

NOTICE: this is the author's version of a work that was accepted for publication in *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*, Vol. 154, Issue 1 (2009), Volume 154, Issue 1, (2009), DOI:10.1016/j.cbpa.2009.05.002

Metabolic, ventilatory and hygric physiology of the chuditch
(*Dasyurus geoffroii*; Marsupialia, Dasyuridae)

S. Schmidt^{1,2}, P.C. Withers^{1,3*} and C.E. Cooper^{1,3}

¹ Zoology, School of Animal Biology, The University of Western Australia, Crawley, WA 6009 Australia

²Metabolic Physiology, Institute of Zoology, Department of Life Sciences, Johann Wolfgang Goethe-Universität, 60323 Frankfurt am Main, Germany

³Centre for Ecosystem Diversity and Dynamics in the Department of Environmental and Aquatic Sciences, Curtin University of Technology, Bentley WA 6145 Australia

* to whom correspondence should be addressed

pwithers@cyllene.uwa.edu.au; tel. +61 8 6488 2235; fax. +61 8 6488 1029

Abstract

The chuditch is a large carnivorous dasyurid marsupial. Historically it had one of the widest geographical distributions of all marsupials, encompassing much of arid Australia, but it is now restricted to the mesic south-west of Western Australia. It is therefore of interest to determine if its physiology better reflects adaptation to its historically arid or present mesic habitat. The basic physiological parameters of the chuditch conform to other marsupials. Body mass of males (1385g) was >400% of that predicted by phylogeny and this may be related to its carnivorous diet. Body temperature was 33.9°C at ambient temperatures \leq thermoneutrality, with hyperthermia occurring above thermoneutrality. Basal metabolic rate was 0.361 ml O₂ g⁻¹ h⁻¹ at an ambient temperature of 31°C. Metabolic rate increased below the thermoneutral zone by 0.038 ml O₂ g⁻¹ h⁻¹ °C⁻¹, and above the thermoneutral zone to 0.444 \pm 0.059 ml O₂ g⁻¹ h⁻¹ at 33.3°C. Standard evaporative water loss was 0.498 \pm 0.071 mg g⁻¹ h⁻¹ at an ambient temperature of 26.0°C, and increased at higher ambient temperatures due to panting and licking. Changes in wet thermal conductance largely reflected changes in evaporative heat loss, and dry thermal conductance increased at high ambient temperature due in part to posture change. Ventilatory parameters were consistent with metabolic demands in and below thermoneutrality, and suggested augmented evaporative heat loss above the thermoneutral zone. Chuditch had a high point of relative water economy of 22.6°C, indicating favourable water economy at even moderate ambient temperatures, due to its low evaporative water loss rather than high metabolic water production. Chuditch were physiologically more similar to marsupials from arid rather than mesic habitats, better reflecting their historical distribution than their current geographical range.

Keywords: basal metabolic rate, body temperature, conductance, evaporative water loss, marsupial, relative water economy, ventilation

Introduction

The chuditch (western quoll, *Dasyurus geoffroii*) is the third largest extant carnivorous marsupial, and the largest in Western Australia; adult males are 1.3 kg and females are 0.9 kg (Serena and Soderquist 1988). Chuditch formerly occurred over about 70% of the Australian mainland, from Western Australia to central New South Wales, with one of the widest geographical distributions of any marsupial. They occurred in a range of habitats extending from mesic to arid, but not tropical, regions. However, since European settlement the distribution of the chuditch has contracted dramatically to the south-west of Western Australia (Morton et al. 1989) and it is now classified as “near threatened” (IUCN 2008). Chuditch are nocturnal and den in hollow logs or burrows during the day (Serena and Soderquist 1989). They feed on a wide range of prey items including invertebrates, small mammals and birds, and carrion (Soderquist and Serena 1994).

The only previous physiological measurements for chuditch are body temperature and metabolic rate (Arnold and Shield 1970; Arnold 1976). Chuditch are effective thermoregulators from ambient temperatures as low as 0°C to as high as 40°C, although they use seasonal torpor, particularly females (Arnold 1976). Arnold and Shield (1970) suggested that the physiology of chuditch may partly explain their wide distribution from temperate to arid regions.

Here we describe the thermal, metabolic, hygric and ventilatory physiology of male chuditch. We measured standard physiological parameters (body temperature, T_b ; metabolic rate, MR; respiratory rate, f_R ; tidal volume, V_T ; minute volume, V_I ; wet and dry thermal conductance, C_{wet} and C_{dry} ; evaporative water loss, EWL) at different ambient temperatures (T_a), and provide the first relative water economy (RWE) data for a medium-sized marsupial. We interpret these basic physiological parameters of the chuditch with respect to its body mass and phylogeny, to determine if the physiology of the chuditch better reflects its past or present climatic distribution or shows adaptation to its carnivorous diet.

Materials and methods

Four male chuditch were captured at Julimar State Forest, 120km north of Perth, Western Australia (31° 24' S, 116° 22' E), kept in quarantine at Perth Zoo for four weeks, then taken to The University of Western Australia (UWA). Each individual was housed in an outdoor enclosure under natural conditions of weather and photoperiod. They were fed at 1800 h daily, with ~120 g of fresh meat supplemented with eggs and live crickets, with *ad lib.* water. Individuals were fasted for 24 hrs prior to metabolic experiments and were weighed to

± 1 g at the start and end of each experiment. One additional adult male chuditch was measured at Perth Zoo. This individual was housed indoors in the nocturnal house under reverse photoperiod.

Oxygen consumption (VO_2), carbon dioxide production (VCO_2) and EWL were measured using standard flow-through respirometry at $T_{a,s}$ of 10.1 ± 0.25 , 14.6 ± 0.39 , 17.9 ± 0.24 , 22.3 ± 0.40 , 26.0 ± 0.20 , 31.0 ± 0.32 and $33.3 \pm 0.24^\circ\text{C}$, in random order; $n = 5$ for all $T_{a,s}$ except 33.3°C where $n = 4$. Experiments were conducted during the animal's rest phase (during the day for the UWA animals and at night for the Perth Zoo animal housed under reverse photoperiod) for a period of 6-10 hours. Chuditch were visually monitored during experiments using a small camera and red light.

A chuditch was placed in a sealed perspex chamber inside a controlled temperature cabinet. T_a was measured inside the metabolic chamber with a thermocouple connected to a Radiospares 611234 thermocouple meter ($\pm 0.1^\circ\text{C}$). The flow of dry compressed air into the chamber was regulated at 5 L min^{-1} with an Aalborg GFC171 mass flow controller. The relative humidity (RH) of the excurrent air was measured with a Vaisala HMP 35B humidity probe. A 100 ml min^{-1} sub-sample was dried with drierite, and the O_2 and CO_2 content determined with a David Bishop 280 Combo Gas Analyser. The gas analyser, humidity probe and thermocouple were interfaced to a PC via Thurlby Thandar 1906 multimeters and the outputs recorded every 30 sec using a custom-written Visual Basic (VB version 6) program. A plastic-sheathed thermocouple (connected to a RS 611234 thermocouple meter) inserted approx. 3 cm into the cloaca was used to measure T_b immediately after the chuditch was removed from the metabolic chamber at the end of each experiment. Baseline background values for O_2 , CO_2 and RH of incurrent air were obtained for at least 30 min before and after each experiment.

The O_2 analyser was calibrated using compressed nitrogen (0% O_2) and room air (20.95% O_2), the CO_2 analyser with compressed nitrogen (0% CO_2) and a 0.53% CO_2 calibration gas (BOCS, Perth, Western Australia), and the relative humidity with dried atmospheric air ($< 1\%$ RH using Drierite) and by breathing on the sensor (100% RH). The mass flow controllers were calibrated using a volumetric meter (Alexander Wright) corrected to standard temperature and pressure, dry (STPD). VO_2 , VCO_2 and EWL were calculated after Withers (2001) for the period (at least 20 min) where MR and EWL were minimal and constant, using custom-written VB software. Wet thermal conductance (C_{wet} ; $\text{J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) was calculated as $\text{MHP}/(T_b - T_a)$ and dry thermal conductance (C_{dry} ; $\text{J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) as $(\text{MHP} - \text{EHL})/(T_b - T_a)$, where MR was converted to metabolic heat production (MHP) using the

measured respiratory exchange ratio ($RER = VCO_2/VO_2$) for that experiment after Withers (1992) and EWL was converted to evaporative heat loss (EHL) using $2.4 \text{ J mg}^{-1} \text{ H}_2\text{O}$ (McNab 2002). The evaporative quotient (EQ) was calculated as EWL/VO_2 , and the relative water economy (RWE) as MWP/EWL , where metabolic water production (MWP; $\text{ml g}^{-1} \text{ h}^{-1}$) was calculated using the measured RER for that experiment after Withers (1992).

Whole-body plethysmography (Malan 1973) was used to measure f_R and V_T at $T_a = 10.1$ ($n = 5$), 17.9 ($n = 5$), 26.0 ($n = 4$) and 33.3°C ($n = 4$), using the metabolic chamber as an open-flow plethysmograph after Larcombe (2002) and Cooper and Withers (2004). Between 8 and 50 ventilatory measurements were made near the end of the experiment, which was generally when VO_2 was lowest. VO_2 varied by approximately 10% over the last few hours of each experiment so any error from using the lowest VO_2 to calculate oxygen extraction efficiency is small. An Analog Devices RTI800 data acquisition board was used to monitor the output from a pressure transducer (Motorola MPX2010DP) at 400 - 1000 Hz. Calculations of V_T and V_I follow Malan (1973) and Szewczak and Powell (2003), and were accomplished using custom-written software. Oxygen extraction (EO_2) was calculated as $VO_2/(0.2095 \cdot V_I)$. V_T and V_I are presented as body temperature and pressure, saturated (BTPS) values, but V_I was converted to STPD to calculate EO_2 .

Values are presented as mean \pm standard error, where n = number of measurements. The effect of T_a on physiological variables was determined by linear regression and full factorial ANOVA with *a priori* polynomial contrasts and Student-Newman-Keuls *post hoc* tests using SPSS (version 11.5) and StatistiXL (version 1.6). Phylogenetically-predicted and phylogenetically-independent variables were calculated using autoregression (Cheverud and Dow 1985; Rohlf 2001) using the phylogenetic tree presented by Withers et al. (2006). Chuditch were compared to conventional and phylogenetically independent log-transformed allometric regressions (except T_b which was not log-transformed; data from Withers et al. 2006) by examining their position relative to the 95% prediction limits for these relationships after Cooper and Withers (2006). The antilog predicted value for chuditch from log-transformed conventional regression was calculated using the minimum variance unbiased estimator (MVUE) of Hayes and Shonkwiler (2006, 2007).

Results

Body mass and temperature

Mean body mass was 1385 ± 140 g (range 1009 g to 1851 g). T_b did not change significantly with T_a between 10.1 and 26°C (linear contrast, $P = 0.522$; Fig. 1). Mean T_b over

this T_a range was $33.9 \pm 0.19^\circ\text{C}$ (5 individuals each measured at 5 $T_{a,s}$). There was a significant quadratic relationship in T_b ($p < 0.001$) when $T_{a,s}$ above 26°C were included, reflecting the elevated T_b at $T_a = 31^\circ\text{C}$ ($T_b = 36.3 \pm 0.28^\circ\text{C}$) and 33.3°C ($T_b = 37.9 \pm 0.06^\circ\text{C}$).

Metabolic rate

There was a significant negative linear relationship between VO_2 ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and T_a from 10.1 to 26°C ; $\text{VO}_2 = 1.38 (\pm 0.076) - 0.038 (\pm 0.004) T_a$; ($R^2 = 0.796$; $F_{1,23} = 89.8$; $p < 0.001$; Fig. 1). The minimal VO_2 was 0.361 ± 0.035 ($n = 5$) $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 31^\circ\text{C}$, so this was considered basal metabolic rate (BMR). Over all $T_{a,s}$, the relationship was quadratic ($P = 0.001$), with VO_2 increasing to $0.44 \pm 0.059 \text{ ml g}^{-1} \text{ h}^{-1}$ at 33.3°C . The pattern of VCO_2 mirrored that of VO_2 and so is not presented separately. There was a significant linear increase of RER with T_a ($R^2 = 0.399$; $F_{1,32} = 21.2$; $p < 0.001$), with RER ranging from 0.75 ± 0.012 at 10.1°C to 1.06 ± 0.097 at 31°C .

Wet and Dry Thermal Conductance

C_{wet} ranged from $0.868 \pm 0.058 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at $T_a = 10.1^\circ\text{C}$ to $2.017 \pm 0.277 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at $T_a = 33.3^\circ\text{C}$ (Fig 1). The effect of T_a on C_{wet} was significant ($F_{6,27} = 12.9$, $P < 0.001$), with a quadratic function ($P < 0.001$), reflecting the sharp increase in C_{wet} at $T_{a,s} \geq 31^\circ\text{C}$. Standard C_{wet} at 26°C was $1.026 \pm 0.123 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. C_{dry} ranged from $0.78 \pm 0.02 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at $T_a = 14.6^\circ\text{C}$ to $1.19 \pm 0.21 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at $T_a = 33.3^\circ\text{C}$. C_{dry} was described by a significant positive linear function ($P = 0.007$), with the increase at high T_a much less pronounced than for C_{wet} .

Ventilation

There was no significant effect of T_a on f_R between 10.1 ($28.3 \pm 5.14 \text{ breaths min}^{-1}$) and 26°C ($17.7 \pm 4.31 \text{ breaths min}^{-1}$; $R^2 = 0.189$; $F_{1,12} = 2.79$; $P = 0.121$; Fig. 2), although there was a significant quadratic effect ($P = 0.038$) when f_R at $T_a = 33.3^\circ\text{C}$ ($48.8 \pm 14.61 \text{ breaths min}^{-1}$) was included. V_T decreased significantly from $T_a = 10.1^\circ\text{C}$ ($32.4 \pm 5.57 \text{ ml}$) to $T_a = 33.3^\circ\text{C}$ ($9.9 \pm 0.68 \text{ ml}$; $F_{3,14} = 6.49$, $P = 0.006$; Fig. 2). There was also a significant effect of T_a on V_I , ($F_{3,14} = 5.31$, $P = 0.012$), with V_I highest at 10.1°C (860 ± 131.7) and lowest at $T_a = 26^\circ\text{C}$ (302 ± 98.9). The increase in V_I at $T_a = 33.3^\circ\text{C}$ (457 ± 196.4) was not significant (SNK $P = 0.336$). There was no effect of T_a on EO_2 ($F_{3,14} = 1.19$; $P = 0.348$); mean EO_2 over all $T_{a,s}$ was $14.4 \pm 0.69 \%$ ($n = 18$ for 5 individuals; Fig 2).

Evaporative Water Loss

There was a significant positive linear relationship between EWL ($\text{mg H}_2\text{O g}^{-1} \text{h}^{-1}$) and T_a below 26°C ; $\text{EWL} = 0.144 (\pm 0.060) + 0.013 (\pm 0.003) T_a$; ($R^2 = 0.427$; $F_{1,23} = 17.2$; $p < 0.001$; Fig 1). The relationship became quadratic above $T_a = 26^\circ\text{C}$ ($P < 0.003$), with EWL increasing to $1.57 \pm 0.135 \text{ mg g}^{-1} \text{h}^{-1}$ at $T_a = 33.3^\circ\text{C}$. We define EWL at $T_a = 26^\circ\text{C}$, of $0.498 \pm 0.071 \text{ mg g}^{-1} \text{h}^{-1}$, to be standard EWL, for comparison with other species. T_a had a significant influence on EQ ($F_{6,27} = 24.3$; $P < 0.001$), which ranged from 0.28 ± 0.052 at $T_a = 10.1^\circ\text{C}$ to $3.7 \pm 0.46 \text{ mg H}_2\text{O ml O}_2^{-1}$ at 33.3°C . There was a significant negative linear relationship between RWE and T_a ($\text{RWE} = 2.807(\pm 0.215) - 0.080(\pm 0.009)T_a$; $R^2 = 0.70$, $F_{1,32} = 75.0$, $P < 0.001$; Fig. 3). The point of relative water economy (PRWE; T_a where $\text{RWE} = 1$) occurred at 22.6°C .

Discussion

Body mass and temperature

The phylogenetically-predicted body mass for a chuditch was 337g, so actual body mass of both females and males (900 and 1300 g respectively; Serena and Soderquist 1988) are 250-400% of that predicted by phylogeny. This higher-than-predicted body mass of chuditch, and most likely the other quoll species as well, is probably an adaptation to a carnivorous diet, and the advantage of large size in capturing and subduing large vertebrate prey. Male chuditch are also larger than females (Serena and Soderquist 1988), presumably reflecting their additional requirements for a large home range and aggressive encounters with other male quolls to enhance reproductive success. The higher-than-expected body mass of chuditch accounts for other physiological variables being higher than predicted by phylogeny, as there are strong allometric effects on most physiological variables for marsupials (McNab 2005; Withers et al. 2006).

Arnold and Shield (1970) measured a T_b of 34.9°C for chuditch at a T_a of 30°C ; this value conforms well to the relationship between T_a and T_b that we observed (Fig. 1). The allometrically-predicted T_b for chuditch was 35.4°C , and although this was 1.54°C higher than the actual T_b of 33.9°C , the chuditch's T_b falls inside the 95% prediction limits for the allometric relationship for T_b and therefore conforms well to other marsupials, both before and after accounting for phylogeny. Chuditch kept T_b constant at low T_a , maintaining a substantial thermal gradient between T_b and T_a below thermoneutrality. Mild hyperthermia at $T_a \geq 31^\circ\text{C}$ maintained a positive $T_b - T_a$ gradient to allow passive heat loss and reduce water

required for evaporative heat loss.

Metabolic Rate

Arnold and Shield (1970) measured BMR for chuditch at about $0.42 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (estimated from their Fig. 1) at 30°C , which is slightly higher but does not differ statistically from the BMR of $0.361 \pm 0.035 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ that we measured. The chuditch's BMR is 94.5 % of that predicted by allometry, and conforms to the allometric relationship for marsupials both before and after accounting for phylogeny. There is a significant difference in the elevation of the allometric relationship for arid and mesic marsupials (Withers *et al.* 2006), and although the chuditch conformed statistically to the 95% confidence limits for both arid and mesic marsupial regressions, its BMR was more similar to that of arid marsupials (105% of predicted) than mesic marsupials (91% of predicted). This suggests that the chuditch's metabolic physiology may reflect its historically mostly-arid distribution more than its currently restricted mesic environment.

Below thermoneutrality, the slope of the linear relationship between VO_2 and T_a of $0.038 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($= 0.764 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) is an approximate estimate of C_{wet} and is similar to C_{wet} calculated as $\text{MHP}/(T_b - T_a)$ of $0.85\text{-}0.97 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$, indicating that the chuditch conformed fairly closely to the Scholander-Irving model of endothermy (Scholander *et al.* 1950), although this model did overestimate T_b (36.5°C predicted compared to 33.9°C actual). Above thermoneutrality, a significant increase in VO_2 indicated a metabolic cost of hyperthermia (which however has hygric advantages; see below). The systematic variation in RER with T_a from 0.75 at $T_a = 10.1^\circ\text{C}$ to 1.06 at 31°C suggests a progressive shift from greater lipid metabolism (lower RER; Withers 1992) at lower T_a and higher VO_2 , to slight hyperventilation at higher T_a . It also confers a slight hygric benefit at higher T_a , as metabolic water production increases with increasing respiratory quotient (RQ) i.e. from $0.566 \text{ mg H}_2\text{O ml O}_2^{-1}$ at $\text{RQ} = 0.7$ to $0.663 \text{ mg H}_2\text{O ml O}_2^{-1}$ at $\text{RQ} = 1$ (Withers 1992).

Thermal Conductance

C_{dry} increased with T_a , reflecting changes in posture (observations during measurement indicated the chuditch were curled into a tight near-spherical ball at low T_a but sprawled out at high T_a) and presumably peripheral blood flow. C_{wet} was always higher than C_{dry} , and increased systematically with T_a , reflecting the additional evaporative component of heat loss. The marked increase in C_{wet} above thermoneutrality indicates substantially augmented heat loss, which reflects both the increase in dry thermal conductance and

significant increase in EWL (hence evaporative heat loss).

The C_{wet} that we calculated from Arnold and Shield (1970) of $1.72 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^{\circ}\text{C}^{-1}$ at $T_a = 30^{\circ}\text{C}$ is similar to that extrapolated for our chuditch at that T_a . C_{wet} for the chuditch was 101% of that predicted for an equivalently-sized marsupial within thermoneutrality and conformed to the marsupial allometric relationship both before and after accounting for phylogenetic history.

Ventilation

Chuditch conformed closely to all allometrically predicted basal ventilatory values (f_R , V_T , V_I and EO_2) for marsupials (data from 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). The ventilatory system of endotherms accommodates changing demand for gas exchange with thermoregulatory responses to T_a , and hyperventilation augments EWL at high T_a to increase evaporative heat loss. As expected, ventilation by chuditch closely matched basal metabolic demand. At T_a s below thermoneutrality, V_I increased to accommodate O_2 demand while oxygen extraction remained constant at about 14%. Previous studies have also shown that marsupials accommodate varying O_2 demand by changes in V_I rather than EO_2 (Chappell and Dawson 1994; Dawson et al. 2000; Larcombe 2002; Cooper and Withers 2004). However, the mechanism by which V_I is increased is determined allometrically; small species increase f_R rather than V_T , whereas larger species increase V_T rather than f_R (Cooper and Withers 2004). The chuditch, with an intermediate body mass, used a combination of the two, with the ratio for $\Delta V_T/\Delta f_R$ of 1.11. This is slightly higher than the predicted ratio of 0.81 (Cooper and Withers 2004) but fell within the 95% prediction limits of the regression (note that the equation and Fig. 2 Y axis of Cooper and Withers 2004 should read $\Delta V_T/\Delta f_R$). At the highest T_a , all chuditch were observed to pant intermittently. The increased f_R , together with licking, contributed to the significant increase in EWL (and thus evaporative heat loss) and C_{wet} .

Evaporative Water Loss

Standard EWL was $0.50 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$, which is only 51 % of that predicted for a marsupial. However, this value fell within the 95% prediction limits for both conventional and phylogenetically independent allometric regressions and so the chuditch statistically conforms to these relationships. Variation in measurement techniques for EWL means that the EWL dataset is more variable than for other physiological parameters such as BMR (Withers

et al. 2006) and it is difficult to interpret comparisons of EWL between studies. We suspect that many of the existing measurements for marsupial EWL are overestimates because of methodological issues (see Cooper *et al.* 2005, 2009; Cooper and Withers 2009). Nevertheless, marsupials from regions with high intra-annual rainfall have lower EWL than those from habitats with more consistent rainfall (Withers *et al.* 2006). The residual EWL of the chuditch from conventional regression (see Withers *et al.* 2006) was 2.3 times lower than that predicted by the rainfall variability (0.827) of its mesic habitat, suggesting that the chuditch's EWL is more typical of a species from a much more variable environment than its current distribution.

The EWL of chuditch increased with T_a (Fig. 1) with virtually the same pattern as C_{wet} . Augmented evaporative heat loss at high T_a allowed for regulation of T_b . The increase in EWL is attributable to both panting and occasional licking of genitalia as observed by video surveillance. Hyperthermia at these high T_a s did however reduce dependence on evaporative cooling. The observed 4.0 °C increase in T_b at $T_a = 33.3^\circ\text{C}$ compared to $T_a \leq 26^\circ\text{C}$ would save the chuditch 2.7 ml $\text{H}_2\text{O h}^{-1}$, which is over 120% of the actual EWL at $T_a = 33.3^\circ\text{C}$.

Chuditch were able to maintain a favourable relative water economy (i.e. metabolic water production exceeding evaporative water loss) even at moderate T_a . They achieved this by having a low EWL rather than a high metabolic water production. The chuditch's PRWE of 22.6 °C is the highest measured so far for a marsupial. PRWE ranges from 11.3 °C for the 68.8g long-furred woolly mouse opossum (*Micoureus paraguayanus*; Cooper *et al.* submitted) to 17.7°C for the 43.6g sandhill dunnart (*Sminthopsis psammophila*; Withers and Cooper in press). What makes the chuditch's PRWE especially remarkable is that RWE should be more favourable for smaller species, with a negative allometric relationship for PRWE (Hinds and MacMillen 1986). The chuditch is 20-fold larger than the largest species for which there is existing data, and so it would be expected to have a PRWE 5.8°C lower than the woolly mouse opossum (calculated using the predictive equation for PRWE of dasyurid marsupials; Hinds and MacMillen 1986; see Withers and Cooper in press).

The point of relative water economy can be interpreted as an index of a species' adaptation to limited water availability and is useful for inter-specific comparison, with a higher PRWE more favourable in arid environments (MacMillen and Hinds 1983; MacMillen 1990). The chuditch's very high PRWE seems unusual, particularly given its carnivorous diet and current distribution being limited to mesic habitats. A carnivorous diet high in preformed water presumably reduces the chuditch's dependence on free water (chuditch with a diet of fresh meat do appear to need to drink; Arnold 1983), although carnivores require the capacity

to excrete urea formed from catabolism of their high protein diet and so a favourable RWE may be advantageous even for this dietary group (Geffen et al. 1992). The chuditch was historically found throughout Australia's arid zone (Serena and Soderquist 2008) and perhaps its high PRWE reflects this. Even so, the chuditch's very high PRWE does seem unusual, and requires further investigation. It would be particularly interesting to compare the chuditch with other quolls, and more data concerning the PRWE of marsupials are needed to determine allometric and ecological patterns.

Ecological correlates of physiological variables

The chuditch is a typical endotherm whose T_b and metabolism generally fits the Scholander-Irving model of thermoregulation (Scholander et al. 1950). General physiological parameters conform well to previously measured values for this species (Arnold and Shield 1970; Arnold 1976), and to other marsupials (e.g. Withers et al. 2006). There is no indication that the chuditch's carnivorous diet is associated with a high BMR, unlike placental mammals that feed on vertebrates (McNab 2008). Marsupials are physiologically conservative, and there is very little residual variation in BMR (body mass explains > 98% of the variation in BMR) to correlate with dietary or other ecological variables. Indeed, Withers et al. (2006) found no correlation between BMR and diet for marsupials (but see McNab 2005). Marsupials have a BMR only 70% of that of a generalised placental mammal (Dawson and Hulbert 1969) and only the nectarivorous honey possum (*Tarsipes rostratus*) has a BMR significantly higher than other marsupials and of the level of a generalised placental mammal (Withers et al. 1990; Cooper and Cruz-Neto in press). Thus even though the chuditch has a diet associated with high basal rates in placentals, it appears to be phylogenetically constrained to a low marsupial BMR. Probably the greatest physiological influence of diet for chuditch is the higher-than-predicted body mass (250-400%) from its phylogenetic position. Presumably this large body mass is an adaptation to capturing and subduing vertebrate prey. The strong allometric effect on most physiological variables means that this high body mass is associated with increased absolute energetic and hygric requirements above those predicted by its phylogeny.

Withers et al. (2006) found significant environmental correlates for physiological variables of marsupials. Species from mesic habitats and/or those with low rainfall variability have a higher BMR and EWL compared with those from arid habitats and/or those with high rainfall variability. None of the chuditch's physiological parameters are statically different to allometrically/phylogenetically predicted values for marsupials in general. However, the

chuditch conforms more closely to the BMR allometric relationship for arid zone marsupials, and has an EWL more typical of a marsupial from a habitat with high intra-annual rainfall. This, together with its remarkably good water economy is surprising for a species now restricted to the mesic south-west of Western Australia and suggests that the chuditch's physiology better reflects its pre-European distribution. Historically chuditch inhabited much of arid central Australia and this may have imposed strong selection for water and energy conservation. It appears that there has been insufficient evolutionary time and/or selection pressure for the chuditch to greatly alter its physiology from that of an arid-habitat species to one restricted to a mesic environment, and it remains more typical of an arid habitat marsupial.

Acknowledgements.

Staff of the Western Australian Department of Environment and Conservation (DEC) kindly loaned us the wild-caught chuditch, and Perth Zoo allowed us to measure their chuditch, and provided quarantine facilities for the wild-caught animals. We thank Dr Elke Schleucher for her support and assistance with this study. We appreciate the constructive comments of the three reviewers of this manuscript. This research was conducted with approval of the UWA Animal Ethics Committee and chuditch were held under licence from DEC. This project was supported by an ARC Discovery Grant to C.E. Cooper and P.C. Withers, and the Hermann Willkomm-Stiftung provided travel assistance to S. Schmidt.

References

- Arnold, J., 1976. Growth and bioenergetics of the chuditch, *Dasyurus geoffroii*. PhD Thesis, Department of Zoology, University of Western Australia, Perth.
- Arnold, J., 1983. Western quoll. In, The Australian Museum Complete Book of Australian Mammals (Ed. R. Strahan), Angus and Robertson Publishers, London, p. 22.
- Arnold, J., Shield, J., 1970. Oxygen consumption and body temperature of the Chuditch (*Dasyurus geoffroii*). *J. Zool.* 160, 391-404.
- Chappell, M.A., Dawson, T.J., 1994. Ventilatory accommodation of changing oxygen consumption in dasyurid marsupials. *Physiol. Zool.* 67, 418–437.
- Cheverud, J.M., Dow, M.M., 1985. An autocorrelation analysis of genetic variation due to lineal fission in social groups of Rhesus monkeys. *Am. J. Phys. Anthro.* 67, 113-121.
- Cooper, C.E., Cruz-Neto, A.P., in press. Metabolic, hygric and ventilatory physiology of a hypermetabolic marsupial, the honey possum (*Tarsipes rostratis*). *J. Comp. Physiol. B.* in press.
- Cooper, C.E., McAllan, B.M., Geiser, F., 2005. Effect of torpor on the water economy of an arid-zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura*). *J. Comp. Physiol. B.* 175, 323–328.
- Cooper, C.E., Withers, P.C., 2004. Ventilatory physiology of the numbat (*Myrmecobius fasciatus*). *J. Comp. Physiol. B.* 174, 107-111.
- Cooper, C.E., Withers, P.C., 2006. Numbats and aardwolves - how low is low? A re-affirmation of the need for statistical rigour in evaluating regression predictions. *J. Comp. Physiol. B* 176, 623-629.
- Cooper, C.E., Withers, P.C., 2009. Effects of measurement duration on the determination of basal metabolic rate and evaporative water loss of small marsupials; how long is long enough? *Physiol. Biochem. Zool.* In press.
- Cooper, C.E., Withers, P.C., Cruz-Neto, A.P., 2009. Metabolic, ventilatory and hygric physiology of the gracile mouse opossum (*Gracilinanus agilis*). *Physiol. Biochem. Zool.*, In press.
- Cooper, C.E., Withers, P.C., Cruz-Neto, A.P., submitted. Metabolic, ventilatory and hygric physiology of a South American marsupial, the long-furred woolly mouse opossum (*Micoureus paraguayanus*). *Zoology*, submitted.
- Dawson, T.J., Hulbert, A.J., 1969. Standard energy metabolism of marsupials. *Nature* 221, 383.
- Dawson, T.J., Munn, A.J., Blaney, C.E., Krockenberger, A., Maloney, S.K., 2000. Ventilatory

- accommodation of oxygen demand and respiratory water loss in kangaroos from mesic and arid environments, the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Macropus rufus*). *Physiol. Biochem. Zool.* 73, 382–388.
- Geffen, E., Degen, A.A., Kam, M., Hefner, R., Nagy, K.A., 1992. Daily energy expenditure and water flux of free-living Blanford's foxes (*Vulpes cana*), a small desert carnivore. *J. Anim. Ecol.* 61, 611-617.
- Hallam, J.F., Dawson, T.J., 1993. The pattern of respiration with increasing metabolism in a small dasyurid marsupial. *Respir. Physiol.* 93, 305-314.
- Hayes, J.P., Shonkwiler, J.S., 2006. Allometry, antilog transformations, and the perils of prediction on the original scale. *Physiol. Biochem. Zool.* 79, 665-674.
- Hayes, J.P., Shonkwiler, J.S., 2007. Erratum: Allometry, antilog transformations, and the perils of prediction on the original scale. *Physiol. Biochem. Zool.* 80, 556.
- Hinds, D.S., MacMillen, R.E., 1986. Scaling of evaporative water loss in marsupials. *Physiol. Zool.* 59, 1-9.
- IUCN 2008. Red List of Threatened Species. www.iucnredlist.org. Downloaded 15 March 2009.
- Larcombe, A.N., 2002. Effects of temperature on metabolism, ventilation, and oxygen extraction in the southern brown bandicoot *Isoodon obesulus* (Marsupialia: Peramelidae). *Physiol. Biochem. Zool.* 75, 405–411.
- Larcombe, A.N., Withers, P.C., 2006. Thermoregulatory, metabolic and ventilatory physiology of the western barred bandicoot (*Perameles bougainville bougainville*) in summer and winter. *Aust. J. Zool.* 54, 15-21.
- Larcombe A.N., Withers, P.C., Nicol, S.C., 2006. Thermoregulatory, metabolic and ventilatory physiology of the eastern barred bandicoot (*Perameles gunnii*). *Aust. J. Zool.* 54, 9–14.
- MacMillen, R.E. 1990. Water economy of granivorous birds: A predictive model. *Condor* 92, 379-392.
- MacMillen, R.E., Hinds, D.S., 1983. Water regulatory efficiency in heteromyid rodents: A model and its application. *Ecology* 64,152-164.
- Malan, A. 1973. Ventilation measured by body plethysmography in hibernating mammals and in poikilotherms. *Respir. Physiol.* 17, 32-44.
- McNab, B.K., 2002. *The Physiological Ecology of Vertebrates*. Cornell University Press, New York, USA.
- McNab, B.K., 2005. Uniformity in the basal metabolic rate of marsupials: its causes and

- consequences. *Rev. Chilena Hist. Nat.* 78, 183-198.
- McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. *Comp. Biochem. Physiol. A.* 151, 5-28.
- Morton, S.R., Dickman, C.R., Fletcher, T.P., 1989. Dasyuridae. In Walton, D.W., Richardson, B.J. (Eds) *Fauna of Australia. Mammalia.* Australian Government Publishing Service, Canberra, pp. 560-582.
- Rohlf, F.J., 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55, 2143-2160.
- Scholander, P.F., Hock, R., Walters, V., Johnson, F., Irving, L., 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99, 237-258.
- Serena, M., Soderquist, T. 1988. Growth and development of pouch young of wild and captive *Dasyurus geoffroii* (Marsupialia: Dasyuridae). *Aust. J. Zool.* 36, 533-543.
- Serena, M., Soderquist, T. 1989. Spatial organization of a riparian population of the carnivorous marsupial *Dasyurus geoffroii*. *J. Zool.* 219, 373-383.
- Serena, M., Soderquist, T. 2008. Western quoll. In, *The Mammals of Australia* (Eds. S. Van Dyck and R. Strahan), Reed New Holland, Sydney, pp. 54-56.
- Soderquist, T., Serena, M., 1994. Dietary niche of the western quoll, *Dasyurus geoffroii*, in the jarrah forest of Western Australia. *Aust. Mamm.* 17, 133-136.
- Szewczak, J.M., Powell, F.L., 2003. Open-flow plethysmography with pressure-decay compensation. *Resp. Physiol. Neurobiol.* 134, 57-67.
- Withers, P.C., 1992. *Comparative Animal Physiology.* Saunders College Publishing, Philadelphia.
- Withers, P.C., 2001. Design, calibration and calculation for flow-through respirometry systems. *Aust. J. Zool.* 49, 445-461.
- Withers, P.C., Cooper, C.E., in press. Metabolic and ventilatory physiology of the sandhill dunnart (*Sminthopsis psammophila*). *Comp. Physiol. Biochem.*, In press.
- Withers, P.C., Cooper, C.E., Larcombe, A.N., 2006. Environmental correlates of physiological variables in marsupials. *Physiol. Biochem. Zool.* 79, 437-453.
- Withers, P.C., Richardson, K.C., Wooller, R.D., 1990. Metabolic physiology of the euthermic and torpid honey possums, *Tarsipes rostratus*. *Aust. J. Zool.* 37, 685-693.

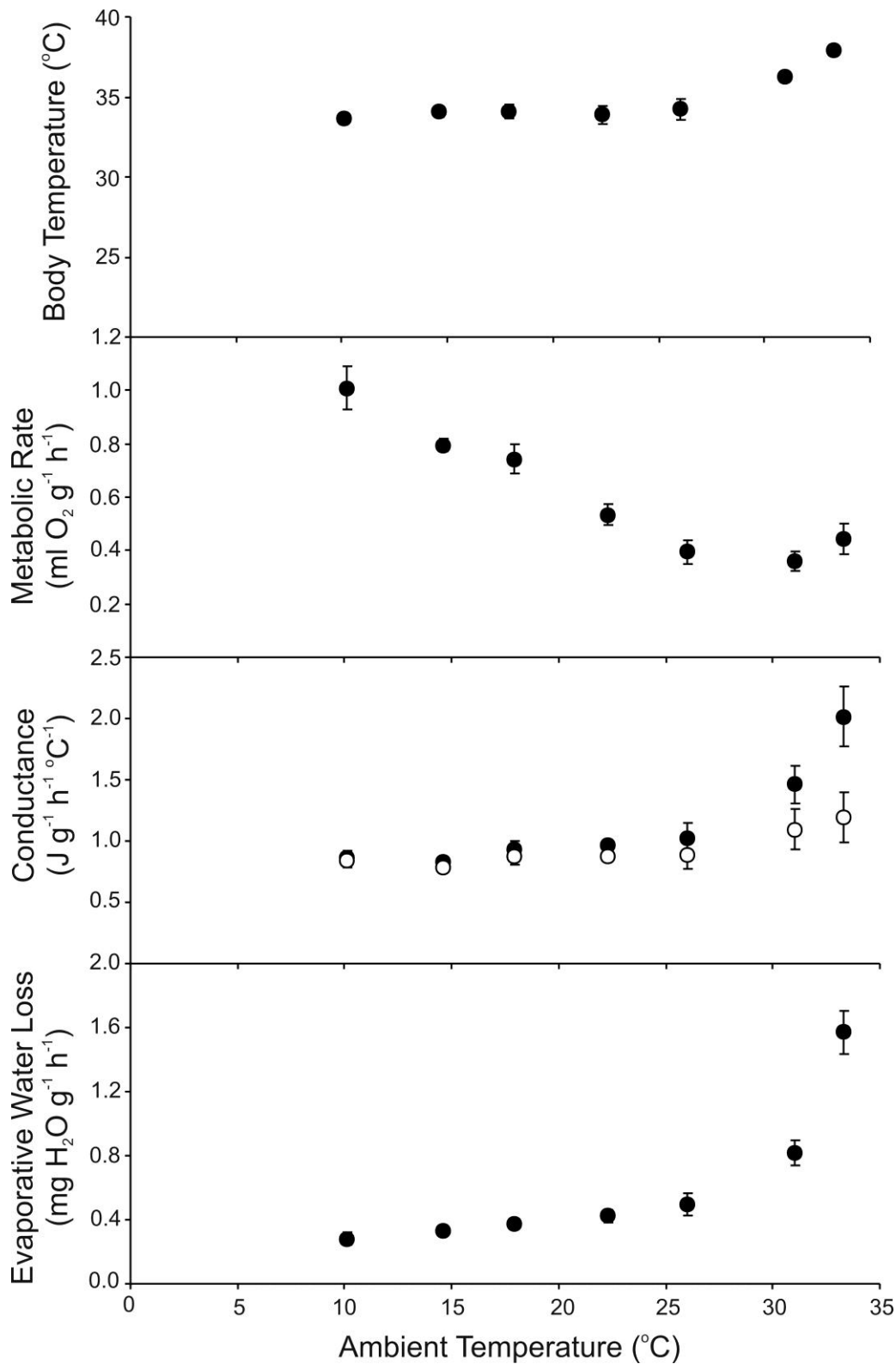


Fig. 1: Body temperature, metabolic rate, wet (dark symbols) and dry (light symbols) thermal conductance and evaporative water loss for chuditch (*Dasyurus geoffroi*) at ambient temperatures from 10.1 to 33.3°C. Values are mean \pm SE (n = 5 for all T_as except for T_a = 33.3°C where n = 4).

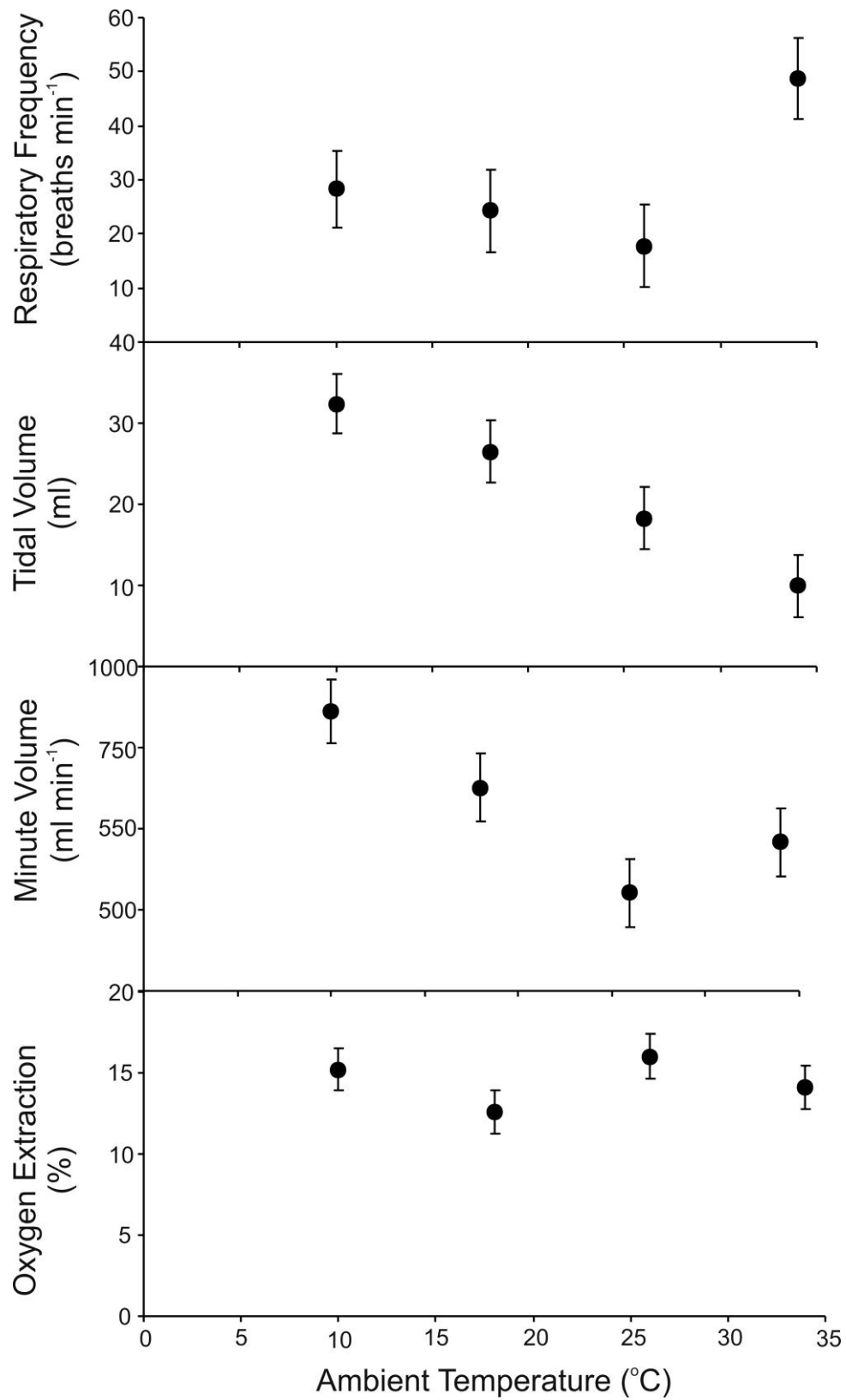


Fig. 2: Respiratory frequency, tidal volume, minute volume and oxygen extraction for chuditch (*Dasyurus geoffroii*) at ambient temperatures from 10.1 to 33.3°C. Values are mean \pm SE (n = 5 for $T_a=10.1$ and 17.9°C, and n = 4 for $T_a= 26.0$ and 33.3°C).

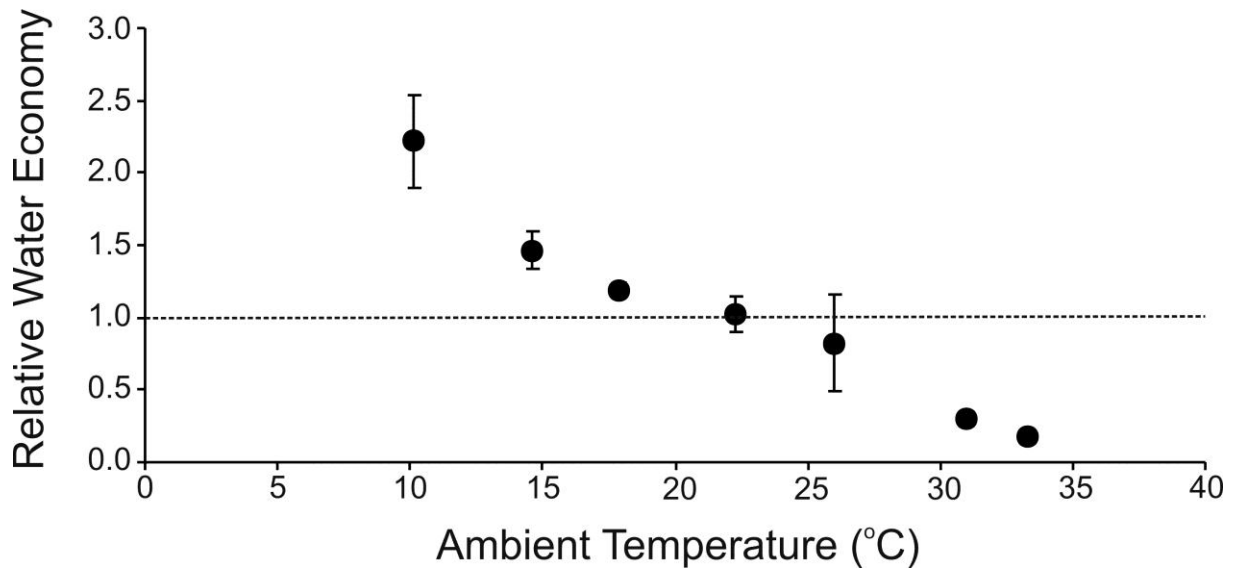


Fig. 3: Relative water economy (metabolic water production/evaporative water loss) as a function of ambient temperature for chuditch (*Dasyurus geoffroii*). The dashed line represents a relative water economy of one, where metabolic water production = evaporative water loss. Values are mean \pm SE ($n = 5$ for all T_a s except for $T_a = 33.3^\circ\text{C}$ where $n = 4$).