

Long-term measurement of body temperature in the southern hairy-nosed wombat (*Lasiorhinus latifrons*)

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Abstract. The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is a nocturnal, fossorial marsupial that has evolved a range of physiological and behavioural adaptations to its semiarid environment. This study describes long-term core body temperature (T_b) of *L. latifrons* in a population with opportunities for behavioural thermoregulation through burrow use. T_b was measured hourly in 12 captive *L. latifrons* using implanted dataloggers over a 9-month period from late winter to late autumn. Data were examined for daily patterns, seasonal changes, sex differences and the relationship with environmental conditions (ambient temperature, den temperature and relative humidity). T_b ranged from 30.9 to 38.8°C, and had a distinct nycthemeral rhythm, with peak temperatures occurring at night in line with nocturnal activity. Females had a higher mean T_b (34.9°C) than males (34.4°C). The relationship between external ambient temperature and body temperature was negative, with body temperature decreasing as ambient temperature increased. This study is an important step towards a comprehensive picture of thermoregulation in *L. latifrons*, which may become vulnerable in the future if environmental temperatures rise and water availability decreases.

Additional keywords: burrowing, environment, fossorial, marsupial, nocturnal, thermoregulation.

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Introduction

Mammals are endothermic and regulate their body temperature (T_b) through a variety of strategies such as the adjustment of metabolic rate, evaporative cooling, shivering, and behavioural modification (Bicego *et al.* 2007). However, the ability to thermoregulate has physiological limits, and exposure to temperatures that exceed a species-specific upper threshold can result in life-threatening pathology from heat stress or heat stroke (Assia *et al.* 1989; Bouchama and Knochel 2002). The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is a large (19–38 kg) (Wells 1989; Taggart and Temple-Smith 2008) fossorial marsupial that inhabits the semiarid regions of southern Australia, where maximum ambient temperatures can reach 48°C in summer and drop to –3°C at night in winter (BOM 2012). Wombats reach their physiological threshold of thermoregulation when exposed to temperatures higher than 33–35°C (Strzelecki 1974; Wells 1978; Jackson 2003), but behaviourally adapt to avoid these extreme temperature

ranges using burrow occupancy and nocturnality (Wells 1978; Jackson 2003; Hogan *et al.* 2009). Their extensive warren systems reduce exposure to extreme ambient temperatures, with the deepest burrows typically remaining between 10 and 27°C throughout the year (Shimmin *et al.* 2002). They are also most active at night to avoid high daytime temperatures, and have seasonal activity patterns, being active approximately one hour more during winter and spring in comparison to summer and autumn (Wells 1978; Hogan *et al.* 2011). In many species, T_b patterns peak during the active period, irrespective of the amount of physical activity performed (Refinetti 1999). This study aimed first, to describe nycthemeral patterns in a fossorial species using a captive population of *L. latifrons* wombats that had opportunities to use behavioural thermoregulatory strategies through free access to dens. It was hypothesised that peaks would occur at night due to the strong nocturnal activity pattern in this species. Although activity patterns are not known to differ between males and females (Hogan *et al.* 2011), sex differences

in body temperature unrelated to activity are possible. This was an additional research question for this study, however it was hypothesised that body temperature would be largely influenced by other variables and sex differences would not be observed.

Previous studies on *L. latifrons* behaviour show that the relationship between activity and ambient temperature is seasonally dependent in this species, being positively correlated in winter, and negatively in summer (Hogan *et al.* 2011). This suggests that wombats thermoregulate behaviourally and have a preferred thermal range at which activity is maximised. Intermittently, captive and wild wombats (*L. latifrons*, common wombat *Vombatus ursinus*) have been observed (by author K.D, J. French Pers. Comm.; A. Fenning Pers. Comm.) to enter a torpor-like state in which they cannot be roused even when picked up or carried. Torpor is associated with a controlled decrease in metabolic rate and body temperature outside of the 'normothermic range' (Barclay *et al.* 2001; Ruf and Geiser 2015); however, as no data exists on long-term T_b patterns in this species, it is unknown whether such decreases of T_b are possible for wombats. While one study has investigated T_b of *L. latifrons* wombats (Wells 1978), this study was temporally restricted to a three-day period. Long-term T_b data is critically important for predicting how species will adapt to changing climatic conditions, particularly in regions that experience significant alterations in temperature or water availability. The region where wild *L. latifrons* inhabit is predicted to increase in temperature by 0.5 to 5.5°C by 2070 (Suppiah *et al.* 2006). Data obtained from *L. latifrons* are also valuable for predicting T_b patterns in the critically endangered northern hairy-nosed wombat (*L. krefftii*), which shares a close phylogenetic relationship with *L. latifrons* (Stephenson 1967). Less than 250 individuals of this species remain, with no animals in captivity so, as a consequence, opportunities for direct study are limited (Queensland Department of Environment and Heritage Protection 2016).

Data from other species indicates that T_b patterns are affected by a range of variables in addition to activity, including environmental conditions such as food quality, ambient temperature and ambient relative humidity (Lin *et al.* 2005; Warnecke *et al.* 2010; Levy *et al.* 2011; Superina and Jahn 2013). Therefore, a further aim of this study was to investigate how body temperature is affected by ambient temperature and humidity. It was hypothesised that increases in ambient temperature and relative humidity would result in lowered thermoregulatory ability in wombats, culminating in elevated body temperatures.

Materials and methods

Study site and wombats

This study was conducted using 12 adult *L. latifrons* housed in four groups (1♂, 2♀ per group) at the Wombat Research Centre, Rockhampton Botanic Gardens and Zoo, Queensland, Australia (23°22'S, 150°30'E). Eleven of the 12 individuals were wild-caught 4–7 years before the study, and one was born at the facility in 2003. Accommodation was similar for each group and consisted of an internal warren system with two sleeping dens adjoined by tunnels, and an external enclosure of 162–249 m², furnished with a digging chamber, a feed house, native grasses

(*Cynodon dactylon*, *Panicum maximum*), and a dirt-covered log. Dens were air-conditioned for temperature control and were constantly accessible to the wombats to allow naturalistic thermoregulatory behaviour. Carrots, lucerne and macropod pellets (Riverina Australia Pty Ltd, West End, Australia) were provided daily.

Environmental monitoring

Ambient temperature and relative humidity were recorded hourly from August (winter) to April (spring), using external temperature dataloggers (ETDs) (Tinytag Ultra 2 TGU-4500, Hastings Dataloggers, Port Macquarie, Australia) and downloaded with interface software (Tinytag Explorer 4.6.98, Gemini Dataloggers, UK Inc.). One ETD was placed ~170 cm above the warren system to monitor external temperature and humidity and one ETD was placed in each main den at ~90 cm above floor level to measure internal temperature and humidity. The ETDs had a temperature reading range of –25°C to +85°C, an accuracy of 0.4–0.5°C within the study range, a resolution of 0.01°C, and they were able to take hourly readings for at least six months. The humidity detection range was 0–95% RH, with an accuracy of ±0.3% (at 25°C), and a resolution <0.3% RH. As it could not be guaranteed that the external ETD was unaffected by direct radiation sources, a second comparison set of hourly ambient temperature and humidity was obtained for confirmation from the Bureau of Meteorology Rockhampton Aero monitoring station (23°38'S, 150°48'E), which was in close proximity (~2 km) and at a similar elevation (within 3 m).

Body temperature

Wombat T_b were measured using stainless steel, cylindrical internal temperature dataloggers (ITDs) (iButton, Maxim DS1922L Alfatek, Vic., Australia, 17 × 5.9 mm, mass 3.3 g). These ITDs were chosen because they had been successfully used with another tetrapedal, burrowing species (*Mephitis mephitis*) with no apparent adverse effects on the animal (Hwang *et al.* 2004), and because they remain accurate over time (Davidson *et al.* 2003). The ITDs were configured in an 8-bit format allowing nine months (August–April inclusive) recording of hourly temperature to 0.5°C in real time. Configuration was achieved using a reader (DS1402D-DR8, Cable 8' Blue dot to RJ11, Alfatek) connected to a USB adaptor (RJ-11, Alfatek) and software ('Meteor Mission Manager' Alfatek). The ITDs were coated twice in a paraffin and resin mixture (Elvax/paraffin, Minimitter, OR, USA) for waterproofing and to prevent tissue reaction, and calibrated using a controlled waterbath heated to 30, 35 and 40°C as measured with a laboratory mercury thermometer (Branna 76-mm immersion thermometer), which encompassed the expected temperature range. Prior to implantation, the coated ITDs were cleaned for 20 min using an enzymatic cleaner (Medizyme, Whiteley Corporation, North Sydney, NSW, Australia), sterilised for 10 min using orthophthalaldehyde (Cidex, Johnson and Johnson Medical, North Ryde, NSW, Australia) and rinsed twice in sterile water (Water for irrigation, Baxter Healthcare, Toongabbie, NSW, Australia). Two ITDs were inserted into each animal to guard against data loss in the case of technical failure.

Anaesthesia and surgical technique

The wombats were anaesthetised using an intramuscular injection of tiletamine and zolazepam (Zoletil 100, Virbac, NSW, Australia) at a dose rate of 4.5–5.5 mg kg⁻¹, dependent on known individual anaesthesia tolerance. Anaesthesia was maintained using a gaseous anaesthetic, Isoflurane (Attane, Bomac, Auckland, New Zealand), at a rate of 1.5–5% on a circular system, adjusted as appropriate to maintain an adequate depth of anaesthesia. Oxygen flow rate was ~1.5 L min⁻¹. During anaesthesia, each wombat underwent an annual physical examination, as well as blood and urine sampling. Anaesthetic monitoring for vital signs occurred at 5-min intervals. The ventral surface of the abdomen and thorax was clipped and aseptically prepared. Incisions were made to the side of the implantation site. Both ITDs were positioned laterally caudal to the costal

arch superficial to the deepest abdominal muscle layer (between the transverse abdominal and the internal oblique abdominal muscles). Butorphanol at 0.5 mg kg⁻¹ (Butomidor, Ausrichter, NSW, Australia) and amoxicillin/clavulanic acid at 0.5 mg kg⁻¹ (Clavulox, Pfizer, NSW, Australia) were injected at the beginning of the procedure for pain relief and to prevent postsurgical infection, respectively. Incisions were closed in multiple layers as indicated for the site with suture material (2–0 PDSII, Johnson and Johnson Medical, North Ryde, NSW). After surgery, the wombats were monitored in isolation within their enclosure until they were sufficiently recovered to join other group members. No wombat experienced postsurgical complications or observable discomfort. The surgical procedure for implantation was reversed for ITD removal. No ITD had migrated from the original implant site,

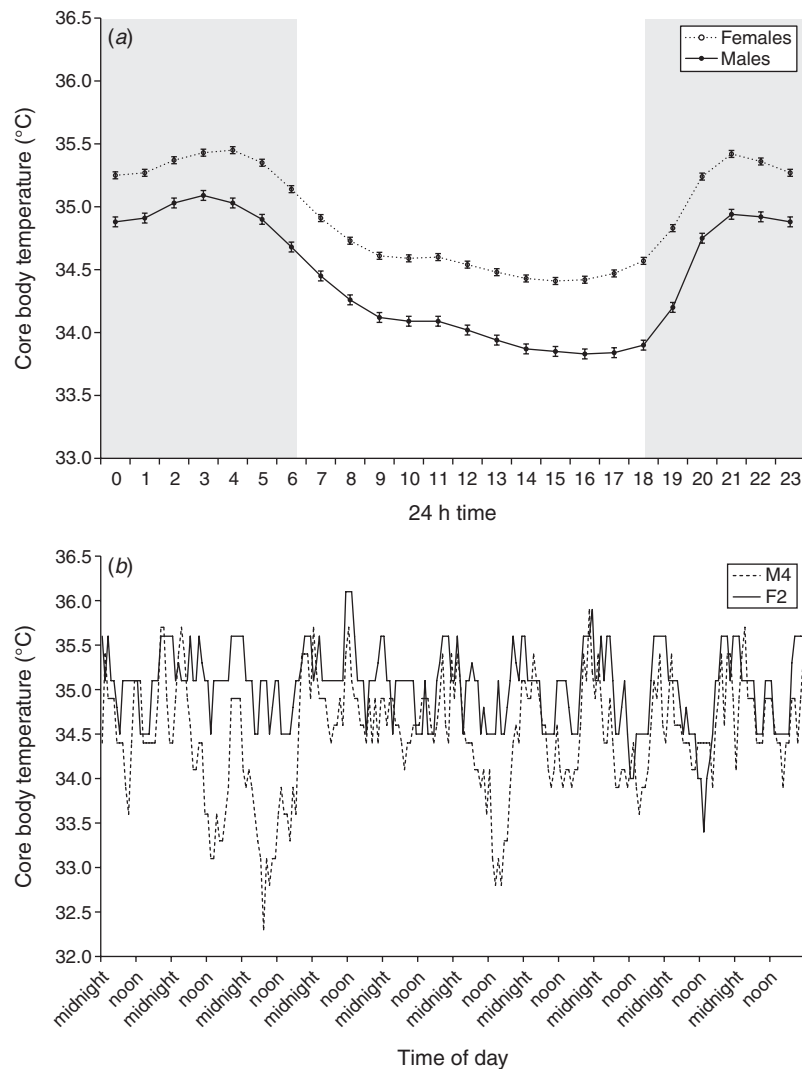


Fig. 1. (a) Mean daily pattern of core body temperature (°C ± 95% CI) in female and male *L. latifrons*. Approximate average night periods are indicated by grey shading. (b) An example trace recording of core body temperature from one male (M4) and one female (F2) *L. latifrons*. Data presented are from 15 September 2008 to 24 September 2008.

and most had become encapsulated in a thin layer of scar tissue and were readily extracted by blunt dissection. Three of the wombats had fluid around their ITD, indicating a mild non-infected tissue reaction.

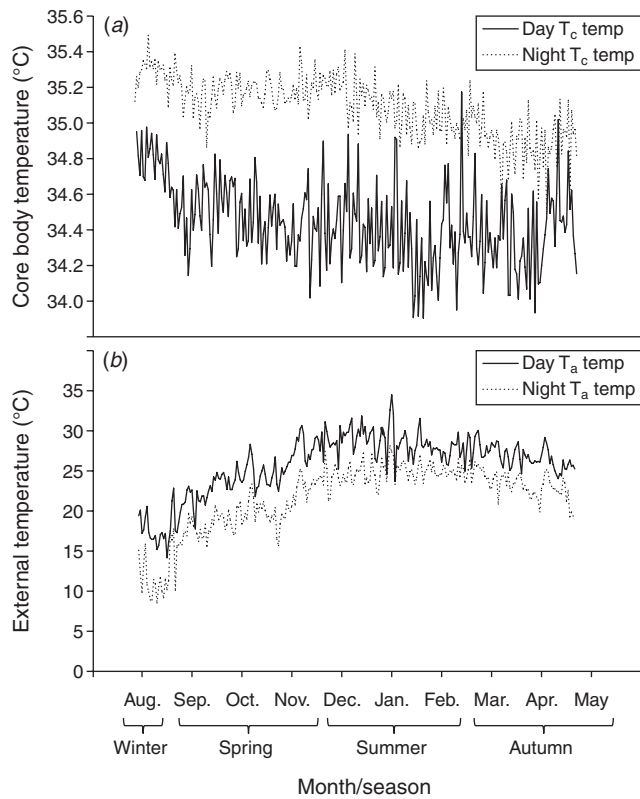


Fig. 2. Mean day and night measurements of (a) core body temperature (°C) and (b) ambient external temperature (°C) from August (winter) to April (autumn).

Data treatment and statistical analysis

The two ITDs for each wombat were compared across the three calibration temperatures, and corrected using the calibration curve. The mean of the two calibrated readings was then used for analysis. For one wombat, an ITD had failed and so the calibrated readings were used from the single functioning ITD. Standardised residuals were visualised for the body temperature data and were normally distributed. Daily and hourly least-square means were obtained using a linear mixed-effects model in the nlme package in R (Pinheiro *et al.* 2015) with an auto-regressive component. Individuals were included as a random effect and fixed effects were sex, month, sex × month, hour, and sex × hour.

The relationship between daytime (0600–1700 hours) and night time (1800–0500 hours) T_b (averaged across all animals) and ambient temperatures and/or relative humidity were examined in the statistical analysis. It was considered pertinent to examine the effects of external and den temperatures both during the day and at night as wombats are largely nocturnal but exhibit a bimodal night-time activity pattern with bouts of activity interspersed with denning behaviour (Hogan *et al.* 2009). To account for the time-series structure of both animal and environmental variables, autoregressive integrated moving average models (ARIMA) of order (1,1,1) were constructed. The resulting residuals for each series were then correlated using the CORR procedure with SAS software (SAS Institute, ver. 9.3, NC, USA).

To further examine whether above/below average ambient temperatures and relative humidity readings were associated with above/below average T_b measurements, residuals were also examined using partial correlations adjusted for hour.

Data from the externally placed ETD at the research site was highly correlated with that of the BOM (2012) data and did not differ in analyses of the relationship with T_b . Therefore, only site data were used and reported in this paper.

This study was approved by the University of Queensland Animal Ethics Committee (licence no. SAS/301/08/WOMBAT).

Table 1. Frequency table of individual core body temperature measurements for four male (M1–M4) and eight female (F1–F8) *Lasiorhinus latifrons*

Temperature range (°C)	M1	M2	M3	M4	F1	F2	F3	F4	F5	F6	F7	F8
30.5–31.0	0	3	0	0	0	0	0	0	0	0	0	0
31.0–31.5	0	9	0	0	0	0	0	0	0	0	0	0
31.5–32.0	0	51	6	0	1	1	0	0	3	5	0	0
32.0–32.5	0	27	56	12	6	5	0	0	23	31	1	0
32.5–33.0	3	208	254	90	5	56	38	0	88	132	15	16
33.0–33.5	31	392	1037	472	99	276	99	0	337	377	156	277
33.5–34.0	479	854	1221	1218	310	63	395	3	932	867	645	898
34.0–34.5	1447	1232	1230	1801	850	997	1048	116	1449	1354	1355	1294
34.5–35.0	2147	1300	1086	1548	1740	1957	1759	46	672	171	1991	227
35.0–35.5	1491	1298	899	842	1808	1927	2007	1428	1497	1329	1590	1313
35.5–36.0	619	762	437	253	1119	955	882	2789	1075	1215	500	1239
36.0–36.5	91	149	61	16	325	69	76	1661	221	759	58	929
36.5–37.0	4	22	20	36	42	6	8	243	13	65	1	117
37.0–37.5	0	4	4	18	4	0	0	19	2	4	0	1
37.5–38.0	0	0	1	5	2	0	0	5	0	2	0	1
38.0–38.5	0	1	0	1	0	0	0	1	0	1	0	0
38.5–39.0	0	0	0	0	1	0	0	1	0	0	0	0

Results

Mean and range in T_b

Over the entire study period, the mean wombat T_b was $34.8 \pm 0.02^\circ\text{C}$. The lowest temperature recorded was 30.9°C and the highest was 38.8°C . On average, T_b fluctuated by $2.2 \pm 0.08^\circ\text{C}$ during the course of a single day. The largest daily range recorded in an individual was 6.3°C . A distinct nycthemeral pattern was observed, with T_b peaking at night, and declining to a nadir during the day (Fig. 1a, b). This day–night pattern was consistent throughout the year (Fig. 2).

Individual and sex differences in T_b

Individual variation in T_b was observed, both in range over the study period, and in the minimum/maximum temperatures recorded (Table 1). Sex differences also occurred (Fig. 3); females had a mean T_b of $34.9^\circ\text{C} \pm 0.01$, which was significantly higher ($F_{1,10} = 1125$, $P < 0.001$) than males, at $34.4^\circ\text{C} \pm 0.01$. This pattern persisted throughout the day, with both sexes maintaining the nycthemeral daily pattern (Fig. 1a). Over the course of the year, male T_b remained stable, while female T_b decreased from winter until early autumn (Fig. 4).

Correlations between ambient conditions and T_b

Correlations were calculated between the residuals from ARIMA models of each time series dataset to account for the effect of repeated-measurements from both animals and the environment (Table 2). Night-time T_b was not significantly correlated with any ambient condition measures. Daytime T_b was negatively associated with external temperature [$r(261) = -0.23$, $P < 0.001$], but positively correlated with external relative humidity [$r(256) = 0.21$, $P < 0.001$]. Therefore, increases in external temperature were associated with decreases in T_b , but the opposite pattern was true for external relative humidity and T_b .

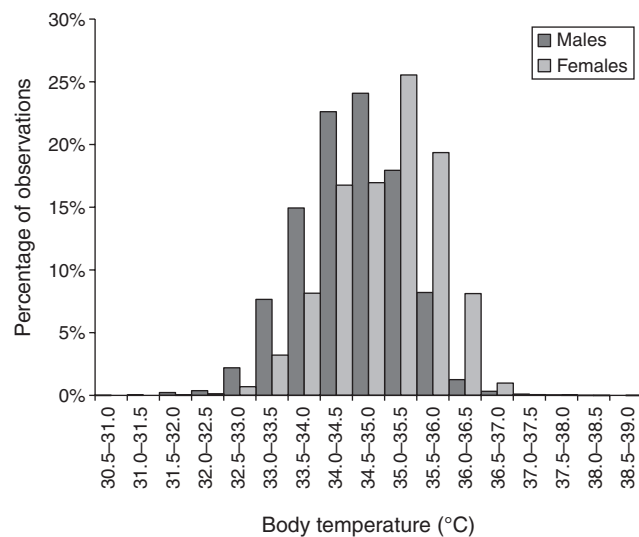


Fig. 3. Mean percentage of observed body temperatures ($^\circ\text{C}$) for male ($n=4$) and female ($n=8$) *L. latifrons* recorded from August (winter) to April (autumn).

Relationship between T_b and non-average ambient conditions

Partial correlations were conducted, which controlled for time of day, and allowed the effect of above- or below-average environmental conditions to be determined. Degrees of freedom were large due to the amount of data collected so that all partial correlations had significant P -values. However, relative humidity both in the dens and externally had very weak partial correlations, suggesting no functional relationship. External and den ambient temperature had a negative relationship with T_b , meaning that above-average ambient temperatures resulted in below-average T_b [external: $r(6134) = -0.27$, $P < 0.0001$; den: $r(6134) = -0.16$, $P < 0.0001$] (Table 2).

Discussion

Body temperature in *L. latifrons* wombats appears to be moderately labile, with an 8°C range (30.9°C to 38.8°C). A nycthemeral T_b pattern was evident, with a nadir during the day and a peak at night, which corresponded with previously reported circadian activity patterns (Hogan *et al.* 2009). Combined with the generally negative relationship between ambient temperature and T_b , this suggests that thermoregulation is associated with activity phases in this species, a hypothesis supported by research in humans and other animals (Nicol and Maskrey 1980; Gemmill *et al.* 1997; Bridge *et al.* 2003; Hosick *et al.* 2010).

Sex differences were evident, with females having a higher mean T_b than males, which decreased over the seasons from winter to early autumn. Again, this may be related to activity, as wombats are more active in winter and spring than summer and autumn; however, seasonal activity levels do not differ between males and females (Finlayson *et al.* 2003; Hogan *et al.* 2011). Seasonal T_b patterns can also be influenced by an endogenous, adaptive circannual rhythm for improved survival in seasons of restricted food and water. A low mean T_b in summer reduces the need for evaporative cooling strategies such as panting (Strzelecki 1974; Wells 1978) and may conserve energy during periods of low food availability (Brown and Dawson 1977;

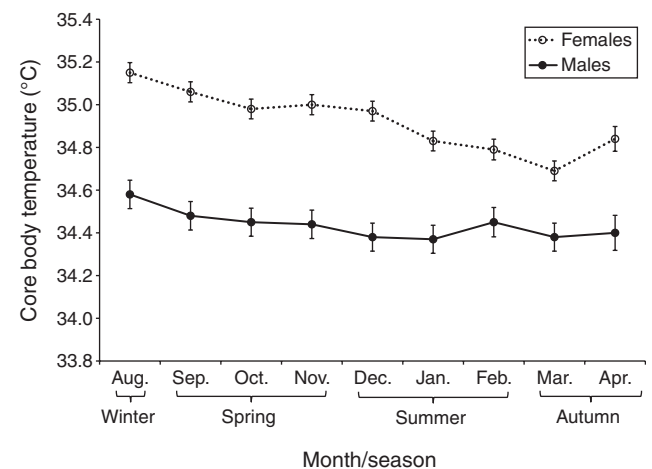


Fig. 4. Mean core body temperature ($^\circ\text{C} \pm 95\%$ CI) for female and male *L. latifrons* from August (winter) to April (autumn).

Table 2. The relationship between body temperature (°C) and ambient temperature (°C)/relative humidity (%)

		Correlation between ARIMA residuals ^A		Partial correlations adjusting for hour ^B
		Daytime body temperature	Night-time body temperature	Hourly body temperature
External ambient temperature (°C)	<i>r</i>	-0.23	-0.02	-0.27
	<i>P</i>	<0.001	0.79	<0.0001
	d.f.	261	260	6134
External relative humidity (%)	<i>r</i>	0.21	0.05	-0.05
	<i>P</i>	<0.001	0.43	<0.0001
	d.f.	256	256	6134
Den ambient temperature (°C)	<i>r</i>	-0.03	0.05	-0.16
	<i>P</i>	0.71	0.49	<0.0001
	d.f.	182	181	6134
Den relative humidity (%)	<i>r</i>	0.03	0.02	0.03
	<i>P</i>	0.67	0.80	0.01
	d.f.	182	181	6134

^ACorrelation between residuals from autoregressive integrated moving average (ARIMA) models of order (1,1,1) of body temperature (°C) and ambient temperature (°C)/relative humidity (%) for daytime (0600 to 1700 hours) and nighttime (1800 to 0500 hours).

^BPartial correlations between hourly residuals of body temperature (°C) and ambient temperature (°C)/relative humidity (%).

Maloney *et al.* 2011; Turbill *et al.* 2011). The current study was conducted in a semitropical location with a wet summer and a dry winter (BOM 2012), whereas *L. latifrons* is naturally found in a semiarid environment. During summer it experiences a hot, dry climate (Wells 1978), with reduced access to food and water, which therefore requires conservation of energy and body fluids. However, environmental variables would apply equally to both males and females, especially in a captive study, therefore the contribution of sex to seasonal body temperature patterns remains only partially explained.

It is known that, for all seasons except winter, wombats reduce activity as humidity rises (Hogan *et al.* 2011), presumably to avoid the risk of heat stress from the combined effect of temperature and humidity. In the current study, a positive relationship was found between external relative humidity and daytime T_b , but none with night-time T_b . Additionally, higher than average temperatures both inside and outside of the dens had a suppressive effect on T_b . In combination with the study of Hogan *et al.* (2011), this supports the suggestion that environmental variables influence T_b through the adjustment of activity patterns in wombats. In some species (e.g. sugar gliders (*Petaurus breviceps*)) T_b decreases in response to rainfall events; however, this corresponds to bouts of torpor (Christian and Geiser 2007), which is not evident in wombats.

Daily fluctuations of T_b in *L. latifrons* were large (sometimes more than 6°C in a single day) but do not suggest torpor, which can be defined by a decrease below 30°C or a bimodal pattern of temperatures falling significantly below the normothermic pattern (Séguy and Perret 2005; Warnecke *et al.* 2007; Brigham *et al.* 2011). Therefore, in this study, at least, no plausible explanation can be given for the non-responsive state intermittently reported in wombats (K. Descovich, pers. obs.; J. French, pers. comm.; A. Fenning, pers. comm.).

It should be noted that physiology including thermoregulatory patterns may be altered by captivity. Studies in other marsupials –

numbat (*Myrmecobius fasciatus*), southern brown bandicoot (*Isodon obesulus*), feathertail glider (*Acrobates pygmaeus*) – conflict on whether captivity affects T_b (Geiser and Ferguson 2001; Larcombe and Withers 2007; Cooper and Withers 2012). Whether this is the case for wombats is speculative; however, in the marsupial species that do not use torpor (bandicoots), T_b in captive animals corresponds with those found in wild populations, suggesting that the current study in captive wombats is relevant to our understanding of thermoregulation in wild populations. It is, however, recommended that wild individuals be incorporated into future studies to confirm the results obtained in this study.

Conclusions

Body temperature in *L. latifrons* has a moderate range and during daytime is negatively associated with ambient temperatures, and positively with relative humidity. T_b had a strong nycthemeral pattern, which peaked at night, suggesting that it is influenced by activity rhythms. Sex differences in T_b were evident, with higher mean temperatures observed in females, and differences in seasonal patterns. This study provides critical long-term data on temperature patterns in this species.

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