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**Ventilatory accommodation of oxygen demand and respiratory water loss in kangaroos from mesic and arid environments, the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Macropus rufus*)**

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## Abstract

We studied ventilation in kangaroos from mesic and arid environments, the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Macropus rufus*), respectively, within the range of ambient temperatures ( $T_a$ ) from -5 degrees to 45 degrees C. At thermoneutral temperatures ( $T_a = 25$  degrees C), there were no differences between the species in respiratory frequency, tidal volume, total ventilation, or oxygen extraction. The ventilatory patterns of the kangaroos were markedly different from those predicted from the allometric equation derived for placentals. The kangaroos had low respiratory frequencies and higher tidal volumes, even when adjustment was made for their lower basal metabolism. At  $T_a > 25$  degrees C, ventilation was increased in the kangaroos to facilitate respiratory water loss, with percent oxygen extraction being markedly lowered. Ventilation was via the nares; the mouth was closed. Differences in ventilation between the two species occurred at higher temperatures, and at 45 degrees C were associated with differences in respiratory evaporative heat loss, with that of *M. giganteus* being higher. Panting in kangaroos occurred as a graded increase in respiratory frequency during which tidal volume was lowered. When panting, the desert red kangaroo had larger tidal volumes and lower respiratory frequencies at equivalent  $T_a$  than the eastern grey kangaroo, which generally inhabits mesic forests. The inference made from this pattern is that the red kangaroo has the potential to increase respiratory evaporative heat loss to a greater level.

## Keywords

respiratory, water, loss, kangaroos, mesic, arid, environments, eastern, grey, kangaroo, macropus, demand, giganteus, oxygen, rufus, ventilatory, accommodation, red

## Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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# Ventilatory Accommodation of Oxygen Demand and Respiratory Water Loss in Kangaroos from Mesic and Arid Environments, the Eastern Grey Kangaroo (*Macropus giganteus*) and the Red Kangaroo (*Macropus rufus*)

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## ABSTRACT

We studied ventilation in kangaroos from mesic and arid environments, the eastern grey kangaroo (*Macropus giganteus*) and the red kangaroo (*Macropus rufus*), respectively, within the range of ambient temperatures ( $T_a$ ) from  $-5^\circ$  to  $45^\circ\text{C}$ . At thermoneutral temperatures ( $T_a = 25^\circ\text{C}$ ), there were no differences between the species in respiratory frequency, tidal volume, total ventilation, or oxygen extraction. The ventilatory patterns of the kangaroos were markedly different from those predicted from the allometric equation derived for placentals. The kangaroos had low respiratory frequencies and higher tidal volumes, even when adjustment was made for their lower basal metabolism. At  $T_a > 25^\circ\text{C}$ , ventilation was increased in the kangaroos to facilitate respiratory water loss, with percent oxygen extraction being markedly lowered. Ventilation was via the nares; the mouth was closed. Differences in ventilation between the two species occurred at higher temperatures, and at  $45^\circ\text{C}$  were associated with differences in respiratory evaporative heat loss, with that of *M. giganteus* being higher. Panting in kangaroos occurred as a graded increase in respiratory frequency, during which tidal volume was lowered. When panting, the desert red kangaroo had larger tidal volumes and lower res-

piratory frequencies at equivalent  $T_a$  than the eastern grey kangaroo, which generally inhabits mesic forests. The inference made from this pattern is that the red kangaroo has the potential to increase respiratory evaporative heat loss to a greater level.

## Introduction

Early thermoregulatory studies on kangaroos focused on licking as the primary evaporative heat loss mechanism at high temperatures (Robertson and Morrison 1957). However, desert kangaroos (*Macropus rufus*) use a range of evaporative heat loss mechanisms, including licking, sweating, and panting (Dawson 1973). Licking plays an interesting role in thermoregulation (Needham et al. 1974), as does sweating in exercise (Dawson 1973; Dawson et al. 1974), but panting is considered to be the principal route in these kangaroos at rest (Dawson 1973). The validity of this suggestion has not been adequately tested, and its applicability to all kangaroos, such as the eastern grey kangaroo (*Macropus giganteus*) from mesic environments, is unknown.

The ventilatory system of mammals must not only carry out gas exchange in thermoneutral conditions but must also accommodate the increased oxygen demand associated with increased heat production in the cold. In addition, the demand for increased evaporative water loss in the heat can involve the ventilatory system via forms of panting. The supply of oxygen by the ventilatory system involves three variables: the ventilation frequency ( $f_R$ ), the volume of those breaths (tidal volume;  $V_T$ ), and the fraction of the oxygen in each breath that the animal ultimately uses (oxygen extraction;  $E_{O_2}$ ). Each of these variables has limits, although the number of combinations is theoretically infinite. The combination chosen by different species to satisfy oxygen consumption and respiratory evaporation may reflect a minimum cost to respiratory muscles (Dejours 1981) or to phylogenetic or ecological differences. There is much variation among small marsupials (Chappell and Dawson 1994).

In arid zone kangaroos, thermoregulatory panting was nasal only (the mouth was closed), and there was a graded increase

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in respiratory rate with increasing heat stress (Dawson 1973). This pattern is different from that seen in dogs, which have been considered to pant efficiently in terms of energy use (Crawford 1962; Schmidt-Nielsen et al. 1970). To clarify the nature and role of the respiratory responses of kangaroos during thermoregulation, we have quantified patterns of ventilation at  $T_a$  from cold ( $-5^\circ\text{C}$ ) to extremely hot ( $45^\circ\text{C}$ ) temperatures in two species of kangaroo, one from an arid habitat and one from a mesic habitat.

### Material and Methods

Seven red kangaroos and five eastern grey kangaroos were used. All were mature females because mature females are 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 familiarized with the experimental procedure for at least 2 wk before data collection, after which time they would stand quietly in the metabolic chamber. Food and water were withheld for 24 h before experimentation. The kangaroos maintained body mass during the approximately 8 wk they were used for the measurements. Red kangaroos at the beginning of the study were  $23.5 \pm 1.05$  kg with a range of 21.2–29.0 kg; eastern grey kangaroos were  $26.4 \pm 0.94$  kg with a range of 23.8–29.0 kg.

Experiments were conducted in winter (May–September) near five  $T_a$  ( $-5^\circ$ ,  $15^\circ$ ,  $25^\circ$ ,  $33^\circ$ ,  $45^\circ\text{C}$ ). Oxygen consumption and evaporative water loss were measured using open circuit respirometry. The metabolic chamber ( $1.5 \times 0.75 \times 0.45$  m) was situated inside a temperature-controlled room that regulated  $T_a$  to  $\pm 0.5^\circ\text{C}$  of a set point. See our companion study (Dawson et al. 2000) for details on techniques. The metabolic chamber also acted as a whole body plethysmograph (Bucher 1981; Maloney and Dawson 1994). Pressure changes caused by the warming (or cooling) and wetting of inspired air were measured with a pressure transducer (Sable Systems PT-100, Sable Systems, Henderson, Nev.). The voltage output from the transducer was monitored every 0.1 or 0.2 s by a personal computer via an analog/digital converter. Files saved to disk contained 64 or 128 s of ventilation data. The system was calibrated by injecting a known volume of air (630 mL) into the chamber after each experiment. The injection procedure was repeated 10 times at rates such that deflection kinetics were similar to those recorded from ventilating kangaroos. The mean of 10 injections was used in calculations.

Use of an open-circuit chamber alleviates the pressure buildup inherent in the design of closed (Drorbaugh and Fenn 1955) or “slow-leak” systems (Jacky 1978, 1980) due to the gradual warming and humidification of chamber air and eliminates the need for base line corrections such as those applied by Drorbaugh and Fenn (1955). Stahel and Nicol (1988) showed that uncorrected  $V_T$  estimates ( $V_T$  estimated directly

from pressure deflections) in an open-circuit system were not significantly different from simultaneous estimates of  $V_T$  obtained using pneumotachography. We estimated  $V_T$  from pressure deflections on ventilation traces using equation 6 from Malan (1973), assuming lung temperature was equal to body temperature ( $T_b$ ).  $V_T$  values were the mean of five sets of readings (files) made throughout the 20-min oxygen consumption determination.

When  $T_a$  approaches or exceeds an animal’s body temperature, the barometric system theoretically becomes unreliable because the pressure change associated with temperature change of inspired air approaches 0 or becomes negative. The low humidities (always  $<15$  mmHg) used in our experiments resulted in the pressure change due to wetting of inspired air being greater than that due to temperature change at high  $T_a$ . At  $T_a = 45^\circ\text{C}$ , the pressure increase due to wetting of an average tidal volume was twice the pressure decrease due to cooling of that air to body temperature. The potential errors in  $V_T$  estimates at high  $T_a$  have been considered for our system in Maloney and Dawson (1994) and compounding errors could result in a maximum 21% overestimate of  $V_T$ .

Tidal volume was measured as  $V_{T_{PS}}$  (body temperature, ambient pressure, saturated) but is presented as  $V_{T_{PD}}$  (standard temperature and pressure, dry), as is  $\dot{V}_I$  (total minute ventilation). Oxygen extraction was calculated as

$$E_{O_2}(\%) = \frac{\dot{V}_{O_2}}{F_{IO_2} \times V_T \times fr} \times 100,$$

where  $F_{IO_2}$  is the fractional concentration of oxygen in chamber incurrent air and  $\dot{V}_{O_2}$  is the oxygen consumption.

Expired air temperature ( $T_{ex}$ ) was measured with a copper-constantan thermocouple (0.25 mm diameter) held at the opening of the nares. The measurement was made in the controlled-temperature room immediately after the metabolic chamber was opened after the final metabolic measurements. Temperature of the thermocouple was logged at 0.1 s intervals on a personal computer via a thermocouple reference/amplifier (AD595 chip [Jaycar, Sydney] and custom-made circuit) and a 12 bit analog/digital converter (Sable Systems). The thermocouple was calibrated against a mercury-in-glass thermometer certified by the National Association of Testing Authorities, Australia. The time lag of the thermocouple was approximately 0.3 s. At all  $T_a$ , the  $T_{ex}$  trace reached a plateau, and  $T_{ex}$  was taken as the average temperature once the trace had stabilized. Respiratory evaporative heat loss (REHL) was calculated as the difference in heat and water content of inspired and expired air, assuming that air was inhaled at chamber temperature and humidity and was expired saturated at  $T_{ex}$ , and  $2.427$  kJ  $g^{-1}$   $H_2O$ .

Results were analyzed using a two-way repeated measures ANOVA for species and temperature. A Student-Newman-

Keuls (SNK) multiple-range test was applied when significant differences were indicated by the ANOVA (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

Total minute ventilation ( $\dot{V}_I$ ) was not found to differ between the two species of kangaroo at any  $T_a$  (Table 1; Fig. 1). The overall pattern seen in the kangaroos indicated little variation from  $T_a -5^\circ$  to that of  $T_a 25^\circ\text{C}$ . The values for  $\dot{V}_I$  at  $25^\circ\text{C}$ , a thermoneutral  $T_a$ , were  $102 \pm 11$  and  $92 \pm 10 \text{ mL kg}^{-1} \text{ min}^{-1}$  for red kangaroos and grey kangaroos, respectively (Table 1). There was a trend to an increase at  $T_a 33^\circ\text{C}$ , but a marked change was seen at  $45^\circ\text{C}$  ( $P < 0.0001$ ), when  $\dot{V}_I$  increased 10-fold over that at  $T_a 25^\circ\text{C}$  (Fig. 1). These changes were accommodated by variation in both  $f_R$  and  $V_T$  (Table 1; Figs. 2, 3). Respiratory frequency rose by some 17 times at  $T_a 45^\circ\text{C}$  (Fig. 2) and was responsible for the increases in  $\dot{V}_I$  in both species at the higher  $T_a$  because of declines in  $V_T$  (Fig. 3).

While no differences in  $\dot{V}_I$  between species were noted, differences were seen in  $f_R$  and  $V_T$  (Table 1; Figs. 2, 3). The  $f_R$  values of red kangaroos were significantly lower at  $T_a 33^\circ\text{C}$  and  $T_a 45^\circ\text{C}$ ; they were 35 and 146 breaths  $\text{min}^{-1}$  at  $T_a 33^\circ\text{C}$  and  $T_a 45^\circ\text{C}$ , respectively, as compared to 80 and 203 breaths  $\text{min}^{-1}$  for the eastern grey kangaroo. While there was much variability in the data, the  $V_T$  values of red kangaroos were consistently above those of the eastern grey kangaroo but only significantly so at  $T_a 33^\circ\text{C}$ . Overall, the  $V_T$  of both species tended to decrease with increasing temperature. The data for  $T_a 33^\circ\text{C}$  were interesting in that in grey kangaroos the  $V_T$  declined significantly

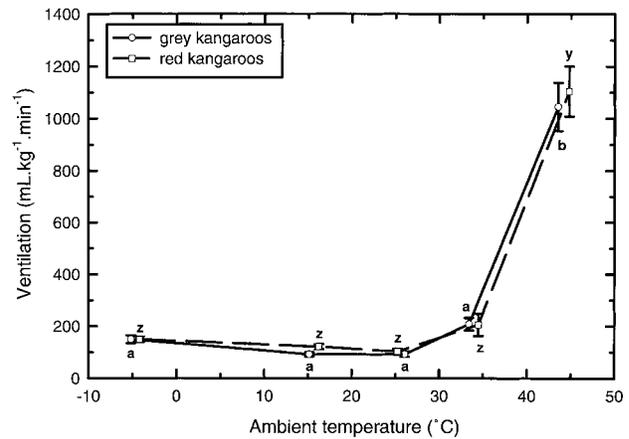


Figure 1. Ventilation of eastern grey kangaroos and red kangaroos at a range of ambient temperatures ( $T_a$ ). Values are  $\bar{X} \pm SE$ ; if error bars are not visible, they are enclosed within the symbols. Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ); letters for grey kangaroos start at *a*; letters for red kangaroos start at *z*.

but increased again at  $45^\circ\text{C}$ . Further, there was much variability in the values of  $V_T$  in red kangaroos: some showed a similar pattern to that of the grey kangaroos, while others remained little changed from the values at  $T_a 25^\circ\text{C}$ .

At higher temperatures, the major changes in  $\dot{V}_I$  were made to facilitate respiratory water loss and concomitant heat loss (Fig. 4). There was generally no difference between the species over a wide range of  $T_a$ , the exception being  $T_a 45^\circ\text{C}$ , where REHL of grey kangaroos is significantly higher ( $P < 0.007$ ).

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

Ambient Temperature (°C)	Mass (kg)	$T_b$ (°C)	$f_R$ (breaths $\text{min}^{-1}$ )	$V_T$ ( $\text{mL kg}^{-1}$ )	$\dot{V}_I$ ( $\text{mL kg}^{-1} \text{ min}^{-1}$ )	$\dot{V}_{O_2}$ ( $\text{mL kg}^{-1} \text{ min}^{-1}$ )	$E_{O_2}$ (%)
<b>Red kangaroo:</b>							
-4.2 ± .6	23.3 ± .8	36.5 ± .2	11.0 ± 1.0 <sup>a</sup>	14.1 ± 1.4 <sup>a</sup>	149 ± 10 <sup>a</sup>	7.40 ± .38 <sup>a*</sup>	24.0 ± 1.1 <sup>a</sup>
16.3 ± .6	23.6 ± .8	36.5 ± .1	10.6 ± 1.1 <sup>a</sup>	11.9 ± 1.0 <sup>ab</sup>	121 ± 10 <sup>a</sup>	4.45 ± .21 <sup>b</sup>	18.4 ± 2.1
25.2 ± .7	23.6 ± 1.1	36.3 ± .1	8.9 ± 1.2 <sup>a</sup>	11.8 ± .5 <sup>ab</sup>	102 ± 11 <sup>a</sup>	3.29 ± .09 <sup>b</sup>	16.6 ± 2.0 <sup>ab</sup>
34.5 ± .2	24.1 ± 1.2	36.5 ± .2	34.9 ± 10.9 <sup>a*</sup>	8.4 ± 1.5 <sup>b*</sup>	206 ± 43 <sup>a</sup>	3.69 ± .22 <sup>b</sup>	10.9 ± 2.1 <sup>b</sup>
44.8 ± .9	23.8 ± 1.3	36.8 ± .1	146.0 ± 17.5 <sup>b*</sup>	8.0 ± .8 <sup>b</sup>	1,105 ± 96 <sup>b</sup>	4.07 ± .18 <sup>b</sup>	1.8 ± .2 <sup>c</sup>
<b>Grey kangaroo:</b>							
-5.2 ± .9	26.5 ± .9	36.6 ± .3 <sup>ab</sup>	15.0 ± 3.5 <sup>a</sup>	11.8 ± 2.1 <sup>a</sup>	149 ± 15 <sup>a</sup>	5.93 ± .38 <sup>a</sup>	19.2 ± .8 <sup>a</sup>
15.1 ± .2	26.0 ± .9	36.5 ± .2 <sup>ab</sup>	11.3 ± 2.0 <sup>a</sup>	8.7 ± .9 <sup>ab</sup>	92 ± 8 <sup>a</sup>	3.92 ± .17 <sup>b</sup>	20.9 ± 1.6 <sup>a</sup>
26.1 ± .9	26.4 ± .9	36.3 ± .1 <sup>a</sup>	13.1 ± 1.6 <sup>a</sup>	8.1 ± .7 <sup>ab</sup>	92 ± 10 <sup>a</sup>	3.56 ± .17 <sup>b</sup>	19.9 ± 2.6 <sup>a</sup>
33.4 ± .5	25.8 ± .8	36.9 ± .3 <sup>ab</sup>	79.9 ± 6.5 <sup>b</sup>	2.6 ± .3 <sup>c</sup>	208 ± 24 <sup>a</sup>	3.71 ± .21 <sup>b</sup>	9.7 ± 1.5 <sup>b</sup>
43.5 ± .4	26.2 ± 1.0	37.1 ± .2 <sup>b</sup>	203.4 ± 34.0 <sup>c</sup>	5.7 ± .9 <sup>b</sup>	1,046 ± 93 <sup>b</sup>	4.11 ± .34 <sup>b</sup>	1.9 ± .2 <sup>c</sup>

Note. Values are  $\bar{X} \pm SE$ . Statistical differences between intraspecific values in columns (i.e., at different temperatures) are indicated by letters; values within columns without common letters are different (SNK;  $P < 0.05$ ). Statistical differences between species are indicated by an asterisk, which is associated with the value for red kangaroos.

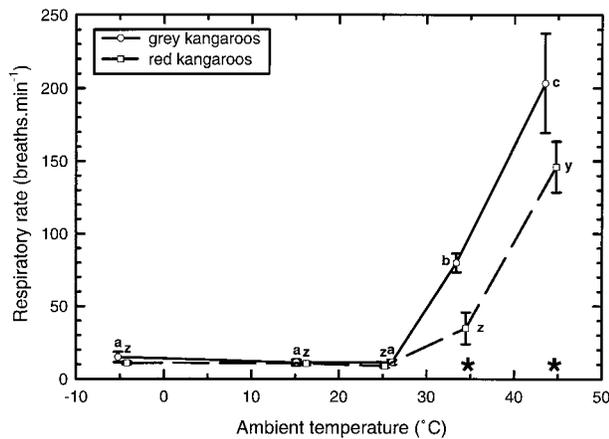


Figure 2. Respiratory rate of eastern grey kangaroos and red kangaroos at a range of  $T_a$ . Values are  $\bar{X} \pm \text{SE}$ . Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ). Stars on the X-axis denote significant differences between species (SNK;  $P < 0.05$ ).

REHL is low at  $T_a$  values of up to 25°C for both species but increases significantly at  $T_a$  33°C and markedly so at the highest  $T_a$ , 45°C, when there is no gradient for dry heat loss from the body. A major contributor to the level of REHL is the expired air temperature (Fig. 5). There were large differences between the species at low  $T_a$  (-5° and 15°C), but statistically significant differences were not apparent at higher  $T_a$ .

The level of oxygen extraction,  $E_{O_2}$ , from the inspired air did not differ between the two species (Table 1; Fig. 6). Oxygen consumption varies neither with species nor with temperature, except in the cold ( $T_a = -5^\circ\text{C}$ ), when the oxygen consumption of red kangaroos is higher (Table 1). The level of oxygen extraction was unchanged from  $T_a -5^\circ$  to  $T_a 25^\circ\text{C}$ , but the data were variable, with values ranging from 24% to 17%. The level of oxygen extraction decreased markedly in both species in association with the increases in ventilation at  $T_a 33^\circ\text{C}$  and  $T_a 45^\circ\text{C}$ , reaching values  $< 2\%$  at  $T_a 45^\circ\text{C}$ .

## Discussion

Data for respiratory characteristics of resting kangaroos in their thermoneutral zone had been limited to respiratory frequencies (Robertson and Morrison 1957; Dawson 1973) until Frappell and Baudinette (1995) produced data for three western grey kangaroos (*Macropus fuliginosus*). While these data were from kangaroos resting in their thermoneutral zone, the animals were not postabsorptive, nor were they fully settled in the measurement chamber. Values from Frappell and Baudinette (1995) were as follows:  $f_R$ , 14 breaths  $\text{min}^{-1}$ ;  $V_T$ , 12.6  $\text{mL kg}^{-1}$ ; and  $\dot{V}_I$ , 176  $\text{mL kg}^{-1} \text{min}^{-1}$ . Mass was 30.0 kg. The  $\dot{V}_I$  values in their study were notably higher than those for the kangaroos in this study (Table 1). This may be a species effect, but the

eastern grey kangaroo and the western grey kangaroo are closely related species (Dawson 1995).

A feature of the basal ventilatory data at  $T_a 25^\circ\text{C}$  (Table 1) is that they differ markedly from the values that would be predicted from the pertinent allometric equations for placental mammals (Stahl 1967). Ventilation is lower, as might be expected from the lower basal (standard) metabolic rate of marsupials, some 30% lower than in placentals (Dawson and Hulbert 1970; Hayssen and Lacy 1985). Tidal volume and respiratory frequency, however, give a set of values that do not simply reflect the lower BMR (basal metabolic rate) of the marsupials. While the  $f_R$  values for the kangaroos are lower than those predicted for placentals, they are much lower than might be expected from the lower BMR. Conversely, the  $V_T$  are higher. The predicted ventilatory values for a placental mammal of the same mass as *Macropus rufus* (for which we have the most data) from the allometric equations of Stahl (1967) are 202  $\text{mL kg}^{-1} \text{min}^{-1}$  for  $\dot{V}_I$ , 8.7  $\text{mL kg}^{-1}$  for  $V_T$ , and 23.5 breaths  $\text{min}^{-1}$  for  $f_R$ . The relationship of the actual red kangaroo values to these predictions are 50.5% ( $\dot{V}_I$ ), 136% ( $V_T$ ), and 34.5% ( $f_R$ ). These are large differences, but they are inline with the original allometric equations suggested for marsupials by Dawson and Needham (1981) on limited data.

That marsupials at rest have a deeper and slower breathing pattern than placentals has been supported by other studies (Hallam and Dawson 1993; Chappell and Dawson 1994; Frappell and Baudinette 1995). Frappell and Baudinette examined the respiratory patterns of 14 species of marsupial and derived a range of allometric equations from this data set. These are in general agreement with the patterns predicted by Dawson and Needham (1981), but Frappell and Baudinette (1995) state

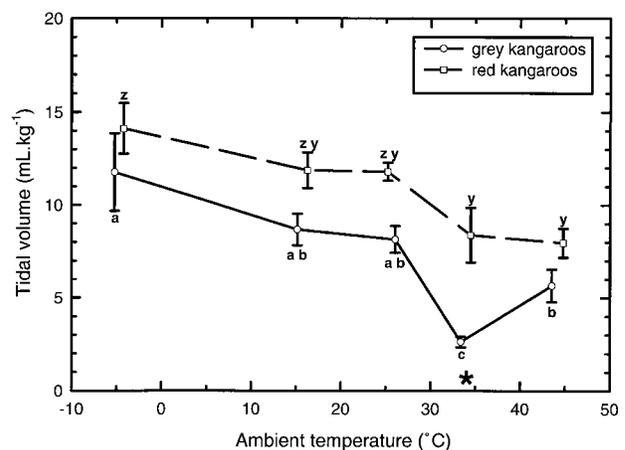


Figure 3. Tidal volume of eastern grey kangaroos and red kangaroos at a range of  $T_a$ . Values are  $\bar{X} \pm \text{SE}$ . Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ). Stars on the X-axis denote significant differences between species (SNK;  $P < 0.05$ ).

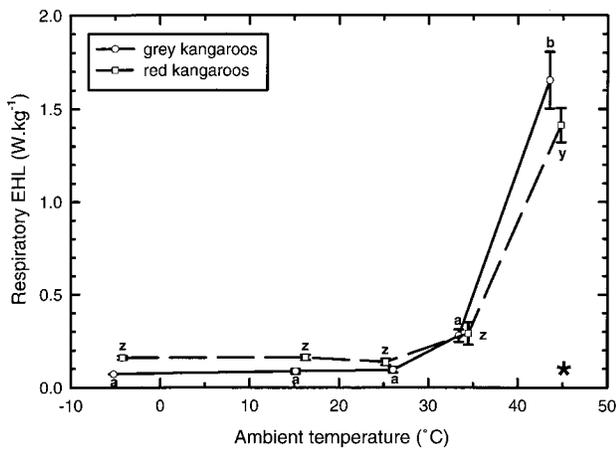


Figure 4. Respiratory evaporative heat loss of eastern grey kangaroos and red kangaroos at a range of  $T_a$ . Values are  $\bar{X} \pm SE$ . Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ). Stars on the X-axis denote significant differences between species (SNK;  $P < 0.05$ ).

that their data do not relate to basal conditions. Obviously, more data are needed before firm allometric equations are accepted for marsupials, but our data on the kangaroos reinforces the point that marsupials (in basal conditions) seem to have a deeper and slower breathing pattern than placentals. Caution is needed, however, because Chappell and Dawson (1994) noted that much of the data used in the equations for placentals (Stahl 1967) was derived from measurements on restrained animals, and restraint may substantially affect ventilation (Chappell 1992).

What implications do these patterns have for *M. rufus* and *Macropus giganteus*? The study of Dawson and Needham (1981) focused principally on cardiovascular responses and suggested that the low heart rate and large cardiac stroke volume that they noted provided a base for a large expansion of the cardiovascular performance of marsupials. Baudinette (1978) found that maximal heart rates of marsupials and placentals were similar. While marsupials have a relatively low BMR, they have a greater aerobic scope than placentals (Dawson and Dawson 1982; Dawson and Olson 1988; Hinds et al. 1995). The red kangaroo has a maximal oxygen consumption superior to that of virtually all placentals (Kram and Dawson 1998). It is feasible that the respiratory system of the kangaroos is organized to accommodate such levels of oxygen consumption.

The respiratory responses to thermoregulatory needs vary with the nature of the thermal stress. The respiratory patterns in the cold,  $T_a = -5^\circ\text{C}$ , vary little from those seen at thermoneutral temperatures in both species of kangaroo. Given the aerobic capacity of kangaroos, the small increase in oxygen consumption at  $T_a = -5^\circ\text{C}$  would be a mild imposition (Table 1). It is at higher  $T_a$  that significant changes in respiratory

patterns are seen, these changes being made to facilitate REHL (Fig. 4).

The ventilatory responses to higher  $T_a$  differ between the two species of kangaroo, however. Although  $\dot{V}_I$  and REHL do not differ at  $T_a 33^\circ\text{C}$ , *M. giganteus* increased its fr by sevenfold, and  $V_T$  decreased to 32% of the value at  $T_a 25^\circ\text{C}$ . For *M. rufus*, the responses at  $T_a 33^\circ\text{C}$  were limited and variable; several individuals increased fr and showed a decline in  $V_T$ , but overall, the changes were not statistically significant. The  $V_T$  of *M. giganteus* was only 31% of that of *M. rufus* at  $T_a 33^\circ\text{C}$ , but conversely, its fr was 2.3 times higher.

The patterns of respiratory responses in the two species tended to continue at  $T_a 45^\circ\text{C}$ , when  $\dot{V}_I$  was increased by approximately five times (Fig. 1). Ventilation in these conditions appeared to be largely of non-gas exchange areas of the respiratory system; note the marked decrease in  $E_{O_2}$  (Fig. 6). However, a difference in respiratory water loss emerged (Fig. 4): that of *M. rufus* was significantly below that of *M. giganteus*. This difference in respiratory water loss appears as a result of nonsignificant factors interacting. Total evaporative water loss was similar in the two species since cutaneous water loss was elevated in *M. rufus* (Dawson et al. 2000).

The pattern of respiratory response seen in the kangaroos is a common response to mild and moderate heat stress in many birds and mammals. An increase in fr accompanied by a drop in  $V_T$  has been termed "Phase I" panting by Hales and Webster (1967) in their initial studies on sheep. This was to distinguish it from the increased fr and  $V_T$  of "Phase II" panting during more severe heat stress. The lower  $V_T$  during Phase I panting is considered to ventilate only non-gas exchange areas of the respiratory system. In this way, REHL can be increased without

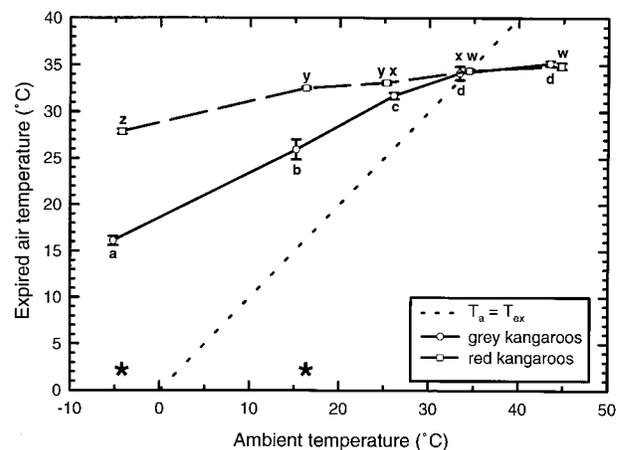


Figure 5. Expired air temperature ( $T_{ex}$ ) of eastern grey kangaroos and red kangaroos at a range of  $T_a$ ; a line of equality ( $T_a = T_{ex}$ ) is included for reference. Values are  $\bar{X} \pm SE$ . Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ). Stars on the X-axis denote significant differences between species (SNK;  $P < 0.05$ ).

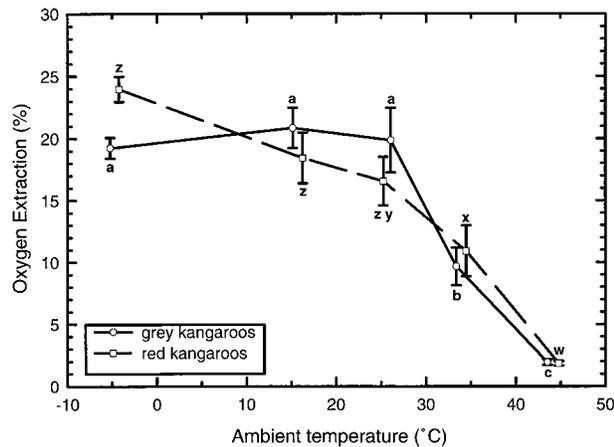


Figure 6. Oxygen extraction from inspired air by eastern grey kangaroos and red kangaroos at a range of  $T_a$ . Values are  $\bar{X} \pm SE$ . Different letters on a species indicate significant differences between means (SNK;  $P < 0.05$ ).

hyperventilating alveoli, and blood gas homeostasis is not jeopardized. This pattern has been noted in another macropodid marsupial (Dawson and Rose 1970) and may occur in kangaroos (T. J. Dawson, personal communication). In the tammar wallaby *Macropus eugenii*, the onset of rapid Phase I panting (up to 350 breaths  $\text{min}^{-1}$ ) did not significantly change blood gas parameters (Dawson and Rose 1970). In response to a much higher heat load ( $T_b$  up to 40.5°C), which induced Phase II panting (a decreased  $f_R$  and “deeper” breathing), there was a marked change in the acid-base status of the blood of the wallaby; arterial and venous  $\text{CO}_2$  partial pressures and pH were much altered.

What of the differences in the ventilatory patterns of *M. rufus* and *M. giganteus*? *Macropus rufus* seems to operate with a lower  $f_R$  and a higher  $V_T$  than *M. giganteus* at equivalent high temperatures. This pattern has similarities to that seen in an earlier study comparing *M. rufus* and the euro, or inland, wallaroo *Macropus robustus erubescens* (Dawson 1973). Under comparable levels of heat stress, the red kangaroo had higher rates of water loss for lower  $f_R$  than the euro; cutaneous water loss was not different. The red kangaroo lives in a habitat that routinely presents extreme environmental heat loads (Dawson 1972). Dawson (1973) suggested that the red kangaroos might have a greater  $V_T$  so that if there was an upper limit to the increase in  $f_R$ , then red kangaroos could reach a higher level of ventilation before Phase II breathing had to be instigated (with its attendant problems with blood acid-base balance).

The panting seen in kangaroos at higher temperatures shows the graded increase in  $f_R$  originally described by Dawson (1973). It does not follow the “resonant frequency” pattern of dogs, which has been suggested to be an energetically less expensive mode of panting (Crawford 1962). However, evidence

now contradicts this suggestion. Sheep show a ventilatory response to heat comparable to that of kangaroos, that is, graded through the nose panting, except in severe heat stress (when Phase II panting is initiated). Sheep increase oxygen consumption at peak panting rates less than dogs do, and this might be construed as an indication that graded panting is more energetically efficient (Hales and Brown 1974; Hales and Dampney 1975). However, actual tissue blood flows to the diaphragm and other respiratory muscles of sheep and dogs are not markedly different at similar peak panting rates (Hales 1973; Hales and Dampney 1975). From the blood-flow patterns, panting appears to be primarily diaphragmatic, especially in the sheep. The blood flow to the diaphragm of the red kangaroo under moderate heat stress follows the pattern seen in sheep (Hales 1973; Needham 1982). The disparity in the oxygen consumption between sheep and dogs during heat stress results from the sheep significantly reducing blood flow (and, thereby, metabolism) in major areas of the viscera; dogs don't show this redistribution to the same degree as sheep (Hales and Dampney 1975), but red kangaroos do (Needham 1982).

Differences exist in the ventilatory responses to thermal stress between red kangaroos and eastern grey kangaroos, and these may reflect adaptation to different habitats. However, the ventilatory patterns of the kangaroos are primarily similar. These are species from divergent evolutionary lines of macropodine kangaroos (Dawson 1995), which suggests a long evolutionary history for their superior respiratory heat-loss mechanisms and their general thermoregulatory abilities. The high aerobic capacity of marsupials, particularly that of kangaroos (Kram and Dawson 1998), may be at the base of such abilities since this would regularly present the kangaroos with exceptional endogenous heat loads.

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