Comparative physiology of Australian quolls (*Dasyurus*; Marsupialia)

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Abstract

Quolls (*Dasyurus*) are medium-sized carnivorous dasyurid marsupials. Tiger (3840 g) and eastern quolls (780 g) are mesic zone species, northern quolls (516 g) are tropical zone, and chuditch (1385 g) were once widespread through the Australian arid zone. We found that standard physiological variables of these quolls are consistent with allometric expectations for marsupials. Nevertheless, inter-specific patterns amongst the quolls are consistent with their different environments. The lower T_b of northern quolls (34 ℃) may provide scope for adaptive hyperthermia in the tropics, and it uses torpor for energy/water conservation, whereas the larger mesic species (eastern and tiger quolls) do not appear to. Thermolability varied from little in eastern (0.035 ℃ ℃$^{-1}$) and tiger quolls (0.051 ℃ ℃$^{-1}$) to substantial in northern quolls (0.100 ℃ ℃$^{-1}$) and chuditch (0.146 ℃ ℃$^{-1}$), reflecting body mass and environment. Basal metabolic rate was higher for eastern quolls (0.662 ± 0.033 ml O_2 g^{-1} h^{-1}), presumably reflecting their naturally cool environment. Respiratory ventilation closely matched metabolic demand, except at high ambient temperatures where quolls hyperventilated to facilitate evaporative heat loss; tiger and eastern quolls also salivated. A higher evaporative water loss for eastern quolls (1.43 ± 0.212 mg H_2O g^{-1} h^{-1}) presumably reflects their more mesic distribution. The point of relative water economy was low for tiger (-1.3 ℃), eastern (-12.5 ℃) and northern (+3.3) quolls, and highest for the chuditch (+22.6 ℃). We suggest that these differences in water economy reflect lower expired air temperatures hence lower respiratory evaporative water loss for the arid-zone chuditch relative to tropical and mesic quolls.

Keywords Allometry · Body temperature · Evaporative water loss · Metabolic rate ·

Relative water economy · Thermal conductance · Ventilation

Abbreviations

BMR	Basal metabolic rate
C_{dry}	Dry (non-evaporative) thermal conductance
C_{wet}	Wet (evaporative and non-evaporative) thermal conductance
EHL	Evaporative heat loss
EO_2	Oxygen extraction efficiency
EQ	Evaporative quotient
EWL	Evaporative water loss
f_R	Respiratory frequency
MHP	Metabolic heat production
MWP	Metabolic water production
MR	Metabolic rate
PRWE	Point of relative water economy
RER	Respiratory exchange ratio
RH	Relative humidity
RWE	Relative water economy
SNK	Student-Newman-Keuls post hoc multiple comparison test
T_a	Ambient temperature
T_b	Body temperature
V_{CO_2}	Carbon dioxide production rate
V_I	Respiratory minute volume
V_{O_2}	Oxygen consumption rate

V_T Respiratory tidal volume

Introduction

Quolls are medium-sized carnivorous dasyurid marsupials (genus *Dasyurus*). They are solitary, generally nocturnal, den in hollow logs, tree hollows or rock crevices during the day, and feed on a range of vertebrate and invertebrate prey, including carrion (Blackhall 1980; Serena and Soderquist 1989; Soderquist and Serena 1994; Edgar and Belcher 1995; Jones and Rose 2001; Jones *et al.* 2001; Oakwood 2002; Belcher *et al.* 2007). Quolls are sexually dimorphic, with males being larger than females, presumably due to selection for large body mass to maintain a large home range, competition for access to females and reduction of dietary competition between the sexes (Jones and Barmuta 1998; Taggart et al. 2003; Glen et al. 2009). Quolls are of particular interest as they are amongst the largest extant marsupial carnivores (only the Tasmanian devil *Sarcophilus harrissi* is larger), and the largest remaining on mainland Australia.

There are four extant species of Australian quoll, with another two species (*Dasyurus albopunctatus* and *D. spartacus*) in New Guinea (Nowak and Dickman 2005). The comparative physiology of these species is of particular significance, because the considerable geographical and climatic differences between their habitats may be reflected by metabolic and hygric adaptations. The tiger or spotted-tail quoll (*Dasyurus maculatus*) is the largest species (mean female body mass 1.8 kg, males 3.5 kg); it is found along Australia's east coast from Tasmania to southern Queensland, in areas receiving > 600mm annual rainfall. An additional isolated population exists in northern Queensland (Edgar and Belcher 1995; Jones *et al.* 2001; Menkhorst and Knight 2004). The range of the eastern quoll (*Dasyurus viverrinus*; females 750g,

males 1.1 kg) historically included south-eastern mainland Australia (Victoria, eastern New South Wales, and south-eastern South Australia ; Rounsevell *et al.* 1991; Godsell 2002; Jones and Rose 2001; Menkhorst and Knight 2004). The northern quoll (*Dasyurus hallucatus*) is the smallest Australian quoll (460g females to 760g male (Oakwood 2002). Northern quolls occur in six disjunct populations in northern Australia, from the Kimberly in Western Australia to the Carnarvon Range in Queensland, although their historical distribution was once almost continuous across the northern third of the Australian continent (Braithwaite and Griffiths 1994; Menkhorst and Knight 2004). The chuditch or western quoll (*Dasyurus geoffroii*; females 0.9 kg, males 1.3 kg) is currently restricted to the mesic sclerophyll and mallee forests of south-west Western Australia, although historically it had one of the widest distributions of all marsupials, throughout much of arid and semi-arid Australia (Serena and Soderquist 2008; Morton et al. 1989; Menkhorst and Knight 2004).

There are dietary, geographic and climatic effects on various standard physiologicavariables, for mammals in general (McNab 1966, 1980a, 1983, 1984, 1986a, 1988, 2002, 2008; Elgar and Harvey 1987; Harvey et al. 1991; Lovegrove 2000, 2003) and marsupials in particular (McNab 1986b, 2005; Withers *et al.* 2006). Marsupials from arid environments, which are characterised by high ambient temperatures (T_a) and high rainfall variability, have a lower body temperature (T_b), basal metabolic rate (BMR) and evaporative water loss (EWL) than species from more mesic environments. However, unlike for placental mammals where there are strong dietary effects on BMR (McNab 1980a, 1983, 1984, 1986a, 2008), general dietary effects for marsupials are restricted to thermal conductance, with folivorous species having lower thermal conductance than other marsupials presumably because

of their exposed arboreal environment (Withers *et al.* 2006). Otherwise, there is little evidence of dietary adaptations amongst species. Carnivorous placental mammals have high BMRs compared to other species, but the limited existing data for marsupial carnivores suggests that these species conform to the low-energy marsupial physiology pattern (MacMillen and Nelson 1969; Nicol and Maskrey 1980; Hinds *et al.* 1993; Schmidt *et al.* 2009). However, the nectarivorous honey possum does have a high BMR and T_b, attributable to its high-energy diet (Withers *et al.* 1990; Cooper and Cruz-Neto 2009), suggesting that marsupials with high-energy niches can achieve placental-level rates of energy expenditure.

Quolls are an interesting group to examine for genus-level environmental correlates of physiological variables, due to their wide geographic/climatic distribution. In addition, a lack of physiological data for marsupial carnivores may have limited the analysis of overall dietary effects on physiological variables for marsupials. Standard physiological data for quolls are scarce; a complete standard physiological dataset including hygric and ventilatory parameters is only available for the chuditch (Schmidt *et al.* 2009). Here we present detailed physiological data for tiger, eastern and northern quolls, and combine these with data that we have previously published for the chuditch (Schmidt *et al.* 2009) to interpret the physiology of quolls in an allometric, phylogenetic and ecological context. We expect to find differences in the energetics and hygric physiology of the quolls, related to their different habitats, and test the hypothesis that a carnivorous diet is associated with an elevated basal metabolic rate and T_b for this specialised marsupial group.

Methods

Adult, non-reproductive quolls were studied at the Malcolm Douglas Wildlife Park, Broome, Western Australia (17° 57'S, 122° 14'E); four tiger quolls (three males, one female), seven eastern quolls (four males, three females) and three northern quolls (two females, one male) were measured. Two additional male tiger quolls were measured at Perth Zoo, Western Australia (31° 58'S 115° 51'E). One additional male northern quoll was captured in the wild near Chichester (Western Australia; 22° 10'S, 117° 48'E) and housed at the University of Western Australia, Perth, then the Broome Wildlife Park. Some measurements were made for this individual in Perth and the rest in Broome. Quolls were housed in large outdoor enclosures and exposed to natural conditions of weather and photoperiod, except for one tiger quoll at Perth Zoo that was housed indoors in the nocturnal house on reverse photoperiod. Comparative data for the chuditch is from Schmidt et al. (2009).

Quolls were fasted for 24 hours before the commencement of experiments. They were measured during their inactive phase (during the day for all except the tiger quoll on reverse photoperiod that was measured at night) for a period of at least 8 hours under dim light, until all physiological variables became stable and minimal (except at a T_a of 35°C where experiments were no longer than 6 hours to avoid excessive heat exposure). Metabolic rate (MR; oxygen consumption VO_2 and carbon dioxide production, VCO_2), evaporative water loss (EWL) and ventilatory variables were measured using standard flow-through respirometry and whole-body plethysmography at ambient temperatures from 8.7°C to 35.7 °C. It was not possible to measure all quolls at all T_a, so for respirometry N = 6 at T_a = 20 and 31°C and N = 5 at all other T_a for tiger quolls, N = 5 at 20°C, 6 at 31°C and 7 at all other T_a for eastern quolls, and for northern quolls N = 4 at all T_a. For plethysmography N = 3 at

T_a = 9, 15 and 35 °C and 4 at all other T_a for tiger quolls, N is the same as for respirometry for eastern quolls, and for northern quolls N = 3 at T_a = 9 and N = 4 at all other T_a. Body temperature (T_b) was measured at the conclusion of each experiment using a plastic-tipped thermocouple (connected to a RadioSpares 611.234 thermocouple meter) inserted into the cloaca, and/or an Omron MC-510 infrared thermometer via the ear canal (the two methods recorded comparable T_b when used simultaneously)

The respirometry system consisted of a mass flow controller (Aalborg GFC171 or Omega FMAA2412) that regulated dried ambient air (using Drierite) at flow rates of 1 to 8 L min^{-1} (depending on animal mass and T_a), achieved using a diaphragm pump. Air passed through a 2000 cm^3 (northern), 8000 cm^3 (eastern) or 25000-45000 cm^3 (tiger) Perspex metabolic chamber located in a temperature control cabinet, then a temperature and relative humidity (RH) probe (Vaisala HMP 45A). A sub-sample (approx 100 mL min^{-1}) of excurrent air was dried (using Drierite) to measure O_2 (Sable Systems Foxbox or Servomex OA184 or 572) and CO_2 levels (Sable Systems CA-2A or Qubit S153). Quolls were observed during experiments without disturbance with a Swann Max-IP-cam camera under infrared light. Flowmeters were calibrated using a bubble flowmeter (corrected to standard temperature and pressure dry, STPD). O_2 analysers were calibrated to room air (20.95% O_2) and for 0% O_2 using nitrogen (Servomex analysers), or electronic zero function (Foxbox). CO_2 analysers were calibrated using nitrogen (0% CO_2) and a precision gas mix (0.53% CO_2; BOC gases). 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 voltage outputs for O_2, CO_2, RH and T_a were recorded

every 10 to 20 sec with a custom-written Visual Basic (VB ver. 6) data acquisition program (P. Withers).

Calculation of VO_2, VCO_2 and EWL was after Withers (2001) using a custom-written VB v6 data analysis program (P. Withers) for the 20 min period during which each value was steady and minimal. Respiratory exchange ratio (RER) and evaporative quotient (EQ) were calculated as VCO_2/VO_2 and EWL/VO_2 respectively. Wet (C_{wet}) thermal conductance (J g^{-1} h^{-1} $°C^{-1}$) was calculated from metabolic heat production (MHP; converted from MR using the oxycalorific coefficient at the measured RER for that experiment; Withers 1992a) as $MHP/(T_b–T_a)$. EWL was converted to evaporative heat loss (EHL) using 2.4 J mg^{-1} H_2O (Withers 1992a), to calculate dry thermal conductance (C_{dry}; J g^{-1} h^{-1} $°C^{-1}$) as $(MHP–EHL)/(T_b-T_a)$. Relative water economy (RWE) was calculated as MWP/EWL, where metabolic water production (MWP; ml g^{-1} h^{-1}) was calculated from VO_2 using the measured RER for that experiment (after Withers 1992a). The point of relative water economy (PRWE) is the T_a where RWE = 1. The CO_2 analyser of the Foxbox was not functional, therefore the VO_2 and EWL were calculated after Koteja (1996) assuming a RER of 0.85 for 20 (of 90) experiments. The mean RER for the other individuals of that species at that T_a was assumed when converting MR to J and calculating MWP for these 20 experiments.

Ventilatory data were measured using the metabolic chamber as a whole-body plethysmograph (Malan 1973; Withers 1977; Larcombe 2002; Cooper and Withers 2004). Pressure changes due to the warming and humidifying of inspired air were detected with a pressure transducer (custom-made with a Motorola MPX2010 sensor). The analog voltage outputs of the pressure transducers were recorded every 15 ms for approximately 30 sec using an ADC 11 data logger and PicoScope software (Pico

Technology). Between two and six sets of ventilatory data were obtained for an individual quoll at each T_a, so a single mean was calculated for each ventilatory variable for each quoll at each T_a. The open-flow plethysmography data were analysed as closed-system signals after Szewczak and Powell (2003) and ventilatory variables (respiratory frequency, f_R; tidal volume, V_T; minute volume, V_I and oxygen extraction, EO_2) were calculated after Malan (1973) and Cooper and Withers (2004), using a custom-written VB v6 data analysis program (P. Withers). V_T and V_I are presented at body temperature and pressure saturated (BTPS). EO_2 was calculated using the VO_2 at the time of ventilatory measurements from V_I corrected to STPD.

All values are presented as mean ± S.E., where N = number of individuals and n = number of measurements. Effects of T_a on physiological variables were examined by linear regression and analysis of variance with Student-Newman-Keuls (SNK) *post hoc* tests. Not all individuals were measured at each T_a, precluding a repeated measures model. Standard (thermoneutral) physiological variables for the quolls, including data for the chuditch (Schmidt et al. 2009), were compared using analysis of variance with SNK *post hoc* tests. Physiological variables were corrected for significant allometric effects (except EO_2 as there is no significant allometric effect), using the marsupial allometric scaling exponents (0.535 for T_b, 0.741 for BMR, 0.575 for C_{wet}, 0.733 for EWL, -0.225 for f_R, 0.881 for V_T and 0.647 for V_I) from Cooper *et al.* (2010). Statistical analyses were accomplished using statisti*XL* (V1.6) and SPSS (v17).

Results

Observations of the quolls during measurements using an infra-red camera indicated that they were initially active when first placed in the chamber, and then rested quietly

for the majority of the experimental period, with some occasional grooming or change in posture. Activity within the metabolic chamber could be easily recognised by characteristic elevation of VO_2, VCO_2 and EWL on the continuous metabolic trace, along with shallow, irregular ventilation. Thus any periods of activity could be eliminated from our analysis. This, combined with long measurement durations (Cooper and Withers 2009), means that we are confident that our physiological data are for calm, resting, inactive quolls.

At lower T_a, all three species rested curled in a ball, while at $T_a \geq 31°C$ quolls rested stretched out. This sprawled posture was most extreme at $T_a = 35°C$. Eastern and especially tiger quolls licked at this high T_a, particularly their limbs and hindquarters.

The mean body mass of tiger quolls over all experiments was 3480 ± 133.8 g (N = 6, n = 32). Eastern quolls had a mean body mass of 780 ± 30.8 g (N = 7, n = 39), while the mean body mass of northern quolls was 516 ± 17.7 g (N = 4, n = 20). There were significant body mass differences between the four quoll species ($F_{3,18} = 38.4$, P < 0.001).

Body temperature

The T_b of tiger quolls (Figure 1) was significantly influenced by T_a ($F_{5,26} = 5.95$, P = 0.001; Figure 1), ranging from 35.6 ± 0.15 °C at $T_a = 9.1°C$ to 37.3 ± 0.29 °C at $T_a = 35.7°C$, which was higher than at all other T_a (SNK P < 0.023). The T_b of eastern quolls (Figure 1) ranged from 36.1 ± 0.24 °C at $T_a = 10°C$ to 37.2 ± 0.18 °C at $T_a = 35°C$, and was independent of T_a ($F_{5,33} = 2.18$, P = 0.080). T_a significantly influenced T_b of northern quolls ($F_{4,14} = 3.31$, P = 0.042), with T_b ranging from 33.3 ± 1.03 °C at $T_a = 25°C$ to 36.5 ± 0.45 °C at $T_a = 35°C$ (Figure 1). One male northern quoll entered torpor at $T_a = 8°C$, with a T_b of 28.4°C. This individual was also found

to be cold and lethargic when removed from its enclosure on cool mornings, but warmed up and was responsive by the time it had been transported to the laboratory.

Standard T_b (at a thermoneutral T_a of 30°C) differed significantly for the four Australian quolls ($F_{3,18} = 5.2$, P = 0.009). T_b was lower (SNK P ≤ 0.013) for northern quolls (34.3 ± 0.55 °C) compared to tiger quolls (36.5 ± 0.21°C), eastern quolls (36.4 ± 0.48 °C) and chuditch (36.3 ± 0.28°C). Standard T_b corrected for allometric scaling (i.e. T_b- 0.535 log mass) for marsupials, also differed between the quolls ($F_{3,18} = 4.1$, P = 0.022). Northern quolls (32.9 ± 0.55 °C) were lower (SNK P ≤ 0.034) than tiger quolls (34.6 ± 0.22°C), eastern quolls (34.9 ± 0.49 °C) and chuditch (34.6 ± 0.25°C).

Metabolic rate

The VO_2 of tiger quolls (Figure 1) was significantly influenced by T_a ($F_{5,26} = 22.5$, P < 0.001), with a slope of -0.023 ± 0.003 ml O_2 g^{-1} h^{-1} °C^{-1} at T_a ≤ 25°C. We interpret the lowest MR, measured at $T_a = 31$°C, as basal metabolic rate (BMR). VCO_2 mirrored VO_2 and so is not presented separately. RER was not influenced by T_a ($F_{5,12} = 2.14$, P = 0.130), with a mean RER over all temperatures of 0.78 ± 0.02 (N = 4, n = 18).

Eastern quolls had a minimal VO_2 of 0.662 ± 0.033 ml O_2 g^{-1} h^{-1} at $T_a = 31$°C, and we consider this BMR. There was an overall T_a effect on VO_2 ($F_{5,33} = 22.3$, P < 0.001; Figure 1), with a slope of -0.049 ± 0.005 ml O_2 g^{-1} h^{-1} °C^{-1} at T_a ≤ 31°C. The pattern of VCO_2 mirrored VO_2 and so is not presented separately, although RER was significantly influenced by T_a ($F_{4,29} = 3.61$, P = 0.017), ranging from 0.72 ± 0.01 at $T_a = 10$°C to 0.86 ± 0.04 at $T_a = 26$°C.

For northern quolls, the significant relationship between T_a and VO_2 ($F_{4,15} = 16.23$, P < 0.001; Figure 1) had a slope of -0.033 ± 0.005 ml O_2 g^{-1} h^{-1} °C^{-1} at T_a ≤ 31°C. We interpret the VO_2 at $T_a = 30$°C of 0.485 ± 0.087 ml O_2 g^{-1} h^{-1} as BMR. The

pattern of VCO_2 mirrored that of VO_2 and so is not presented separately here, and there was no significant T_a effect for RER ($F_{4,15} = 3.0$, $P = 0.053$), with the mean RER for all northern quolls at all T_a being 0.80 ± 0.030 (N = 4, n = 20).

Mass independent BMR (i.e. ml O_2 $g^{-0.74}$ h^{-1}) differed significantly between the four quoll species at thermoneutrality ($F_{3,18} = 0.013$, $P = 0.005$), with eastern quolls higher (3.50 ± 0.224 ml O_2 $g^{-0.74}$ h^{-1}) than tiger quolls, (2.66 ± 0.116 ml O_2 $g^{-0.74}$ h^{-1}; SNK $P = 0.013$), chuditch (2.36 ± 0.424 ml O_2 $g^{-0.74}$ h^{-1}; SNK $P = 0.008$) and northern quolls (2.30 ± 0.202 ml O_2 $g^{-0.74}$ h^{-1}; SNK $P = 0.010$). Mass independent BMR did not differ (SNK $P \geq 0.409$) for chuditch, tiger and northern quolls.

Evaporative water loss

T_a influenced the EWL of tiger quolls ($F_{5,26} = 21.0$, $P < 0.001$; Figure 1) with EWL at $T_a = 36°C$ significantly higher than at all other T_a (SNK $P < 0.001$); there were no differences at any other T_a. Standard EWL ($T_a = 31°C$) was 0.692 ± 0.054 mg H_2O g^{-1} h^{-1}. For eastern quolls, there was a significant T_a effect on EWL ($F_{5,33} = 3.51$, $P = 0.012$; Figure 1)), with standard EWL at $T_a = 31°C$ being 1.76 ± 0.234 mg H_2O g^{-1} h^{-1}. EWL at $T_a = 35°C$ was significantly higher than that at all other T_a but there was no T_a effect for EWL at $T_a \leq 31°C$ (SNK $P \geq 0.771$). EWL of northern quolls was significantly higher at $T_a = 35°C$ than at $T_a = 17°C$ (SNK $P = 0.025$) and $25°C$ (SNK $P = 0.04$). Standard EWL ($T_a = 31°C$) was 0.692 ± 0.054 mg H_2O g^{-1} h^{-1}. There was a significant species effect ($F_{3,18} = 3.18$, $P = 0.049$) on mass independent standard EWL (i.e. mg H_2O $g^{-0.733}$ h^{-1}), which ranged from 4.54 ± 0.891 mg H_2O $g^{-0.733}$ h^{-1} for northern quolls to 8.45 ± 1.25 mg H_2O $g^{-0.733}$ h^{-1} for eastern quolls.

Thermal conductance

C_{wet} and C_{dry} of tiger quolls increased with increasing T_a ($F_{5,26} = 9.15$, $P < 0.001$; $F_{5,26} = 6.29$, $P = 0.001$; Figure 1), gradually at $T_a \leq 31°C$ and more dramatically at $T_a =$

36°C. Both C_{wet} and C_{dry} were significantly higher at $T_a = 35°C$ than that at all other T_a (SNK $P \le 0.001$). Standard C_{wet} (at $T_a = 31°C$) was 1.17 ± 0.099 J g^{-1} h^{-1} $°C^{-1}$ and C_{dry} was 0.88 ± 0.087 J g^{-1} h^{-1} $°C^{-1}$.

T_a had a significant effect on C_{wet} and C_{dry} for eastern quolls ($F_{5,33} = 17.9$, P <0.001; $F_{5,33} = 9.45$, P <0.001), with a gradual increase at $T_a \le 31°C$ and more dramatic increase at $T_a = 35°C$ (Figure 1). C_{wet} was significantly higher at $T_a = 35°C$ than at all lower T_a (SNK $P < 0.001$). Standard C_{wet} and C_{dry} (at $T_a = 31°C$) were 2.27 ± 0.218 J g^{-1} h^{-1} $°C^{-1}$ and 1.62 ± 0.120 J g^{-1} h^{-1} $°C^{-1}$ respectively.

The pattern of C_{wet} and C_{dry} for northern quolls was similar to that for tiger and eastern quolls, with a significant T_a effect ($F_{4,15} = 7.82$, P = 0.001; $F_{4,14} = 4.96$, P = 0.011; Figure 1). Both C_{wet} and C_{dry} were significantly higher at 35°C than at all other T_a (SNK $P \le 0.020$). Standard C_{wet} (at $T_a = 31°C$) was 2.21 ± 0.425 J g^{-1} h^{-1} $°C^{-1}$ and C_{dry} 1.71 ± 0.279 J g^{-1} h^{-1} $°C^{-1}$. Standard mass-independent C_{wet} (i.e. J $g^{-0.575}$ h^{-1} $°C^{-1}$) did not differ for the four quoll species ($F_{3,18} = 1.50$, P = 0.248).

Ventilation

All ventilatory variables for tiger quolls were significantly influenced by T_a ($F_{5,15} \ge 6.08$, $P \le 0.003$; Figure 2). f_R remained constant at $T_a \le 31°C$ (SNK $P \ge 0.867$) but increased dramatically from 21.7 ± 2.63 breaths min^{-1} above thermoneutrality ($T_a = 36°C$; SNK $P < 0.001$). V_T decreased linearly from $T_a = 9°C$ to $T_a = 36°C$. Standard V_T (at $T_a = 31°C$) was 20.3 ± 1.87 ml. V_I decreased with increasing T_a to 420 ± 23.8 ml min^{-1} at $T_a = 31°C$, before increasing dramatically at $T_a = 36°C$ (SNK $P < 0.001$). EO_2 was 24.7 ± 2.0 % at $T_a = 31°C$, and there was no T_a effect on EO_2 at $T_a \le 31°C$ (SNK $P \ge 0.533$), although EO_2 at $T_a = 36°C$ was significantly lower than at all other T_a (SNK $P < 0.001$).

For eastern quolls, T_a influenced V_T ($F_{5,32} = 4.10$, $P = 0.005$) and V_I ($F_{5,32} = 6.92$, $P < 0.001$), but not f_R ($F_{5,32} = 2.37$, $P = 0.061$) or EO_2 ($F_{5,32} = 1.34$, $P = 0.274$; Figure 2). Standard f_R was 25.0 ± 2.77 breaths min^{-1} and EO_2 18.0 ± 2.09 % at $T_a = 31°C$. V_T decreased from $T_a = 10°C$ to $35°C$; at $T_a = 31°C$ it was 20.3 ± 1.87 ml. V_I was significantly higher at $T_a = 10°C$ than at all other T_a (SNK $P \leq 0.015$); it was 320 ± 47.8 ml min^{-1} at $T_a = 31°C$.

No significant T_a effects were found for ventilatory variables of northern quolls ($F_{4,14} \leq 0.317$, $P \geq 0.862$; Figure 2). Standard f_R was 27.8 breaths min^{-1}, V_T was 8.3 ± 1.00 ml, V_I was 228 ± 27.8 ml min^{-1} and EO_2 10.7 ± 1.47.

The four Australian quoll species did not differ at thermoneutrality with respect to mass-independent f_R (i.e. breaths min^{-1} $g^{-0.225}$; $F_{3,14} = 1.12$, $P = 0.378$) or V_I (ml min $g^{-0.647}$; $F_{3,14} = 2.50$, $P = 0.102$). There were significant species differences for V_T (ml $g^{-0.881}$; $F_{3,14} = 3.70$, $P = 0.038$) and EO_2 (%, $F_{3,14} = 4.94$, $P = 0.015$), with eastern quolls having a high V_T (0.037 ml $g^{-0.881}$) and tiger quolls a high EO_2 (24.7 %).

Relative Water Economy

For tiger quolls, there was a significant T_a effect on EQ ($F_{5,26} = 56.3$, $P < 0.001$). EQ at $T_a = 36°C$ was higher than all other T_a (SNK $P < 0.001$), and higher at $T_a = 31$ (2.1 ± 0.13 mg mlO_2^{-1}) and $26°C$ than at $T_a \leq 20°C$ (SNK $P \leq 0.041$). There was a significant linear relationship between RWE and T_a (Figure 3); RWE = 0.975 (± 0.044) - 0.023 (± 0.002) T_a ($R^2 = 0.84$, $F_{1,30} = 160.6$, $P < 0.001$) which extrapolated to a PRWE of -$1.3°C$.

EQ of eastern quolls was also influenced by T_a ($F_{5,33} = 16.8$, $P < 0.001$), being higher at $T_a = 35°C$ than at all other T_a, and higher at $T_a = 31°C$ (2.3 ± 0.27 mg mlO_2^{-1}) than at $T_a \leq 20°C$ (SNK $P \leq 0.021$). RWE was significantly related to T_a ($R^2 = 0.62$,

$F_{1,27} = 60.5$, P < 0.001; Figure 3) as RWE = 0.79 (±0.054) − 0.017 (± 0.002) T_a. This relationship extrapolated to a PRWE of -12.5°C.

There was also a significant effect of T_a on EQ for northern quolls; EQ was higher at $T_a = 35$°C than all lower T_a (SNK P ≤ 0.027); EQ was 1.9 ± 0.31 at 31°C. There was a significant negative linear relationship between RWE and T_a ($R^2 = 0.71$, $F_{1,18} = 44.6$, P <0.001; Figure 3); RWE = 1.083 (±0.091) - 0.025 (±0.004) T_a. This extrapolated to a PRWE of 3.3°C.

Discussion

Our study of captive Australian quolls, housed under similar environmental conditions, enables us to evaluate inter-specific differences that may be attributed to genetic differences between the species, and therefore reflects heritable physiological adaptations, rather than individual acclimation effects. This enables us to interpret our findings in an evolutionary and adaptational context.

Body mass

The almost 8-fold variation in inter-specific mass of quolls accounts for some of the variation in their absolute and mass-specific physiological variables, reflecting the well-documented effect of body mass on marsupial physiology (e.g. McNab 1986a, 2005; Withers *et al.* 2000; 2006; Cooper *et al.* 2010). For comparative analyses, it was therefore necessary to allometrically-correct physiological variables (except EO_2). Body mass of the quolls was greater than predicted by autoregression (Cheverud and Dow 1985; Rohlf 2001) from their phylogenetic position amongst marsupials (phylogeny from Bininda-Emonds et al. 2007). The northern quoll was 165% of the predicted 312 g, the eastern quoll 171% of 455 g and the tiger quoll 2361% of predicted 147 g; the chuditch was 400% of predicted 337g (Schmidt et al.

2009). This is presumably a consequence of their carnivorous diet, with the most carnivorous of the Australian quolls, the tiger quoll, having the greatest increase in body mass compared to predicted..

Body Temperature

The thermoneutral body temperatures of the three quoll species that we measured in this study were generally consistent with those measured previously (MacMillen and Nelson 1969; Hinds *et al.* 1993). However, T_b of the northern quoll was significantly lower than that of MacMillen and Nelson (1969; one-sample t-test P = 0.006), and our value for the eastern quoll was differed from (P = 0.035), but was encompassed by, values measured by Hinds *et al.* (1993; lower) and MacMillen and Nelson (1969; higher). . T_bs of quolls ranged from 0.9°C lower (northern quoll) to 1.1°C higher (eastern quoll) than allometrically-predicted T_b (Cooper *et al.* 2010), although all four conformed to allometric predictions (fell inside the 95% prediction limits; see Cooper and Withers 2006). T_bs of chuditch, eastern and tiger quolls were consistent with phylogenetic prediction (≤ +0.72°C of predicted by autoregression, using the marsupial phylogeny of Bininda-Emonds et al. 2007), but T_b of the northern quoll was 2°C lower than predicted (P = 0.036). There was no significant allometric effect on T_b for marsuipals after phylogenetic correction to compare the quolls with (Cooper *et al.* 2010).

The low standard T_b of the northern quoll compared to the other three Australian quoll species may provide scope for greater adaptive hyperthermia. This could be advantageous in a tropical habitat, where a combination of high T_a and ambient RH reduces the potential for conductive, convective and evaporative heat loss. Metabolic and ventilatory variables indicated that the northern quoll was not

particularly heat stressed and did not lick at $T_a = 35°C$, unlike the larger quolls, particularly the tiger quoll.

The four quolls were thermolabile; $\Delta T_b/\Delta T_a$ ranged from $0.04°C\ °C^{-1}$ (eastern) and 0.05 (tiger) quolls, to 0.10 (northern quolls) and $0.15\ °C\ °C^{-1}$ (chuditch; Schmidt et al. 2009). Quolls would be expected to be less thermolabile than small dasyurids (mean of $0.076°C\ °C^{-1}$; Withers and Cooper 2009a) due to their larger body mass and thermal inertia. However, thermolability is presumably advantageous for northern quolls and chuditch in tropical or arid environments, with an increased T_b at high T_a reducing heat gain and the need for evaporative cooling, and decreased T_b at low T_a reducing the energetic costs of thermoregulation (Withers and Cooper 2009b).

All four quolls maintained a substantial $T_b - T_a$ differential at low T_a. The northern quoll did, however, show evidence of torpor ($T_b < 30°C$) and early morning lethargy. This is the first record of torpor we are aware of for northern quolls, but the strong phylogenetic pattern of torpor use amongst marsupials (Cooper and Geiser 2008) and widespread use of daily torpor amongst dasyurids (Geiser 1994, 2003, 2004), including the chuditch (Arnold 1976), means that torpor in the small northern quoll is not unexpected.

Metabolic Physiology

Our estimates of BMR for the northern and tiger quoll conformed to previous estimates for these species (MacMillen and Nelson 1969; Hinds *et al.* 1993). However, previous measures of BMR for the eastern quoll (MacMillen and Nelson 1969; Hinds *et al.* 1993 were significantly ($P \leq 0.002$) lower than our estimate. It is unclear why our measure of BMR for eastern quolls was higher, especially considering that the other quolls conformed to previous measures, and our long measurement durations are more likely to yield truly minimal resting rates than the

short 1-2 hour experiments used in the previous studies (Cooper and Withers 2009). This difference may simply reflect individual variation and the small sample size of previous studies.

Eastern quolls had a higher mass-independent BMR compared to the other three species, presumably reflecting their naturally cool climate distribution. Withers et al. (2006) found significant temperature and aridity effects on marsupial BMR, with mesic and cooler environment species having a higher BMR than those from arid and warmer habitats. The comparatively high BMR of eastern quolls may be an energetic necessity to maintain homeothermy in cold conditions. This species was the least thermolabile quoll, and T_b telemetry of wild, free-living eastern quolls during winter in sub-alpine Tasmania suggested that they are strict homeotherms (Jones et al. 1997; but see Reardon 1999). There are fundamental physiological and ecological advantages to homeothermy (Withers and Cooper 2008), but maintaining the necessary metabolic machinery in a cold climate, especially for a relatively small species, imposes an energetic cost that may be expressed as an elevated BMR.

Amongst placental mammals, carnivores have high a BMR (Hayssen and Lacey 1985; McNab 1983, 1986a, 2008; Elgar and Harvey 1987; Muñoz-Garcia and Williams 2005; Careau et al. 2007) presumably due to their high-energy, easily digestible meat diet, and the need to be aerobically active and maintain large home ranges to obtain vertebrate prey. However, the BMR of quolls ranged from 94% (northern quoll) to 140 % (eastern quoll) of that predicted from the marsupial allometric relationship of Cooper et al. (2010), calculated using the minimal variance unbiased estimator (Hayes and Shonkwiler 2006, 2007), and fell inside the 95% prediction limits for the allometric relationship for marsupials, both before and after accounting for phylogenetic history (autoregression as for T_b). Therefore, unlike

placental carnivores, there is no evidence that marsupial carnivores have an elevated BMR. This is consistent with our previous data for the chuditch (Schmidt *et al.* 2009), but since chuditch have a historically arid-habitat distribution, a counteracting reduction in BMR due to habitat aridity for this species could not be ruled out. The largest extant marsupial carnivore, the Tasmanian Devil (*Sarcophilus harrissi*), also has a typical marsupial BMR (87 % of predicted; MacMillen and Nelson 1969; Nicol and Maskrey 1980), so it is now clear that carnivorous marsupials do not attain high rates of energy expenditure, and certainly don't approximate the high BMRs observed for placental carnivores. It seems that the only dietary niche associated with a high BMR for marsupials is nectarivory (honey possum *Tarsipes rostratus*; Withers *et al.* 1990; Withers *et al.* 2006; Cooper and Cruz-Neto 2009).

All quoll species had a typical endothermic response to variation in T_a, with proportional thermoregulation to maintain a T_b-T_a differential at T_a below thermoneutrality. According to the Scholander-Irving model of endothermy, the slope of the line relating T_a and MR below thermoneutrality is a measure of the C_{wet} of an endotherm, and this line should extrapolate to $T_a = T_b$ at MR = 0 (McNab 1980b). However, the slope of the MR vs T_a line substantially underestimated C_{wet} compared to C_{wet} calculated as MR/(T_b-T_a) and the extrapolated line overestimated T_b for all quolls (by 3.8°C for the chuditch to 12.9°C for the northern quoll). Thus, quolls did not conform closely to the Scholander-Irving model of heat balance.

Our measure of standard C_{wet} for the northern and tiger quolls conformed closely to previous estimates for these species (MacMillen and Nelson 1969; Hinds *et al.* 1993). The two previous estimates of C_{wet} for eastern quolls (MacMillen and Nelson 1969;Hinds *et al.* 1993) were significantly lower ($P \leq 0.010$) than our value, reflecting our higher BMR for this species.

There were no significant differences in mass-independent C_{wet} between the four quolls, and all quolls conformed to the marsupial allometric relationship for C_{wet} both before and after accounting for phylogenetic history. C_{wet} ranged from 94 % (chuditch) to 164 % (eastern quoll) of predicted for a marsupial (analyses as for BMR).

Ventilatory Physiology

There are significant allometric effects for all ventilatory variables for marsupials except EO_2 (Cooper et al. 2010). All standard ventilatory variables for the quolls conformed to these allometric relationships, falling inside the 95% prediction limits for the allometric regressions, and the EO_2 of the quolls fell within the range of EO_2 previously measured for marsupials (9.4% to 28%, Cooper et al. 2010). This conformity is expected, considering that ventilatory variables closely match metabolic demand, and the BMR of all quolls conformed to allometric predictions. The eastern quoll's high V_T compared to the other quolls is the mechanism by which it meets the oxygen demand of a comparatively high (for quolls) BMR.

An increase in metabolic rate associated with thermoregulation at low T_a can be accommodated by increasing V_I or EO_2. Typically, marsupials increase V_I rather than EO_2 to meet this increased O_2 demand (Cooper and Withers 2004), and the quolls were no exception. EO_2 remained constant at $T_a \leq$ thermoneutrality for all three quolls examined here, and for the chuditch (Schmidt et al. 2009). The only significant change in EO_2 was a dramatic reduction to only 6.2 ± 0.85 % at high T_a (36°C) for tiger quolls, associated with panting to enhance evaporative heat loss.

Increased V_I at low T_a can be achieved via either an increase in f_R or V_T. The proportion by which these ventilatory variables contribute to the accommodation of an increased metabolic rate for marsupials depends on body mass, with large species

increasing V_T rather than f_R, and small species increasing f_R rather than V_T (Larcombe 2002; Cooper and Withers 2004). The large tiger quoll, and the eastern quoll, increased f_R rather than V_T, with a $\Delta V_T/\Delta f_R$ ratio of 2.00 and 2.3 respectively. The smaller northern quoll, however, increased f_R more than V_T ($\Delta V_T/\Delta f_R$ ratio = 0.50), while chuditch showed an intermediate response with a $\Delta V_T/\Delta f_R$ ratio = 1.11 (Schmidt *et al.* 2009).

Tiger quolls had a pronounced panting response at high T_a, indicating the need to increase evaporative heat loss. Eastern quolls showed a similar but less pronounced hyperventilatory response, as did chuditch (Schmidt et al 2009). There was no evidence of panting by northern quolls. Presumably body mass and habitat influence this differential thermoregulatory heat response of quolls, with large and mesic species having more difficulty in dissipating metabolic heat at high T_a than smaller and arid/tropical species. The low T_b and high thermolability of the northern quoll also provides additional scope for heat dissipation through hyperthermia.

Hygric Physiology

Our standard EWL for the eastern quoll conformed to that measured by Hinds and MacMillen (1986), but there are no previous measures of EWL for northern or tiger quolls. EWL of the four Australian quolls ranged from 51% (chuditch) to 130% (eastern quoll) of allometric predictions, but all species statistically conformed to the allometric EWL relationship for marsupials, both before and after accounting for phylogenetic history (calculations as for BMR). The limited sample size and high variability of the marsupial EWL data set results in wide prediction limits that make it difficult to statistically demonstrate that a single species differs from other marsupials (Cooper and Withers 2006). Therefore even the chuditch, with an EWL almost half of that predicted, statistically conforms to the regression. Methodological differences in

the measurement of EWL also make it difficult to interpret comparative data between studies (Cooper and Withers 2008), and the majority of marsupial EWL data are probably too high due to insufficient measurement duration and/or non-instantaneous measurement (Cooper and Withers 2009). The high standard EWL of the eastern quoll compared to the other three quolls is presumably related to its very mesic habitat (and therefore less selection for water conservation), high BMR and associated high V_T.

All quolls enhanced EHL at high T_a by hyperventilation and, for eastern and particularly tiger quolls, by licking. EHL accounted for 43 ± 4.2 % (eastern quoll) to 53 ± 4.7 % (tiger quoll) of metabolic heat production at $T_a \sim 35°C$. This compares with 42.3 ± 4.92 % for the chuditch (calculated from Schmidt *et al.* 2009). These capacities to evaporatively dissipate metabolic heat are modest compared to many other marsupials e.g. 65% for *Cercartetus nanus* (Bartholomew and Hudson 1962), 105% for *Petauroides volans* (Rübsamen et al. 1984) and 147 % for *Phascolarctos cinereus* (Degabriele and Dawson 1979).

Thermoneutral EQ of the three quolls examined here (range 1.9 mg H_2O ml O_2^{-1} for the northern quoll to 2.3 for the eastern quoll) and chuditch (2.4; Schmidt et al. 2009) was consistent with values for other marsupials (Cooper et al. 2005, 2009; Cooper and Cruz-Neto 2009; Withers and Cooper 2009a,b; Cooper et al. 2010) of 1.9 (sandhill dunnart, *Sminthopsis psammophila*) to 2.8 mg H_2O ml O_2^{-1} (woolly mouse opossum, *Micoureus paraguayanus*). EQ increased with decreasing T_a, reflecting the thermoregulatory increase in MR but relatively constant EWL (tiger, eastern and northern quolls) or decreasing EWL (chuditch). It is interesting that EQs of marsupials are substantially higher than those measured for a range of placental mammals. Thermoneutral EQ of the cactus mouse *Peromyscus eremicus* is 1.2 mg H_2O ml O_2^{-1} (MacMillen 1965), but white laboratory mice and rats have ratios of 0.85

and 0.94, while some desert rodents have EQs as low as 0.5–0.59 (Hudson 1962). Placental/marsupial differences in EQ, and the mechanisms responsible, is an area requiring further investigation.

The point of relative water economy provides a comparative measure of water economy, with arid-adapted species having a higher PRWE than mesic species (MacMillen and Hinds 1983; MacMillen 1990). Previous measures of PRWE for marsupials range from 11.3 ºC for the woolly mouse opossum (Cooper *et al.* 2010) to 22.6 °C for the chuditch (Schmidt *et al.* 2009). All three quoll species measured here had a lower PRWE than has been measured previously for marsupials, including the chuditch. There is a theoretical negative relationship between PRWE and body mass (MacMillen 1990), presumably due to increased MHP (and therefore MWP) at low T_a for smaller species compared to large species, due to their higher thermal conductance. This negative allometric relationship has been demonstrated for granivorous birds (MacMillen 1990) and heteromyid rodents (MacMillen and Hinds 1983), and has been calculated for dasyurid marsupials (Hinds and MacMillen 1986). Standardised data for EWL and PRWE of marsupials (Cooper and Cruz-Neto 2009; Cooper et al. 2009; Schmidt et al. 2009; Withers and Cooper 2009a,b; Cooper *et al.* 2010 and calculated from data of Withers 1992b; Cooper and Withers 2002; Larcombe 2004) indicate a significant, negative allometric relationship for PRWE (R^2 = 0.62, $F_{1,9}$ = 14.7, P = 0.004); PRWE = -11.2 (± 2.93) log mass(g) + 30.0 (± 6.77). The tiger, eastern and northern quolls conform to this allometric relationship, so their low PRWEs can be explained by their relatively large body mass. However, the chuditch's PRWE falls above the 95% allometric prediction limits. This may be related to its historical distribution, which prior to European settlement was one of the broadest distributions of any marsupial, encompassing the majority of semi-arid and

arid inland Australia (Serena and Soderquist 2008). A very favourable water economy may have been an important adaptation allowing the chuditch to occupy a wider range of Australia's arid habitats than most other marsupials. The high PRWE of chuditch is a consequence of its EWL decreasing at T_a below thermoneutrality, whereas EWL remained constant at low T_a for the other three quolls (presumably due to the increase in respiratory EWL counterbalancing the reduced cutaneous evaporation at low T_a). This suggests that the chuditch has better nasal counter-current water exchange to minimise respiratory water loss, presumably reflecting a lower expired air temperature. Partitioning of respiratory and cutaneous EWL will provide valueable insight into the mechanisms for constancy or reduction of EWL at low T_a in quolls, and also other marsupials.

Ecological correlates of quoll physiology

There are significant inter-specific differences among the four Australian quolls that are consistent with expected environmental adaptations. Cool, wet and predictable climates are associated with higher BMR and EWL amongst marsupials (Withers et al. 2006), and the most mesic quoll (eastern) had the highest BMR and EWL. Presumably eastern quolls have high energetic costs associated with the necessity to thermoregulate at low T_a and have experienced little selection for water conservation. We found that the northern quoll uses torpor, as does the chuditch (Arnold 1976), but there was no evidence of torpor for the other quolls.,Therefore, it seems that torpor is most advantageous for small quolls in variable arid and tropical environments where there is variability in the availability of food and water, rather than cold climates. Shallow daily torpor is an important factor contributing to the success of dasyurid marsupials in harsh dry and variable habitats (Geiser 2004; Withers *et al.* 2004). Northern quolls also had the smallest body mass and lowest thermoneutral T_b,

presumably adaptations for maximising heat dissipation and providing scope for hyperthermia under tropical conditions of high T_a and RH. The PRWE of the chuditch indicated a more favourable water balance than for any of the other quolls, and indeed for any marsupial so far measured. This presumably reflects its historically arid habitat.

Despite these inter-specific differences, the standard physiological variables of quolls conformed to those of other marsupials. There was no evidence of an elevated BMR associated with the high-energy carnivorous dietary niche of quolls, reflecting the general lack of a diet effect and an overall conservative marsupial physiology (McNab 2005; Withers *et al.* 2006; Cooper *et al.* 2010).

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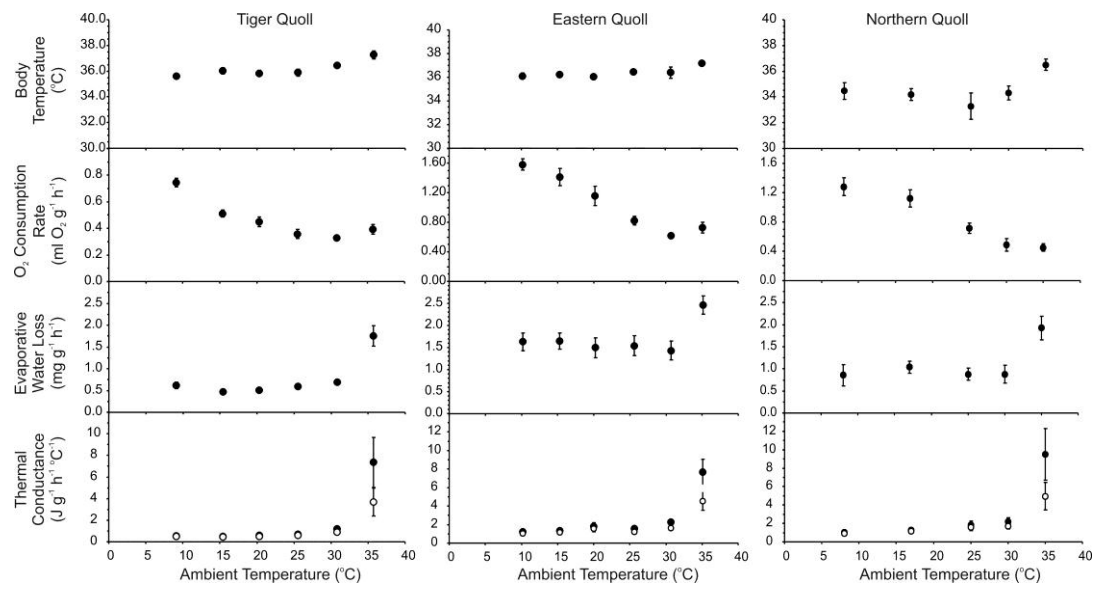
Figure 1. Thermal, metabolic and hygric variables for tiger, eastern and northern quolls, over a range of ambient temperatures. Values are mean ± standard error.
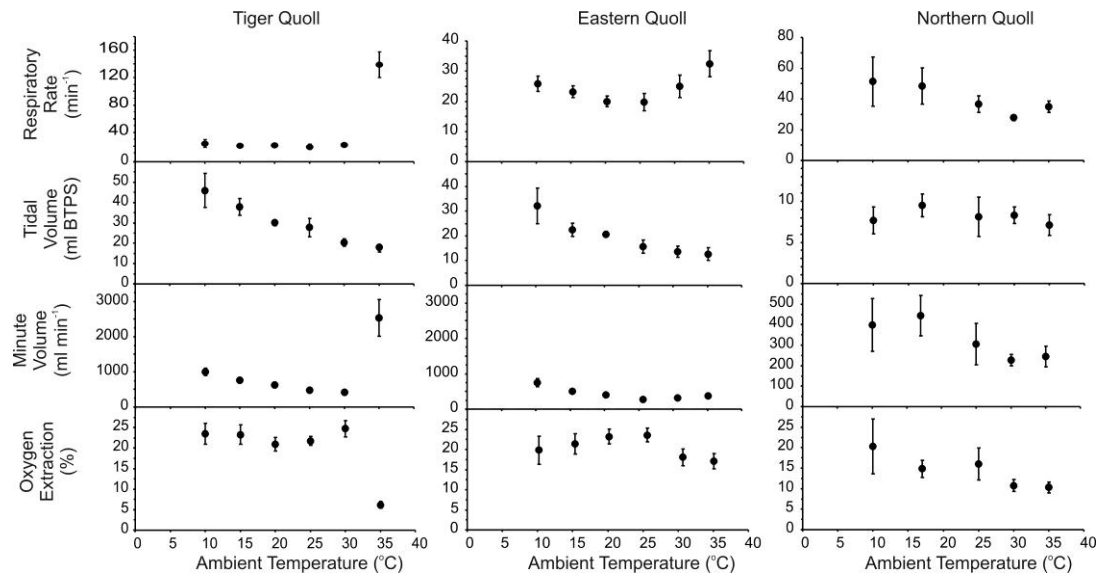
Figure 2. Respiratory variables for tiger, eastern and northern quolls, over a range of ambient temperatures. Values are mean ± standard error.
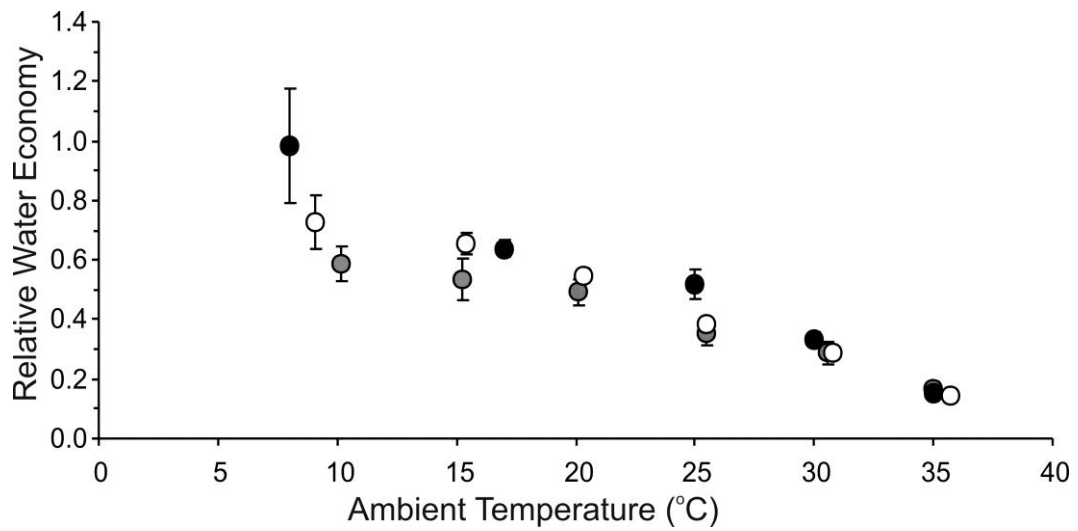
Figure 3. Figure 3. Relative water economy (metabolic water production/evaporative water loss) for tiger (open symbols), eastern (grey symbols) and northern (dark symbols) quolls, over a range of ambient temperatures. Values are mean ± standard error.