

NOTICE: This is the author's version of a work that was accepted for publication in Mammalian Biology. 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 Mammalian Biology, Vol. 78, Issue 6. (2013). doi: 10.1016/j.mambio.2012.11.008

1 Original Investigation

2 Metabolic, hygric and ventilatory physiology of the red-tailed phascogale (*Phascogale*
3 *calura*; Marsupialia; Dasyuridae): adaptations to aridity or arboreality?

4

5 Hannah Pusey^{1,2}, Christine E. Cooper^{*1,3}, Philip C. Withers^{1,3}

6

7 ¹Environment and Agriculture, Curtin University PO Box U1987 Perth, Western Australia,
8 Australia 6845

9 ²Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia 3125

10 ³Animal Biology, University of Western Australia, Crawley, Western Australia, Australia
11 6009

12

13 *Corresponding author. Tel.: +61 8 92667965; fax: +61 8 92662495

14 *E-mail address:* C.Cooper@curtin.edu.au

15

16 Running title: Physiology of the red-tailed phascogale.

17 Word count: 6,748 words.

18 Key words:

19 Marsupial

20 Dasyuridae

21 Energetics

22 Water balance

23 Ventilation

24 ABSTRACT

25 The red-tailed phascogale is a small arboreal dasyurid marsupial that inhabits semi-arid to
26 arid regions of Western Australia's wheat belt. Its body mass (34.7 g) is only ~15% of that
27 predicted based on its phylogenetic position among other dasyuromorphs; we interpret this as
28 an adaptation to its scansorial and semi-arid/arid lifestyle. The standard physiology of this
29 species at a thermoneutral ambient temperature of 30°C conforms to that of other dasyurid
30 marsupials; body temperature ($34.7 \pm 0.37^\circ\text{C}$), basal metabolic rate ($0.83 \pm 0.076 \text{ mL O}_2 \text{ g}^{-1}$
31 h^{-1}), evaporative water loss ($1.68 \pm 0.218 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$) and wet thermal conductance ($3.8 \pm$
32 $0.26 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) all fall within the 95% predication limits for the respective allometric
33 relationships for other dasyurid species. Thermolability confers an energy savings at low T_a
34 and water savings at high T_a . Torpor, observed at low T_a , was found to be more beneficial for
35 energy savings than for water economy. The red-tailed phascogale therefore has a physiology
36 suitable for the challenges of arid environments without any obvious requirement for
37 adaptations to its scansorial lifestyle, other than its considerably lower-than-expected body
38 mass.

39

1

2 List of Abbreviations

3	BMR	Basal metabolic rate
4	C	Thermal conductance
5	C_{dry}	Dry thermal conductance
6	cm	Centimetres
7	C_{wet}	Wet thermal conductance
8	°C	Degrees Celsius
9	EHL	Evaporative heat loss
10	EO_2	Oxygen extraction
11	EQ	Evaporative quotient
12	EWL	Evaporative water loss
13	f_R	Ventilatory frequency
14	g	Grams
15	h	Hours
16	J	Joules
17	Mg	Milligrams
18	min	Minute
19	ml	Millilitres
20	MHP	Metabolic heat production
21	MR	Metabolic rate
22	MVUE	Minimum variance unbiased estimator
23	MWP	Metabolic water production
24	N	Number of individuals
25	n	Number of measurements
26	PRWE	Point of relative water economy
27	RER	Respiratory exchange ratio
28	RH	Relative humidity

29	RWE	Relative water economy
30	SE	Standard error
31	T_a	Ambient temperature
32	T_b	Body temperature
33	VO_2	Rate of oxygen consumption
34	VCO_2	Rate of carbon dioxide production
35	VB	Visual Basic
36	V_I	Minute volume
37	V_T	Tidal volume

38

39 **Introduction**

40 Various environmental and ecological drivers of physiological adaptation have been
41 identified for mammals in general (e.g. McNab, 1986a, 2002a, 2008; Elgar and Harvey,
42 1987; Harvey et al., 1991; Lovegrove, 2000, 2003) and for marsupials specifically (McNab,
43 1986b, 2005; Withers et al., 2006). Marsupials have a relatively conservative physiology,
44 with very strong allometric and phylogenetic effects explaining the majority of variation in
45 physiological variables such as basal metabolic rate (BMR), body temperature (T_b), thermal
46 conductance (C) and evaporative water loss (EWL). Nevertheless, it is still possible to
47 identify environmental factors such as habitat aridity, temperature, and rainfall variability as
48 drivers of physiological adaptation from the residual variation after phylogeny and allometry
49 are accounted for (McNab, 2005; Withers et al., 2006). Marsupials from habitats
50 characterised by aridity, high ambient temperatures (T_a) and/or high rainfall variability tend
51 to have a low T_b , BMR, and EWL. Surprisingly, diet has little impact on most physiological
52 variables for marsupials (but see McNab 1986b), despite its recognised correlation with BMR
53 for mammals in general (See McNab 2002a and references therein). However, marsupial wet
54 thermal conductance (C_{wet}) is influenced by diet, rather than environmental factors, with

55 folivores having a lower C_{wet} than insectivores and vertebrativores. This pattern in C_{wet} may
56 nevertheless be related to habitat, since many folivores are arboreal, and would be more
57 exposed to the elements than terrestrial species (Withers et al., 2006). Examination of the
58 physiology of non-folivorous arboreal marsupials may test this hypothesis.

59 The red-tailed phascogale (*Phascogale calura*) is a small, arboreal,
60 insectivorous/carnivorous dasyurid marsupial currently inhabiting semi-arid, and historically
61 arid, regions of Australia (Bradley et al., 2008; Stannard et al., 2010). It has a semelparous
62 reproductive strategy, with complete male die-off after a short, synchronised breeding season
63 in July (Bradley, 1997). Since European settlement, the red-tailed phascogale's range has
64 contracted from being widespread throughout Central and Southern Australia to a small
65 pocket in Western Australia's wheat belt that receives 300-600 mL annual rainfall
66 (Kitchener, 1981; Menkhorst and Knight, 2001; Bradley et al., 2008). Red-tailed phascogales
67 are nocturnal, predominately arboreal, and feed opportunistically on invertebrates, small birds
68 and mammals (Kitchener, 1981) in their preferred habitat of dense wandoo (*Eucalyptus*
69 *wandoo*) and sheoak (*Allocasuarina huegeliana*) woodlands with poison plant (*Gastrolobium*
70 and *Oxylobium* spp.) understory (Kitchener, 1981). Reportedly, phascogales do not require
71 drinking water, and estimates of field metabolic rate (FMR) and field water turnover rate
72 (FWTR) suggest that their energy and water requirements may be lower than those of other
73 dasyurid marsupials (Green et al., 1989).

74 Here we present the first standard metabolic, thermal, hygric and ventilatory data for
75 the red-tailed phascogale. We relate its standard physiological variables to those of other
76 dasyuromorph marsupials, including the closely related brush-tailed phascogale, and examine
77 effects of ambient temperature to determine its thermoregulatory strategies (including torpor).
78 The unusual combination of its ecological and environmental traits, being an arboreal

79 insectivore/carnivore of the semi-arid/arid zone, provides an ideal opportunity to examine
80 further the relationship between diet, distribution, habitat and physiology for marsupials.

81

82 **Material and methods**

83 Seven phascogales (4 male and 3 female) were caught on private property near
84 Narrogin, approximately 200 km south east of Perth, Western Australia (33°2'S, 117°14'E)
85 during April 2010. Phascogales were captured using Elliot traps with universal bait (rolled
86 oats, peanut butter and sardines), placed at the base of sheoak and wandoo trees, in patches of
87 remnant bush, and along road side verges. Traps were covered with a plastic bag and lined
88 with Dacron fibre to provide insulation. Phascogales were returned to Curtin University,
89 where they were housed indoors in large plastic crates, with a 12:12 light: dark cycle at an
90 ambient temperature (T_a) of approximately 21°C. They were fed daily with kangaroo mince,
91 canned cat food, mealworms, crickets, and occasionally thawed neonate mice. Water was
92 provided *ad lib*. Phascogales were fasted for 24 h prior to experiments and were allowed at
93 least 3 nights with food between successive measurements. They were weighed before and
94 after each measurement to ± 0.1 g.

95 Oxygen consumption (VO_2), carbon dioxide production (VCO_2) and evaporative water
96 loss (EWL) were measured simultaneously during the phascogales' inactive (day) phase
97 using open-flow respirometry at $T_{a,s}$ of 13, 18, 24, 30 and 35 °C for a period of 5-9 h (Cooper
98 and Withers, 2010a). Measurements were conducted in random order; $N = 7$ for all T_a unless
99 stated otherwise. A phascogale was placed in a sealed glass cylindrical chamber (110 ml)
100 inside a temperature controlled room. Compressed air passed through a column of drierite
101 (anhydrous calcium sulphate, W. H. Hammond, Xenia, OH), then through a GFC17
102 (Aalborg, Orangeburg, NY) or 32708-26 (Cole-Parmer, Vernon Hills, IL) mass flow

103 controller that maintained air flow rates between 100 and 1000 mL min⁻¹ depending of T_a.
104 These relatively high flow rates optimised washout rate, reducing the response time of the
105 system and minimising the potential of overestimating physiological values due to activity.
106 Excurrent air passed through a HMP 45A temperature and relative humidity (RH) probe
107 (Vaisala, Helsinki, Finland). A subsample then passed through another column of drierite
108 before the O₂ and CO₂ content were determined by a PA-10 paramagnetic oxygen analyser
109 and CA-2A or CA-10A carbon dioxide analyser (Sable Systems, Las Vegas, NV). Analysers
110 were interfaced to a PC with a UI2 A/D converter (Sable Systems). O₂, CO₂, RH and T_a were
111 recorded every 20 seconds for the duration of the experiment, using custom written Visual
112 Basic (v6) software. We measured T_b immediately after the phascogale was removed from
113 the chamber at the end of each experiment, using a HH25TC thermocouple meter (Omega,
114 Stamford, CT) with a plastic-tipped thermocouple inserted approx. 1.5 cm into the cloaca.
115 Background values for O₂, CO₂, and RH were recorded for at least 30 minutes before and
116 after each experiment. Torpor was defined as T_b < 30°C and/or a reduction in MR to < 75%
117 of the normothermic MR at that T_a. If phascogales became torpid during experiments (as
118 indicated by a low MR), then they were removed from the chamber (once MR and EWL were
119 constant and minimal) and T_b was measured immediately. Although they had the capacity to
120 rewarm spontaneously (phascogales defended T_b > T_a, and some individuals aroused from
121 torpor before being removed from the chamber), they were then warmed and returned to the
122 chamber to continue the experiment to obtain normothermic data; most subsequently
123 remained normothermic for the rest of the experiment.

124 The oxygen analyser was calibrated using dried atmospheric air (20.95% O₂) and the
125 analyser's electronic zero function, and the carbon dioxide analysers with nitrogen (0% CO₂)
126 and a certified gas mixture (0.53% CO₂, BOC, Perth, Western Australia). The factory
127 calibration of the humidity probe was confirmed using dried atmospheric air (<1% RH, using

128 drierite) and by breathing on the probe (100% RH). Flow meters were calibrated using a
129 Gilian Gilibrator 2 (Sensidyne, Clearwater, FL) traceable to a national standard. Calculations
130 of VO_2 , VCO_2 and EWL were after Withers (2001) for the period that EWL and MR were
131 minimal and stable (at least 20 mins). Wet (C_{wet} ; $J g^{-1} h^{-1} °C^{-1}$) and dry thermal conductance
132 (C_{dry} ; $J g^{-1} h^{-1} °C^{-1}$) were calculated as $MR/(T_b-T_a)$ and $(MHP- EHL)/(T_b- T_a)$ respectively,
133 where metabolic rate (MR) was converted to metabolic heat production (MHP; J) using the
134 measured respiratory exchange ratio ($RER= VCO_2/VO_2$) during that experiment, after Withers
135 (1992). EWL was converted to evaporative heat loss (EHL) assuming $2.4 J mg^{-1} H_2O$
136 (Withers, 1992). Evaporative quotient (EQ) was calculated as EWL/VO_2 , and relative water
137 economy (RWE) was calculated as MWP/EWL , where metabolic water production (MWP;
138 $mL g^{-1} h^{-1}$) was calculated from MR using the measured RER for that experiment after
139 Withers (1992). The point of relative water economy (PRWE; the T_a at which $RWE = 1$) was
140 determined from the relationship between RWE and T_a by least-squares regression.

141 Ventilatory frequency (f_R) and tidal volume (V_T) were measured for each phascogale
142 at each T_a using the metabolic chamber as a whole body plethysmograph (Malan, 1973).
143 Ventilatory measurements were made near the end of each experimental period before
144 measurement of T_b and when a low and constant VO_2 indicated the phascogale was resting.
145 Pressure changes resulting from the warming and humidifying of inspired air were detected
146 by a custom-made pressure MPX 2010 transducer (Motorola, Schaumburg, IL). Analog
147 voltage outputs from the pressure transducer were converted to digital signals using an ADC
148 11 converter (Pico Technology, St Neots, UK) and were recorded on a computer using
149 PicoScope software (Pico Technology). Five ventilatory datasets were analysed for each
150 individual at each T_a and averaged to provide a single value for each individual at each T_a .
151 Calculations for f_R , V_T , minute volume (V_I) and oxygen extraction (EO_2) were after Malan
152 (1973) and Cooper and Withers (2004), using a custom-written VB (v6) data analysis

153 program. The plethysmograph system was calibrated after Szewczak and Powell (2003) and
154 Cooper and Withers (2004). All values are reported as body temperature and pressure
155 saturated (BTPS), except for EO_2 which was calculated using standard temperature and
156 pressure dry (STPD) VO_2 and V_I , from VO_2 at the time the ventilatory measurements were
157 made.

158 Values are presented as mean \pm standard error (SE), where N = the number of
159 individuals and n = number of measurements. The effect of T_a on physiological variables was
160 determined using linear regression and multivariate repeated measures ANOVA; the ranks of
161 C_{wet} and C_{dry} were analysed since the data were not normally distributed. *A priori* polynomial
162 and reverse Helmert contrasts were used to determine the nature of the relationship between
163 the variables and T_a (Withers and Cooper, 2011). The effect of torpor on physiological
164 variables was examined with two-way ANOVA, with torpor and T_a as factors, as not all
165 individuals entered torpor at each T_a precluding a repeated measures design. Statistical
166 analyses were accomplished using StatistiXL V1.9 and a custom-written Excel macro
167 (Withers and Cooper 2011). Phascogales were compared to the conventional and
168 phylogenetically independent allometric regressions using \log_{10} -transformed (except T_b) data
169 for dasyuromorphs (Appendix 1) by examining their position relative to the 95% prediction
170 limits after Cooper and Withers (2006). The antilog predicted value for both species from the
171 log-transformed conventional regression was calculated using the minimum variance
172 unbiased estimator (MVUE) after Hayes and Shonkwiler (2006, 2007). Phylogenetic analysis
173 was accomplished (via a custom-written VB program, P. Withers) using autoregression
174 (Cheverud and Dow, 1985; Rohlf, 2001) and a phylogenetic tree for dasyuromorphs extracted
175 from the mammal supertree of Bininda-Emonds et al. (2007).

176

177 **Results**

178 Body mass of all phascogales was 34.7 ± 1.04 g ($N = 7$, $n = 35$), over all experiments.
179 This is only 15% of that predicted by autoregression from their phylogenetic position among
180 dasyuromorphs (227 g).

181 The T_b of normothermic phascogales ranged from $30.2 \pm 1.02^\circ\text{C}$ at $T_a = 13^\circ\text{C}$ to 37.4
182 $\pm 0.52^\circ\text{C}$ at $T_a = 35^\circ\text{C}$; T_b was $34.7 \pm 0.37^\circ\text{C}$ at a thermoneutral T_a of 30°C (Fig. 1). There
183 was a significant effect of T_a on T_b ($F_{4,3} = 32$, $P = 0.009$), with the relationship described by a
184 significant linear contrast ($P < 0.001$). Thermoneutral T_b was only 0.3°C lower than predicted
185 from the conventional allometric T_b relationship for dasyuromorph marsupials, falling within
186 the 95% prediction limits for both conventional and phylogenetically-independent allometric
187 relationships (Table 1; Fig. 2). Thermolability below thermoneutrality ($\Delta T_b/\Delta T_a$) was $0.26 \pm$
188 $0.036^\circ\text{C } ^\circ\text{C}^{-1}$ for normothermic phascogales over the T_a range $13 - 30^\circ\text{C}$ (linear regression;
189 $F_{1,26} = 25.8$, $P < 0.001$). Six of the seven phascogales entered torpor at $T_a = 13^\circ\text{C}$ ($T_b = 25.1 \pm$
190 1.22°C , $N = 6$) and 18°C ($T_b = 23.8 \pm 2.2^\circ\text{C}$, $N = 2$), but only three individuals became torpid
191 at $T_a = 25^\circ\text{C}$ (no T_b measurements).

192 The O_2 consumption rate ranged from a maximum of 3.46 ± 0.063 mL O_2 $\text{g}^{-1} \text{h}^{-1}$ at T_a
193 $= 13^\circ\text{C}$ to a minimum of 0.83 ± 0.076 mL O_2 $\text{g}^{-1} \text{h}^{-1}$ at $T_a = 30^\circ\text{C}$, which we consider basal
194 metabolic rate (BMR; Fig. 1). There was a significant effect of T_a on VO_2 for normothermic
195 phascogales ($F_{4,3} = 1722$, $P < 0.001$). Both linear and quadratic contrasts were significant ($t_6 \geq$
196 14.0 , $P < 0.001$) for the VO_2 vs. T_a relationship. Only a significant linear contrast remained (t_6
197 $= 43.6$, $P < 0.001$) after VO_2 data at $T_a = 35^\circ\text{C}$ were removed from the model, indicating that
198 VO_2 had increased at $T_a = 35^\circ\text{C}$ compared to the otherwise linear pattern of VO_2 decreasing
199 with increasing T_a . The pattern of VCO_2 mirrored that of VO_2 , ranging from 0.708 ± 0.103 ml
200 CO_2 $\text{g}^{-1} \text{h}^{-1}$ at $T_a = 30^\circ\text{C}$ to 2.29 ± 0.176 ml CO_2 $\text{g}^{-1} \text{h}^{-1}$ at $T_a = 13^\circ\text{C}$, so CO_2 data are not
201 analysed separately here. RER increased significantly with T_a (linear contrast $t_6 = 3.84$, $P =$
202 0.009), from 0.67 ± 0.02 at $T_a = 13^\circ\text{C}$ to 0.82 ± 0.05 at $T_a = 35^\circ\text{C}$. BMR, which was 86 % of

203 that predicted for an equivalently-sized dasyuromorph marsupial, conformed to the allometric
204 relationship for BMR for both the conventional and phylogenetically-independent regressions
205 (Table 1; Fig. 2). During torpor, VO_2 ranged from $0.44 \pm 0.110 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 25^\circ\text{C}$ to
206 $1.16 \pm 0.263 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 13^\circ\text{C}$ (Fig. 1), with a significant T_a effect ($F_{2,30} = 38.0$, $P <$
207 0.001). Torpor VO_2 was significantly lower (29 to 33%) than normothermic VO_2 ($F_{1,30} = 200$,
208 $P < 0.001$), although this difference was more pronounced at lower T_a , with a significant
209 interaction between torpor state and T_a ($F_{2,30} = 8.2$, $P = 0.001$).

210 For thermal conductance (Fig. 1), there was a significant overall effect of T_a for C_{wet}
211 ($F_{4,3} = 54.3$, $P = 0.004$), with a significant reverse Helmert contrast comparing $T_a = 35^\circ\text{C}$
212 with lower temperatures ($T_6 = 13.3$, $P < 0.001$). For C_{dry} there was no significant overall T_a
213 effect ($F_{4,3} = 8.27$, $P = 0.057$), but there was a highly significant reverse Helmert contrast $t_6 =$
214 4.85 , $P = 0.003$). Thermoneutral values (at 30°C) were 3.8 ± 0.26 for C_{wet} and $2.9 \pm 0.22 \text{ J g}^{-1}$
215 $\text{h}^{-1} \text{ }^\circ\text{C}^{-1}$ for C_{dry} . Although C_{wet} was only 69 % of that predicted for an equivalent-sized
216 dasyuromorph marsupial, the red-tailed phascogale was well within the 95% prediction limits
217 for the allometric relationship both before and after accounting for phylogenetic history
218 (Table 1; Fig. 2).

219 For EWL (Fig. 3), there was a significant effect of T_a ($F_{4,3} = 12.3$, $P = 0.033$),
220 reflecting an increase at $T_a = 35^\circ\text{C}$ ($3.86 \pm 0.474 \text{ mg g}^{-1} \text{ h}^{-1}$) as indicated by a significant
221 reverse Helmert contrast for $T_a = 35^\circ\text{C}$ compared to the other T_a s ($t_6 = 5.28$, $P = 0.002$).
222 EWL remained constant for normothermic phascogales from $T_a = 13$ to 30°C ($F_{3,4} = 2.63$, $P =$
223 0.186). Standard EWL at thermoneutrality (30°C) was $1.68 \pm 0.218 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$. Although
224 only 61% of the allometrically-predicted value for an equivalent-sized dasyuromorph
225 marsupial, the phascogale's EWL was well inside the 95% prediction limits for the allometric
226 relationship both before and after accounting for phylogenetic history (Table 1; Fig. 2). EWL
227 of torpid phascogales was not significantly affected by T_a ($F_{2,30} = 0.29$, $P = 0.750$), but there

228 was a significant difference between torpid and normothermic EWL ($F_{1,30} = 11.2$, $P = 0.002$),
229 with EWL of torpid individuals being 67 to 90% of that for normothermic phascogales.

230 There was a significant, negative, linear regression between RWE and T_a for
231 normothermic phascogales ($EWL = 1.930 - 0.051 T_a$; $F_{1,33} = 171$, $P < 0.001$; $R^2 = 0.838$), with
232 a PRWE of 18.2°C (Fig. 3). This PRWE was greater than that predicted (14.9°C) but was
233 within the 95% confidence limits for the significant allometric relationship for marsupials of
234 $PRWE = 26.3 (\pm 7.49) - 7.42 (\pm 2.86) \log \text{mass}$ (dataset as for Withers et al. 2012). RWE was
235 considerably lower during torpor ($F_{1,30} = 66.2$, $P < 0.001$), ranging from $0.24 \pm 0.036 \text{ mg H}_2\text{O}$
236 $\text{g}^{-1} \text{h}^{-1}$ at 25°C to $0.59 \pm 0.138 \text{ mg H}_2\text{O g}^{-1} \text{h}^{-1}$ at 13°C (Fig 3). The significant T_a effect on
237 torpid RWE ($F_{2,30} = 22.5$, $P < 0.001$) gave a torpor PRWE of -0.9°C ($R^2 = 0.38$, $F_{1,13} = 6.36$,
238 $P = 0.026$; $RWE = 0.971 - 0.031 T_a$).

239 There was a significant effect of T_a on all respiratory variables (Fig. 4; ANOVA $F_{4,3} \geq$
240 9.68 , $P \leq 0.046$) except EO_2 ($F_{4,3} = 6.68$, $P = 0.075$), although there was a significant positive
241 linear contrast for EO_2 ($t_6 = 2.74$, $P = 0.034$). The relationship for f_R was cubic over the
242 entire T_a range ($t_6 = 3.30$, $P = 0.016$), but linear ($t_6 = 3.49$, $P = 0.013$) when $T_a = 35^\circ\text{C}$ was
243 removed from the model, indicating that f_R increased significantly at high T_a . The patterns for
244 both V_T and V_I with T_a were best described by negative linear contrasts ($t_6 \geq 4.78$, $P \leq 0.003$).
245 Standard (thermoneutral) values for ventilatory variables were; f_R , $37.8 \pm 2.52 \text{ breaths min}^{-1}$;
246 V_T , $0.544 \pm 0.045 \text{ ml}$; V_I , $21.1 \pm 2.70 \text{ ml min}^{-1}$; EO_2 , $19.5 \pm 2.55\%$.

247

248 DISCUSSION

249 Amongst Australian marsupials, a carnivorous diet is generally associated with a body
250 mass larger than predicted from phylogeny, presumably due to the need to capture and
251 subdue vertebrate prey (Schmidt et al., 2009; Cooper and Withers, 2010b). However, a lower
252 than predicted body mass is associated with an arid environment for both marsupial and

253 placental carnivores (Williams et al., 2002, 2004; Withers and Cooper, 2009a), consistent
254 with the resource limitation hypothesis (Roth, 1990). The red-tailed phascogale's body mass
255 (34.7 g) was considerably lower (85%) than predicted (227 g) by its phylogenetic position
256 reducing absolute energy consumption by ~87% and water requirements by ~86% (calculated
257 from the allometric scaling relationships for dasyurid marsupials). These absolute energy and
258 water savings are presumably important for survival in an environment with limited and
259 unpredictable food and water availability. A small body mass could also be favourable for a
260 scansor because the mass-specific metabolic cost of transport for climbing does not increase
261 for small mammals whereas the cost of walking does (Hanna et al., 2008), and it allows the
262 use of small refugia such as the hollows typically available in small arid-zone eucalypts
263 (Bradley et al., 2008).

264 The thermoneutral T_b of the red-tailed phascogale was significantly lower (one
265 sample t-test, $t_6 = 7.2$, $P < 0.001$) than that measured for the larger brush-tailed phascogale
266 (37.4°C ; MacMillen and Nelson, 1969). This difference of 2.7°C was substantially greater
267 than the 0.4°C differential (35.0°C vs 35.4°C) predicted for these phascogales from the
268 allometry of dasyurid T_b (Table 1). This difference may reflect habitat aridity for the red
269 tailed phascogale, as a low T_b is consistent with the reduced energy requirements and heat
270 production of other dasyurids in an arid environment (e.g. Withers and Cooper, 2009a;
271 Cooper and Withers, 2010b). However, methodological differences between the studies
272 (measurement durations of as little as 1 hour for the brush-tailed phascogale) confound
273 interpretation of this difference. Short measurement durations may overestimate standard
274 physiological variables, including T_b (Hayes et al., 1992; Cooper and Withers, 2010a; Page et
275 al., 2011).

276 The red-tailed phascogale is thermolabile during normothermia (Fig 1).
277 Thermolability from $T_a = 13$ to 30°C of $0.29^\circ\text{C } ^\circ\text{C}^{-1}$ is much greater than the mean for other

278 dasyurids of $0.064 (\pm 0.018) ^\circ\text{C } ^\circ\text{C}^{-1}$ (Withers and Cooper, 2009a). Like the greater reductions
279 in T_b associated with torpor, thermolability at low T_a can be interpreted as a physiological
280 strategy for energy conservation. A reduction in T_b of 4.5°C at $T_a = 13^\circ\text{C}$ represents a 26%
281 reduction in metabolic rate ($0.91 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) compared to having maintained a
282 thermoneutral T_b of 34.7°C (calculated from thermal conductance and the respective thermal
283 gradients for these T_b s); this savings is 110% of BMR. While substantial, this is not as great
284 as the energy savings of 258% of BMR at $T_a = 11^\circ\text{C}$ achieved through even greater
285 thermolability by the also carnivorous and hyper-arid little red kaluta (Withers and Cooper,
286 2009a). Hyperthermia at high T_a also achieves substantial water conservation for the
287 phascogale. Allowing T_b to increase by 2.8°C to 37.5°C at $T_a = 35^\circ\text{C}$ maintains a favourable
288 gradient for heat dissipation and saves the phascogale about $14.4 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ compared to
289 defending a thermoneutral T_b of 34.7°C .

290 The typical endothermic response of the red-tailed phascogale, although somewhat
291 attenuated by its thermolability, was accommodated by an increase in V_I (rather than EO_2)
292 which in turn resulted from an increase in both f_R and V_T . It is interesting that V_T increased
293 by a similar proportion to f_R at low T_a . A small marsupial would be expected to accommodate
294 an increase V_I predominantly by an increase in f_R with little change in V_T (Chappell and
295 Dawson, 1994; Larcombe, 2002; Cooper and Withers, 2010b), but the $\Delta V_T/\Delta f_R$ for
296 phascogales (0.84) indicates that V_T contributes substantially to accommodating increased
297 VO_2 at low T_a .

298 The BMR of the red-tailed phascogale was not high compared to other dasyurid
299 marsupials, which was unexpected for a species with a diet that includes vertebrate flesh
300 (Hayssen and Lacy 1985; McNab 1986a, 2008; Elgar and Harvey 1987; Muñoz-Garcia and
301 Williams 2005; Careau et al. 2007), and there was also no evidence of a reduced BMR as
302 may be associated with habitat aridity (e.g. MacMillen 1983; Bozinovic and Rosenman 1988;

303 Lovegrove 2000; White 2003; Withers et al. 2006; Careau et al. 2007). It should be noted,
304 however, that the dasyurid dataset consists of several carnivorous species (e.g. *Dasyurus* spp.,
305 *Dasykaluta*), and over 60% of dasyurids inhabit arid environments, so metabolic adaptations
306 to these factors are presumably already characteristic of many of the dasyurids that comprise
307 the dataset. Direct comparison with the closely-related but mesic habitat brush-tailed
308 phascogale may therefore be more informative in revealing patterns in BMR consistent with
309 habitat adaptation. The red-tailed phascogale had a significantly lower BMR than the brush-
310 tailed phascogale ($t_6 = 4.57$, $P = 0.004$; brush-tailed phascogale data from MacMillen and
311 Nelson, 1969) after correcting for body mass differences using the scaling exponent for the
312 dasyurid allometric relationship of 0.75. Although a low BMR is consistent with an arid
313 habitat for marsupials (Withers et al., 2006), and also arid-habitat carnivorous mammals, and
314 mammals in general (e.g. Lovegrove, 2000; White, 2003; Careau et al., 2007; but see
315 Williams et al., 2004), this difference could also be attributed to very short measurement
316 durations for the brush-tailed phascogale (MacMillen and Nelson, 1969) and consequent
317 over-estimation of BMR (Hayes et al., 1992; Cooper and Withers, 2010a; Page et al., 2011).
318 It would be informative to re-investigate the physiology of the brush-tailed phascogale using
319 modern standardised measurement techniques to determine if its physiology is indeed
320 consistent with a more mesic habitat.

321 The red-tailed phascogale maintained a constant EWL below the thermoneutral zone,
322 which is the most common pattern for dasyurid marsupials (e.g. Hinds and MacMillen, 1986;
323 Withers and Cooper, 2009a,b). This presumably reflects a trade-off between the expected
324 increased cutaneous EWL at high T_a (due to a higher water vapour deficit between the animal
325 and the ambient air at higher T_a) and increased respiratory EWL at low T_a (as a result of
326 increased V_I to accommodate an increased MR). Increased EWL at $T_a > 30^\circ\text{C}$, can be
327 attributed to enhanced respiratory (as indicated by increased V_I) and cutaneous EWL. The

328 phascogale's standard EWL conforms to that of other dasyurids, despite its arid habitat. The
329 PRWE of the phascogale is relatively high, but consistent with its small body mass. The
330 higher thermal conductance of small compared to large species means that MR, and thus
331 MWP, increases more rapidly with decreasing T_a . As EWL generally remains constant at T_a
332 below thermoneutrality, this rapid increase in MWP results in a relatively high PRWE.
333 Therefore a small body mass not only minimises absolute energy and water requirements, but
334 it also contributes to a more favourable water economy at low T_a .

335 C_{wet} and C_{dry} were considerably increased at $T_a = 35^\circ\text{C}$ (Fig 3), but more variable,
336 reflecting differences in individual phascogale's responses to the heat challenge of a small
337 $T_b - T_a$ differential at $T_a = 35^\circ\text{C}$. EWL was responsible for ~35% of heat loss at $T_a = 35^\circ\text{C}$
338 compared to ~24% at a thermoneutral $T_a = 30^\circ\text{C}$, which is similar to the evaporative heat
339 dissipation capacity of other arid habitat dasyurids (e.g. Withers and Cooper, 2009ab; Cooper
340 and Withers, 2010b; Warnecke et al., 2010). The standard C_{wet} of the phascogale appeared
341 low (69% of predicted) compared to other dasyurid marsupials, as might be expected for an
342 arboreal species (Degabriele and Dawson, 1979; McNab, 2002b; Withers et al., 2006);
343 however, this difference was not significant (Fig. 2), reflecting the difficulty in demonstrating
344 statistical divergence for a single species from an allometric relationship (Cooper and
345 Withers, 2006; Munn et al., 2012).

346 Daily torpor is considered to be a factor contributing to the success of dasyurid
347 marsupials inhabiting arid and semi-arid environments, where both food and water resources
348 may be limited and their availability unpredictable (Geiser, 2004; Munn et al 2010), and the
349 red-tailed phascogale is no exception. Torpor was a frequent response of red-tailed
350 phascogales to T_a below 25°C and resulted in substantial absolute energy (up to 70%) and
351 water savings (up to 32%), as is expected for a small dasyurid marsupial (Geiser, 1994, 2003,
352 2004; Withers and Cooper, 2009a,b). The torpor T_b s of red-tail phascogales in our study (24-

353 25°C) were relatively high (cf Geiser and Baudinette, 1990), which may reflect maintenance
354 in captivity with regular and abundant food and water, and thus a propensity to regulate
355 torpor T_b at a higher set point (e.g. Geiser et al., 2000). There are currently no data
356 concerning torpor use in the field for red-tailed phascogales for comparison and, while
357 expected, our evidence of torpor is the first reported for this species. Interestingly, the more
358 substantial reduction in MR compared to EWL during torpor results in a significantly lower
359 RWE and PRWE (of only 2.0 °C compared to 16.2 °C when normothermic). This reduction in
360 RWE may be a significant contribution to limiting hibernation duration for small hibernators
361 (Withers et al., 2012), and presumably is also of significance for the water balance of daily
362 torpidators. Despite reducing overall EWL during torpor, when MWP is the only avenue of
363 water gain and EWL the only water loss, the negative water balance of phascogales (and
364 other heterothermic species) suggests that torpor is primarily a mechanism for energy rather
365 than water conservation. Further study of the frequency, duration and depth of torpor for
366 phascogales, particularly for wild, free-living individuals, would be of interest to better
367 understand their energy and water budgets.

368 These first metabolic, hygric, thermal and ventilatory data for the red-tailed
369 phascogale do not indicate any unusual aspects of their physiological profile that would
370 suggest adaptation to its unusual combination of diet, habit, habitat and distribution. That the
371 phascogale's physiology conformed to that of other dasyurid marsupials suggests that the
372 general dasyurid physiological bauplan is appropriate for exploiting a wide range of
373 ecological niches, including scansoriality. We identify thermolability during normothermia
374 (over a range of T_a), and torpor (at low T_a), as physiological adaptations of the red-tail
375 phascogale to conserve energy, but these are common traits for arid zone dasyurid marsupials
376 (Geiser, 2004; Withers and Cooper, 2009a,b; Warnecke et al., 2010). A smaller-than-
377 predicted body mass may be interpreted as a significant adaptation to both habitat aridity and

378 arboreality. Further work investigating the C_{wet} of arboreal dasyurids may provide more
379 robust evidence of a link between habitat use and C_{wet} , but currently it appears that the red-
380 tailed phascogale has typical dasyurid pre-adaptations to an arid habitat and little further
381 physiological adaption that might be interpreted as specifically advantageous for an arboreal
382 lifestyle.

383

384 **Acknowledgements**

385 We thank Mr. and Mrs. Roades for allowing us to trap the phascogales on their land, and Dr
386 Beng Chua for providing space in the Animal Facility at Curtin University. Mr Neil Thomas
387 provided valuable advice concerning trapping protocols. This study was funded by an
388 Australian Research Council Discovery Grant to CEC and PCW.

389

390 **References**

- 391 Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D.,
392 Grenyer, R., Price, S.A.R., Vos, A., Gittleman, J.L., Purvis, A., 2007. The delayed rise
393 of present-day mammals. *Nature* 446, 507-512.
- 394 Bozinovic, F., Rosenmann, M., 1988. Comparative energetics of South American cricetid
395 rodents. *Comp.Biochem. Physiol. A* 91, 195-202.
- 396 Bradley, A.J., 1997. Reproduction and life history in the red-tailed phascogale, *Phascogale*
397 *calura* (Marsupialia: Dasyuridae): the adaptive-stress senescence hypothesis. *J. Zool.*
398 *Lond.* 241,: 739-755.
- 399 Bradley, A.J., Foster, W.K., Taggart, D.A., 2008. Red-tailed phascogale (*Phascogale calura*).
400 In: Van Dyck, S., Strahan, R. (Eds.), *The Mammals of Australia*. New Holland,
401 Sydney, pp. 101-102.

402 Careau, V., Morand-Ferron, J., Thomas, D, 2007. Basal metabolic rate of canids from hot
403 deserts to cold arctic climates. *J. Mamm.* 88, 394–400.

404 Chappell, M.A., Dawson, T.J. 1994. Ventilatory accomodation of changing oxygen
405 consumption in dasyurid marsupials. *Physiol. Zool.* 67, 418-437.

406 Cheverud, J.M., Dow, M.M., 1985. An autocorrelation analysis of genetic variation due to
407 lineal fission in social groups of Rhesus monkeys. *Am. J. Physical Anthro.* 67, 113-121.

408 Cooper, C.E. and Withers, P.C., 2004. Ventilatory physiology of the numbat (*Myrmecobius*
409 *fasciatus*). *J. Comp. Physiol. B* 174, 107-111.

410 Cooper, C.E., Withers, P.C., 2006. Numbats and aardwolves- how low is low? A re-
411 affirmation of the need for statistical rigour in evaluating regression predictions. *J.*
412 *Comp. Physiol. B* 176, 623-629.

413 Cooper, C.E., Withers, P.C., 2010a. Effect of sampling regime on estimation of basal
414 metabolic rate and standard evaporative water loss using flow-through respirometry.
415 *Physiol. Biochem. Zool.* 83, 385-393.

416 Cooper, C.E., Withers, P.C., 2010b. Comparative physiology of Australian quolls (*Dasyurus*;
417 *Marsupialia*). *J. Comp. Physiol. B* 180, 857-868.

418 Degabriele, R., Dawson, T.J., 1979. Metabolism and heat balance of an arboreal marsupial,
419 the koala (*Phascolarctos cinereus*). *J. Comp. Physiol. B* 134, 293- 301.

420 Elgar, M.A., Harvey, P.H., 1987. Basal metabolic rates in mammals: allometry, phylogeny
421 and ecology. *Func. Ecol.* 1, 25–36.

422 Geiser, F., 1994. Hibernation and daily torpor in marsupials - a review. *Aust. J. Zool.* 42, 1-
423 16.

424 Geiser, F., 2003. Thermal biology and energetics of carnivorous marsupials. In: Jones, M.,
425 Dickman, C., Archer, M. (Eds.), *Predators with Pouches: the Biology of Carnivorous*
426 *Marsupials*. CSIRO, Melbourne, Australia, pp. 238–253.

427 Geiser, F., 2004. The role of torpor in the life of Australian arid zone mammals. Aust.
428 Mamm. 26, 125–134.

429 Geiser, F., Baudinette, R.V., 1990. The relationship between body mass and rate of
430 rewarming from hibernation and daily torpor in mammals. J. Exp. Biol. 151, 349–359.

431 Geiser, F., Holloway, J.C., Kortner, G., Maddocks, T.A., Turbill, C., Brigham, R.M., 2000.
432 Do patterns of torpor differ between free-ranging and captive mammals and birds? In:
433 Heldmaier, G., Klingensper, M. (Eds.), Life in the Cold. 11th International Hibernation
434 Symposium. Springer Verlag, Berlin.

435 Green, B., King, D., Bradley, A., 1989. Water and energy metabolism and estimated food
436 consumption rates of free-living Wambengers, *Phascogale calura* (Marsupialia:
437 Dasyuridae). Aust. Wildl. Res. 16, 501-507.

438 Hanna, J.B., Schmitt, D., Griffin, T.M., 2008. The energetic cost of climbing in primates.
439 Science 320, 898.

440 Harvey, P.H., Pagel, M.D., Rees, J.A. 1991. Mammalian metabolism and life histories. Am.
441 Nat. 137, 556–566.

442 Hayssen, V., Lacy, C.R., 1985. Basal metabolic rates in mammals: taxonomic differences in
443 the allometry of BMR and body mass. Comp. Biochem. Physiol. A 81, 741–754.

444 Hayes, J.P., Shonkwiler, J.S., 2006. Allometry, antilog transformations, and the peril of
445 prediction on the original scale. Physiol. Biochem. Zool. 79, 665-674.

446 Hayes, J.P., Shonkwiler, J.S., 2007. Erratum: allometry, antilog transformations, and the
447 perils of prediction on the original scale. Physiol. Biochem. Zool. 80, 556.

448 Hayes, J.P., Speakman, J.R., Racey, P.A., 1992. Sampling bias in respirometry. Physiol.
449 Zool. 65, 604–619.

450 Hinds, D.S., MacMillen, R.E., 1986. Scaling of evaporative water loss in marsupials.
451 Physiological Zoology 59: 1-9.

452 Hume, I.D., 2003. Nutrition of carnivorous marsupials. In: Jones M., Dickman, C., Archer,
453 M. (Eds), *Predators with Pouches: The Biology of Carnivorous Marsupials*. CSIRO,
454 Collingwood, pp. 221–228.

455 Kitchener, D.J., 1981. Breeding, diet and habitat preference of *Phascogale calura* (Gould,
456 1844) (Marsupialia: Dasyuridae) in the southern wheat belt, Western Australia. *Records*
457 *Western Aust. Mus.* 9, 173-186.

458 Larcombe, A., 2002. Effects of temperature on metabolism, ventilation and oxygen extraction
459 in the southern brown bandicoot *Isodon obesulus* (Marsupialia: Peramelidae). *Physiol.*
460 *Biochem. Zool.* 75, 405-411.

461 Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. *Amer. Nat.*
462 156, 201–219.

463 Lovegrove, B.G., 2003. The influence of climate on the basal metabolic rate of small
464 mammals: a slow-fast metabolic continuum. *J. Comp. Physiol. B* 173, 87–112.

465 MacMillen, R.E., 1983. Adaptive physiology of heteromyid rodents. *Great Basin Nat. Mem.*
466 7, 65-90.

467 MacMillen, R.E., Nelson, J.E., 1969. Bioenergetics and body size in dasyurid marsupials.
468 *Amer. J. Physiol.* 217, 1246-1251.

469 Malan, A., 1973. Ventilation measured by body plethysmography in hibernating mammals
470 and poikilotherms. *Respir. Physiol.* 17, 32-44.

471 McNab, B.K., 1986a. The influence of food habits on the energetics of eutherian mammals.
472 *Ecol. Mono.* 56, 1-19.

473 McNab, B.K., 1986b. Food habits, energetics, and the reproduction of marsupials. *J. Zool.*
474 (Lond.) 208, 595–614.

475 McNab, B.K., 2002a. *The Physiological Ecology of Vertebrates: A View from Energetics*.
476 Cornell University Press, Ithaca.

477 McNab, B.K., 2002b. Short-term energy conservation in endotherms in relation to body mass,
478 habits, and environment. *J. Thermal Biol.* 27, 459–466.

479 McNab, B.K., 2005. Uniformity in the basal metabolic rate of marsupials: its causes and
480 consequences. *Rev. Chil. Hist. Nat.* 78, 183-198.

481 McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of
482 mammalian BMR. *Comp. Biochem. Physiol. A* 151, 5-28.

483 Menkhorst, P., Knight F., 2001. *A Field Guide to the Mammals of Australia*. Oxford
484 University Press, South Melbourne.

485 Munn, A.J., Cooper, C.E., Russell, B., Dawson, T.J., McLeod, S.R., Maloney, S.K., 2012.
486 Energy and water use by invasive goats (*Capra hircus*) in an Australian rangeland, and
487 a caution against using broad-scale allometry to predict species-specific requirements.
488 *Comp. Biochem. Physiol. A* 161, 216-229.

489 Munn, A.J., Kern, P., and McAllan, B.M. (2010) Coping with chaos: unpredictable food
490 supplied intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart
491 (*Sminthopsis crassicaudata*). *Naturwissenschaften* 97: 601-605.

492 Muñoz-García A., Williams, J.B., 2005. Basal metabolic rate in carnivores is associated with
493 diet after controlling for phylogeny. *Physiol. Biochem. Zool.* 78, 1039–1056.

494 Page, A.J., Cooper, C.E., Withers, P.C., 2011. Effects of experiment start time and duration
495 on measurement of standard physiological variables. *J. Comp. Physiol. B* 181, 657-665.

496 Rohlf, F.J., 2001. Comparative methods for the analysis of continuous variables: geometric
497 interpretations. *Evol.* 55, 2143-2160.

498 Roth, V.L., 1990. Insular dwarf elephants: a case study in body mass estimation and
499 ecological inference. In: Damuth, J., MacFadden, B.J. (Eds), *Body Size in Mammalian*
500 *Paleobiology. Estimation and Biological Implications*. Cambridge University Press,
501 Cambridge, pp. 151–179.

502 Schmidt, S., Withers, P.C., Cooper, C.E., 2009. Metabolic, ventilatory and hygric physiology
503 of the chuditch (*Dasyurus geoffroii*; Marsupialia, Dasyuridae). *Comp. Biochem.*
504 *Physiol. A* 154, 92-97.

505 Stannard, H., Caton, W., Old, J., 2010. The diet and reproduction of the red-tailed phascogale
506 in a trial translocation at Alice-Springs Desert Park, Northern Territory, Australia. *J.*
507 *Zool. (Lond.)* 280, 326-331.

508 Szewczak, J.M., Powell, F.L., (2003). Open-flow plethysmography with pressure-decay
509 compensation. *Respir. Physiol. Neurobiol* 134, 57-67.

510 Tomlinson, S., Withers, P.C., Maloney, S.K., 2012. Flexibility in thermoregulatory
511 physiology of two dunnarts, *Sminthopsis macroura* and *Sminthopsis ooldea*
512 (Marsupialia; Dasyuridae). *J Exp. Biol.* 215, 2236-2246.

513 Warnecke, L., Cooper, C.E., Geiser, F., Withers, P.C., 2010. Environmental physiology of a
514 small marsupial inhabiting arid floodplains. *Comp. Biochem. Physiol.* 157, 73-78.

515 White, C.R., 2003. The influence of foraging mode and arid adaptation on the basal
516 metabolic rates of burrowing mammals. *Physiol. Biochem. Zool.* 76, 122-134.

517 Williams, J.B., Lenain, D., Ostrowski, S., Tieleman, B.I., 2002. Energy expenditure and
518 water flux of Rüppell's foxes in Saudi Arabia. *Physiol. Biochem. Zool.* 75, 33-42.

519 Williams, J.B., Muñoz-Garcia, A., Ostrowski, S., Tieleman, B.I., 2004. A phylogenetic
520 analysis of basal metabolism, total evaporative water loss, and life-history among foxes
521 from desert and mesic regions. *J. Comp. Physiol. B* 174, 29-39.

522 Withers, P.C., 1992. *Comparative Animal Physiology*. Philadelphia, Saunders College
523 Publishing.

524 Withers, P.C., 2001. Design, calibration and calculation for flow-through respirometry
525 systems. *Aust. J. Zool.* 49, 455-461.

526 Withers, P.C., Cooper, C.E., 2009a. Thermal, metabolic, and hygric physiology of the little
527 red kaluta, *Dasykaluta rosamondae* (Dasyuromorphia: Dasyuridae). *J. Mamm.* 90, 752-
528 760.

529 Withers, P.C., Cooper, C.E., 2009b. Thermal, metabolic, hygric and ventilatory physiology of
530 the sandhill dunnart (*Sminthopsis psammophila*: Marsupialia, Dasyuridae). *Comp.*
531 *Biochem. Physiol. A* 153, 317-323.

532 Withers, P.C., Cooper, C.E., 2011. Using a priori contrasts for multivariate repeated-
533 measures ANOVA to analyze thermoregulatory responses of the dibbler
534 (*Parantechinus apicalis*; Marsupialia, Dasyuridae). *Physiol. Biochem. Zool.* 84, 514-
535 521.

536 Withers, P.C., Cooper, C.E., Nespolo, R.F. 2012. Evaporative water loss, relative water
537 economy and evaporative partitioning of a heterothermic marsupial, the monito del
538 monte (*Dromiciops gliroides*). *J. Exp. Biol.* 215, 2806-2813.

539 Withers, P.C., Cooper, C.E., Larcombe, A., 2006. Environmental correlates of physiological
540 variables in marsupials. *Physiol. Biochem. Zool.* 79, 437-453.

541

542

543 Figure 1. Body temperature, oxygen consumption (black symbols are normothermic
544 individuals and white symbols are torpid individuals) and thermal conductance (black
545 symbols are wet thermal conductance; C_{wet} and grey symbols are dry thermal
546 conductance; C_{dry}) of the red-tailed phascogale (*Phascogale calura*) over a range of
547 ambient temperatures. Values are mean \pm SE (N = 7 for normothermia).

548

549 Figure 2. Conventional (left column) and phylogenetically independent (right column)
550 allometric relationships for body temperature, metabolic rate, thermal conductance and
551 evaporative water loss of dasyurid marsupials (black circles; see Appendix 1 for data).
552 Solid lines represents linear regressions for the relationships, the dashed lines are the
553 95% prediction limits for a further datum. The red-tailed phascogale (*Phascogale*
554 *calura*) is indicated by a white triangle.

555

556 Figure 3. Evaporative water loss and relative water economy of the red-tailed phascogale
557 (*Phascogale calura*) over a range of ambient temperatures. Values are mean \pm SE (N =
558 7 for normothermia). Black symbols are normothermic individuals and white symbols
559 are torpid individuals.

560

561 Figure 4. Respiratory rate, tidal volume, minute volume and oxygen extraction for the red-
562 tailed phascogale (*Phascogale calura*) over a range of ambient temperatures. Values
563 are mean \pm SE (N = 7).







