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11 **RH: SEASON AND CAPTIVITY EFFECTS FOR NUMBATS**

12

13 **Does season or captivity influence the physiology of an endangered marsupial, the**  
14 **numbat (*Myrmecobius fasciatus*)?**

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23 We examined the effects of season and captivity on several commonly measured  
24 physiological variables (body temperature, metabolic rate, thermal conductance and  
25 evaporative water loss) for the numbat, an endangered myrmecophagous Australian  
26 marsupial, because the maintenance of a wild-type physiology may increase the  
27 likelihood of successful re-introduction of numbats into the wild. Our results indicate  
28 that the physiology of male captive numbats is representative of wild individuals, at  
29 least at thermoneutrality, except for some diet-related effects on substrate metabolism  
30 and thermoregulation. Season significantly influenced physiological variables, in  
31 particular basal metabolic rate and evaporative water loss. Basal metabolic rate was 30-

32 37 % higher in winter than in summer, and evaporative water loss increased at a high  
33 ambient temperature in winter, presumably reflecting seasonal differences in ambient  
34 temperature, food availability and water consumption. Seasonal variation in  
35 physiological responses of captive numbats was similar to that observed for wild  
36 numbats. We conclude that there is seasonal flexibility in the physiology of numbats,  
37 and that captivity under semi-natural conditions does not compromise their basic  
38 physiology.

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40 Key words: body temperature, captivity, evaporative water loss, metabolism, thermal  
41 conductance, season

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45           Physiological parameters of mammals, such as metabolic rate (MR), body  
46 temperature ( $T_b$ ), evaporative water loss (EWL) and thermal conductance (C), are  
47 influenced by a variety of factors, such as body mass, ambient temperature ( $T_a$ ),  
48 circadian phase, reproductive state, growth and food digestion (e.g. Blaxter 1989;  
49 Cooper and Withers 2009; Kleiber 1961; McNab 1997; Withers 1992). Although the  
50 effects of many of these factors are well understood, less is known about the potential  
51 effects of season and captivity on the physiology of mammals, in particular marsupials.

52           It is particularly important that potential physiological effects of season and  
53 captivity are considered for maintenance of captive colonies of threatened species. If  
54 captive individuals are to be successfully released into the wild, then their normal  
55 physiology, and any plasticity associated with seasonal acclimation, needs to be  
56 maintained to maximize survival and reproduction under natural conditions. Released  
57 individuals need to meet their daily energy and water requirements, and regulate body  
58 temperature appropriately, if they are to survive. Long-term survival requires these  
59 individuals to maintain the physiological flexibility to respond to seasonal variation in  
60 environmental conditions (such as  $T_a$ ) and food and water availability. The design and  
61 interpretation of comparative studies must also consider any seasonal or captivity  
62 effects that might influence standardization of comparative datasets.

63           Captive breeding, with the aim to release individuals into the wild to establish  
64 self-sustaining populations, is a widespread management technique. However, many  
65 captive-breeding conservation programs fail due to difficulty in maintaining self-  
66 supporting breeding colonies, or failure of the released individuals to survive, reproduce  
67 and maintain long-term viable populations in the wild (Kleiman 1989; Snyder et al.  
68 1996). Indeed, reintroduction programs are more likely to fail for captive-bred than  
69 wild-caught individuals (Fischer and Lindenmayer 2000; Griffith et al. 1989).

70 Captive animals do not experience the same environmental conditions as wild  
71 individuals; they do not have to forage for food, they have different diets and do not  
72 have the same variation in food availability, their activity levels are often lower, they do  
73 not experience the same predation pressures, their reproductive activity is controlled,  
74 and they may experience very different weather conditions compared to their free-living  
75 counterparts (Kleiman 1989; Snyder et al. 1996). These marked differences in the  
76 conditions experienced by captive and wild animals may have physiological  
77 consequences for captive individuals, which can influence the likelihood of successful  
78 reintroduction of individuals into the wild (Kleiman 1989; Snyder et al. 1996).

79 Captive breeding of threatened species is of maximal value if there are no  
80 changes that reduce fitness under natural conditions. Although behavioral and genetic  
81 effects of captivity are widely appreciated (Sarrazin and Barbault 1996), little  
82 consideration is given to physiological changes resulting from differences in selection  
83 pressure, acclimation to more benign environments, or from developmental effects. For  
84 native Australian mammals in particular, which have suffered the worst rates of faunal  
85 attrition for any continent during the last 200 years (Johnson 2006), coupled with the  
86 lowest success rates of translocation and re-introduction programs (Fischer and  
87 Lindenmayer 2000; Griffith et al. 1989; Wolf et al. 1996), it is critical to understand all  
88 factors that might impact on the success of conservation and management programs.

89 Studies of possible effects of captivity on the physiology of birds and mammals  
90 are equivocal. Factors such as the animal's origin (e.g., wild-caught or captive bred),  
91 history (e.g., rehabilitated from injury or hand-raised orphans), diet or housing may all  
92 contribute to the observed variability in captivity effects. Some studies, often of  
93 rehabilitated animals or those bred in captivity for several generations, conclude that  
94 there is a strong physiological influence of captivity (e.g., Geiser et al. 1990, 2000;  
95 Skadhauge and Bradshaw 1974; Warkentin and West 1990) and that any extrapolation

96 of data from captive to wild individuals should be treated with caution. For species such  
97 as the feathertail glider (*Acrobates pygmaeus*), physiological changes for captive-bred  
98 individuals are sufficient to suggest that they would be unlikely to survive in the wild  
99 (Geiser and Ferguson 2001). However, other studies (e.g., Dawson and Carey 1976;  
100 Stonerook et al. 1994; Wasser 1986; Weathers et al. 1983) suggest that captivity does  
101 not have a physiological influence. For another marsupial, the southern brown  
102 bandicoot (*Isodon obesulus*—Larcombe and Withers 2007), captivity effects for wild-  
103 caught individuals were limited to diet-related physiological variables such as CO<sub>2</sub>  
104 production (VCO<sub>2</sub>), respiratory exchange ratio (RER) and EWL; variables such as basal  
105 metabolic rate (BMR), C and T<sub>b</sub> were not influenced by captivity.

106 Wild, free-living mammals must make behavioral, anatomical and/or  
107 physiological adjustments to seasonal variation in environmental factors such as T<sub>a</sub>,  
108 relative humidity (RH) and photoperiod (Lovegrove 2005; Merritt et al. 2001). Seasonal  
109 changes in weather are not only associated with changes in thermoregulatory demands,  
110 but also changes in availability of food and water, and sometimes reproductive  
111 condition. Consequently, it is important that captive individuals retain normal seasonal  
112 physiological responses. Many small mammals have a higher BMR in winter than in  
113 summer, associated with increased thermogenic capacity (Heldmaier and Steinlechner  
114 1981; Lynch 1973; McDevitt and Speakman 1996; Merritt 1986; Merritt et al. 2001).  
115 However, for others, BMR decreases during winter (Degan 1997; Holloway and Geiser  
116 2001), often as a result of a reduced winter body mass.

117 We quantified the effects of season and captivity on aspects of the basic  
118 physiology (MR, EWL, C and T<sub>b</sub>) of male numbats (*Myrmecobius fasciatus*). The  
119 numbat is an endangered Australian marsupial, for which there is a long-term captive  
120 breeding program (Cooper 2011). Numbats are exclusively termitivorous, and despite  
121 their wide-spread historical distribution throughout southern Australia they are currently

122 restricted in the wild to a few isolated areas of woodland in south-west Western  
123 Australia (Cooper 2011). Previous physiological studies indicate that the numbat's  
124 metabolic, hygric and thermal physiology is typical of that of other arid habitat  
125 dasyuromorph marsupials, and of other termitivorous mammals in general (Cooper and  
126 Withers 2002, 2004a, 2004b; Cooper et al. 2003b).

127

## 128 MATERIALS AND METHODS

129 Basic physiological variables were measured for both captive and wild adult numbats.  
130 Only male numbats were used for this study, as adult females had dependant young  
131 during the study period and there is a metabolic cost of lactation (Rogowitz 1996;  
132 Thompson and Nicoll 1986). Captive numbats were studied at Perth Zoo (South Perth;  
133 31° 58' S 115° 51' E) and wild numbats were studied at Dryandra Woodland (170 km  
134 south-east of Perth; 31° 46' S 117° 1' E). Data for O<sub>2</sub> consumption (VO<sub>2</sub>), VCO<sub>2</sub> and  
135 EWL of summer wild numbats were presented by Cooper et al. (2003b). Summer  
136 experiments were conducted in February and early March 2001 and winter experiments  
137 were in late July and August 2002. Mean ambient temperatures of these study locations  
138 are similar, with summer T<sub>a</sub> ranging from mean minima of 15.2°C (Dryandra) and  
139 18.3°C (Perth), to mean maxima of 29.9°C (Dryandra) and 31.1°C (Perth), and winter  
140 temperatures ranging from mean minima of 3.4°C (Dryandra) and 8.3°C (Perth), to  
141 mean maxima of 14.1°C (Dryandra) and 17.0°C (Perth; climate data from Australian  
142 Bureau of Meteorology). Measurements of captive numbat physiology commenced in  
143 the week immediately following those of wild numbats. All experiments were  
144 conducted at night, during the numbats' inactive phase, between 1800 and 0400 h, with  
145 all physiological variables calculated for periods after 0000 h, by which time the  
146 numbats had not eaten for at least 8 h. An individual numbat was only measured at one  
147 T<sub>a</sub> per night, and was allowed at least four days between successive measurements.

148 Captive numbats used for this study were wild-caught long-term captives (in  
149 captivity for > 6 yrs) except for 1 shorter-term wild-caught captive (in captivity for  
150 approximately 1 year) and 1 captive-born individual (6 yrs old). All captive, wild-  
151 caught numbats originated from Dryandra Woodland. The numbats were housed in  
152 large outdoor wire enclosures (2.5 m x 10 m x 2.5 m) where they experienced natural  
153 conditions of weather and photoperiod. They were fed an artificial diet of custard,  
154 consisting of lactose-free milk powder, water, eggs, baked termite mound and vitamin  
155 and mineral supplements, in addition to frozen termites. Numbats were removed from  
156 their nest boxes, weighed to  $\pm 0.5$  g, placed in the metabolic chamber at the  
157 commencement of an experiment, and returned to their box at its conclusion.  
158 Physiological variables were measured at  $T_a$ s of 10, 20, 30 and 32.5 °C.

159 The wild numbats used for this study were fitted with radio collars (Biotrack  
160 TWS, 7g) for long-term monitoring by the Department of Conservation and Land  
161 Management. For summer studies, 5 wild male numbats were measured, and 4 were  
162 measured in winter. During the day preceding each experiment, a wild numbat was  
163 radio-tracked to locate its position, captured by hand, and held in a calico bag until the  
164 commencement of the experiment. Numbats were weighed to  $\pm 0.5$  g before being  
165 placed in the metabolic chamber and were returned to the site of capture at around 0900  
166 h the following day. Physiological variables were only measured for wild numbats at a  
167 thermoneutral temperature of 30 °C (Cooper and Withers 2002).

168 The  $VO_2$ ,  $VCO_2$  and EWL of numbats were measured using open flow-through  
169 respirometry. Compressed air from SCUBA tanks passed through the metabolic  
170 chamber (8 L) at 2 to 3 L  $\text{min}^{-1}$  (depending on  $T_a$ ), controlled by an Omega FMA 4669  
171 mass flowmeter. A subsample of excurrent air passed through a Vaisala HMP 33 or 35B  
172 temperature and humidity probe, then through a column of drierite to remove water  
173 vapour, before  $CO_2$  was measured by a Qubit S152 infrared  $CO_2$  analyser or a David

174 Bishop 280 Combo analyser, and finally O<sub>2</sub> was measured by a Servomex paramagnetic  
175 O<sub>2</sub> analyser (model 527, 570A or 574). The analog voltage outputs from the O<sub>2</sub> and CO<sub>2</sub>  
176 analysers, and the humidity and temperature probe, were recorded by Thurlby 1906  
177 multimeters, and their RS 232 outputs were recorded with a PC. Baselines of  
178 background O<sub>2</sub>, CO<sub>2</sub> and water vapour levels were established for at least 20 min before  
179 and after each experiment. The metabolic system was calibrated after Withers (2001).

180         Calculations of VO<sub>2</sub>, VCO<sub>2</sub> and EWL were after Withers (2001), averaged for  
181 the 20 min period when these variables were constant and minimal. T<sub>b</sub> was measured at  
182 the conclusion of each experiment, immediately after removing the numbat from the  
183 metabolic system, by inserting a plastic-sheathed thermocouple, connected to a RS  
184 Components 611-234 thermocouple meter (resolution and accuracy 0.1 °C),  
185 approximately 2 cm into the cloaca. RER was calculated as VCO<sub>2</sub>/VO<sub>2</sub>. Wet (C<sub>wet</sub>) and  
186 dry (C<sub>dry</sub>) thermal conductance were calculated as MHP/(T<sub>b</sub>-T<sub>a</sub>) and (MHP – EHL)/(T<sub>b</sub>-  
187 T<sub>a</sub>) respectively, where metabolic heat production (MHP) and evaporative heat loss  
188 (EHL) were calculated in J from MR, RER and EWL after Withers (1992). Experiments  
189 were approved by the University of Western Australia's animal ethics committee, and  
190 followed ethical guidelines of the American Society of Mammalogists (Sikes et al.  
191 2011).

192         *Statistics.*- Values are presented as mean ± SE unless stated otherwise, with *n* =  
193 number of individuals. Sample sizes are *n* = 6 for captive winter measurements, *n* = 5  
194 for captive and wild summer measurements, and *n* = 4 for wild winter measurements.  
195 Not all variables could be measured for all numbats; variations in degrees of freedom  
196 reflect the sample size for each analysis.

197         Standard physiological variables, measured within the thermoneutral zone  
198 (TNZ; 30°C), were analysed for captive and wild numbats by 1-way ANOVA, with  
199 season and captivity as factors. If there was a significant interaction term, then 1-way



200 ANOVA with a Student-Newman-Keuls (SNK) post hoc test was used to further  
201 explore patterns in captivity and season. 2-way ANOVA with season and temperature as  
202 factors were used to compare seasonal variation in body mass and physiological  
203 variables of captive numbats over a range of  $T_a$ . SNK post hoc tests and  $t$ -tests were  
204 used to examine the pattern of any  $T_a$  effects. Statistical tests were performed using  
205 *statistiXL* v1.8.

## 206 RESULTS

207 Body mass of wild and captive numbats (Table 1) was not influenced by season  
208 ( $F_{1,16} = 0.415$ ,  $P = 0.529$ ) or captivity ( $F_{1,16} = 4.35$ ,  $P = 0.053$ ), and there was no  
209 significant interaction between season and captivity ( $F_{1,16} = 2.94$ ,  $P = 0.105$ ). Overall  
210 mean mass was  $516 \pm 12$  g. Thermoneutral  $T_b$  (Table 1) differed significantly with  
211 season ( $F_{1,16} = 27.6$ ,  $P < 0.001$ ) and captivity ( $F_{1,16} = 5.19$ ,  $P = 0.027$ ). The interaction  
212 term was significant ( $F_{1,16} = 7.46$ ,  $P = 0.015$ ), reflecting the lower  $T_b$  (by  $2.4$  °C) for  
213 wild numbats in summer compared to winter (SNK  $P < 0.001$ ), and a  $T_b$  difference of  
214  $1.6$  °C between captive and wild numbats during summer (SNK  $P = 0.002$ ). There was  
215 no season effect for  $T_b$  ( $F_{3,30} = 0.67$ ,  $P = 0.420$ ) of captive numbats. There was a highly  
216 significant effect of  $T_a$  on  $T_b$  for captive numbats ( $F_{3,30} = 37.1$ ,  $P < 0.001$ ), with  $T_b$   
217 higher at  $T_a = 30$  and  $32.5$ °C than at  $T_a = 10$  and  $20$ °C (SNK  $P < 0.001$ ).

218 *Metabolic Rate.*- BMR (at  $T_a = 30$  °C) differed for  $VO_2$  and  $VCO_2$  with season  
219 ( $F_{1,15} = 6.01$ ,  $P = 0.027$ ;  $F_{1,16} = 4.87$ ,  $P = 0.042$ ) but not captivity ( $F_{1,15} = 0.34$ ,  $P =$   
220  $0.567$ ;  $F_{1,16} = 0.44$ ,  $P = 0.515$ ; Table 1). However, there was a significant interaction  
221 between season and captivity for  $VCO_2$  ( $F_{1,16} = 10.8$ ,  $P = 0.005$ ), with captive and wild  
222 numbats differing in winter (SNK  $P < 0.035$ ) but not summer (SNK  $P = 0.178$ ), and  
223 season affecting  $VCO_2$  of captive numbats (SNK  $P = 0.004$ ) but not wild numbats (SNK  
224  $P = 0.477$ ). RER was not influenced by captivity ( $F_{1,32} = 0.81$ ,  $P = 0.376$ ), but there was  
225 a seasonal effect ( $F_{1,32} = 5.12$ ,  $P = 0.031$ ). The significant interaction term ( $F_{1,32} = 5.90$ ,

226  $P = 0.021$ ) resulted from strong seasonal effects for captive (SNK  $P < 0.001$ ) but not  
227 wild numbats (SNK  $P = 0.932$ ).

228 For captive numbats (Fig.1), there was a highly significant influence of  $T_a$  from  
229 10 to 32.5 °C on  $VO_2$  and  $VCO_2$  ( $F_{3,29} = 81.2, P < 0.001$ ;  $F_{3,30} = 184, P < 0.001$ ) but a  
230 season effect only for  $VCO_2$  ( $F_{3,30} = 16.8, P < 0.001$ ), which was higher in summer. For  
231 RER, there was a positive  $T_a$  effect in summer ( $F_{1,17} = 14.4, P < 0.001$ ) but not winter  
232 ( $F_{1,15} = 0.02, P = 0.888$ ), explaining the significant interaction for this variable ( $F_{3,28} =$   
233  $8.19, P < 0.001$ ).

234 *Thermal Conductance.*-  $C_{wet}$  and  $C_{dry}$  at thermoneutrality ( $T_a = 30$  °C; Table 1)  
235 were not influenced by season ( $F_{1,13} = 1.87, P = 0.192$ ;  $F_{1,14} = 605, P = 0.450$ ) or  
236 captivity ( $F_{1,15} = 23.2, P = 0.094$ ;  $F_{1,14} = 1.74, P = 0.208$ ). For captive numbats,  $T_a$  had a  
237 highly significant influence on both  $C_{wet}$  and  $C_{dry}$  ( $F_{3,29} = 26.1, P < 0.001$ ;  $F_{3,29} = 16.1, P$   
238  $< 0.001$ ; Fig.1) but there was no significant influence of season ( $F_{1,15} = 0.189, P =$   
239  $0.667$ ;  $F_{1,15} = 0.027, P = 0.872$ ), and no significant interaction ( $F_{3,29} = 0.91, P = 0.449$ ;  
240  $F_{3,29} = 0.50, P = 0.686$ ). Both  $C_{wet}$  and  $C_{dry}$  were higher at  $T_a = 32.5$ °C than at the other  
241  $T_a$  (SNK  $P < 0.001$ ).

242 *EWL.*- Thermoneutral EWL did not differ with season ( $F_{1,14} = 3.58, P = 0.079$ )  
243 or captivity ( $F_{1,14} = 0.02, P = 0.884$ ; Table 1). For captive numbats, there was no  
244 significant effect of season on EWL at  $T_a = 10$ -32.5 °C ( $F_{1,15} = 0.05, P = 0.826$ ), but the  
245 effect of  $T_a$  was highly significant ( $F_{3,29} = 8.17, P < 0.001$ ; Fig.1), with a significant  
246 interaction ( $F_{3,29} = 10.8, P < 0.001$ ). EWL increased greatly at 32.5 °C during winter  
247 ( $1.18 \pm 0.166$  mg  $H_2O$   $g^{-1} h^{-1}$ ; SNK  $P \leq 0.003$ ) but not during summer ( $0.48 \pm 0.042$  mg  
248  $H_2O$   $g^{-1} h^{-1}$ ; SNK  $P \geq 0.082$ ; Fig. 1). The winter values for EWL were significantly  
249 higher at  $T_a = 32.5$  °C than during summer ( $t_7 = 4.09, P = 0.005$ ).

250

## DISCUSSION

251           The standard physiology of wild, free-living male numbats was very similar to  
252 that of captive male numbats. As for southern brown bandicoots (Larcombe and Withers  
253 2007), the physiological variables influenced by captivity were those aspects reflecting  
254 diet and nutrition;  $VCO_2$  varies as a consequence of substrate metabolism, and  
255 thermoregulation is influenced by energy availability. Seasonal differences in  $VCO_2$  and  
256 RER suggest that captive numbats metabolize a greater proportion of carbohydrate  
257 during summer (high RER) when wild numbats may have to metabolise fat reserves  
258 (low RER). Maintenance by wild numbats of a lower  $T_b$  during summer also conserves  
259 energy during a period of limited food availability (Abensperg-Traun and De Boer  
260 1990). Other standard physiological variables such as BMR, C and EWL were similar  
261 for both wild and captive numbats, suggesting that these standard physiological data for  
262 captive numbats are representative of those for wild individuals, and that there have  
263 been few effects on basic physiology, at least at thermoneutrality, for male numbats  
264 held in this captive breeding colony.

265           Studies that do show a difference in physiological variables between captive and  
266 wild individuals have often involved injured individuals not capable of natural  
267 movements (Warkentin and West 1990), or individuals that have been captive bred for  
268 several generations (Geiser and Ferguson 2001; Geiser et al. 1990; Skadhauge and  
269 Bradshaw 1974). The captive numbats used for this study were mostly wild-caught  
270 individuals (with 1 first-generation captive bred animal), that had been maintained  
271 under reasonably natural environmental conditions. The numbats were able to move  
272 freely about their outdoor enclosures and their daily energy expenditure ( $258 \text{ kJ day}^{-1}$ )  
273 was similar to that of wild numbats ( $269 \text{ kJ day}^{-1}$ —Cooper and Withers 2004b; Cooper  
274 et al. 2003b). Therefore the numbats may be expected to maintain a more natural  
275 physiology than species maintained under more artificial conditions.

276           Our study has important implications for the management of captive colonies of  
277 endangered species, such as the numbat. For male numbats at least, current captive  
278 conditions appear appropriate to preserve a wild-type physiology for most standard  
279 physiological variables, the exceptions being those variables associated with diet. For a  
280 species with a specialized diet, such as the termitivorous numbat, it can be logistically  
281 and financially difficult to replicate a natural diet, despite measurable physiological  
282 impacts. It would be of interest to further examine captivity effects on the physiology of  
283 numbats and other endangered marsupials for environmental conditions outside  
284 thermoneutrality.

285           Both captive and wild numbats had a significantly higher  $T_b$ , BMR, and EWL  
286 in winter than in summer, indicating that natural seasonal plasticity in these variables  
287 was maintained in captivity. Wild numbats had a low thermoneutral  $T_b$  in summer  
288 compared to other seasons, and compared to numbats measured previously in spring  
289 (Cooper and Withers 2002). This low  $T_b$  would not only conserve energy for wild  
290 numbats by reducing BMR (via the  $Q_{10}$  effect) during the period when termites are least  
291 abundant in the soil (Abensperg-Traun and DeBoer 1990), but also provide a greater  
292 scope for adaptive hyperthermia and conservation of water during the hot, dry summer  
293 months.

294           Winter BMR of both captive and wild numbats increased by 30-37 % above  
295 summer BMR, which was similar to previously measured BMRs for numbats (Cooper  
296 and Withers 2002; McNab 1984). This increased winter BMR is presumably related to  
297 increased thermogenic capacity for thermoregulation during the cool winter months, and  
298 for wild numbats a seasonal change in food availability. An increased winter BMR is  
299 consistent with seasonal effects observed for a number of small placental mammals  
300 (Grodzinski and Wunder 1975; Heldmaier and Steinlechner 1981; Lynch 1973;  
301 McDevitt and Speakman 1996; Merritt 1986; Merritt et al. 2001), and some marsupials

302 such as the grey short-tailed opossum (*Monodelphis domestica*—Dawson and Olson  
303 1988) and cold-acclimated kowari (*Dasyuroides byrnei*—Smith and Dawson 1984).

304         There was no change in thermal conductance with season, despite many other  
305 mammals having a lower thermal conductance during winter (Heldmaier and  
306 Steinlechner 1981; Holloway and Geiser 2001; Withers 1992). Maximizing external  
307 radiative heat gain at the expense of improving endogenous heat conservation may be  
308 an energetically more favorable strategy for diurnal numbats, as decreasing thermal  
309 conductance during winter may reduce the ability of numbats to gain solar heat. Solar  
310 heat gain is potentially important for numbats to conserve energy otherwise needed for  
311 thermoregulation (Cooper et al. 2003a). As for southern brown bandicoots (Larcombe  
312 and Withers 2008), there was also no seasonal effect on standard EWL for numbats,  
313 although western barred bandicoots (*Perameles bougainville*) from the same study site  
314 had higher rates of EWL during summer (Larcombe and Withers 2006).

315         For captive numbats,  $T_a$  had a significant effect on all of the physiological  
316 parameters that we measured, with the patterns of response expected from previous  
317 physiological data for numbats (Cooper and Withers 2002). However, seasonal effects  
318 were not restricted to standard physiological variables; we also found seasonal  
319 differences in physiological responses to more extreme  $T_a$ s.

320         For captive numbats,  $T_b$  increased with  $T_a$  (Fig 1) in both winter and summer,  
321 but  $T_b$  would have had to increase in winter to about 36 °C at a  $T_a$  of 32.5 °C (compared  
322 to the actual  $T_b$  of 35.1 °C) to maintain thermal balance had their EWL not increased  
323 markedly (calculated assuming a constant  $C_{dry}$ ). Metabolic rate increased in both  
324 seasons at low  $T_a$ , as has been previously reported for numbats (Cooper and Withers  
325 2002) and is the typical thermal response of an endotherm. RER increased with  $T_a$  for  
326 numbats in summer, but there was no pattern for winter numbats, which had a relatively  
327 low RER at all  $T_a$ . This suggests a seasonal nutritional effect; summer numbats are



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498           **Table 1.**—Mass, body temperature ( $T_b$ ), basal metabolic rate (BMR),  
499 evaporative water loss (EWL) and wet thermal conductance ( $C_{wet}$ ) within the  
500 thermoneutral zone ( $T_a = 30$  °C) of captive and wild, free-living numbats in summer and  
501 winter, where  $n$  = number of individuals. \* indicates a significant difference between  
502 season and • indicates a significant difference between captive and wild numbats by  
503 two-way ANOVA. Sample sizes are as indicated, except  $n = 5$  for EWL and  $C_{dry}$  captive  
504 winter;  $n = 4$  for  $VO_2$ ,  $C_{wet}$  and  $C_{dry}$  for wild summer.

505

506           **Fig 1.** —Effect of  $T_a$  on body temperature, metabolic rate, thermal conductance  
507 ( $C_{wet}$  represented with solid lines and circles,  $C_{dry}$  with dashed lines and triangles) and  
508 evaporative water loss for captive numbats in summer (white symbols) and winter (dark  
509 symbols). Values are mean  $\pm SE$ ,  $n = 4-5$ .

**Table 1.**—Mass, body temperature ( $T_b$ ), basal metabolic rate (BMR), evaporative water loss (EWL) and wet thermal conductance ( $C_{wet}$ ) within the thermoneutral zone ( $T_a = 30\text{ °C}$ ) of captive and wild, free-living numbats in summer and winter, where  $n$  = number of individuals. \* indicates a significant difference between season and • indicates a significant difference between captive and wild numbats by two-way ANOVA. Sample sizes are as indicated, except  $n = 5$  for EWL and  $C_{dry}$  captive winter;  $n = 4$  for  $VO_2$ ,  $C_{wet}$  and  $C_{dry}$  for wild summer.

	Captive		Wild	
	Summer ( $n = 5$ )	Winter ( $n = 6$ )	Summer ( $n = 5$ )	Winter ( $n = 4$ )
Mass (g)	563 ± 20.8	512 ± 18.5	482 ± 28.2	505 ± 9.22
$T_b$ (°C) *•	34.5 ± 0.43	35.3 ± 0.20	32.9 ± 0.18	35.3 ± 0.39
BMR ( $VO_2$ ; ml $O_2$ $g^{-1}$ $h^{-1}$ ) *	0.38 ± 0.026	0.50 ± 0.058	0.37 ± 0.032	0.48 ± 0.067
BMR ( $VCO_2$ ; ml $CO_2$ $g^{-1}$ $h^{-1}$ ) *	0.38 ± 0.027	0.24 ± 0.027	0.31 ± 0.014	0.34 ± 0.016
RER ( $VCO_2/VO_2$ ) *	1.00 ± 0.036	0.58 ± 0.088	0.76 ± 0.10	0.77 ± 0.146
EWL (mg $H_2O$ $g^{-1}$ $h^{-1}$ )	0.42 ± 0.069	0.31 ± 0.063	0.56 ± 0.132	0.53 ± 0.059
$C_{wet}$ ( $J$ $g^{-1}$ $h^{-1}$ $°C^{-1}$ )	1.86 ± 0.185	1.96 ± 0.223	2.67 ± 0.284	1.76 ± 0.181
$C_{dry}$ ( $J$ $g^{-1}$ $h^{-1}$ $°C^{-1}$ )	1.63 ± 0.186	1.68 ± 0.189	2.13 ± 0.284	1.52 ± 0.179

