

VARIATION IN BODY TEMPERATURE IN FREE-RANGING WESTERN GREY KANGAROOS *MACROPUS FULIGINOSUS*

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Using implanted temperature loggers we measured temperature in the carotid artery in five (4 male, 1 female) western grey kangaroos (*Macropus fuliginosus*) every 5 min for between 39 and 74 days. Dry bulb temperature during the study ranged from an average minimum of (mean \pm SD) $11 \pm 3^\circ\text{C}$ to maximum of $24 \pm 5^\circ\text{C}$. Black globe temperature measured in the southern shade of a grass tree, the habitat chosen by kangaroos during the day, ranged from an average minimum of $10 \pm 4^\circ\text{C}$ to an average maximum of $30 \pm 6^\circ\text{C}$. There were nine days where maximum shade globe temperature exceeded 40°C . Carotid blood temperature averaged $36.5 \pm 0.1^\circ\text{C}$ ($n = 5$), ranging from an average minimum of $35.5 \pm 0.3^\circ\text{C}$ to a maximum of $37.3 \pm 0.1^\circ\text{C}$. The resultant average daily range was $1.8 \pm 0.3^\circ\text{C}$. Body temperature was highest during the night and dropped rapidly early in the morning, reaching a nadir at 1000 hours, after ambient temperature and solar radiation had begun increasing. Body temperature then rose gradually during the day to reach a peak in the early evening. The nycthemeral variation in carotid blood temperature was largely independent of ambient conditions. There was a weak but significant association between early morning radiation levels and the minimum body temperature reached, suggesting that peripheral warming influences the morning decrease in core temperature.

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METATHERIAN mammals (marsupials) were long considered primitive in their thermoregulatory abilities compared to eutherian (placental) mammals. These notions emerged primarily because core body temperature was lower in marsupials than in eutherians and the macropod marsupials were observed to use licking, a means of cooling considered inferior to panting or sweating, as an evaporative mechanism in hot conditions (Dawson 1995). However, during the last decade experimental evidence has emerged showing that the thermoregulatory competency of marsupials, and the large macropods in particular, are comparable to their eutherian relatives (Dawson *et al.* 2000a,b). Eastern grey (*Macropus giganteus*) and red (*Macropus rufus*) kangaroos maintain a constant core temperature over a wide range of ambient temperatures, and even at 45°C their core temperature increases only slightly (Dawson *et al.* 2000a). These data do not reflect the full evaporative cooling capacity of kangaroos since they were obtained from animals at rest and

macropods at rest do not sweat, but do so potently during exercise (Dawson *et al.* 1974).

These data were mostly obtained from captive animals and there is mounting evidence that measurements on captive animals may not reflect the physiological repertoire of the free-living animal. For example, the urine concentrating ability of captive zebra finches (*Taeniopygia guttata*) is not as well developed as in their wild counterparts (Skadhauge and Bradshaw 1974), captive-bred mountain pygmy possums (*Burramys parvus*) do not enter torpor as readily, have shorter torpor bouts, and shallower torpor temperature decreases than do wild caught animals of the same species (Geiser *et al.* 1990), and large African antelope appear to exhibit different body temperature patterns during high temperature exposure in captivity as compared to those in the field (Fuller *et al.* 1999; Mitchell *et al.* 2001). The ultimate measure of how an animal thermoregulates must relate to how it performs in its natural habitat

since free-living animals have access to the full gamut of autonomic and behavioural mechanisms that may be limited in laboratory experiments (Fuller *et al.* 1999).

There have been sporadic reports of body core temperature in free-living macropods, but to date there has been no systematic study of the core temperature responses of large macropods in their natural environment. McCarron *et al.* (2001) provide the most comprehensive data set on body temperatures in kangaroos, demonstrating a nycthemeral cycle with a nocturnal zenith in both *M. rufus* and *M. giganteus*, the amplitude being greater in the latter. But earlier researchers (Brown and Dawson 1977) had found an early evening zenith for *M. giganteus*, western grey kangaroos (*Macropus fuliginosus*) and *M. rufus*. The structure of the cycle has implications for the adaptive mechanisms kangaroos might have for dealing with a heat load. A low diurnal body temperature provides greater scope for storage of heat during a hot day, but to achieve a low diurnal body temperature might require increased thermoregulatory water use. McCarron *et al.* (2001) suggested that heat storage becomes important in hot conditions especially if water is restricted.

We have measured core temperature in free-living *M. fuliginosus* to determine the structure of the nycthemeral core temperature cycle and whether changes in environmental conditions alter that cycle. Earlier researchers have suggested that the body temperature of *M. rufus* decreases in the early morning subsequent to solar radiation exposure (Brown and Dawson 1977). We have tested this hypothesis in *M. fuliginosus* by correlating morning body temperature with the level of incident solar radiation in the morning.

MATERIAL AND METHODS

Animals and habitat

The experiments took place between September and November (Southern Hemisphere spring and early summer) at the Harry Waring Marsupial Reserve 30 km south-east of Perth, Western Australia. *M. fuliginosus* is endemic to the area and the reserve is typical habitat. Five kangaroos (4 male and 1 female with masses of 61, 69, 32, 36, and 25 kg respectively) were captured, instrumented and released back into the reserve. Mass change between September and February averaged 1 ± 3 kg. Periodic observations were made of the animals over the course of the study and the animals were often interacting with conspecifics and/or engaged in similar behaviours as conspecifics, leading us to believe that the instrumented animals were behaving normally.

Body temperature measurement

Kangaroos were darted with tiletamine chlorhydrate 125 mg and zolapezam chlorhydrate 125 mg (sold as Zoletil 100, Virbac, Australia) and transported to a nearby temporary theatre. The animals were placed on their side and anaesthetised with 1–2% halothane (Rhone Merieux, Australia) in oxygen, administered via an endotracheal tube. Ventilation during anaesthesia was spontaneous. Respiratory rate, heart rate and rectal temperature were monitored throughout surgery.

Using aseptic surgical procedures we implanted miniature data loggers with thermistor sensors for temperature measurement as described in Maloney *et al.* (2002). Briefly, a thermistor in a blind-ended and thin-walled polytetrafluoroethylene (PTFE) tube was advanced 50 mm into the left common carotid artery. Outside the artery, the PTFE tube was connected to a silicone rubber tube covering leads from the thermistor to a temperature logger implanted behind the scapula. The loggers with their thermistors were calibrated against a certified mercury in glass thermometer (WIKA Australia, resolution 0.05°C) in an insulated water bath and proved to have a calibrated accuracy within one sampling step of the logger (0.04°C). Scan interval of the loggers was set at 5 min.

A 50 mg enrofloxacin tablet (Baytril, Bayer, Germany) was inserted into each surgical site and the skin suture line sealed with topical antiseptic spray (Terramycin Pinkeye Aerosol, Pfizer, Australia). The animals also received long-acting antibiotic (2 ml Benicillin, Troy Laboratories, Smithfield, NSW) and an analgesic and anti-inflammatory medication (1 ml Temgesic containing 0.32 mg buprenorphine hydrochloride, Reckitt and Colman, UK plus 1 ml Finadyne, Heriot Agvet, Rowville, Victoria, Australia).

The animals were redarted during the subsequent February, killed with an overdose of sodium pentobarbitone (Lethabarb, Virbac, Australia) and the loggers recovered. The implanted loggers were in perfect order, the animals' wounds had healed and there were no signs of infection. In all animals, however, the thermistor/logger combination no longer was functioning at recovery, generally as a result of thermistor breakage between 39 and 74 days after surgery. *In vivo* examination of the carotid arteries at logger retrieval revealed no occlusion or clotting along the length of the intravascular guide tube, that is, the thermistors measured the temperature of free-flowing blood.

Meteorological data measurement

Meteorological data were measured on site. Dry bulb temperature and relative humidity were measured using a Hobo Temp/RH logger placed inside a

Stevenson screen within the reserve. Globe temperature also was measured at the centre of 150 mm blackened copper spheres with Stowaway XTI temperature loggers (as described above except with a wider temperature range). One globe was placed in full sunshine and the other placed in the southern shade of a large grass tree (*Xanthorrhoea preissii*). Observation of the kangaroos showed that they invariably were lying in shade at the hottest times of day and so globe temperature in the sun was not used in analysis. Globe temperature integrates dry bulb temperature, radiation temperature, and wind speed. It will not equal operative temperature of a kangaroo but we suggest that globe temperature will correlate better with operative temperature than will dry bulb temperature alone. Temperature logger/thermistor combinations were calibrated as described above but over a wider temperature range (0 - 45°C). Solar radiation data were obtained from Medina Agricultural Station ~ 1 km east of the reserve.

Data analysis

The animals were slightly hypothermic immediately post-anaesthesia but warmed rapidly during the first day after release. Subsequently, temperatures were slightly elevated above the long-term average for about two weeks. We considered the temperatures during the initial two weeks to be influenced by the consequences of surgery and did not employ these results in further analysis.

To avoid introducing a circadian bias to body temperature analysis, the analysed data for each animal consist of the data from midnight on the first post-hyperthermic day following surgery to the midnight before equipment failure. Analysed data consists of 37 days (male 1), 23 days (male 2), 60 days (male 3), 51 days (male 4), and 63 days (female 1).

The hourly mean, standard deviation, minimum, and maximum carotid blood temperature (T_{car}) were calculated for each animal to investigate the pattern of temperature over the nycthemeral cycle. The original 5 min recordings then were used to find the daily mean, SD, minimum, maximum, and range of T_{car} for each animal. Similar calculations were made on dry bulb (T_{db}) and shade globe temperatures (T_{g}) and these data then were used to analyse for effects of meteorological variables on body temperatures by correlation and regression analysis.

Data for each variable describing T_{car} from the five animals (daily mean, minimum, maximum, and range) were regressed on the same variable for T_{db} and T_{g} . We analysed these relationships using two approaches. Firstly, T_{car} for each animal was regressed on shade T_{g} for each variable. This approach led to occasionally inconsistent results when one or two animals would exhibit significant (not corrected for Type I error rate) correlations while the others would not (Table 1). The contradictory nature compounded when, occasionally significant relationships for a variable in two different animals had opposite slopes. Secondly, the regression slopes for all five animals were compared within each variable by ANOVA, and the slopes were found not to differ between animals for any variable. The regression slopes of the five animals were then compared to zero using a *t*-test. The same procedure was used to analyse the effect of morning solar radiation level on the minimum T_{car} each day. Since the minimum T_{car} occurred usually around 1000 hours, we compared the average solar radiation intensity between sunrise and 1000 hours to the minimum T_{car} observed each morning. The Animal Ethics Committee of the University of Western Australia (approval #01/100/163) approved all experimental procedures.

	Male 1	Female 1	Male 2	Male 3	Male 4	Compare slopes	Slopes vs zero
Mean	$F_{1,30} = 0.01$ $p = 0.90$ $r^2 = +0.001$	$F_{1,56} = 7.3$ $p = 0.01$ $r^2 = -0.11$	$F_{1,16} = 0.5$ $p = 0.5$ $r^2 = -0.03$	$F_{1,53} = 1.7$ $p = 0.2$ $r^2 = -0.03$	$F_{1,44} = 2.3$ $p = 0.14$ $r^2 = -0.05$	$F_{4,199} = 0.32$ $p = 0.86$	$t_4 = 4.12$ $p = 0.01$
Minimum	$F_{1,30} = 0.34$ $p = 0.56$ $r^2 = +0.01$	$F_{1,56} = 4.0$ $p = 0.05$ $r^2 = -0.07$	$F_{1,16} = 6.3$ $p = 0.02$ $r^2 = +0.29$	$F_{1,53} = 2.3$ $p = 0.13$ $r^2 = -0.04$	$F_{1,44} = 0.01$ $p = 0.9$ $r^2 = +0.003$	$F_{4,199} = 2.3$ $p = 0.06$	$t_4 = 0.17$ $p = 0.87$
Maximum*	$F_{1,28} = 8.5$ $p = 0.01$ $r^2 = -0.23$	$F_{1,52} = 0.1$ $p = 0.75$ $r^2 = +0.002$	$F_{1,15} = 0.004$ $p = 0.95$ $r^2 = +0.002$	$F_{1,50} = 1.6$ $p = 0.21$ $r^2 = +0.03$	$F_{1,41} = 0.02$ $p = 0.9$ $r^2 = +0.001$	$F_{4,186} = 1.1$ $p = 0.35$	$t_4 = 0.31$ $p = 0.77$
Range*	$F_{1,28} = 1.3$ $p = 0.25$ $r^2 = -0.04$	$F_{1,52} = 5.2$ $p = 0.03$ $r^2 = +0.09$	$F_{1,15} = 0.8$ $p = 0.4$ $r^2 = +0.05$	$F_{1,50} = 1.8$ $p = 0.2$ $r^2 = +0.03$	$F_{1,41} = 1.4$ $p = 0.24$ $r^2 = +0.03$	$F_{4,186} = 1.1$ $p = 0.35$	$t_4 = 1.6$ $p = 0.18$
Morning radiation vs minimum	$F_{1,30} = 3.0$ $p = 0.09$ $r^2 = -0.09$	$F_{1,56} = 3.4$ $p = 0.07$ $r^2 = -0.06$	$F_{1,16} = 9.3$ $p = 0.007$ $r^2 = -0.37$	$F_{1,53} = 1.6$ $p = 0.21$ $r^2 = -0.03$	$F_{1,44} = 2.8$ $p = 0.09$ $r^2 = -0.06$	$F_{4,199} = 0.27$ $p = 0.90$	$t_4 = 6.4$ $p = 0.003$

Table 1. Results of regression analyses of effects of variations in T_{g} on variation in T_{car} . *[Days on which there was a high diurnal maximum T_{car} , presumably due to exercise, were excluded].

Fig. 1. Daily average, minimum, and maximum dry-bulb temperature (A) and globe temperature measured in the shade (B) over the course of the study. Day zero corresponds to September 15. Daily average, minimum, and maximum T_{car} in one of the animals (C) is shown over the same period. Plots for the other four animals were similar.

RESULTS

Ambient conditions began with cool nights and warm days in September and gradually warmed till the study ended in early December (Fig. 1). Average daily dew-point temperature during the study ranged from 6.5 to 15.8°C, and averaged $10.6 \pm 2.2^\circ\text{C}$ (mean \pm SD) which is a vapour pressure of approximately 1.25 mmHg. Total rainfall was 125 mm during the study (measured at Medina Agricultural Station \sim 1 km east of the reserve). Maximum rainfall on any day was 25 mm. Data on air temperature and globe temperature are given in more detail below.

Average daily T_{db} ranged from 11.7 to 25.0°C, with a minimum recorded temperature of 3.7 and maximum of 35.4°C. There were nine days where dry bulb temperature exceeded 30°C. Average daily globe temperature measured in the shade ranged from 12.2 to 26.8°C with a minimum of 2.0°C and maximum of 45.2°C. There were seven days where shade globe temperature exceeded 40°C. Dry bulb temperature and globe temperature measured in the shade were highly correlated, with the minimum shade T_{g} being slightly cooler, and maximum slightly higher, than T_{db} as would be expected from the effects of radiation temperature during night and day (mean $T_{\text{g}} = 1.06 \times \text{mean } T_{\text{db}} + 0.60$, $F_{1,56} = 1840$, $p < 10^{-4}$, $r^2 = 0.97$; minimum $T_{\text{g}} = 1.02 \times \text{minimum } T_{\text{db}} - 1.22$, $F_{1,56} = 2372$, $p < 10^{-4}$, $r^2 = 0.98$; maximum $T_{\text{g}} = 1.16 \times \text{maximum } T_{\text{db}} + 2.67$, $F_{1,56} = 312$, $p < 10^{-4}$, $r^2 = 0.85$). We believe T_{g} measured in the shade provides the better index of the thermal environment of these kangaroos, and so subsequent analyses based on T_{g} are reported. However, the results were similar if T_{db} was used.

The mean 24-hour core temperature of the kangaroos was remarkably invariant from day to day (Fig. 1c). The data from all animals were similar and Female 1 is shown as an example. Logger implantation occurred on September 19 (Day 4 on the plot) and the last data were collected on December 2 (Day 78). Analysis was performed on data collected after October 1 (Day 16). During that period her mean daily T_{car} was $36.6 \pm 0.1^\circ\text{C}$ with the lowest and highest daily averages being 36.4°C and 37.0°C respectively. For the five animals the mean daily T_{car} was $36.5 \pm 0.1^\circ\text{C}$ (mean \pm SD of the average daily temperature for the five animals).

A noticeable feature of the daily plots for each animal was the occasional large increases in maximum temperature. Maximum temperature of the nycthemeral cycle usually occurred in the early evening at about 1800 hours (see later). In 12 out of 13 occurrences of maximum T_{car} greater than 38°C, the large excursions from the norm occurred in the mid-afternoon between 1400 and 1700 hours. A

characteristic of all such increases was a rapid increase (over 10 – 15 min) followed by a relatively rapid resolution over the course of about 60 min back to the average temperature for that time of day. These excursions probably were caused by exercise, and, presumably because their duration was short, did not generate a noticeable increase in the mean temperature for those days.

Ambient temperature reached a nadir at approximately 0600 hours and warmed to a zenith at 1600 hours (Fig. 2a). The nycthemeral core temperature cycle revealed a nocturnal maximum corresponding to the observation that the animals rested during the day and were active at night (Fig. 2b). T_{car} was relatively stable during the night, began to decrease at around 0530 hours just before sunrise, reached a nadir during the midmorning at around 1000 hours and then increased gradually during the afternoon to reach the cycle zenith early in the evening at around 1800 hours. The nycthemeral T_{car} amplitude averaged over the five animals was $1.8 \pm 0.3^\circ\text{C}$ (mean \pm SD, $n = 5$). Minimum amplitude was $1.1 \pm 0.3^\circ\text{C}$ and maximum $4.2 \pm 0.5^\circ\text{C}$. Variability in core temperature, as gauged by the standard deviation of the hourly temperatures, was lower during the night than during the day, indicating tight control of core temperature during activity. The variability peaked at midmorning, around 1000 hours (Fig. 2c), and remained higher than at night until 1700 hours.

Effects of environmental conditions, as represented by shade T_{g} , on T_{car} , were inconsistent and minor (Table 1, Fig. 3). For maximum and range (maximum minus minimum daily temperature) of core temperature there was an indication of associations between body temperature and globe temperature for some animals, the regression slopes did not differ between animals, and the regression slopes were significantly different from zero. However, we felt that these analyses were confounded by the occasional large excursions of T_{car} tending to occur more often later in the study, when the days were warmer. We thus repeated these analyses removing days when there was a diurnal maximum of T_{car} greater than 38°C. This was an arbitrary limit, but one which prevented the analysis of body temperature as a function of the environmental temperature being confounded by vigorous exercise. With these days removed there was no association between T_{car} and T_{g} (Table 1).

The minimum morning T_{car} was significantly but weakly associated with the level of radiation during the early morning (Fig. 4). One of the animals exhibited a significant negative relationship between these variables (corrected for Type I error rate) while the relationship was suggestive of a negative

Fig. 2. (A) Mean hourly shade globe temperature over the course of the study. Points show mean \pm SD and the lines above and below are maximum and minimum hourly temperatures, respectively. (B) Mean hourly T_{car} averaged across days for each of the five animals. Points show mean \pm SD on every fifth hour. (C) Hourly standard deviation of T_{car} across days for each of the five animals.

Fig. 3 Relationships between T_{car} of the five animals and T_{g} for mean (A), minimum (B), range (C), and maximum (D) daily temperatures. Legend for individuals is as in Fig. 2. Results of statistical comparisons of these relationships are detailed in Table 1.

Fig. 4. Minimum morning T_{car} level as a function of the average solar radiation level between 0600 and 1000. Legend for individuals is as in Fig. 2. Statistical analysis of these data is detailed in Table 1.

association in three of the others (Table 1). There was no difference in the slopes of the regressions between animals and the mean slope of the five regressions was significantly less than zero ($p = 0.003$, Table 1).

DISCUSSION

Our results provide the longest continuous measurements of body temperature achieved for macropod marsupials. The animals exhibited a nycthemeral pattern of body temperature with an evening zenith as previously described for other species of macropod (Brown and Dawson 1977; McCarron *et al.* 2001). We found these kangaroos to be very capable thermoregulators over the range of conditions to which they were exposed during this study, with no evidence that high ambient temperatures caused increases in maximal body temperatures, or that low ambient temperatures caused lower minimum temperatures. Despite dry bulb temperatures as low as 2°C and as high as 36°C with globe temperatures measured in the shade of up to 45°C, the day-to-day variation in T_{car} of the animals was minimal. Apart from the occasional days when maximum T_{car} spiked very high (> 38°C), which we assume was associated with intense physical activity, the day to day variation in hourly T_{car} was less than 1°C within individuals (Fig. 2).

We do not know whether our findings apply to marsupials in general or are species specific, as there has been no systematic study on the amplitude of the circadian cycle in the metatheria. What is known is that there are differences in the structure of the cycle

between some species. The common brushtail possum (*Trichosurus vulpecula*) (Gemmell *et al.* 1997), the chuditch (*Dasyurus geoffroii*) (Arnold 1976), and the greater bilby (*Macrotis lagotis*) (Morrison 1962), display less variability in core temperature at the cycle zenith than at the nadir, as we found in *M. fuliginosus*. On the other hand the northern brown bandicoot (*Isodon macrourus*) displays the opposite, and has a more variable core temperature at the cycle zenith (Gemmell *et al.* 1997). The South American opossum (*Didelphis marsupialis*), the Virginian opossum (*Didelphis virginiana*) (Gemmell *et al.* 1997), and the southern brown bandicoot (*Isodon obesulus*) (Morrison 1962), display constant variability in body temperature across the nycthemeral period.

The average body temperature in *M. fuliginosus* of 36.5°C is low by eutherian standards, but slightly higher than that reported for marsupials in general (35.3°C; Withers *et al.* 2000). Early reports on macropod marsupials indicated a lower level of body temperature than we report here (Dawson and Hulbert 1970; Dawson 1973), but more recent studies on *M. giganteus* and *M. rufus* over a range of ambient temperatures in the laboratory (Dawson *et al.* 2000a) report levels of body temperature similar to our field measurements. Field measurements in *M. rufus* and *M. giganteus* also reveal nocturnal body temperatures similar to those we report here for *M. fuliginosus* (McCarron *et al.* 2001), but the early morning decrease in *M. giganteus* was much more pronounced than in either *M. rufus* or *M. fuliginosus*.

The most striking feature of the nycthemeral body temperature pattern was the relatively rapid and variable decrease beginning just before sunrise. At this time of day the ambient heat load was increasing from the minimum temperature several hours earlier (Fig. 1a). Previously Brown and Dawson (1977) noted similar morning decreases in body temperature in captive *M. rufus* and suggested that the fall in body temperature may have been caused by a redistribution of warm core blood to the cool periphery, stimulated by a skin temperature increase from solar radiation absorption. We have here presented evidence in favour of this hypothesis, the greater was the average solar radiation intensity in the morning hours, the lower was the minimum core temperature reached at mid-morning (Fig. 4). Body temperature began to decrease before sunrise, and so probably is a component of an endogenous rhythm, but the magnitude of the decrease appeared to be related to environmental cues. A lower morning body temperature when morning radiation load is high, whatever the cause, would increase the scope for passive heat storage in the heat of the day. If the solar radiation intensity in the early morning is indicative of how hot the day will be, then such a mechanism would have adaptive significance. Support for this scenario is that the cumulative shade globe temperature between sunrise and sunset (as an index of how hot the day would be for resting kangaroos) indeed was related to the mean radiation level in the morning ($F_{1,56} = 3.7$, $p = 0.05$). The kangaroos appeared to be pre-empting hot days by lowering morning body temperature. Water savings accrued by greater diurnal heat storage would aid *M. giganteus* and *M. fuliginosus* since they are more dependent on free water than is *M. rufus* (Caughley 1964; Caughley *et al.* 1985). Their numbers have been increasing in the arid zone in recent times (Dawson 1995), a phenomenon probably caused mainly by provision of water for stock in the drier parts of the continent (Dawson 1995). Their thermoregulatory strategies nevertheless would reduce the requirement to return to water often in hot conditions.

The advantage bestowed by lower morning body temperature would be negated if the low temperature was defended by evaporative cooling for the rest of the day. Refinetti and Menaker (1992) have argued that body temperature is more labile during the quiet phase of the circadian cycle because temperature and sleep are co-related. Whether kangaroos sleep during the day is not established. Caughley (1964) never saw wild *M. rufus* or *M. giganteus* sleeping, but individuals of both species monitored closely in a large reserve were observed sleeping (Dawson *et al.* in prep). Whether our kangaroos slept in the day or not, they did not appear to defend a body temperature

that started low. We found that diurnal body temperature was more labile than at night (Fig. 2c).

Counter-intuitively the morning decrease in body temperature in the arid adapted *M. rufus* seems not as pronounced as in *M. giganteus* and *M. fuliginosus* (McCarron *et al.* 2001). If so, then the remarkably lower water requirements of *M. rufus* must reflect other strategies, for example better urine concentrating ability or behavioural strategies that reduce water use for thermoregulation (TJ Dawson, pers. comm.). There is also a suggestion that *M. rufus* evaporates water more efficiently at high ambient temperature. *M. rufus* takes full advantage of a well developed superficial vasculature (Needham 1982) to aid heat loss resulting from licking, resulting in a lower requirement for respiratory evaporative heat loss than in *M. giganteus* (Dawson *et al.* 2000a).

We have characterised the circadian pattern of body temperature in *M. fuliginosus* and shown competent homeothermy: the pattern is remarkably resilient to ambient temperature variation. We additionally have identified a potential thermoregulatory strategy of pre-emptive morning lowering of body temperature when high environmental heat loads are anticipated. Neither of these observations is consistent with thermoregulation in kangaroos being 'primitive'.

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