1 **Patterns of body temperature variation and torpor in the numbat, *Myrmecobius***

2 ***fasciatus* (Marsupialia: Myrmecobiidae).**

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4 Cooper, C.E. and Withers, P.C.*

5

6 Zoology, School of Animal Biology M092

7 University of Western Australia

8 Stirling Highway

9 Crawley 6009 Western Australia

10 e-mail ccooper@graduate.uwa.edu.au
11   pwithers@cyllene.uwa.edu.au
12
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27 *Corresponding Author**:**

28   Professor Philip Withers

29   Zoology, School of Animal Biology M092

30   University of Western Australia

31   Crawley WA 6009 Western Australia

32 Ph +61 8 6488 2235
33 Fax +61 8 6488 1029
34 E-mail   pwithers@cyllene.uwa.edu.au

Abstract

35
36 1. Body temperature (T_b) radio-telemetric data for the diurnal numbat indicated a strong
37 nychthemeral rhythm, being higher during the day. 2. Mean daily T_b was 34.4 ºC, but was
38 higher in spring and summer than winter. 3. All three numbats showed spontaneous,
39 shallow daily torpor; minimum torpor T_b was 19.1 ºC, and maximum torpor duration was
40 15.3 h. 4. Cooling and arousal rates were slow for numbats compared to other marsupials
41 (1.6 and 7.1 ºC h^{-1} respectively). 5. Torpor was calculated to reduce the daily energy
42 expenditure of a wild numbat in a burrow by 13 to 42 % over 12.5 h.

43
44 **Keywords**: numbat, marsupial, *Myrmecobius fasciatus*, body temperature, conductance,
45 hypothermia, torpor
46
47
48 **Introduction**

49 The numbat (*Myrmecobius fasciatus*) is a small to medium sized marsupial that once
50 inhabited much of southern Australia. However, since European settlement, the range of
51 the numbat has been drastically reduced to only a few areas of open forest and woodland
52 in the south-west of Western Australia. It is now considered to be endangered. Numbats
53 belong to the monospecific marsupial family Myrmecobiidae and are unique amongst
54 marsupials as they are diurnal and feed exclusively on termites.

55

56 A termitivorous diet is commonly perceived to have a low energy density (McNab 1984;
57 Redford and Dorea 1984), and therefore numbats may limit endogenous heat production
58 for thermoregulation to reduce their energy expenditure. This, together with their semi-
59 fossorial habit, diurnal activity (Calaby 1960a,b; Maisy and Bradbury 1983; Christensen
60 *et al*. 1984; Cooper 2004), a pelt that is adapted for solar heat acquisition (Cooper *et al*.
61 2003a) and anecdotal reports of sun-basking (Calaby 1960a,b; Serventy and Raymond
62 1973), suggest that numbats may rely extensively on behavioural rather than
63 physiological means for thermoregulation, and be thermolabile. However, laboratory
64 studies of metabolism and body temperature (T_b) regulation indicate that numbats are
65 capable of precise physiological regulation of T_b during rest, over a range of ambient
66 temperatures (T_a) from 10 to 32.5 ºC (Cooper and Withers 2002, Cooper 2004), at least
67 in the short-term ($\leq$10 h).

68 No quantitative data are available on the thermal biology of numbats in the field. There is

69 an anecdotal report of torpor (Serventy and Raymond 1973), and as numbats are most

70 closely related to dasyurids (Baverstock *et al.* 1990) it is possible that they too may use

71 torpor to conserve energy either when food is scarce or under adverse environmental

72 conditions. Shallow daily torpor, where the minimum T_b (T_{bmin}) is 11-28 ºC and torpor

73 bouts last 2-19.5 h, occurs in all dasyurid marsupials so far investigated, and is

74 spontaneous (occurs when food is freely available) in some species and induced (by food

75 shortage) in others (Geiser 1994; 2003). Torpor may be of particular importance for the

76 numbat, which feeds on a termite diet with a low energy density and is temporally and

77 spatially variable (Redford and Dorea 1984). We investigate T_b for unrestrained, captive

78 numbats, and for a wild, free-living numbat, to determine long-term patterns of seasonal

79 and daily T_b variation, and evaluate what role controlled hypothermia and/or torpor might

80 play in energy conservation.

81

82 **Materials and Methods**

83 T_b was measured for three unrestrained adult male numbats using temperature radio-

84 telemetry. Only three individuals were available due to the endangered status of numbats;

85 however this number has proven sufficient to investigate the basic patterns of T_b

86 variation, controlled hypothermia and torpor in numbats. Two numbats (CB and CW)

87 were maintained in captivity at Perth Zoo (South Perth 31º 58' S 115º 51' E). CB was a

88 captive-bred numbat, 6 years old. CW was a wild-caught numbat (originally from

89 Dryandra Woodland, 31º 46' S 117º 1' E), approximately 2 years old, that had been held

90 in captivity for 1 year. The captive numbats were housed in large (10 x 2.5 x 2.5 m)

91 outdoor wire enclosures, where they experienced natural conditions of weather and

92 photoperiod. Their enclosures contained two nest boxes, with dried seagrass and couch

93 grass for nest material. Cages had a natural substrate (combination of sand and laterite)

94 and contained rocks, stumps, hollow logs, branches, small shrubs and tussock grasses for

95 environmental enrichment and shelter. During daylight hours, each cage had areas of both

96 full sunlight and shade. The numbats were fed by staff at 0900 and 1300 hours daily, with

97 80 g of artificial custard diet consisting of eggs, powdered low-lactose milk formula,

98 calcium and vitamin supplements, baked termite mound, and termites. Fresh water was

99 available at all times.

100

101 The other radio-telemetered numbat (WLD) was free-living (age unknown, but ≥ 2 years)

102 and maintained a territory in the southern area of the main block of Dryandra Woodland.

103 WLD had been previously fitted with a radio-collar (Biotrack TWS, 7 gm) as part of the

104 Department of Conservation and Land Management's numbat research program. He was

105 captured by hand, and transported to Perth Zoo, where he was held in quarantine in the

106 Veterinary Department for a week prior to implantation of the temperature telemeter.

107

108 The temperature telemeters (Sirtrack, 3 g) were coated with a biologically inert wax

109 (Elvax), and calibrated in a water bath, at T_as from 5 to 45 ºC, in 5 ºC increments. The

110 temperature of the water bath was measured to ± 0.1 ºC with a thermometer traceable to a

111 national standard. Calibration curves were obtained for telemeters using the data logging

112 system used for each telemeter (see below), and were also checked by manual counts

113 with a stopwatch.

114

115 The temperature telemeters were implanted into the abdominal cavity of each numbat.

116 Surgery was performed under general anesthesia (isoflurane, administered via a face

117 mask using a Bain's anaesthetic circuit attached to a CIG Midget 3 anaesthetic machine).

118 A small midline abdominal incision was made, the telemeter inserted, and then the

119 incision sutured closed. Captive numbats were returned to their enclosures on recovery

120 from anesthesia, whereas the wild numbat was held in quarantine at Perth Zoo for a week

121 after surgery before being released at the site of capture. Data obtained in the fortnight

122 after surgery were discarded for all numbats.

123

124 The T_b of CW and CB was monitored from 5/7/2001 to 28/2/2002 (the battery life of the

125 telemeters), with 90 days of T_b data recorded for CW and 65 days for CB, using a

126 Biotelemetry Rx3 receiver, antenna and data logger, powered by a 12 V deep-cycle car

127 battery. The Rx3 recorded the number of pulses for each telemeter's frequency in

128 alternate minutes, along with the date and time. The logger was activated, and the data

129   downloaded to a PC (using Biomain software). The number of pulses min^{-1} was

130   converted to a T_b using the calibration curve for each telemeter. T_b was plotted against

131   time, and any obviously unusual values resulting from interference or from missing

132   values (usually resulting from the numbat moving so that there were two sections of wire

133   mesh between him and the antenna) were deleted manually.

134

135   WLD's T_b was monitored for two consecutive nights every 1-3 weeks from 28/4/2003

136   until 20/8/2003, with at total of 20 nights of T_b data obtained. On dusk (just after the time

137   he would have retired for the night) he was radio-tracked to his night retreat, and his T_b

138   was then monitored using an AOR AR8000 receiver and R8000 interface (with a Sirtrack

139   antenna), interfaced with a Toshiba laptop PC, which ran a custom-written VB data

140   acquisition program. The AR8000 and laptop were powered by a 12 V car battery, and

141   were set up and left running next to his retreat. The time of each pulse from the implanted

142   temperature telemeter was recorded, as were pulses from another ambient temperature

143   (T_a) telemeter which was placed nearby, for alternating 1 min periods. The resulting data

144   were analysed using a custom-written VB analysis program, where the interval between

145   each pulse was calculated, and values which varied by more than 95 % of the median for

146   each 1 min set of T_b values were discarded. These pulse intervals were then converted to

147   frequencies, and T_bs calculated from the calibration curve for each telemeter. The data

148   logging system was left in place until the numbat left his retreat the following day (when

149   he would move out of range of the receiver). Some daytime T_b's were recorded by radio-

150   tracking the numbat until we were close enough to receive the signal from his T_b

151   telemeter (he would hide in a hollow log when we were this close) and recording the time

152   for 30 pulses with a stopwatch. T_a was recorded in a similar manner with another

153   telemeter immediately after.

154

155   T_b data were then analysed for all numbats using another custom written VB program to

156   calculate the required T_b characteristics (*e.g.* minimum and maximum T_b, mean daily and

157   nightly T_b, and T_b when torpid; Figure 1), and the associated times of day. Torpor was

158   defined as $T_b < 30$ °C (Geiser 1987, 1988). Cooling and arousal rates were calculated

159   from the slope of the regression line of T_b and time during cooling and arousal.

160   Temperature values are presented as mean ± S.E., unless stated otherwise. Differences

161   between numbats and seasons were determined by ANOVA, and relationships between

162   T_b and T_a by correlation. Mean values for times of day were calculated by circular

163   descriptive statistics, and time values are presented as mean ± S.D. (there is no S.E.

164   equivalent for circular statistics) All statistical tests were preformed using *statisti*XL v1.3

165   (www.statistixl.com).

166

167   **Results**

168   *Captive numbats*

169   The captive numbats had a strong nychthemeral T_b rhythm, being higher during the day

170   and lower at night (Figure 2). The two captive numbats had overall mean daytime active

171   T_bs ($T_{b,active}$) of 37.4 ± 0.13 (CW) and 37.7 ± 0.07 ℃ (CB), and there was no significant

172   seasonal effect ($F_{2,144} = 2.6$, $p = 0.078$). Daily T_b maxima ($T_{b,max}$) all occurred between

173   sunrise and sunset (1148 h ± 29.4 min, CW and 1150 h ± 37.2 min, CB). There was no

174   significant seasonal influence on $T_{b,max}$ ($F_{1,144} = 2.5$, $p = 0.084$).

175

176   Overall mean minimum T_b ($T_{b,min}$; Table 1) occurred at 0525 h ± 22.2 min (CW) and

177   0526 h ± 25.2 min (CB) respectively. There was a highly significant effect of season on

178   $T_{b,min}$ ($F_{2,142} = 27.7$, $p < 0.001$), with all seasons differing significantly from one another

179   (SNK $p < 0.008$) and $T_{b,min}$ being lowest in winter and highest in summer. The lowest

180   $T_{b,min}$ recorded was 19.4 ℃ for CW and 20.2 ℃ for CB. Mean daily T_b range (when not

181   torpid) was 5.7 ± 0.2 (CW) and 5.8 ± 0.25 ℃ (CB). This range differed significantly with

182   season ($F_{2,84} = 6.8$, $p = 0.002$), with the range being smaller in summer than in winter or

183   spring (SNK $p < 0.018$).

184

185   Both captive numbats entered spontaneous, daily torpor (Figure 2), most frequently in

186   winter (85.7 % of nights during winter, 37.8 % during spring and 20.8 % during summer

187   for CW and 57.9 % of nights during winter, 32.3 % during spring and never during

188   summer for CB). The overall mean torpor duration for CW was 4.3 ± 0.39 h, with torpor

189   beginning at 0344 h ± 33.6 min and ending at 0756 h ± 30.6 min. For CB, overall mean

190   torpor duration was 4.1 ± 0.47 h, with torpor beginning at 0321 h ± 57 min and ending at

191 0700 h ± 41.4 min. The longest torpor bouts recorded for these numbats were 9.7 h (CW)

192 and 9.2 h (CB).

193

194 There was a highly significant seasonal effect on mean T_b during torpor ($T_{b,torpor}$; $F_{1,50}$ =

195 16.8 p < 0.001) for the captive numbats, with $T_{b,torpor}$ being lower in winter (25.1 ± 0.35

196 ºC, CW; 27.5 ± 0.31 ºC, CB) than in spring (27.9 ± 0.43 ºC, CW; 28.2 ± 0.52 ºC, CB).

197 Season also had a significant influence on the $T_{b,min}$ attained during torpor ($F_{1,54}$ = 9.3, p =

198 0.004). Mean arousal rates were significantly influenced by season ($F_{1,55}$ = 24.4, p <

199 0.001), being higher in winter (10.2 ± 0.75 ºC h^{-1}, CW; 7.8 ± 1.14 ºC h^{-1}, CB) than in

200 summer (5.0 ± 0.69 ºC h^{-1}, CW; 5.0 ± 0.72 ºC h^{-1}, CB). Season did not significantly

201 influence cooling rates ($F_{1,55}$ = 0.92, p = 0.341).

202

203 Although we were only able to study 2 captive numbats, there were many significant

204 differences between the individuals in their pattern of thermoregulation (Table 1). $T_{b,active}$

205 ($F_{1,144}$ = 9.6, p = 0.002), $T_{b,max}$ ($F_{1,144}$ =16.3, p <0.001), $T_{b,min}$ ($F_{1,142}$ = 13.5, p < 0.001),

206 $T_{b,torpor}$ ($F_{1,55}$ = 10.1, p = 0.002), $T_{b,min}$ during torpor ($F_{1,54}$ = 9.2, p = 0.004) and cooling

207 rates ($F_{1,55}$ = 5.0, p = 0.029) differed between individuals, and there were significant

208 interactions between season and numbat (p < 0.004).

209

210 *Wild Numbat*

211 WLD used burrows, hollow logs and tree hollows as night retreats during the study

212 period. There was no significant effect of T_a on retreat type ($F_{2,16}$ = 0.06, p = 0.945), and

213 there was no relationship between mean nightly T_a and T_b ($F_{1,15}$ = 0.029, p = 0.868). The

214 time that WLD first became active (left his retreat), obtained from the time that his T_b

215 telemetry signal disappeared due to the short range and specific positioning of the

216 receiving/logging equipment, was 0940 h ± 22.8 min, and his mean T_b when activity

217 commenced was 35.0 ± 0.26 ºC. WLD's daytime T_b, measured during his activity period,

218 ranged from 36.6-40.0 ºC (Table 1). Active T_bs were recorded over the T_a range 10.1-

219 16.8 ºC, and there was no significant relationship between T_b whilst active and T_a ($F_{1,8}$ =

220 3.81, p = 0.087). WLD's $T_{b,min}$ (Table 1) ranged from 19.1–34.4 ºC and was significantly

221 higher in autumn (29.2 ± 2.38) than in winter (23.0 ± 1.41; $F_{1,15}$ = 5.7, p = 0.031). The

222 mean time of $T_{b,min}$ was 0649 h ± 35.4 min. Mean $T_{b,min}$ when torpor did not occur (*i.e.*

223 when $T_{b,min} > 30$ ºC) was 32.5 ± 0.60 ºC.

224

225 The wild numbat entered torpor on 28.6 % of nights in autumn and 90 % during winter.

226 Torpor began at 2213 h ± 3 h 35 min, ending at 0848 h ± 24 min, with the longest

227 recorded torpor duration being 15.3 h (1817 h to 0934 h; Table 1). The mean $T_{b,torpor}$ for

228 WLD was 24.8 ± 0.62 ºC. His mean cooling rate was 1.1 ± 0.12 ºC h^{-1} and his mean

229 arousal rate 7.6 ± 0.53 ºC h^{-1}. There was no relationship between these rates and T_a ($F_{1,11}$

230 = 0.005, p = 0.43; $F_{1,11}$ = 1.37, p = 0.266 respectively). One day (26/7/2003) the numbat

231 did not leave his burrow due to inclement weather, and his T_b was monitored

232 continuously during this time (Figure 3). The time of arousal from torpor on the first day

233 was typical (0800 h), and his T_b increased at a typical rate of 7.9 ºC h^{-1} to a maximum of

234 37.3 ºC at 1300 h, whilst in his burrow. After this, T_b declined at a rate of 0.78 º C h^{-1}, he

235 entered torpor again at 1817 h, and attained a minimum T_b of 19.5 ºC again at 0740 h the

236 following morning.

237

238 **Discussion**

239 *Daily patterns of T_b*

240 The numbat's T_b rhythm was typical of that for other endothermic mammals (Refinetti

241 and Menaker 1992), being higher during its active phase than during its inactive phase

242 (Figure 2). Unlike nocturnal marsupials (Guiler and Heddle 1974; Geiser 1986; Rose *et*

243 *al*. 1990; Gemmell *et al*. 1997) which have maximal T_bs during the night, the diurnal

244 numbat's T_b was highest during the daytime and lowest at night, with maximum T_bs

245 recorded around midday and minimum T_bs around 0600 h.

246

247 The numbat's T_b showed a mean daily variation of almost 6 ºC when not entering torpor,

248 which is greater than the range of around 2 ºC typical for other non-torpid Australian

249 marsupials (Guiler and Heddle 1974; Brown and Dawson 1977; Geiser 1986; Rose *et al*.

250 1990; Gemmell *et al*. 1997) but is similar to that of antelope ground squirrels (Chappell

251 and Bartholomew 1981). This large range results from fairly typical mean $T_{b,max}$ values

252 (37.7-38.2 ºC), but quite low mean $T_{b,min}$ values (32.1-32.4 ºC). This mild and controlled

253 nocturnal hypothermia is presumably associated with a reduced metabolic rate, which

254 would be important for energy conservation, especially since being inactive at night when

255 T_as are lower would be associated with higher resting energetic demands. Like the

256 numbat, variation in the T_b of antelope ground squirrels is also around 6 ºC, and also

257 results from a reduced minimum T_b rather than an increased maximum T_b (Chappell and

258 Bartholomew 1981).

259

260 *Torpor*

261 This study confirms an anecdotal report (Serventy and Raymond 1973) that numbats

262 enter torpor. All of the dasyurid species that have been examined (approximately 50 % of

263 all Australian dasyurids) utilise torpor to some extent (Geiser 2003). As numbats are most

264 closely related to the family Dasyuridae within the Marsupialia (Baverstock *et al.* 1990),

265 it is not surprising that they too use torpor to help balance their energy budgets. The

266 shallow, daily torpor pattern that we observed for numbats is typical of dasyurid

267 marsupials (Geiser 1994; 2003), with torpor bouts lasting < 24 h and T_{bmin} during torpor

268 > 11 ºC (minimum recorded T_{bmin}19.1 ºC). Since torpor in numbats is spontaneous,

269 occurring when food is freely available (*e.g.* torpor occurred frequently in captive

270 numbats fed equivalent amounts of food year round), it appears to be part of the daily

271 cycle in colder months to reduce energy expenditure rather than a response to acute

272 energy stress (Geiser 2003). However torpor depth and duration are variable day to day,

273 and vary somewhat between individuals, so these may be adaptive to daily energy intake.

274

275 Numbats typically entered torpor in the early mornings (around 0330 h), and became

276 normothermic again about mid morning (around 0800 h). Nocturnal dasyurids generally

277 enter torpor in the early morning, and torpor continues into the daily rest phase, with

278 arousal occurring in the late morning or afternoon. Diurnal numbats, however, arouse

279 from torpor at around 0800 h (even when remaining inactive for the day), as their activity

280 phase is during the day (Figure 2). If torpor is extended, the increased duration occurs by

281 entering torpor earlier (*i.e.* late at night rather than early morning) rather than staying

282 torpid towards midday or early afternoon. This enables the numbats to be ready for

283 activity during the day, when termites are most abundant (Maisey and Bradbury 1983;

284   Christensen *et al.* 1984; Friend 1986). WLD's maximum torpor duration (15.3 h) is

285   longer than that predicted for marsupials (8.8 h) from the relationship log duration (h) =

286   2.88 − 1.51 log T_{bmin} (determined for captive dasyurids; Geiser 1994). This extended

287   torpor duration increases nightly energy savings, which is presumably important for the

288   termitivorous numbat.

289

290   The cooling rates of the numbats were very slow, and all three numbats also had slow

291   arousal rates, compared to other marsupials. The mean arousal rate for the three numbats

292   was 7.1 °C h^{-1}, which is only 35 % of that predicted for marsupials (overall arousal rate)

293   from the equation log arousal rate (°C min^{-1}) = -0.174 $\log_{10}$ mass(g) + 0.006 (Geiser and

294   Baudinette 1990), suggesting that perhaps the metabolic scope of numbats is lower than

295   that of other marsupials. There was no relationship between T_a and arousal rate for WLD.

296   Generally there is a strong effect of T_a on arousal rates for marsupials, with arousal rate

297   increasing with increasing T_a (Geiser and Baudinette 1987, 1988). However the effect of

298   temperature on arousal rate is greater for small species (which have a high surface

299   area/volume ratio) than larger species, so perhaps for the numbat, which has a

300   comparatively large body mass, the effect of T_a is very much reduced. In addition, the use

301   of night refuges, especially burrows, buffers numbats from outside T_a (Cooper 2004) so

302   that environmental T_a during arousal has little if any impact on the numbats.

303

304   *Calculated metabolic rates*

305   To estimate the energetic significance of nightly hypothermia and torpor, it is necessary

306   to know the metabolic rate of numbats at various T_bs. Unfortunately, the numbats would

307   not enter torpor in a laboratory metabolic system, but we can estimate the metabolic rate

308   of hypothermic and torpid numbats (Figure 4). Calculated metabolic rates (VO_{2calc}; ml O_2

309   min^{-1}) were estimated for WLD when in a burrow after Withers *et al.* (1990) from the

310   equation $\Delta T_b = 20.1[VO_{2calc}–C(T_b-T_a)]/(m.SH)$, where ΔT_b is the change in T_b (°C min^{-1};

311   calculated from a running average of 20 min of T_b values), C is thermal conductance (ml

312   O_2 °C^{-1} min^{-1}), m is body mass (g), SH is the specific heat of tissues (3.47 J g^{-1} °C^{-1}) and

313   1 ml O_2 is assumed to be equivalent to 20.1 J. Thermal conductance was the sum of

314   numbat resistance (R = 1/C; C from Cooper and Withers 2002) and nest resistance (R_{nest}

315 = $1/C_{nest}$; C_{nest} from Cooper 2004). T_a was assumed to be 11.7 °C (mean T_a within a

316 numbat burrow in winter, Cooper 2004), and as burrows remain at a constant temperature

317 overnight, VO_{2calc} was only estimated for WLD when in a burrow, not when in a log or

318 tree hollow, or for captive numbats in a nest box where T_a is variable (Cooper 2004).

319

320 From these estimates of VO_2, WLD was calculated to conserve 6.6 kJ over 9 h (0.73 kJ h$^-$

321 ^{1}) by nightly hypothermia (T_b drop of 1.7 °C; this calculation accounts for the energetic

322 cost of re-warming). Calculated energy savings resulting from nightly hypothermia by

323 antelope ground squirrels were similar, approximately 9.5 kJ over 14 h (0.68 kJ h^{-1};

324 Chappell and Bartholomew 1981). The energy conserved by lowering T_{bmin} during

325 nocturnal hypothermia may be particularly important for numbats which feed on a low-

326 energy termitivorous diet, with this small change in T_b reducing the numbat's required

327 daily food intake by approximately 425 termites (assuming 0.015 kJ of assimilated

328 energy per termite, Cooper and Withers 2004).

329

330 Calculated VO_2 values for WLD in a burrow indicated substantial energy savings from

331 torpor (Figure 4). By decreasing T_b by an average of 9.5 °C for 12.5 h, WLD reduced

332 energy expenditure by 34.1 kJ, while a reduction in T_b of 11.3 °C for the same time

333 resulted in a saving of 114.7 kJ. This energy saving equates to 13 - 42 % of the numbat's

334 field metabolic rate (Cooper *et al*. 2003b) and savings of 2208 - 7440 termites (Cooper

335 and Withers 2004). Note that these calculations included entry into and the metabolic

336 'overshoot' for arousal from torpor (Figure 4), which reduces the energetic advantage of

337 torpor. When T_b was low (19.8°C) for WLD in his burrow, VO_{2calc} was only 0.28 ml O_2 g$^-$

338 ^{1} h$^-$ which is 72 % of BMR (0.39 ml O_2 g^{-1} h^{-1}) and 20.4 % of resting metabolic rate

339 (RMR; 1.37 ml O_2 g^{-1} h^{-1} at T_a = 11.7 °C; Cooper and Withers 2002). However this

340 reduction in MR is smaller than in other marsupials during torpor and reflects the

341 comparatively high $T_{b,min}$ of the numbat.

342

343 *Season*

344 Season appears to have a strong affect on the occurrence and pattern of daily torpor in the

345 numbat. Torpor bouts were significantly more frequent, deeper and longer in winter than

in spring or summer for captive numbats (housed outdoors with natural weather and photoperiod). The wild numbat also showed seasonal variation, with more frequent, longer and deeper torpor bouts in winter compared to autumn. Seasonal variation has been observed in aspects of daily torpor for other dasyurids. Fat-tailed and striped-faced dunnarts (*Sminthopsis crassicaudata* and *S. macroura*), and kowari (*Dasyuroides byrnei*) all showed an increased tendency to enter torpor during winter than in other seasons, presumably due to exposure to lower T_a and reduced food availability during winter (Geiser and Baudinette 1987). Like the two dunnarts, numbats appeared to have a lower setpoint for $T_{b,min}$ during torpor in winter than in other seasons. However, unlike other daysurids utilising daily torpor, numbats also showed seasonal variation in the duration of torpor bouts, with longer bouts in winter compared to other seasons. Therefore, unlike dunnarts that achieve seasonal adjustment of energy budgets by reducing the depth of torpor, numbats use a combination of increased depth and increased duration to reduce their energy expenditure in winter.

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452 **Table 1:** Body temperature variables for unrestrained, captive, wild-caught (CW) and

453 captive born (CB), and free-living (WLD) numbats. Sample size is given in parentheses.

|	CW	CB	WLD
$T_{b, active}$ (ºC)	37.4 ± 0.13 (90)	37.7 ± 0.07 (65)	35.0 ± 0.26 (17)[a]
$T_{b, max}$ (ºC)	37.7 ± 5 (90)	38.2 ± 4.7 (65)	38.3 ± 0.25 (6)
$T_{b, min}$ (ºC)	29.1 ± 0.47 (90)	30.1 ± 0.43 (65)	25.4 ± 1.45 (17)
Lowest $T_{b, min}$ (ºC)	19.4	20.2	19.1
Non-torpid $T_{b, min}$ (ºC)	32.1 ± 0.2 (51)	32.4 ± 0.26 (37)	32.5 ± 0.6 (6)
Torpor duration (h)	4.3 ± 0.39 (33)	4.1 ± 0.47 (23)	9.7 ± 1.2 (17)
$T_{b, torpor}$ (ºC)	26.4 ± 0.36 (33)	27.9 ± 0.32 (23)	24.8 ± 0.70 (13)
Torpor $T_{b, min}$ (ºC)	24.8 ± 4.07 (33)	26.8 ± 0.53 (23)	21.8 ± 3.3 (11)
Cooling rate (ºC h^{-1})	2.1 ± 0.11 (33)	1.7 ± 0.13 (23)	1.1 ± 0.12 (13)
Arousal rate (ºC h^{-1})	7.8 ± 0.69 (33)	6.1 ± 0.68 (23)	7.6 ± 0.53 (13)

454 [a]mean T_b when activity commences (ºC).

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Figure 1: The body temperature (T_b) of a numbat over 24 h, showing the periods used to
calculate various T_b parameters (see text). The dark bars indicate the period between
sunset and sunrise.
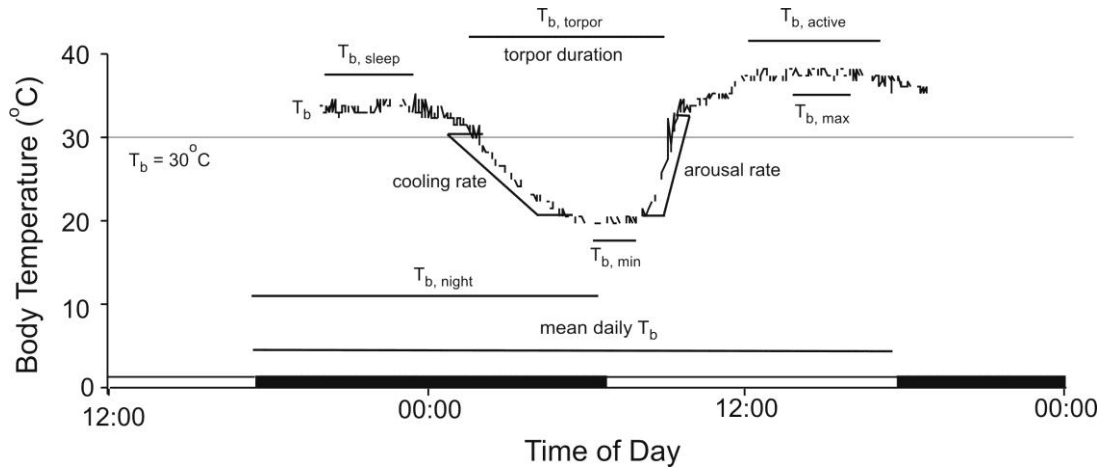
465 **Figure 2:** Body temperature (T_b) of a captive numbat (CW) over four consecutive days,
466 where the dark bars indicate the period between sunset and sunrise.
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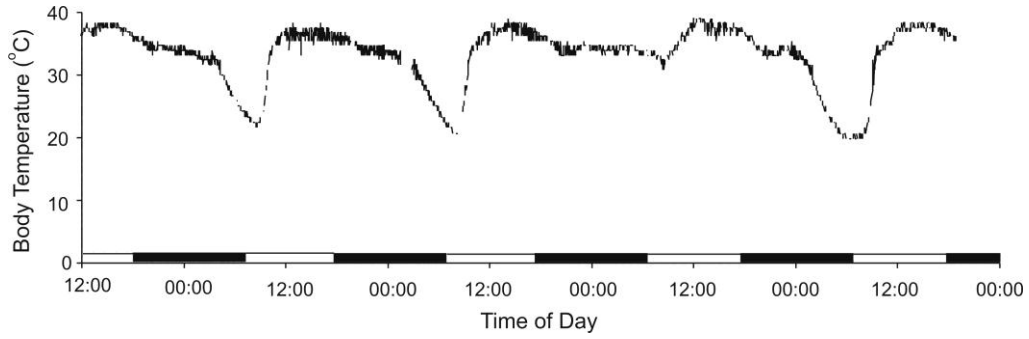
473 **Figure 3:** Body temperature (T_b) and ambient temperature (T_a) of a wild numbat (WLD)
474 that was in a burrow, over 48 hours. The dark bars indicate the period between sunset and
475 sunrise.
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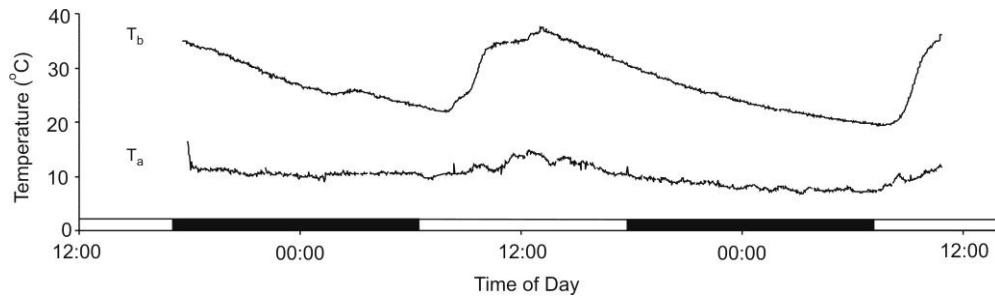
478   **Figure 4:** Body temperature (T_b) and calculated metabolic rate (MR_{calc}) of a wild numbat
479   overnight while in a burrow, showing an episode of torpor.
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