Patterns of body temperature variation and torpor in the numbat, *Myrmecobius fasciatus* (Marsupialia: Myrmecobiidae).

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

Zoology, School of Animal Biology M092
University of Western Australia
Stirling Highway
Crawley 6009 Western Australia

e-mail ccooper@graduate.uwa.edu.au
pwithers@cyllene.uwa.edu.au

*Corresponding Author:
Professor Philip Withers
Zoology, School of Animal Biology M092
University of Western Australia
Crawley WA 6009 Western Australia

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

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

Keywords: numbat, marsupial, *Myrmecobius fasciatus*, body temperature, conductance, hypothermia, torpor

Introduction

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

A termitivorous diet is commonly perceived to have a low energy density (McNab 1984; Redford and Dorea 1984), and therefore numbats may limit endogenous heat production for thermoregulation to reduce their energy expenditure. This, together with their semi-fossorial habit, diurnal activity (Calaby 1960a,b; Maisy and Bradbury 1983; Christensen *et al*. 1984; Cooper 2004), a pelt that is adapted for solar heat acquisition (Cooper *et al*. 2003a) and anecdotal reports of sun-basking (Calaby 1960a,b; Serventy and Raymond 1973), suggest that numbats may rely extensively on behavioural rather than physiological means for thermoregulation, and be thermolabile. However, laboratory studies of metabolism and body temperature ($T_b$) regulation indicate that numbats are capable of precise physiological regulation of $T_b$ during rest, over a range of ambient temperatures ($T_a$) from 10 to 32.5 °C (Cooper and Withers 2002, Cooper 2004), at least in the short-term (≤10 h).
No quantitative data are available on the thermal biology of numbats in the field. There is an anecdotal report of torpor (Serventy and Raymond 1973), and as numbats are most closely related to dasyurids (Baverstock et al. 1990) it is possible that they too may use torpor to conserve energy either when food is scarce or under adverse environmental conditions. Shallow daily torpor, where the minimum $T_b (T_{b\min})$ is 11-28 °C and torpor bouts last 2-19.5 h, occurs in all dasyurid marsupials so far investigated, and is spontaneous (occurs when food is freely available) in some species and induced (by food shortage) in others (Geiser 1994; 2003). Torpor may be of particular importance for the numbat, which feeds on a termite diet with a low energy density and is temporally and spatially variable (Redford and Dorea 1984). We investigate $T_b$ for unrestrained, captive numbats, and for a wild, free-living numbat, to determine long-term patterns of seasonal and daily $T_b$ variation, and evaluate what role controlled hypothermia and/or torpor might play in energy conservation.

**Materials and Methods**

$T_b$ was measured for three unrestrained adult male numbats using temperature radio-telemetry. Only three individuals were available due to the endangered status of numbats; however this number has proven sufficient to investigate the basic patterns of $T_b$ variation, controlled hypothermia and torpor in numbats. Two numbats (CB and CW) were maintained in captivity at Perth Zoo (South Perth 31° 58’ S 115° 51’ E). CB was a captive-bred numbat, 6 years old. CW was a wild-caught numbat (originally from Dryandra Woodland, 31° 46’ S 117° 1’ E), approximately 2 years old, that had been held in captivity for 1 year. The captive numbats were housed in large (10 x 2.5 x 2.5 m) outdoor wire enclosures, where they experienced natural conditions of weather and photoperiod. Their enclosures contained two nest boxes, with dried seagrass and couch grass for nest material. Cages had a natural substrate (combination of sand and laterite) and contained rocks, stumps, hollow logs, branches, small shrubs and tussock grasses for environmental enrichment and shelter. During daylight hours, each cage had areas of both full sunlight and shade. The numbats were fed by staff at 0900 and 1300 hours daily, with 80 g of artificial custard diet consisting of eggs, powdered low-lactose milk formula,
calcium and vitamin supplements, baked termite mound, and termites. Fresh water was available at all times.

The other radio-telemetered numbat (WLD) was free-living (age unknown, but ≥ 2 years) and maintained a territory in the southern area of the main block of Dryandra Woodland. WLD had been previously fitted with a radio-collar (Biotrack TWS, 7 gm) as part of the Department of Conservation and Land Management’s numbat research program. He was captured by hand, and transported to Perth Zoo, where he was held in quarantine in the Veterinary Department for a week prior to implantation of the temperature telemeter.

The temperature telemeters (Sirtrack, 3 g) were coated with a biologically inert wax (Elvax), and calibrated in a water bath, at $T_a$ from 5 to 45 °C, in 5 °C increments. The temperature of the water bath was measured to ± 0.1 °C with a thermometer traceable to a national standard. Calibration curves were obtained for telemeters using the data logging system used for each telemeter (see below), and were also checked by manual counts with a stopwatch.

The temperature telemeters were implanted into the abdominal cavity of each numbat. Surgery was performed under general anesthesia (isoflurane, administered via a face mask using a Bain’s anaesthetic circuit attached to a CIG Midget 3 anaesthetic machine). A small midline abdominal incision was made, the telemeter inserted, and then the incision sutured closed. Captive numbats were returned to their enclosures on recovery from anesthesia, whereas the wild numbat was held in quarantine at Perth Zoo for a week after surgery before being released at the site of capture. Data obtained in the fortnight after surgery were discarded for all numbats.

The $T_b$ of CW and CB was monitored from 5/7/2001 to 28/2/2002 (the battery life of the telemeters), with 90 days of $T_b$ data recorded for CW and 65 days for CB, using a Biotelemetry Rx3 receiver, antenna and data logger, powered by a 12 V deep-cycle car battery. The Rx3 recorded the number of pulses for each telemeter’s frequency in alternate minutes, along with the date and time. The logger was activated, and the data
downloaded to a PC (using Biomain software). The number of pulses min\(^{-1}\) was converted to a \(T_b\) using the calibration curve for each telemeter. \(T_b\) was plotted against time, and any obviously unusual values resulting from interference or from missing values (usually resulting from the numbat moving so that there were two sections of wire mesh between him and the antenna) were deleted manually.

WLD’s \(T_b\) was monitored for two consecutive nights every 1-3 weeks from 28/4/2003 until 20/8/2003, with at total of 20 nights of \(T_b\) data obtained. On dusk (just after the time he would have retired for the night) he was radio-tracked to his night retreat, and his \(T_b\) was then monitored using an AOR AR8000 receiver and R8000 interface (with a Sirtrack antenna), interfaced with a Toshiba laptop PC, which ran a custom-written VB data acquisition program. The AR8000 and laptop were powered by a 12 V car battery, and were set up and left running next to his retreat. The time of each pulse from the implanted temperature telemeter was recorded, as were pulses from another ambient temperature \((T_a)\) telemeter which was placed nearby, for alternating 1 min periods. The resulting data were analysed using a custom-written VB analysis program, where the interval between each pulse was calculated, and values which varied by more than 95\% of the median for each 1 min set of \(T_b\) values were discarded. These pulse intervals were then converted to frequencies, and \(T_b\)s calculated from the calibration curve for each telemeter. The data logging system was left in place until the numbat left his retreat the following day (when he would move out of range of the receiver). Some daytime \(T_b\)’s were recorded by radio-tracking the numbat until we were close enough to receive the signal from his \(T_b\) telemeter (he would hide in a hollow log when we were this close) and recording the time for 30 pulses with a stopwatch. \(T_a\) was recorded in a similar manner with another telemeter immediately after.

\(T_b\) data were then analysed for all numbats using another custom written VB program to calculate the required \(T_b\) characteristics \((e.g.\) minimum and maximum \(T_b\), mean daily and nightly \(T_b\), and \(T_b\) when torpid; Figure 1), and the associated times of day. Torpor was defined as \(T_b < 30^\circ C\) (Geiser 1987, 1988). Cooling and arousal rates were calculated from the slope of the regression line of \(T_b\) and time during cooling and arousal.
Temperature values are presented as mean ± S.E., unless stated otherwise. Differences between numbats and seasons were determined by ANOVA, and relationships between \( T_b \) and \( T_a \) by correlation. Mean values for times of day were calculated by circular descriptive statistics, and time values are presented as mean ± S.D. (there is no S.E. equivalent for circular statistics) All statistical tests were preformed using statistiXL v1.3 (www.statistixl.com).

**Results**

*Captive numbats*

The captive numbats had a strong nychthemeral \( T_b \) rhythm, being higher during the day and lower at night (Figure 2). The two captive numbats had overall mean daytime active \( T_b \)s (\( T_{b,active} \)) of 37.4 ± 0.13 (CW) and 37.7 ± 0.07 °C (CB), and there was no significant seasonal effect (\( F_{2,144} = 2.6, \ p = 0.078 \)). Daily \( T_b \) maxima (\( T_{b,max} \)) all occurred between sunrise and sunset (1148 h ± 29.4 min, CW and 1150 h ± 37.2 min, CB). There was no significant seasonal influence on \( T_{b,max} \) (\( F_{1,144} = 2.5, \ p = 0.084 \)).

Overall mean minimum \( T_b \) (\( T_{b,min} \); Table 1) occurred at 0525 h ± 22.2 min (CW) and 0526 h ± 25.2 min (CB) respectively. There was a highly significant effect of season on \( T_{b,min} \) (\( F_{2,142} = 27.7, \ p < 0.001 \)), with all seasons differing significantly from one another (SNK \( p < 0.008 \)) and \( T_{b,min} \) being lowest in winter and highest in summer. The lowest \( T_{b,min} \) recorded was 19.4 °C for CW and 20.2 °C for CB. Mean daily \( T_b \) range (when not torpid) was 5.7 ± 0.2 (CW) and 5.8 ± 0.25 °C (CB). This range differed significantly with season (\( F_{2,84} = 6.8, \ p = 0.002 \)), with the range being smaller in summer than in winter or spring (SNK \( p < 0.018 \)).

Both captive numbats entered spontaneous, daily torpor (Figure 2), most frequently in winter (85.7 % of nights during winter, 37.8 % during spring and 20.8 % during summer for CW and 57.9 % of nights during winter, 32.3 % during spring and never during summer for CB). The overall mean torpor duration for CW was 4.3 ± 0.39 h, with torpor beginning at 0344 h ± 33.6 min and ending at 0756 h ± 30.6 min. For CB, overall mean torpor duration was 4.1 ± 0.47 h, with torpor beginning at 0321 h ± 57 min and ending at
0700 h ± 41.4 min. The longest torpor bouts recorded for these numbats were 9.7 h (CW) and 9.2 h (CB).

There was a highly significant seasonal effect on mean $T_b$ during torpor ($T_{b,torpor}$; $F_{1.50} = 16.8$, $p < 0.001$) for the captive numbats, with $T_{b,torpor}$ being lower in winter ($25.1 ± 0.35 ^\circ C$, CW; $27.5 ± 0.31 ^\circ C$, CB) than in spring ($27.9 ± 0.43 ^\circ C$, CW; $28.2 ± 0.52 ^\circ C$, CB). Season also had a significant influence on the $T_{b,min}$ attained during torpor ($F_{1.54} = 9.3$, $p = 0.004$). Mean arousal rates were significantly influenced by season ($F_{1.55} = 24.4$, $p < 0.001$), being higher in winter ($10.2 ± 0.75 ^\circ C \text{ h}^{-1}$, CW; $7.8 ± 1.14 ^\circ C \text{ h}^{-1}$, CB) than in summer ($5.0 ± 0.69 ^\circ C \text{ h}^{-1}$, CW; $5.0 ± 0.72 ^\circ C \text{ h}^{-1}$, CB). Season did not significantly influence cooling rates ($F_{1.55} = 0.92$, $p = 0.341$).

Although we were only able to study 2 captive numbats, there were many significant differences between the individuals in their pattern of thermoregulation (Table 1). $T_{b,active}$ ($F_{1.144} = 9.6$, $p = 0.002$), $T_{b,max}$ ($F_{1.144} = 16.3$, $p < 0.001$), $T_{b,min}$ ($F_{1.142} = 13.5$, $p < 0.001$), $T_{b,torpor}$ ($F_{1.55} = 10.1$, $p = 0.002$), $T_{b,min}$ during torpor ($F_{1.54} = 9.2$, $p = 0.004$) and cooling rates ($F_{1.55} = 5.0$, $p = 0.029$) differed between individuals, and there were significant interactions between season and numbat ($p < 0.004$).

**Wild Numbat**

WLD used burrows, hollow logs and tree hollows as night retreats during the study period. There was no significant effect of $T_a$ on retreat type ($F_{2.16} = 0.06$, $p = 0.945$), and there was no relationship between mean nightly $T_a$ and $T_b$ ($F_{1.15} = 0.029$, $p = 0.868$). The time that WLD first became active (left his retreat), obtained from the time that his $T_b$ telemetry signal disappeared due to the short range and specific positioning of the receiving/logging equipment, was 0940 h ± 22.8 min, and his mean $T_b$ when activity commenced was $35.0 ± 0.26 ^\circ C$. WLD’s daytime $T_b$, measured during his activity period, ranged from 36.6–40.0 °C (Table 1). Active $T_b$s were recorded over the $T_a$ range 10.1–16.8 °C, and there was no significant relationship between $T_b$ whilst active and $T_a$ ($F_{1.8} = 3.81$, $p = 0.087$). WLD’s $T_{b,min}$ (Table 1) ranged from 19.1–34.4 °C and was significantly higher in autumn ($29.2 ± 2.38$) than in winter ($23.0 ± 1.41$; $F_{1.15} = 5.7$, $p = 0.031$).
mean time of $T_{b,\text{min}}$ was 0649 h ± 35.4 min. Mean $T_{b,\text{min}}$ when torpor did not occur (i.e. when $T_{b,\text{min}} > 30$ °C) was 32.5 ± 0.60 °C.

The wild numbat entered torpor on 28.6 % of nights in autumn and 90 % during winter. Torpor began at 2213 h ± 3 h 35 min, ending at 0848 h ± 24 min, with the longest recorded torpor duration being 15.3 h (1817 h to 0934 h; Table 1). The mean $T_{b,\text{torpor}}$ for WLD was 24.8 ± 0.62 °C. His mean cooling rate was 1.1 ± 0.12 °C h$^{-1}$ and his mean arousal rate 7.6 ± 0.53 °C h$^{-1}$. There was no relationship between these rates and $T_a$ ($F_{1,11} = 0.005, p = 0.43; F_{1,11} = 1.37, p = 0.266$ respectively). One day (26/7/2003) the numbat did not leave his burrow due to inclement weather, and his $T_b$ was monitored continuously during this time (Figure 3). The time of arousal from torpor on the first day was typical (0800 h), and his $T_b$ increased at a typical rate of 7.9 °C h$^{-1}$ to a maximum of 37.3 °C at 1300 h, whilst in his burrow. After this, $T_b$ declined at a rate of 0.78 °C h$^{-1}$, he entered torpor again at 1817 h, and attained a minimum $T_b$ of 19.5 °C again at 0740 h the following morning.

**Discussion**

**Daily patterns of $T_b$**

The numbat’s $T_b$ rhythm was typical of that for other endothermic mammals (Refinetti and Menaker 1992), being higher during its active phase than during its inactive phase (Figure 2). Unlike nocturnal marsupials (Guiler and Heddle 1974; Geiser 1986; Rose *et al.* 1990; Gemmell *et al.* 1997) which have maximal $T_b$s during the night, the diurnal numbat’s $T_b$ was highest during the daytime and lowest at night, with maximum $T_b$s recorded around midday and minimum $T_b$s around 0600 h.

The numbat’s $T_b$ showed a mean daily variation of almost 6 °C when not entering torpor, which is greater than the range of around 2 °C typical for other non-torpid Australian marsupials (Guiler and Heddle 1974; Brown and Dawson 1977; Geiser 1986; Rose *et al.* 1990; Gemmell *et al.* 1997) but is similar to that of antelope ground squirrels (Chappell and Bartholomew 1981). This large range results from fairly typical mean $T_{b,\text{max}}$ values (37.7-38.2 °C), but quite low mean $T_{b,\text{min}}$ values (32.1-32.4 °C). This mild and controlled
nocturnal hypothermia is presumably associated with a reduced metabolic rate, which
would be important for energy conservation, especially since being inactive at night when
$T_a$'s are lower would be associated with higher resting energetic demands. Like the
numbat, variation in the $T_b$ of antelope ground squirrels is also around 6 °C, and also
results from a reduced minimum $T_b$ rather than an increased maximum $T_b$ (Chappell and

Torpor
This study confirms an anecdotal report (Serventy and Raymond 1973) that numbats
enter torpor. All of the dasyurid species that have been examined (approximately 50 % of
all Australian dasyurids) utilise torpor to some extent (Geiser 2003). As numbats are most
closely related to the family Dasyuridae within the Marsupialia (Baverstock et al. 1990),
it is not surprising that they too use torpor to help balance their energy budgets. The
shallow, daily torpor pattern that we observed for numbats is typical of dasyurid
marsupials (Geiser 1994; 2003), with torpor bouts lasting < 24 h and $T_{b\text{min}}$ during torpor
> 11 °C (minimum recorded $T_{b\text{min}}$19.1 °C). Since torpor in numbats is spontaneous,
 occurring when food is freely available (e.g. torpor occurred frequently in captive
numbats fed equivalent amounts of food year round), it appears to be part of the daily
cycle in colder months to reduce energy expenditure rather than a response to acute
energy stress (Geiser 2003). However torpor depth and duration are variable day to day,
and vary somewhat between individuals, so these may be adaptive to daily energy intake.

Numbats typically entered torpor in the early mornings (around 0330 h), and became
normothermic again about mid morning (around 0800 h). Nocturnal dasyurids generally
enter torpor in the early morning, and torpor continues into the daily rest phase, with
arousal occurring in the late morning or afternoon. Diurnal numbats, however, arouse
from torpor at around 0800 h (even when remaining inactive for the day), as their activity
phase is during the day (Figure 2). If torpor is extended, the increased duration occurs by
entering torpor earlier (i.e. late at night rather than early morning) rather than staying
torpid towards midday or early afternoon. This enables the numbats to be ready for
activity during the day, when termites are most abundant (Maisey and Bradbury 1983;
Christensen et al. 1984; Friend 1986). WLD’s maximum torpor duration (15.3 h) is longer than that predicted for marsupials (8.8 h) from the relationship log duration (h) = 2.88 – 1.51 log T\(_{\text{bmin}}\) (determined for captive dasyurids; Geiser 1994). This extended torpor duration increases nightly energy savings, which is presumably important for the termitivorous numbat.

The cooling rates of the numbats were very slow, and all three numbats also had slow arousal rates, compared to other marsupials. The mean arousal rate for the three numbats was 7.1 °C h\(^{-1}\), which is only 35 % of that predicted for marsupials (overall arousal rate) from the equation log arousal rate (°C min\(^{-1}\)) = -0.174 log\(_{10}\) mass(g) + 0.006 (Geiser and Baudinette 1990), suggesting that perhaps the metabolic scope of numbats is lower than that of other marsupials. There was no relationship between T\(_{\text{a}}\) and arousal rate for WLD. Generally there is a strong effect of T\(_{\text{a}}\) on arousal rates for marsupials, with arousal rate increasing with increasing T\(_{\text{a}}\) (Geiser and Baudinette 1987, 1988). However the effect of temperature on arousal rate is greater for small species (which have a high surface area/volume ratio) than larger species, so perhaps for the numbat, which has a comparatively large body mass, the effect of T\(_{\text{a}}\) is very much reduced. In addition, the use of night refuges, especially burrows, buffers numbats from outside T\(_{\text{a}}\) (Cooper 2004) so that environmental T\(_{\text{a}}\) during arousal has little if any impact on the numbats.

### Calculated metabolic rates

To estimate the energetic significance of nightly hypothermia and torpor, it is necessary to know the metabolic rate of numbats at various T\(_{\text{b}}\)s. Unfortunately, the numbats would not enter torpor in a laboratory metabolic system, but we can estimate the metabolic rate of hypothermic and torpid numbats (Figure 4). Calculated metabolic rates (VO\(_{2\text{calc}}\); ml O\(_2\) min\(^{-1}\)) were estimated for WLD when in a burrow after Withers et al. (1990) from the equation \(\Delta T_{\text{b}} = 20.1\left[\frac{\text{VO}_{2\text{calc}} - C(T_{\text{b}}-T_{\text{a}})}{m\cdot\text{SH}}\right]\), where \(\Delta T_{\text{b}}\) is the change in T\(_{\text{b}}\) (°C min\(^{-1}\); calculated from a running average of 20 min of T\(_{\text{b}}\) values), C is thermal conductance (ml 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 1 ml O\(_2\) is assumed to be equivalent to 20.1 J. Thermal conductance was the sum of numbat resistance (R = 1/C; C from Cooper and Withers 2002) and nest resistance (R\(_{\text{nest}}\))
= 1/C_{nest}; C_{nest} from Cooper 2004). T_a was assumed to be 11.7 °C (mean T_a within a
numbat burrow in winter, Cooper 2004), and as burrows remain at a constant temperature
overnight, VO_{2calc} was only estimated for WLD when in a burrow, not when in a log or
tree hollow, or for captive numbats in a nest box where T_a is variable (Cooper 2004).

From these estimates of VO_2, WLD was calculated to conserve 6.6 kJ over 9 h (0.73 kJ h^{-1}) by nightly hypothermia (T_b drop of 1.7 °C; this calculation accounts for the energetic
cost of re-warming). Calculated energy savings resulting from nightly hypothermia by
antelope ground squirrels were similar, approximately 9.5 kJ over 14 h (0.68 kJ h^{-1};
Chappell and Bartholomew 1981). The energy conserved by lowering T_{b_{min}} during
nocturnal hypothermia may be particularly important for numbats which feed on a low-
energy termitivorous diet, with this small change in T_b reducing the numbat’s required
daily food intake by approximately 425 termites (assuming 0.015 kJ of assimilated
energy per termite, Cooper and Withers 2004).

Calculated VO_2 values for WLD in a burrow indicated substantial energy savings from
torpor (Figure 4). By decreasing T_b by an average of 9.5 °C for 12.5 h, WLD reduced
energy expenditure by 34.1 kJ, while a reduction in T_b of 11.3 °C for the same time
resulted in a saving of 114.7 kJ. This energy saving equates to 13 - 42 % of the numbat’s
field metabolic rate (Cooper et al. 2003b) and savings of 2208 - 7440 termites (Cooper
and Withers 2004). Note that these calculations included entry into and the metabolic
‘overshoot’ for arousal from torpor (Figure 4), which reduces the energetic advantage of
torpor. When T_b was low (19.8°C) for WLD in his burrow, VO_{2calc} was only 0.28 ml O_2 g^{-1} h^{-1} which is 72 % of BMR (0.39 ml O_2 g^{-1} h^{-1}) and 20.4 % of resting metabolic rate
(RMR; 1.37 ml O_2 g^{-1} h^{-1} at T_a = 11.7 °C; Cooper and Withers 2002). However this
reduction in MR is smaller than in other marsupials during torpor and reflects the
comparatively high T_{b_{min}} of the numbat.

Season
Season appears to have a strong affect on the occurrence and pattern of daily torpor in the
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. macoura), 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
dasyurids 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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Management of Marsupials.

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Table 1: Body temperature variables for unrestrained, captive, wild-caught (CW) and captive born (CB), and free-living (WLD) numbats. Sample size is given in parentheses.

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

$^a$mean $T_b$ when activity commences ($^\circ$C).
**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.
Figure 2: Body temperature ($T_b$) of a captive numbat (CW) over four consecutive days, where the dark bars indicate the period between sunset and sunrise.
Figure 3: Body temperature ($T_b$) and ambient temperature ($T_a$) of a wild numbat (WLD) that was in a burrow, over 48 hours. The dark bars indicate the period between sunset and sunrise.
Figure 4: Body temperature ($T_b$) and calculated metabolic rate ($MR_{calc}$) of a wild numbat overnight while in a burrow, showing an episode of torpor.