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Abstract

We examined thermoregulation in red kangaroos (*Macropus rufus*) from deserts and in eastern grey kangaroos (*Macropus giganteus*) from mesic forests/woodlands. Desert kangaroos have complex evaporative heat loss mechanisms, but the relative importance of these mechanisms is unclear. Little is known of the abilities of grey kangaroos. Our detailed study of these kangaroos' thermoregulatory responses at air temperatures (T-a) from -5 degrees to 45 degrees C showed that, while some differences occur, their abilities are fundamentally similar. Both species show the basic marsupial characteristics of relatively low basal metabolism and body temperature (T-b). Within the thermoneutral zone, T-b was 36.3 degrees +/- 0.1 degrees C ((X) over bar +/- SE) in both species, and except for a small rise at T-a 45 degrees C, T-b was stable over a wide range of T-a. Metabolic heat production was 25% higher in red kangaroos at T-a -5 degrees C. At the highest T-a (45 degrees C), both species relied on evaporative heat loss (EHL) to maintain T-b; both panting and licking were used. The eastern grey kangaroo utilised panting (76% of EHL) as the principal mode of EHL, and while this was so for red kangaroos, cutaneous evaporative heat loss (CEHL) was significant (40% of EHL). CEHL appeared to be mainly licking, as evidenced from surface temperatures. Both species utilised peripheral vascular adjustments to control heat flow, as indicated by changes in dry conductance (C-dry). At lower temperatures, C-dry was minimal, but it increased significantly at T-a just below T-b (33 degrees C); in these conditions, the C-dry of red kangaroos was significantly higher than that of eastern grey kangaroos, indicating a greater reliance on dry heat loss. Under conditions where heat flows into the body from the environment (T-a 45 degrees C), there was peripheral vasoconstriction to reduce this inflow; C-dry decreased significantly from the values seen at 33 degrees C in both kangaroos. The results indicated that, while both species have excellent thermoregulatory abilities, the desert red kangaroos may cope better with more extreme temperatures, given that they respond to T-a 45 degrees C with lower respiratory evaporation than do the eastern grey kangaroos.

Keywords

kangaroos, mesic, arid, habitats, influence, temperature, routes, heat, loss, eastern, grey, macropus, thermoregulation, giganteus, rufus, red

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Thermoregulation by Kangaroos from Mesic and Arid Habitats: Influence of Temperature on Routes of Heat Loss in Eastern Grey Kangaroos (*Macropus giganteus*) and Red Kangaroos (*Macropus rufus*)

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ABSTRACT

We examined thermoregulation in red kangaroos (*Macropus rufus*) from deserts and in eastern grey kangaroos (*Macropus giganteus*) from mesic forests/woodlands. Desert kangaroos have complex evaporative heat loss mechanisms, but the relative importance of these mechanisms is unclear. Little is known of the abilities of grey kangaroos. Our detailed study of these kangaroos' thermoregulatory responses at air temperatures (T_a) from -5° to 45°C showed that, while some differences occur, their abilities are fundamentally similar. Both species show the basic marsupial characteristics of relatively low basal metabolism and body temperature (T_b). Within the thermoneutral zone, T_b was $36.3^\circ \pm 0.1^\circ\text{C}$ ($\bar{X} \pm \text{SE}$) in both species, and except for a small rise at T_a 45°C , T_b was stable over a wide range of T_a . Metabolic heat production was 25% higher in red kangaroos at T_a -5°C . At the highest T_a (45°C), both species relied on evaporative heat loss (EHL) to maintain T_b ; both panting and licking were used. The eastern grey kangaroo utilised panting (76% of EHL) as the principal mode of EHL, and while this was so for red kangaroos, cutaneous evaporative heat loss

(CEHL) was significant (40% of EHL). CEHL appeared to be mainly licking, as evidenced from surface temperatures. Both species utilised peripheral vascular adjustments to control heat flow, as indicated by changes in dry conductance (C_{dry}). At lower temperatures, C_{dry} was minimal, but it increased significantly at T_a just below T_b (33°C); in these conditions, the C_{dry} of red kangaroos was significantly higher than that of eastern grey kangaroos, indicating a greater reliance on dry heat loss. Under conditions where heat flows into the body from the environment (T_a 45°C), there was peripheral vasoconstriction to reduce this inflow; C_{dry} decreased significantly from the values seen at 33°C in both kangaroos. The results indicated that, while both species have excellent thermoregulatory abilities, the desert red kangaroos may cope better with more extreme temperatures, given that they respond to T_a 45°C with lower respiratory evaporation than do the eastern grey kangaroos.

Introduction

While basic studies have been made on arid-zone kangaroos such as the red kangaroo (*Macropus rufus*, then called *Megaleia rufa*; Dawson 1973), it is surprising that very little is known about the environmental physiology of common mesic species such as the eastern grey kangaroo (*Macropus giganteus*). The eastern grey has a fossil history going back more than 5 million yr, while the red kangaroo appears to be a newly evolved species with a fossil history restricted to the Pleistocene (Dawson 1995). It has been assumed that many of the thermoregulatory characteristics seen in red kangaroos reflect adaptation to a harsh arid environment. Eastern grey kangaroos have extended their range into more arid regions in the latter part of this century (Dawson 1995), putatively because of the provision of water sources for domestic sheep and cattle. Little is published about the water requirements of eastern greys in dry country, except that they are reported to drink more frequently than red kangaroos (Caughley 1962). However, recent work indicates differences in kidney physiology between these species—red kangaroos have a markedly higher urine-concentrating ability. Additionally, in the arid rangelands, eastern grey kangaroos

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show greater behavioral avoidance of summer heat loads (shade seeking; T. J. Dawson, personal communication).

Red kangaroos have excellent thermoregulatory abilities: evaporative heat loss mechanisms such as panting, sweating, and licking (Dawson 1973, 1989; Dawson et al. 1974; Needham et al. 1974) enable them to cope with high externally (Dawson 1972) and internally produced (Kram and Dawson 1998) heat loads. While the evaporative heat loss mechanisms utilised by red kangaroos have been suggested to follow an efficient pattern, we do not know the relative contribution of these mechanisms at high environmental temperatures. In regard to the grey kangaroos, little has been reported except that they pant and lick. Licking has been suggested to be the grey kangaroo's major route of evaporative heat loss (EHL) at high temperatures (Robertson and Morrison 1957).

In this article, we compare the thermoregulatory characteristics of two kangaroo species that represent the two major evolutionary lineages of extant kangaroos. We also explore the pattern of responses to high ambient temperature by these kangaroos; the aim: to gain further insight into the relative contributions of the several modes of EHL utilised by both species.

Material and Methods

Red kangaroos are the dominant kangaroo of the arid, open plains of inland Australia. The bulk of their population lives in areas with less than 250-mm rainfall. On the other hand, eastern grey kangaroos are predominantly found in the wetter forests and woodlands of eastern Australia. Their range includes the wet tropics of northern Australia as well as cold alpine regions in southern Australia. They are rarely found in areas with less than 250-mm rainfall, and when this does occur, they are associated with the thick cover provided by eucalyptus-lined rivers and creeks (Dawson 1995).

Seven red kangaroos and five eastern grey kangaroos were used. All were mature females, the predominant age/sex class in kangaroo populations (Dawson 1995). The kangaroos had been raised in captivity and were tame; none carried pouch young during the experimental period. The kangaroos were housed in pens ($4.3 \times 1.2 \times 2.5$ m) with food ("kangaroo" pellets, fruit, lettuce, and bread) and water ad lib. Food and water were withheld for 24 h before experimentation. The kangaroos maintained body mass during the approximately 8 wk they were used for measurements. Red kangaroos, at the beginning of the study, were 23.5 ± 1.05 kg, with a range of 21.2–29.0 kg; eastern grey kangaroos were 26.4 ± 0.94 kg, with a range of 23.8–29.0 kg. Experiments were carried out in winter (May–September). The kangaroos were familiarised with the experimental procedure for at least 2 wk before collection. After this time, they would stand quietly in the experimental chamber.

Experiments were carried out during the quiet phase of the kangaroo's diurnal cycle (between 800 and 1600 hours). Animals were placed in a $1.5 \times 0.75 \times 0.45$ -m Lexan metabolism chamber that had a mesh floor above a bath of vegetable oil to cover any excreta. The inside walls of the chamber were painted flat black to reduce radiation reflection in the chamber (Porter 1969). The chamber was placed in an environmental room in which ambient temperature (T_a) was controlled to within $\pm 0.5^\circ\text{C}$ of a set point. Measurements were made near five temperatures (-5° , 15° , 25° , 33° , and 45°C). T_a was measured ($\pm 0.1^\circ\text{C}$) with a Jenco electronic thermometer; the probe was situated in the excurrent port of the chamber. This thermometer was calibrated against a mercury-in-glass thermometer certified by the National Association of Testing Authorities, Australia.

Flow rate of dry air into the chamber was adjusted so that water-vapour pressure in the excurrent air remained below 15 mmHg. Flow rate was measured upstream of the chamber with a Hastings Mass Flowmeter (model HFM-201). Approximately 125 mL min^{-1} of chamber excurrent air was drawn through a capacitance-type humidity sensor (CHK-Engineering dgt-RH/ τ ; $\pm 0.1\%$ RH). This sensor was calibrated at regular intervals with saturated solutions of lithium chloride and sodium chloride (Winston and Bates 1960). The sample airstream was then dried, scrubbed of CO_2 with ascarite, redried, and passed through an Applied Electrochemistry S3A-II oxygen analyser.

Outputs from the three sensors (mass flow, relative humidity, and O_2) were logged every 5 s on a computer via a 16-bit analog/digital (A/D) converter (National Instruments AD board and Warthog software, Warthog Systems, Riverside, Calif.). Approximately 120 readings were averaged for each recorded value. Maximum resolution for this combination of sensors and A/D converter was 0.006% for O_2 . The system was calibrated regularly by the iron-burn method of Young et al. (1984).

Before each experiment, a kangaroo was weighed to the nearest 0.1 kg on a platform balance (Wedderburn Scales, Sydney). Data collection periods lasted from 3 to 5 h. In most cases, total exposure to each T_a was more than 4 h. At the end of an experiment, fur surface temperatures (T_c) of eight representative areas were measured with an Everest infrared thermometer; these regional T_c were for tail, hip, hind leg, back, belly, head, ears, and foreleg.

Body temperature (T_b), measured as intraperitoneal temperature, was measured continuously via temperature transmitters (J. Stuart Enterprises, Gross Valley, Calif.) that had been surgically implanted in the body cavity. Signals from the transmitters were received on a Telonics receiver, and the pulse period was logged on a personal computer via a Telonics TDP-2 processor and an A/D converter (ADC-1, Remote Measurements Systems, Seattle, Wash.). Transmitters were calibrated to $\pm 0.1^\circ\text{C}$ against a certified thermometer.

Table 1: Basic thermoregulatory variables of red kangaroos and eastern grey kangaroos at a wide range of ambient temperatures

Ambient Temperature (°C)	Mass (kg)	T_b (°C)	Mean T_e (°C)	MHP (W kg ⁻¹)	EHL (W kg ⁻¹)	REHL (W kg ⁻¹)	C_{dry} (W m ⁻² °C ⁻¹)
Red kangaroo:							
-4.2 ± .6	23.3 ± .8	36.5 ± .2	6.7 ± .3 ^a	2.48 ± .13 ^a	.17 ± .03 ^a	.15 ± .01 ^a	1.34 ± .07 ^a
16.3 ± .6	23.6 ± .8	36.5 ± .1	21.9 ± .5 ^b	1.49 ± .07 ^b	.24 ± .02 ^a	.16 ± .01 ^a	1.48 ± .06 ^a
25.2 ± .7	23.6 ± 1.1	36.3 ± .1	29.6 ± .5 ^c	1.10 ± .03 ^b	.34 ± .04 ^a	.14 ± .02 ^a	1.71 ± .16 ^a
34.5 ± .2	24.1 ± 1.2	36.5 ± .2	35.2 ± .3 ^d	1.24 ± .07 ^b	.70 ± .03 ^b	.30 ± .06 ^a	7.20 ± 1.52 ^c
44.8 ± .9	23.8 ± 1.3	36.8 ± .1	39.5 ± .4 ^e	1.36 ± .06 ^b	2.36 ± .09 ^c	1.41 ± .09 ^b	3.13 ± .33 ^b
Grey kangaroo:							
-5.2 ± .3	26.5 ± .9	36.6 ± .3 ^{ab}	4.3 ± .6 ^a	1.99 ± .13 ^a	.20 ± .02 ^a	.07 ± .01 ^a	1.04 ± .08 ^a
15.1 ± .2	26.0 ± .9	36.5 ± .2 ^{ab}	19.6 ± .3 ^b	1.32 ± .06 ^b	.18 ± .01 ^a	.09 ± .01 ^a	1.28 ± .04 ^a
26.1 ± .5	26.4 ± .9	36.3 ± .1 ^a	29.4 ± .3 ^c	1.20 ± .06 ^b	.40 ± .05 ^a	.09 ± .01 ^a	1.87 ± .22 ^a
33.4 ± .5	25.8 ± .8	36.9 ± .3 ^{ab}	34.8 ± .2 ^c	1.25 ± .07 ^b	.61 ± .06 ^b	.28 ± .03 ^a	4.76 ± .59 ^c
43.5 ± .4	26.2 ± 1.0	37.1 ± .2 ^b	39.4 ± .3 ^e	1.38 ± .11 ^b	2.21 ± .15 ^b	1.65 ± .15 ^b	3.17 ± .37 ^b

Note. Values are $\bar{X} \pm SE$. Statistical difference between intraspecific values at different temperatures is indicated by letters within each column; values without common letters are different (SNK; $P < 0.05$).

Oxygen consumption (\dot{V}_{O_2}) was calculated as

$$\frac{\dot{V}_{STDP}(F_{IO_2} - F_{EO_2})}{1 - F_{EO_2}},$$

where \dot{V}_{STDP} = flow rate of dry air into the chamber (STPD), and F_{IO_2} and F_{EO_2} were the fractional concentrations of O_2 in dry air entering and leaving the chamber, respectively (Hill 1972). Evaporative water loss (EWL) was calculated as

$$EWL = (FE_{H_2O} - FI_{H_2O})\dot{V}$$

(FI_{H_2O} was zero),

where FE_{H_2O} and FI_{H_2O} were the water contents, respectively, of the excurrent and incurrent air (calculated from humidity using a predictive equation based on vapour-pressure data in the CRC Handbook of Chemistry and Physics [Weast and Astle 1983]), and \dot{V} was the flow rate at specified T_a and pressure.

Metabolic rate (MR) and EWL at each T_a were defined as the lowest continuous 20 min of \dot{V}_{O_2} and EWL, respectively, in any collection period. Metabolic heat production (MHP) and evaporative heat loss (EHL) were calculated assuming 20.08 kJ L⁻¹ O_2 and 2.42 kJ g⁻¹ H_2O . Dry conductance (C_{dry} ; SA = surface area) was calculated as

$$C_{dry}(\text{W m}^{-2} \text{ °C}^{-1}) = \frac{(\text{MHP} - \text{EHL})}{(T_b - T_a) \times \text{SA}}.$$

Since body temperatures were stable during measurements of C_{dry} , allowance for changes in heat storage were not necessary. The fur SA of each of the eight regions was initially

measured for each kangaroo. Areas were traced with tissue paper, and the area was calculated by a Graphetic Digitiser, KD4300 (Southern Graphetic Systems). Total SA of the kangaroos were used to calculate Meeh formulae (see Dawson and Hulbert [1970] for discussion of Meeh formulae). These formulae were used in subsequent experiments: for the red kangaroo,

$$SA(\text{cm}^2) = 12.0 \pm 0.2 \text{ Mass}(\text{g})^{0.667},$$

and for the eastern grey kangaroo,

$$SA(\text{cm}^2) = 12.3 \pm 0.5 \text{ Mass}(\text{g})^{0.667}.$$

The average contribution of each region to total SA was used to estimate the mean surface temperature (T_e) of kangaroos. T_e was used in the Stefan-Boltzman equation, with an effective SA of 0.8, to assess the role of radiation in heat exchange independently of overall dry heat loss, as determined by C_{dry} .

EWL was partitioned into respiratory evaporative water loss (REWL) and cutaneous evaporative water loss (CEWL). The values for REWL were obtained from our companion study on the ventilatory accommodation of oxygen demand and respiratory water loss in the two species of kangaroo (Dawson et al. 2000).

Data were initially analysed with two-way repeated measures ANOVA for species and the five T_a . A Student-Newman-Keuls (SNK) multiple-range test was applied when significant differences were indicated by the ANOVA (using Statistica 4.1 for Macintosh, Statsoft, Tulsa, Okla.). All figures and Table 1 show $\bar{X} \pm SE$. Means considered significantly different have a $0.01 < P < 0.05$, unless otherwise noted.

Results

The T_b of the two species when at rest did not differ significantly at temperatures within the T_a range of -5° to 45°C (Fig. 1; Table 1). At T_a 25°C , the T_b of *Macropus rufus* was $36.3^\circ \pm 0.13^\circ\text{C}$ and that of *Macropus giganteus* was $36.3^\circ \pm 0.06^\circ\text{C}$. A small but significant rise occurred in the T_b of *M. giganteus* at 45°C , relative to the value at 25°C .

The two species did not differ in MHP (as derived from oxygen consumption), except at the lowest temperature (around -5°C), where that of red kangaroos was 25% higher ($P=0.0004$; Fig. 2). The lower critical temperature in both species was below T_a 15°C ; metabolism in both species rose significantly ($P<0.0002$) below this temperature (Table 1).

Total EHL, in both absolute terms (Table 1) and relative to MHP (Fig. 3), was similar at all T_a in the two species of kangaroo. Total EHL was below 10% of MHP at low T_a but rose significantly to about 30% of MHP at 25°C . At higher tem-

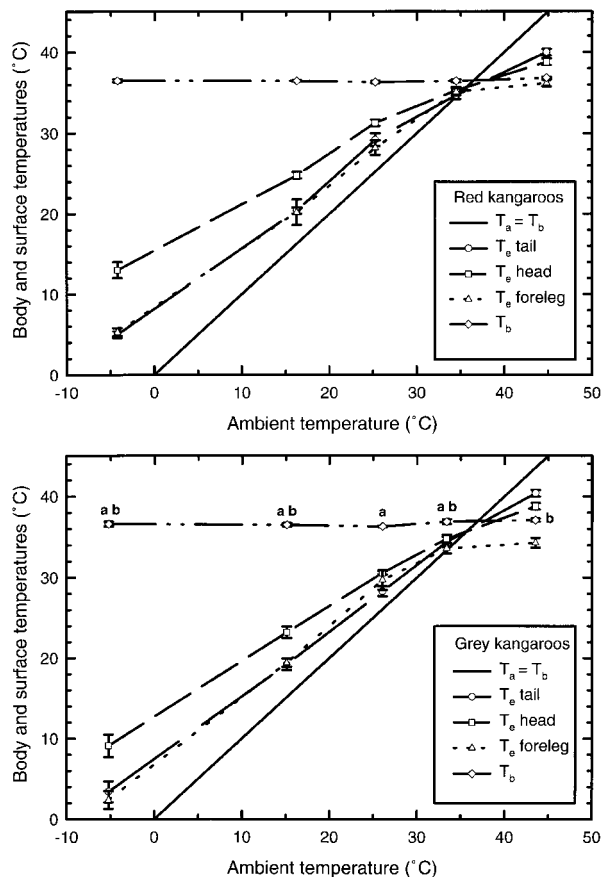


Figure 1. Body temperature (T_b) and regional fur surface temperatures (T_e) at different ambient temperatures (T_a) for red kangaroos (top panel) and eastern grey kangaroos (bottom panel). Values are $\bar{X} \pm \text{SE}$; if error bars are not visible they are enclosed within symbols. Statistical differences for T_e are discussed in "Results."

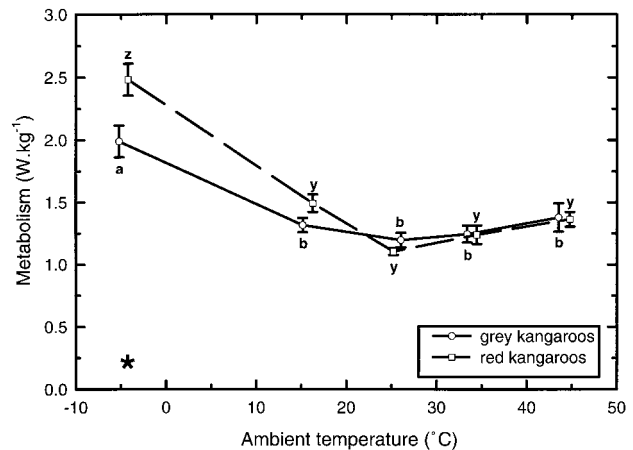


Figure 2. Metabolic rates of eastern grey kangaroos and red kangaroos at a range of T_a . Values are $\bar{X} \pm \text{SE}$; different letters for the same species denote significant differences between means (SNK; $P<0.05$). Note that letters for eastern grey kangaroos start with *a* and those for red kangaroos start with *z*. Star on X-axis indicates significant differences between species.

peratures, it became the more dominant route of heat loss (Fig. 3) and, at 45°C , was responsible for the loss of all heat production together with any heat that flowed into the body. The combined heat from both sources approached 1.7 times MHP as T_a reached 45°C .

EHL can be divided into respiratory losses (REHL) and cutaneous (CEHL) losses (Fig. 4). The latter, in kangaroos, comprises sweating and licking, which it was not feasible to separate. Other data, principally surface-temperature measurements, give some insight into relative levels of sweating and licking.

Except at 45°C , no significant differences were apparent between the species in modes of EHL (Fig. 4). For each species, REHL and CEHL were both less than 10% of MHP at low temperatures (-5° and 15°C). Both rose significantly at 25°C and further at 33°C . It was only at 45°C that REHL became the dominant form of EHL. While this pattern occurred in both species, REHL is significantly more important in *M. giganteus* than in *M. rufus*. Conversely, in *M. rufus* cutaneous evaporation played a more substantial role at T_a 45°C ($P<0.001$).

The patterns of dry heat loss (and heat inflow at T_a above T_b) were similar in both species. Only at 33°C was there a significant difference between *M. giganteus* and *M. rufus* (Fig. 5). Conductance was least at the lower temperatures, reflecting peripheral vasoconstriction. C_{dry} tended to increase in thermoneutrality (T_a of 25°C), but there was a marked significant rise at T_a 33°C , a T_a slightly below T_b . At this temperature, the C_{dry} of *M. rufus* was significantly higher ($P=0.006$) than that of *M. giganteus*. Of note, at T_a well above T_b (45°C), C_{dry} de-

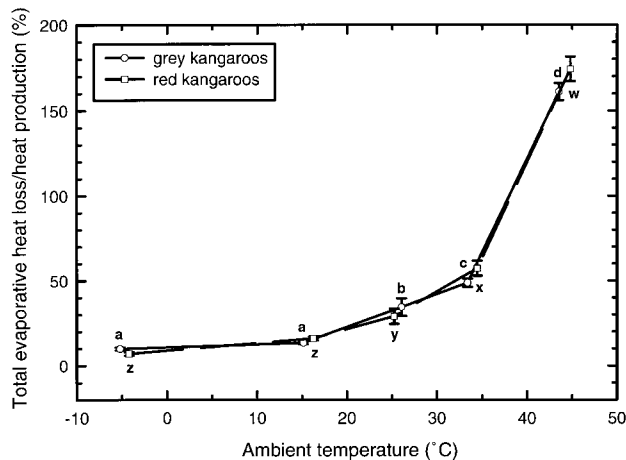


Figure 3. Variation with T_a of total evaporative water loss in eastern grey kangaroos and red kangaroos. Values are $\bar{X} \pm \text{SE}$; different letters for the same species denote significant differences between means (SNK; $P > 0.05$).

creased relative to its value at 33°C but was still significantly above the values at 25°C.

Mean T_e differed between the species only at the lowest temperatures, (-5° and 15°C), when *M. rufus* values were significantly higher ($P = 0.002$). Patterns of change of regional fur T_e 's with changes in T_a were similar within species. Representative T_e are shown in Figure 1. At the lowest T_a , *M. rufus* tended to have higher regional surface temperatures: those of the head and the belly were significantly different ($P < 0.001$ in each case). At the lowest T_a , peripheral and less well furred areas in both species (such as tail, lower hind legs, forelegs, and ears), had T_e significantly lower than those of the head and belly; the back tended to be intermediate (Fig. 1). This pattern largely continued at $T_a 15^\circ\text{C}$.

At thermoneutral temperatures ($T_a 25^\circ\text{C}$), there were no differences in T_e between species and no significant within species effects in grey kangaroos. However, for *M. rufus*, head T_e was still significantly higher than those of tail, foreleg, and hind leg, but ear T_e had risen to be the highest T_e , indicating vasodilatation. By $T_a 33^\circ\text{C}$, the T_e of the ears of *M. rufus* was significantly higher than all other T_e and was similar to T_b . Other T_e did not differ; that is, peripheral temperatures were comparable with those of core areas. In *M. giganteus*, the T_e of the ears was also the highest T_e but was only significantly different from that of the foreleg.

When T_a was well above T_b , different patterns occurred; most noticeably, T_e of the foreleg was significantly lower than that of all other T_e in both species and was the only T_e lower than T_b —markedly so in *M. giganteus* ($P < 0.0002$). Back and tail T_e were the highest T_e in both species and were significantly higher than most other regional T_e 's.

Discussion

In its thermoregulatory patterns, the mesic forest/woodland kangaroo *Macropus giganteus* is not markedly different from the desert kangaroo *Macropus rufus*. There were differences between the species, but generally they were not major, which is perhaps surprising given their long evolutionary separation and different habitats (Dawson 1995).

T_b 's and general patterns of change in metabolism with T_a were similar to those that have been reported previously for red kangaroos (Dawson 1973) and other macropodids (Dawson 1989; McCarron and Dawson 1989). The picture is one seen generally in marsupials and first noted by Martin (1902); T_b tends to be low relative to that seen in many placentals but is relatively stable over a wide range of T_a 's. The body temperatures were 36.3°C at $T_a 25^\circ\text{C}$ for both species (Table 1), with a rise of less than 1°C occurring at 45°C . Metabolism was not significantly different in either species between 15° and 45°C . The minimum values for *M. rufus* and *M. giganteus* at $T_a 25^\circ\text{C}$ were within the range generally reported for marsupials, that is, 20%–30% below the levels given for many placentals. The lower critical temperatures of both species were below $T_a 15^\circ\text{C}$. The kangaroos were in winter fur, and a lower critical temperature of 11° – 12°C has been previously reported for *M. rufus* in winter (Dawson 1973).

This study is more comprehensive and detailed than previous studies and gives much insight into the thermoregulatory responses of kangaroos. New information is provided for higher T_a , but the data at lower T_a are also informative. Although T_b

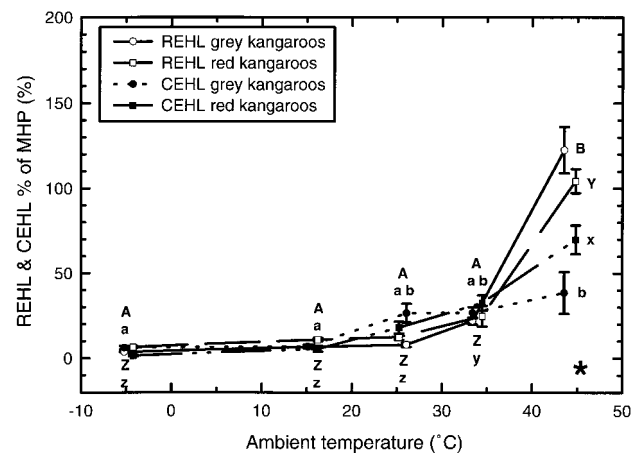


Figure 4. Partition of evaporative heat loss between REHL and CEHL at a range of T_a for eastern grey kangaroos and red kangaroos. Values are $\bar{X} \pm \text{SE}$; different letters for the same species and route of EHL denote significant differences between means (SNK; $P < 0.05$). Letters for REHL of eastern grey kangaroos start with A; those for their CEHL start with a. Letters for REHL of red kangaroos start with Z; those for their CEHL start with z. Star on the X-axis indicates a significant difference between species for CEHL.

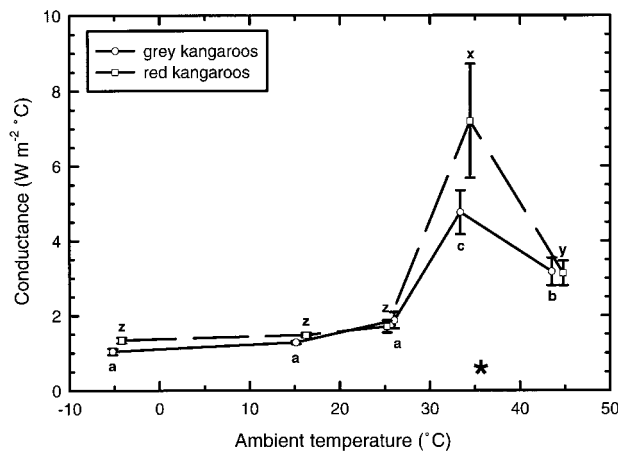


Figure 5. Change in conductance at different T_a in eastern grey kangaroos and red kangaroos. Values are $\bar{X} \pm SE$; different letters for the same species denote significant differences between means (SNK; $P > 0.05$). Star on the X-axis indicates a significant difference between species.

did not differ between species at the lowest T_a , metabolism did—that of *M. rufus* was higher. This seems related to levels of fur insulation. A study by McCarron (1990) found that, in winter, the trunk insulation was similar in the two species, but the hip/thigh values were significantly lower in red kangaroos. In still air, the values in $^{\circ}\text{C W}^{-1} \text{m}^{-2}$ ($\bar{X} \pm SE$) for *M. rufus* were 0.33 ± 0.025 for trunk and 0.24 ± 0.012 for thigh; for *M. giganteus*, 0.31 ± 0.005 for trunk and 0.30 ± 0.011 for thigh. In summer, the fur insulation of *M. rufus* is generally lower than that of *M. giganteus* (McCarron 1990).

Below the lower critical temperatures, heat loss was primarily via radiation, convection, and conduction. These forms of heat loss account for more than 90% of the heat loss. Calculations based on mean surface temperature indicated that radiation from a kangaroo's surface was by far the main avenue of heat loss. It was about two-thirds of total heat loss at $T_a -5^{\circ}\text{C}$. The kangaroos combat this by minimizing C_{dry} in the cold via peripheral vasoconstriction and regional heterothermia. This was indicated by the patterns of T_c 's (Fig. 1). While complex vascular arrangements occur in the tail and limbs, countercurrent vascular arrangements do not exist (Dawson 1989).

Apart from the decreased metabolism in the thermoneutral range ($T_a 15^{\circ}\text{--}25^{\circ}\text{C}$), there were few significant changes in heat balance parameters from the values seen at $T_a -5^{\circ}\text{C}$. There were changes in the patterns of T_e , which indicated an increased peripheral blood flow. At $T_a 25^{\circ}\text{C}$, the T_e of the ears of both species had increased to be the highest of the regional T_e , after being among the lowest at $T_a -5^{\circ}\text{C}$. Values for C_{dry} tended to increase in both species but not significantly so. Of note, even with the much reduced gradient, radiation still accounted for around 60% of total heat loss; this is much higher than the

losses via conduction and convection. EHL was significantly elevated in both species to approximately 30% of MHP.

As T_a increases to 33°C , that is, just below T_b , major thermoregulatory adjustments occur in both species. Total EWL increased significantly in both species and accounted for about 50% of heat loss. The increases occurred in both respiratory and cutaneous evaporation. The surface temperatures of the forelegs were relatively low in both species (Fig. 1), an indication that licking was starting to be brought into play.

Although the gradient for heat loss by radiation, convection, and conduction was much decreased at 33°C , the kangaroos still lost half of their metabolic heat by this route, thus effecting considerable water savings. The vascular adjustments needed to achieve this heat loss were reflected in the marked increase in C_{dry} (Fig. 5), which was noticeably higher in *M. rufus* than in *M. giganteus*. Adjustments to skin blood flow in hot conditions occur largely in arteriovenous anastomoses (AVAs), as elegantly shown (with radioactive microsphere techniques in sheep) by Hales et al. (1978a) and Hales and Fawcett (1979). Using the same techniques, Needham and Dawson (1984) demonstrated large changes in AVA flows in *M. rufus* that parallel the changes that we have found in C_{dry} . In cold and thermoneutral conditions, AVA flow was some 3%–4% of cardiac output, but it rose significantly to 31% at T_a just below T_b ; at $T_a 42^{\circ}\text{--}45^{\circ}\text{C}$, AVA flow decreased to 24% of the cardiac output.

The pattern of thermoregulation in kangaroos changed markedly at $T_a 45^{\circ}\text{C}$. No heat loss by radiation, conduction, or convection was possible; indeed, there was substantial heat inflow from the environment, principally via radiation. In these conditions, maintenance of T_b near thermoneutral levels could only be achieved via substantial increases in total EHL (Fig. 3). EHL was 161% of metabolic heat production in *M. giganteus* and 174% in *M. rufus*—the difference between species was not significant.

Both species limited the inflow of heat (and saved water) by using vasomotor adjustments. AVA flow was presumably principally involved, but skin capillary blood flow may also play a role. Apart from the large changes in AVA flows in *M. rufus*, Needham and Dawson (1984) noted marked reductions in skin capillary flow to the tail and trunk at $T_a 42^{\circ}\text{--}45^{\circ}\text{C}$; blood flow to foreleg skin increased at the same time. The overall impact of such adjustments was that C_{dry} decreased significantly from the values seen at $T_a 33^{\circ}\text{C}$. The values were, however, still higher than those seen at $T_a 25^{\circ}\text{C}$ (Fig. 5). Peripheral vasoconstriction in the heat has been reported for numerous arid-inhabiting mammals and birds since it was first reported in the antelope jackrabbit (*Lepus alleni*; Schmidt-Nielsen et al. 1965; Dawson and Schmidt-Nielsen 1966). The mechanisms involved in such vasomotor adjustments have largely been uncovered by the studies of Hales and coworkers (Hales et al. 1978a, 1978b; Hales and Fawcett 1979).

Total EHL can be partitioned into respiratory and cutaneous components (Fig. 4). At high T_a , REHL was the principal mode

of EHL in both species and accounted for 76% of total EHL in *M. giganteus*, while in the arid-zone species *M. rufus*, the level was only 60%. Ventilation patterns of *M. rufus* and *M. giganteus* differ at high T_a and are examined in detail by Dawson et al. (2000). While REHL dominated, CEHL also played a substantial role, particularly in *M. rufus*.

Cutaneous evaporation includes water loss through the skin (passive diffusion and sweating) and water spread onto the skin (licking). Is it possible to tease these apart in the case of the kangaroos? Regional surface temperatures provide insight. For effective heat loss from a surface, T_e needs to be below T_b and T_a . For example, when exercise induces sweating in *M. rufus* at high T_a , the skin T_e rapidly falls below T_b (Dawson 1973). For both species, at a T_a of 45°C, tail and back T_e were high, >40°C; head and ear T_e were lower but still above T_b . This contraindication of sweating on these surfaces in our resting *M. giganteus* and *M. rufus* is in agreement with the findings for *M. rufus* and *Macropus robustus erubescens* by Dawson (1973) and Dawson et al. (1974).

If sweating does not occur, licking provides the high CEWL in *M. rufus*. The T_e of the forelegs was below T_b in both species, but that of *M. giganteus* was the lower, $34.3^\circ \pm 0.6^\circ\text{C}$ versus $36.2^\circ \pm 0.4^\circ\text{C}$ for *M. rufus*. The higher T_e in *M. rufus* may reflect high blood flows. Kangaroos and some wallabies have a special anastomosing network of superficial vessels in their forelegs to facilitate heat loss via licking (Needham et al. 1974), and this is most developed in *M. rufus* (Needham 1982). Large increases in foreleg blood flow occur in *M. rufus* when T_a is raised above thermoneutral levels (Needham et al. 1974; Needham and Dawson 1984). While circumstantial, the data suggest that licking provides most of the nonrespiratory EHL of *M. rufus* at 45°C.

All kangaroos lick their forearms as part of their heat loss mechanisms. What are the benefits of its greater use by resting *M. rufus* when panting and sweating are in its repertoire? The answer may lie in the environmental heat loads that this species normally faces in its usual habitat. Dawson (1972) estimated an effective radiation temperature of 60°C in the shade of the sparse desert trees under which *M. rufus* rests on hot summer days, with a T_a as high as that used in this study. In full sun, the effective radiation temperature rises to 75°C. The few *M. giganteus* that may extend into such regions generally restrict themselves to areas along creeks that provide dense shade (Dawson 1995). In these severe conditions, licking may be seen as an auxiliary route of EHL that poses less problems than sweating. Apart from the forelimbs, peripheral vasoconstriction can still be exerted over most of the body surface, thereby reducing heat inflow. The level of C_{dry} and the pattern of regional surface temperatures at T_a 45°C attest to this probability.

Why should kangaroos need to supplement panting by an expanded role for licking? There are, in fact, limitations to panting as a heat loss mechanism in severe heat (Hales and Webster 1967; Hales and Findlay 1968). That some large bovines both pant and sweat in response to severe heat loads (Robert-

shaw and Taylor 1969) also reflects these limitations in the use of panting by large mammals. The difficulties that arise with panting involve the acid-base balance of the blood and energetic cost. These aspects of the ventilatory responses of kangaroos during thermoregulation are examined in the accompanying article (Dawson et al. 2000).

The overall requirement for superior heat loss mechanisms by kangaroos may also be related to their generation of high internal heat loads. Marsupials are highly aerobic mammals, despite their relatively low basal metabolic rates (Dawson and Dawson 1982; Hinds et al. 1995). *Macropus rufus* has a maximum metabolic rate that is among the highest of all terrestrial mammals (Kram and Dawson 1998), achieving levels equivalent to those of race horses. The ability of kangaroos to alter the mode of EHL in response to different types of heat stress is significant since it indicates a refinement of the thermoregulatory response to heat not matched in other mammals.

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