963; Lovegrove, 2000) and arid populations of rodents can decrease water loss by 36% compared to mesic conspecifics (Tracy and Walsberg, 2001). Marsupials show similar inter-specific adaptations to aridity; correlates between environmental conditions and physiological variables indicate that species from arid regions and/or habitats with high rainfall variability have a higher body temperature (T_b) and a lower evaporative water loss (EWL) and BMR (Withers et al., 2006). However, in contrast to placentals, marsupials such as the fat-tailed dunnart (*Sminthopsis crassicaudata*) show little intra-specific physiological variability among populations from various climatic zones (Morton, 1980). Nevertheless, there are intra-specific differences in daily energy expenditure of wild fat-tailed dunnarts from mesic and arid habitats, mainly due to modified activity periods and torpor use (Nagy et al., 1988; Warnecke et al., 2008).

Arid-zone habitats are particularly challenging for small endotherms as they have a high mass-specific metabolic rate (MR), EWL, respiratory frequency (f_R) and surface area to volume ratio. Living underground provides small mammals with benefits in terms of temperature, energy and water balance because of the buffered thermal conditions underground compared to the surface, and also provides some protection from predators (Degen, 1997). However, the underground environment potentially challenges animals with restricted gaseous exchange as well as limited scope for conductive and evaporative heat dissipation (McNab, 1966; Williams and Rausch, 1973; Withers, 1978; Kuhnen, 1986). Consequently, many fossorial and semi-fossorial mammals have a characteristically low MR and T_b , and high thermal conductance (C) and EWL (McNab, 1966; Seymour et al., 1998; Withers et al., 2000). On average, marsupials have a lower T_b and MR than placentals (Dawson and Hulbert, 1969), so we might predict that underground conditions are less challenging for marsupials. Also, the drastic reductions in energy requirements achieved by daily torpor or hibernation (Geiser and Ruf, 1995) may well assist small dasyurid marsupials, such as planigales and dunnarts, in exploiting underground microhabitats (Dawson and Wolfers, 1978; Geiser and Baudinette, 1988; Geiser, 2003).

Planigales are among the smallest marsupials, and some species are found in extremely arid environments (Read, 1984) such as floodplains where dry clay soils form narrow, deep (>1 m) soil cracks (Read, 1987a). The combination of small body size and arid habitat imposes harsh living conditions for Giles' planigale (*Planigale gilesi*, 6–15 g). The

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dorso-ventrally flattened skull and body of planigales allow them to exploit soil-crack microhabitats. While such morphological adaptations of planigales are obvious, there are no such obvious physiological adaptations to the physical demands of underground arid-zone environments. We hypothesise that this small species has further specific physiological adaptations to its habitat, and therefore examine its thermal, metabolic, hygric and ventilatory physiology with particular emphasis on energy and water balance.

2. Methods

2.1. Animals

Eight planigales (six males, two females) were caught in Kinchega National Park (32° 30' S, 142° 20' E; western New South Wales, Australia) in April 2007 (eight weeks prior to measurements). Planigales were transported to the University of New England, Armidale, and maintained at an ambient temperature (T_a) of $20 \pm 2^\circ\text{C}$ (12:12 LD, lights on 06:00 h) in separate cages ($57 \times 35 \times 20$ cm). They were fed daily with a mixture of lean minced meat, hard boiled eggs, dog kibble (Jackson, 2003) and mealworms; water was freely available. The mean body mass over all experiments was 9.1 ± 0.3 g. Even long-term captivity has little effect on most standard physiological variables for marsupials (Cooper, 2004; Larcombe and Withers, 2007) and so the physiological data we present here for captive planigales are likely to be representative of wild individuals.

2.2. Measurements

Standard open-flow respirometry was used to measure oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$) and EWL at four different T_a s: 10°C ($n=6$), 21°C ($n=8$), 30°C ($n=8$) and 32°C ($n=8$). Planigales were fasted for 24 h prior to the measurements, then placed in a cylindrical metabolic chamber (180 mL) inside a temperature-controlled cabinet at approximately 08:00, where they remained for at least 7 h (their rest phase) for each T_a . Animals were allowed a minimum of three days rest between each T_a measurement. The flow of dry compressed air (dried with Drierite) through the chamber was maintained at 150 mL min^{-1} at $T_a = 32^\circ\text{C}$ to 350 mL min^{-1} at $T_a = 10^\circ\text{C}$ with an Aalborg GFCS 01007 mass flow controller. Excurrent air passed through a Vaisala HMP 35B relative humidity (RH) and temperature probe before a sub-sample (100 mL min^{-1}) was dried with Drierite and then analysed for O_2 and CO_2 concentration (Sable Systems FoxBox). The O_2 , CO_2 , T_a and RH values were recorded every 10 s on a PC using a custom-written Visual Basic (V6) program (P.C. Withers). Planigales were weighed before and after the experiment (± 0.01 g; Sartorius), and the mean was used for mass-specific calculations. T_b was measured ($\pm 0.1^\circ\text{C}$; Radiospares 611234 thermocouple meter) immediately after measurements using a fine plastic-tipped thermocouple. Torpor was defined by a decrease in MR of more than 75% compared to normothermic values at the same T_a (Hudson and Scott, 1979). Torpid individuals were removed from the chamber to measure T_b during steady-state, and were then returned to measure resting rates after arousal.

Means of $\dot{V}O_2$ ($\text{mL O}_2\text{ g}^{-1}\text{ h}^{-1}$), $\dot{V}CO_2$ ($\text{mL CO}_2\text{ g}^{-1}\text{ h}^{-1}$) and EWL ($\text{mg H}_2\text{O g}^{-1}\text{ h}^{-1}\text{ }^\circ\text{C}^{-1}$) were calculated over ~ 20 min periods when MR and EWL were stable and minimal (after Withers, 2001), using a custom-written analysis VB program (P.C. Withers). The respiratory exchange ratio (RER) was calculated as $\dot{V}CO_2/\dot{V}O_2$. EWL was converted to evaporative heat loss (EHL) using the latent heat of fusion of 2.4 J mg^{-1} . Wet (C_{wet}) and dry (C_{dry}) thermal conductance ($\text{J g}^{-1}\text{ h}^{-1}\text{ }^\circ\text{C}^{-1}$) were calculated as $\dot{V}O_2/(T_b - T_a)$ and $(\dot{V}O_2 - \text{EHL})/(T_b - T_a)$ respectively, where $\dot{V}O_2$ was converted to J using the oxy-calorific coefficient for the measured RER (e.g. $19.5\text{ J mL O}_2^{-1}$ at $\text{RER} = 0.7$ and $20.1\text{ J mL O}_2^{-1}$ at $\text{RER} = 1$; Table 4.2 in Withers, 1992). Metabolic water production (MWP) was calculated from $\dot{V}O_2$, at the

measured RER (Withers, 1992). Relative water economy (RWE) was calculated as MWP/EWL with the point of RWE (PRWE) being the T_a where $\text{RWE} = 1$.

The metabolic chamber was used as an open whole body plethysmograph to measure respiratory variables after Malan (1973) and Withers (1977). Pressure changes due to inspiration/expiration were detected with a custom-made pressure transducer (Motorola MPX2010 sensor). A Pico Technology ADC 11 data logger and PicoScope software were used to record the analog voltage outputs of the pressure transducer every 15 ms for approximately 30 s. A single mean was calculated for each ventilatory variable for each planigale at each T_a from the two to six sets of ventilatory data obtained for an individual planigale at each T_a . Ventilatory variables (respiratory frequency, f_R ; tidal volume, V_T ; minute volume, \dot{V}_I ; oxygen extraction, EO_2) were calculated after Malan (1973) and Cooper and Withers (2004), using a custom-written VB 6 data analysis program (P.C. Withers). V_T and \dot{V}_I are presented at T_b and pressure saturated (BTPS) conditions. EO_2 was calculated using the $\dot{V}O_2$ at the time of ventilatory measurements from \dot{V}_I corrected to STPD.

Planigales were observed without disturbance during experiments using an infrared camera (Swann Max-IP-cam) to ensure that they were calm and resting. Flowmeters were calibrated using a custom-made bubble meter and CO_2 analysers were calibrated using nitrogen ($0\% CO_2$) and a precision gas mix ($1.50\% CO_2$; BOC gases). O_2 analysers were calibrated to room air ($20.95\% O_2$); the FoxBox has an electronic zero function. Calibration of the RH probes was confirmed using two points, $1\% RH$ (dried with Drierite) and $100\% RH$ (saturated; by breathing on the probe). The plethysmography system was calibrated by injecting known volumes of air into the chamber at the end of each experiment, and the open-flow plethysmography data were analysed as closed-system signals after Szewczak and Powell (2003) to account for the time course of calibration injections and breathing pressure pulses.

2.3. Statistical analysis

Data are presented as mean \pm standard error, with n = number of individuals. Not all individual planigales were measured at each T_a ($n=6, 8, 8$ and 8 for $10, 20, 30$ and 32°C respectively) for logistical reasons, precluding a repeated measures ANOVA. We used standard univariate ANOVA to analyse these data but adjusted the total degrees of freedom to reflect the number of individuals (i.e. $8 - 1 = 7$) rather than the normal value of the number of measurements (i.e. $30 - 1 = 29$). This is a very conservative adjustment to avoid artificial inflation of the error degrees of freedom, which may occur if the repeated measure nature of the data is ignored. The expected effect of T_a was examined using *a priori* contrasts by univariate ANOVA, also adjusting the total degrees of freedom as above. Linear and quadratic polynomial contrasts were used to examine the pattern of change with T_a , and reverse-Helmert contrasts were used to test for an increase in a variable at high T_a . Paired *t*-tests (correcting for equality of variance if necessary) were used to compare normothermic and torpid values for planigales. Linear regression of RWE with T_a was used to determine the PRWE. These analyses were performed using StatistixL (v 1.7) and SPSS (v16).

Planigales were compared to other marsupials (N = number of species) by determining if they conformed to the 95% prediction limits (after Cooper and Withers, 2006) of marsupial allometric relationships for T_b ($N=71$), BMR ($N=72$), C_{wet} ($N=60$) and EWL ($N=30$), using the dataset of Withers et al. (2006), with additional data from Bozinovic et al. (2004, 2005), Cooper and Cruz-Neto (2009), Cooper et al. (2005, 2009, 2010), Larcombe and Withers (2006), Larcombe et al. (2006, 2008), Ribeiro and Bicudo (2007), McNab (2008) and Withers and Cooper (2009a,b). Ventilatory variables were compared to the dataset used by Cooper et al. (2009), with additional data from Cooper and Cruz-Neto (2009), Cooper et al. (2010), Larcombe et al. (2008) and Withers and Cooper (2009a); $N=17$. Comparisons were made

with conventional and phylogenetically-independent allometric relationships of log-transformed (except T_b) physiological variables, where the mean of multiple values for a species was used. Allometrically-predicted values were calculated using the minimum variance unbiased estimate of Hayes and Shonkwiler (2006). Phylogenetically predicted body mass, and phylogenetically independent traits were determined using autocorrelation (Cheverud and Dow, 1985; Rohlf, 2001), based on the marsupial section of the mammal phylogeny of Bininda-Emonds et al. (2007).

3. Results

3.1. Empirical results

3.1.1. Thermal and metabolic physiology

T_b ranged from 32.4 ± 0.45 °C at $T_a = 10$ °C to 34.4 ± 0.17 °C at $T_a = 32$ °C (Fig. 1A). ANOVA indicated a significant effect of T_a on T_b ($F_{3,4} = 7.4$, $p = 0.026$), with T_b increasing linearly with increasing T_a (linear contrast $t_4 = 5.2$, $p = 0.006$). T_a also had a significant effect on $\dot{V}O_2$ ($F_{3,4} = 39.7$, $p = 0.002$), with a linear decrease in $\dot{V}O_2$ with increasing T_a (linear contrast $t_4 = 10.9$, $p < 0.001$); $\dot{V}O_2$ ranged from 1.20 ± 0.082 at $T_a = 32$ °C to 6.62 ± 0.646 mL O₂ g⁻¹ h⁻¹ at $T_a = 10$ °C (Fig. 1B). We consider MR at $T_a = 32$ °C to be the BMR. $\dot{V}CO_2$ mirrored $\dot{V}O_2$, hence is not presented separately here. The mean RER for all planigales over all experiments was 0.82 ± 0.025 .

No animal entered torpor at $T_a = 10$ °C, but three of the eight planigales entered torpor at 20 °C, with a mean T_b of 22.8 ± 1.1 °C ($n = 3$). This was significantly lower than T_b of these individuals when normothermic at 20 °C ($t_2 = 13.7$, $p = 0.005$). During torpor $\dot{V}O_2$ was significantly reduced to 0.83 ± 0.20 mL O₂ g⁻¹ h⁻¹ (Fig. 1B; $t_2 = 5.1$, $p = 0.037$), which was a 79% decrease compared to normothermic values for all planigales at the same T_a .

T_a had a significant overall effect on C_{wet} but not on C_{dry} (Fig. 1C and 1D; ANOVA $F_{3,4} = 7.5$, $p = 0.041$ and $F_{3,4} = 2.6$, $p = 0.193$, respectively). C_{wet} was significantly higher (reverse Helmert contrast $t_4 = 4.4$; $p = 0.012$) at $T_a = 32$ °C (10.31 ± 0.912 J g⁻¹ h⁻¹ °C⁻¹) than at all other T_a s, but C_{dry} was not ($t_4 = 2.6$, $p = 0.058$). We define the C_{wet} (6.32 ± 0.610 J g⁻¹ h⁻¹ °C) and C_{dry} (5.38 ± 0.520 J g⁻¹ h⁻¹ °C) at $T_a = 30$ °C (which is near the lower limit of the thermoneutral zone) as standard C_{wet} and C_{dry} . EHL ranged from $7.2 \pm 2.17\%$ ($T_a = 10$ °C) to $25.7 \pm 2.08\%$ ($T_a = 32$ °C) of planigales' total heat loss, with the proportion increasing significantly with increasing T_a ($F_{3,4} = 15.8$, $p = 0.011$). The C_{wet} and C_{dry} of torpid planigales was 7.61 ± 1.08 J g⁻¹ h⁻¹ °C⁻¹ and 6.85 ± 1.20 J g⁻¹ h⁻¹ °C⁻¹ respectively; these did not differ significantly ($t_2 \leq 0.068$, $p \geq 0.952$) from normothermic planigales (Fig. 1C and D).

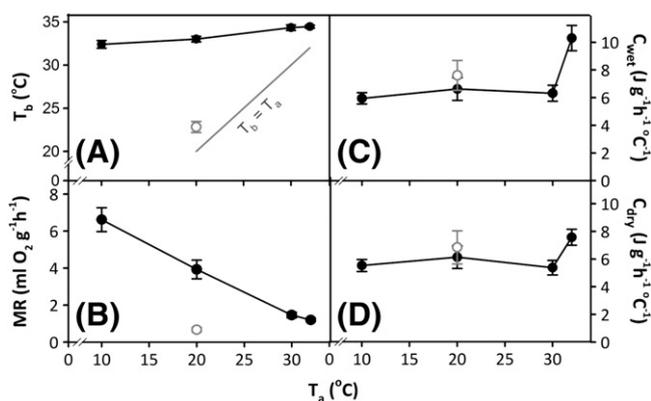


Fig. 1. The effect of ambient temperature (T_a) on (A) body temperature (T_b), (B) metabolic rate (MR), (C) wet thermal conductance (C_{wet}) and (D) dry thermal conductance (C_{dry}) in normothermic (dark circles) and torpid (light circles) *Planigale gilesi*. Data are mean \pm SE.

3.1.2. Hygric physiology

EWL was lower at $T_a = 30$ °C (1.79 ± 0.325 mg H₂O g⁻¹ h⁻¹) than at all other T_a s (Fig. 2A); we define this minimum EWL near the lower end of the thermoneutral zone as standard EWL. The effect of T_a on EWL was better explained by a linear relationship for $T_a = 10, 20$ and 30 °C (linear contrast $t_5 = 2.8$, $p = 0.038$) than when all T_a s were included in the model (linear contrast $t_4 = 2.4$, $p = 0.077$), suggesting that EWL started to increase at $T_a = 32$ °C.

The effect of T_a on MWP mirrored that of $\dot{V}O_2$, with MWP ranging from 0.72 ± 0.048 mg g⁻¹ h⁻¹ ($T_a = 32$ °C) to 4.07 ± 0.461 mg g⁻¹ h⁻¹ ($T_a = 10$ °C). RWE increased with decreasing T_a (Fig. 2B; $F_{3,4} = 9.0$, $p = 0.030$), ranging from 0.29 ± 0.033 at $T_a = 32$ °C to 1.34 ± 0.27 at $T_a = 10$ °C. The relationship between T_a and RWE was described by the significant linear regression ($RWE = -0.0045 T_a + 1.85$; $R^2 = 0.48$; $F_{1,6} = 26.1$, $p = 0.002$), with the PRWE occurring at $T_a = 19.1$ °C.

For the three torpid planigales at $T_a = 20$ °C, EWL decreased significantly ($t_2 = 4.6$, $p < 0.001$) to 0.94 ± 0.33 mg H₂O g⁻¹ h⁻¹, which is 38% of normothermic EWL. MWP was reduced from 2.50 ± 0.333 mg g⁻¹ h⁻¹ during normothermia to only 0.47 ± 0.010 mg g⁻¹ h⁻¹ during torpor. RWE during torpor was 0.70 ± 0.30 (Fig. 2B) and did not differ significantly from normothermic RWE ($t_9 = 0.87$, $p = 0.407$).

3.1.3. Ventilatory physiology

Standard ventilatory variables near the lower critical temperature at $T_a = 30$ °C were: $\dot{f}_R = 76$ breaths min⁻¹, $V_T = 0.22 \pm 0.039$ mL, $\dot{V}_I = 16.1 \pm 2.37$ mL min⁻¹ and $EO_2 = 11.1 \pm 0.72\%$. T_a had an overall significant effect on two respiratory variables, \dot{f}_R ($F_{3,4} = 9.1$, $p = 0.029$) and \dot{V}_I ($F_{3,4} = 38.8$, $p = 0.002$), but not V_T ($F_{3,4} = 3.0$, $p = 0.621$) or EO_2 ($F_{3,4} = 3.6$, $p = 0.123$; Fig. 3). The relationship between \dot{f}_R and T_a was inverse (linear contrast $t_4 = 5.2$, $p = 0.007$), with \dot{f}_R decreasing from 211 breaths min⁻¹ at $T_a = 10$ °C to 76 breaths min⁻¹ at $T_a = 30$ °C (Fig. 3A). \dot{V}_T ranged from 0.175 mL at $T_a = 32$ °C to 0.304 mL at $T_a = 10$ °C, but there was no overall T_a effect (linear contrast $t_4 = 2.1$, $p = 0.099$; Fig. 3B). \dot{V}_I decreased substantially with increasing T_a (linear contrast $t_4 = 10.3$, $p < 0.001$) from 57.8 mL min⁻¹ at $T_a = 10$ °C to 14.5 ± 3.18 mL min⁻¹ at $T_a = 32$ °C (Fig. 3C). EO_2 ranged from 9.1% at $T_a = 10$ °C to 19.1% at $T_a = 20$ °C (Fig. 3D), but there was no significant linear T_a relationship (linear contrast $t_4 = 0.03$, $p = 0.974$).

3.2. Comparative analysis

The mean body mass (9.1 ± 0.3 g) was 76% of the phylogenetically-predicted body mass for this species of 12.6 g (using the BMR dataset for body mass, as this has the largest number of species). The planigales'

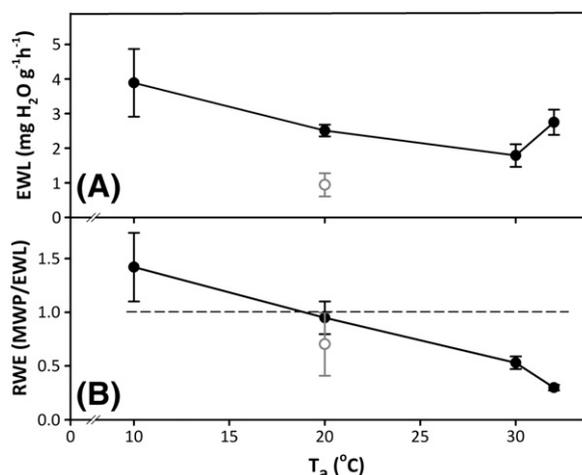


Fig. 2. The effect of ambient temperature (T_a) on (A) evaporative water loss (EWL) and (B) the relative water economy (RWE), calculated as the ratio of metabolic water production (MWP) and EWL, for normothermic (dark circles) and torpid (light circles) *Planigale gilesi*. The dashed line indicates $RWE = 1$. Data are mean \pm SE.

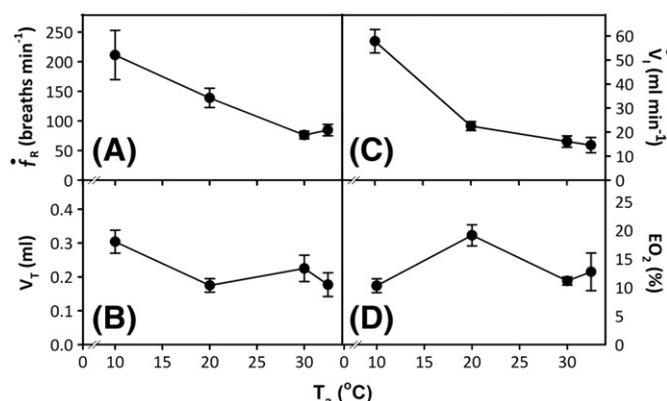


Fig. 3. The effect of ambient temperature (T_a) on (A) ventilation frequency (f_R), (B) tidal volume (V_T), (C) inspiratory minute volume (\dot{V}_I) and (D) oxygen extraction (EO_2) in *Planigale gilesi*. Data are mean \pm SE.

standard T_b conformed closely to their allometrically (34.3 °C) predicted T_b and did not differ significantly from the phylogenetically independent T_b allometry for marsupials. BMR (86% of the allometrically predicted value), standard C_{wet} (69%) and standard EWL (52%) also statistically conformed to other marsupials, falling within the 95% prediction limits for both conventional and phylogenetically-independent regressions. Ventilatory parameters likewise conformed to those of other marsupials, ranging from 78% (EO_2) to 129% (\dot{V}_I) of that predicted from body mass.

4. Discussion

Our study demonstrates that thermal, metabolic, hygric and ventilatory variables of Giles' planigale conform to predictions for a similar-sized marsupial. Despite the severe physiological challenges imposed on this tiny endotherm by the combination of its small size, semi-fossorial habit and arid habitat, it appears that planigales can survive without specific physiological adaptations. The generally low energy requirements of marsupials, as well as the planigales' behavioural strategies (e.g. semi-fossorial, crack-dwelling habits) and the use of torpor appear to suffice to reduce energy and water expenditure and secure its survival in a harsh environment.

4.1. Thermal, metabolic and ventilatory physiology

The small body mass of Giles' planigale is not unexpected based on its phylogenetic position within the dasyurid marsupials. It is clustered together with the other small planigales, and amongst other small dasyurids such as *Sminthopsis* and *Ningau* (Bininda-Emonds et al., 2007). Planigales regulated T_b between 32.4 °C and 34.5 °C over the measured T_a s during normothermia, but they nevertheless were significantly thermolabile with reduced T_b at low T_a s. T_b varied essentially linearly over the T_a range by 0.090 °C °C⁻¹, which is similar to the thermolability of 0.076 \pm 0.023 °C °C⁻¹ measured for other dasyurids (Withers and Cooper, 2009a,b). This observed thermolability is similar to that measured for the same species by Dawson and Wolfers (1978), but contrasts with the observation by Geiser and Baudinette (1988) who found T_b to be constant over a T_a range from 7 °C to 32 °C. Thermolability is not unexpected for a small mammal inhabiting a harsh environment as it can correlate with behavioural thermoregulatory plasticity and confer energy and water savings. For example, a T_b of 32.4 °C rather than 34.4 °C at $T_a = 10$ °C reduces MR by 0.67 mL O₂ g⁻¹ h⁻¹, which compared to the actual MR of 7.47 mL O₂ g⁻¹ h⁻¹ represents a 9% reduction in energy expenditure.

The BMR of planigales (1.20 mL O₂ g⁻¹ h⁻¹) was between values previously reported for the same species (1.43 mL O₂ g⁻¹ h⁻¹; Geiser and Baudinette, 1988) and the slightly larger common planigale (*P.*

maculata, 1.01 mL O₂ g⁻¹ h⁻¹; Morton and Lee, 1978). MR of planigales increased at lower T_a s, as expected for an endotherm, at about the expected rate given their typical thermal conductance. Torpor, at $T_a = 20$ °C, resulted in a 79% decrease in MR and a 62% decrease in EWL. Such use of torpor for energy and water savings is common, if not universal, among small dasyurid marsupials (Geiser, 1994, 2003; Cooper and Geiser, 2008) and may be an important factor contributing to their success in arid environments (Geiser, 2004; Withers et al., 2004).

Planigales accommodated their higher thermoregulatory costs at lower T_a s by increasing \dot{V}_I by 318% ($T_a = 10$ °C compared to 30 °C) rather than EO_2 , which did not change with T_a . This is typical of marsupials (e.g. Chappell and Dawson, 1994; Dawson et al., 2000; Schmidt et al., 2009). Body mass is the major determinant of whether the increase in \dot{V}_I is accommodated by an increase in f_R or in V_T , with small marsupials increasing f_R and larger species increasing V_T (Cooper and Withers, 2004), presumably due to differences in the physics and mechanics of ventilation for large and small animals (Larcombe, 2002). The small planigales were no exception to this pattern, with f_R increasing by 240% as T_a decreased from 30 °C to 10 °C, while V_T was not influenced by T_a . The only other published study concerning ventilation in planigales, by Chappell and Dawson (1994) for the slightly smaller narrow-nosed planigale (*P. tenuirostris*), indicated similar patterns to our results. Ventilatory variables also conformed to those of other marsupials, which is not surprising considering that metabolic variables were similar to allometric predictions, and ventilation closely matches the metabolic demand of resting endotherms (Withers and Cooper, 2009a,b).

The fact that standard T_b , BMR, C and ventilation of planigales statistically conformed to that of other marsupials suggests that Giles' planigale does not have specific thermal, metabolic or ventilatory adaptations associated with its small size, semi-fossorial habit or arid habitat. Presumably the low T_b and BMR associated with the planigale being a marsupial, and enhanced heat dissipation of a small body mass, means that specific physiological adaptations to further reduce energy expenditure and heat production are unwarranted. Behavioural adaptations of exploiting favourable microclimates and basking, and the flexible use of torpor, by free-ranging planigales in winter (Warnecke and Geiser, 2009), result in considerable reductions in energy expenditure, as also observed for the sympatric fat-tailed dunnart (Warnecke et al., 2008; Warnecke and Geiser, 2010). Hence, it is likely that these adaptations make further thermal and metabolic adaptations unnecessary. The steep increase in MR at $T_a < 30$ °C, and the beginning of a heat stress response (increased C_{wet} , C_{dry} , and EWL) at a fairly moderate T_a (32 °C) indicate the importance of exploitation of a favourable microclimate and avoidance of low and high T_a .

4.2. Water economy

The EWL of planigales increased with decreasing T_a , which is consistent with findings for the stripe-faced dunnart (*S. macroura*; Cooper et al., 2005) but is in contrast with the constancy or decrease in EWL with decreasing T_a observed for most marsupials (e.g. Hinds and MacMillen, 1986; Dawson et al., 2000; Larcombe et al., 2006; Withers and Cooper, 2009b). An increase in EWL with decreasing T_a might seem counter-intuitive (EWL might be expected to decrease with a decrease in T_a as a lower skin temperature and expired air temperature would be expected to decrease cutaneous EWL and respiratory EWL at lower T_a), but it presumably reflects an increase in respiratory water loss at low T_a s as \dot{V}_I increases to accommodate an increased MR (Figs. 2 and 3). Differences between species in EWL- T_a patterns presumably result from variation in thermal conductance (and therefore the rate of increase in MR with decreasing T_a) and the effectiveness of nasal counter-current heat/water exchange.

The standard EWL of planigales did not differ significantly from that of other marsupials, despite being only 50% of that predicted by

body mass. However, comparison with allometrically predicted values is complicated by methodological differences (e.g. measurement technique, chamber humidity and measurement duration) that may influence the measurement of EWL and lead to a variable dataset for this variable (see Cooper et al., 2005 and Cooper and Withers, 2008). Many of the existing standard EWL data for small marsupials are probably overestimates (Cooper and Withers, 2009). Therefore it is difficult to unequivocally evaluate the planigale's standard EWL in comparison with other species.

An increase in EWL with increasing T_a reduces RWE. For example, stripe-faced dunnarts never attain a PRWE, as their increase in MWP at low T_a is insufficient to balance the increase in EWL (Cooper et al., 2005). In contrast, planigales had a sufficiently large increase in MWP below thermoneutrality (presumably resulting from greater thermoregulatory costs associated with a small body size) to counterbalance the increasing EWL and were able to achieve a relatively high PRWE of 19.1 °C. This is the second highest PRWE yet measured for a marsupial; PRWEs for marsupials range from 11.3 °C for the woolly mouse opossum (Cooper et al., 2010) to 22.6 °C for the chuditch (Schmidt et al., 2009). A high PRWE presumably reflects a combination of Giles planigales' small size and arid habitat as both body mass and habitat aridity have been related to RWE (MacMillen and Hinds, 1983; Cooper and Withers, in press).

4.3. Torpor

Use of torpor by small arid-zone marsupials is a well-described thermoregulatory strategy with considerable energetic and hygric benefits (Geiser, 2003). All four Australian planigale species use torpor in captivity (Dawson and Wolfers, 1978; Morton and Lee, 1978; Geiser and Baudinette, 1988), as do all other small dasyurids so far investigated (Geiser, 1994, 2003; Cooper and Geiser, 2008). In the field, planigales use torpor extensively during winter, with a mean torpor bout duration of over 16 h (Warnecke and Geiser, 2009). In contrast, in the present study only three of the eight planigales entered torpor, and only at $T_a = 20$ °C. All six remained normothermic at $T_a = 10$ °C, possibly to avoid the high cost of arousal at low T_a . During torpor, energy expenditure was reduced by 79% and EWL by 62% compared to normothermic values, which is comparable to energy and water savings reported by previous studies (Geiser and Baudinette, 1988; Cooper et al., 2005, 2009; Withers and Cooper, 2009a,b). Despite these absolute reductions in MR and EWL, torpor did not improve the RWE, similar to findings for other marsupials and placental mammals (e.g. MacMillen, 1965; Buffenstein, 1985; Cooper et al., 2005; Withers and Cooper, 2009a). Thus, while torpor results in substantial absolute energy and water savings it does not improve relative water economy.

4.4. Ecological consequences

The basic physiology of Giles' planigales conforms closely to allometric and phylogenetic predictions, indicating that this species lacks specific physiological adaptations to its arid habitat, small size and semi-fossorial habit. Rather, other aspects of planigales' biology make substantial contributions to their ability to inhabit a challenging environment. Phylogenetic and body mass influences of being a small dasyurid marsupial (as compared to a placental mammal) reduce overall energy expenditure, as does torpor use. A small body mass also enhances heat exchange underground, and is associated with a more favourable water economy. The planigale's insectivorous diet (Read, 1987b) is high in pre-formed water, which has been identified as an important contributor to water balance for the sympatric fat-tailed dunnart (Morton, 1980). Further, behavioural adaptations such as selection of favourable microclimates in soil cracks and basking (Warnecke and Geiser, 2009) also enhance survival. The combination of these factors appears to sufficiently decrease energy demands of

planigales in their resource-poor habitat that further specific physiological adaptations are unnecessary.

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