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Abstract

The population dynamics of red kangaroos (*Macropus rufus*) in the Australian arid zone is tightly linked with environmental factors, which partly operate via the survival of juvenile animals. A crucial stage is the young-at-foot (YAF) stage when kangaroos permanently exit the pouch. We have examined the thermal biology of YAF red kangaroos during ages from permanent pouch exit until weaning. Over a wide range of environmental temperatures (ambient temperature [T_a] -5 degrees to 45 degreesC), YAF red kangaroos had a mass-specific metabolism that was generally twice that of adults, considerably higher than would be expected for an adult marsupial of their body size. The total energy requirements of YAF red kangaroos were 60%-70% of those of adult females, which were three times their size. Over the same range in T_a, YAF red kangaroos also had total evaporative water losses equal to those of adult females. At the highest T_a (45 degreesC), differences were noted in patterns of dry heat loss (dry conductance) between YAF red kangaroos and adult females, which may partially explain the relatively high levels of evaporative cooling by YAF. By weaning age, young kangaroos showed little change in their basal energy and water requirements (at T_a 25 degreesC) but did show reduced mass-specific costs in terms of energy and water use at extremes of T_a (-5 degrees and 45 degreesC, respectively). In their arid environment, typified by unpredictable rainfall and extremes of T_a, young red kangaroos may need to remain close to water points, which, in turn, may restrict their ability to find the high-quality forage needed to meet their high energy demands.

Keywords

water, requirements, red, kangaroos, macropus, rufus, juvenile, after, thermoregulation, pouch, exit, higher, metabolism, evaporative

Disciplines

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

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Thermoregulation in Juvenile Red Kangaroos (*Macropus rufus*) after Pouch Exit: Higher Metabolism and Evaporative Water Requirements

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ABSTRACT

The population dynamics of red kangaroos (*Macropus rufus*) in the Australian arid zone is tightly linked with environmental factors, which partly operate via the survival of juvenile animals. A crucial stage is the young-at-foot (YAF) stage when kangaroos permanently exit the pouch. We have examined the thermal biology of YAF red kangaroos during ages from permanent pouch exit until weaning. Over a wide range of environmental temperatures (ambient temperature [T_a] -5° to 45°C), YAF red kangaroos had a mass-specific metabolism that was generally twice that of adults, considerably higher than would be expected for an adult marsupial of their body size. The total energy requirements of YAF red kangaroos were 60%–70% of those of adult females, which were three times their size. Over the same range in T_a , YAF red kangaroos also had total evaporative water losses equal to those of adult females. At the highest T_a (45°C), differences were noted in patterns of dry heat loss (dry conductance) between YAF red kangaroos and adult females, which may partially explain the relatively high levels of evaporative cooling by YAF. By weaning age, young kangaroos showed little change in their basal energy and water requirements (at T_a 25°C) but did show reduced mass-specific costs in terms of energy and water use at extremes of T_a (-5° and 45°C , respectively). In their arid environment, typified by unpredictable rainfall and extremes of T_a , young red kangaroos may need to remain close to water points, which, in turn, may restrict their ability to find the high-quality forage needed to meet their high energy demands.

Introduction

Red kangaroos (*Macropus rufus*) are one of the largest extant marsupials and inhabit much of arid inland Australia. Adult red kangaroos show a number of behavioural and physiological adaptations for dealing with high heat loads and unpredictable rainfall (Dawson 1973; Blaney et al. 2000; Dawson et al. 2000a, 2000b). However, the ability of juvenile kangaroos to cope with thermal extremes is unclear, but insight into these abilities may be important for understanding the population dynamics of the species. The age/size class of the young red kangaroos studied here is comparable to that which is most impacted by harsh environmental conditions (Shepherd 1987).

Like all marsupials, the newborn red kangaroo is extremely underdeveloped at birth, weighing just 0.8 g (Frith and Sharman 1964; Sharman et al. 1964). The tiny, hairless neonate then crawls from the mother's cloaca to a large, well-developed pouch, a characteristic of macropodid marsupials. By 190 d old, weighing around 2 kg, the young is fully furred and will venture out of the pouch for short periods of time. At this "in-out" stage, the young kangaroo is still unable to maintain deep body temperature (T_b) for long periods out of the pouch and regularly returns to the pouch for warmth and safety (Frith and Sharman 1964; Sharman et al. 1964). By 230–250 d old, the young kangaroo permanently leaves the pouch, becoming a "young-at-foot" (weight, 4–5 kg). Young-at-foot (YAF) red kangaroos forage in association with their mothers but also continue to suckle by putting their head back into the pouch. After another 100 d or so, the YAF red kangaroo is fully weaned at around 360 d old (weight, 10–11 kg; Frith and Sharman 1964; Sharman et al. 1964). YAF red kangaroos aged from permanent pouch exit (PPE) to shortly after weaning will herein be referred to as "juveniles," distinguishing them from the red kangaroos at earlier stages of development when time is still spent in the pouch.

Much research on the development of marsupials, and macropodids in particular, has concentrated on the development of metabolism and thermoregulation while the young is in the pouch (i.e., from birth to PPE; see, e.g., Tyndale-Biscoe 1973; Janssens et al. 1997). Little is known about the development of kangaroos beyond PPE, which is perhaps the most ecologically important age. Severe or prolonged drought can result in juvenile mortalities of up to 83%, the highest mortalities of any population cohort (Newsome 1977; Shepherd 1987; Dawson 1995). Consequently, the size and structure of adult red

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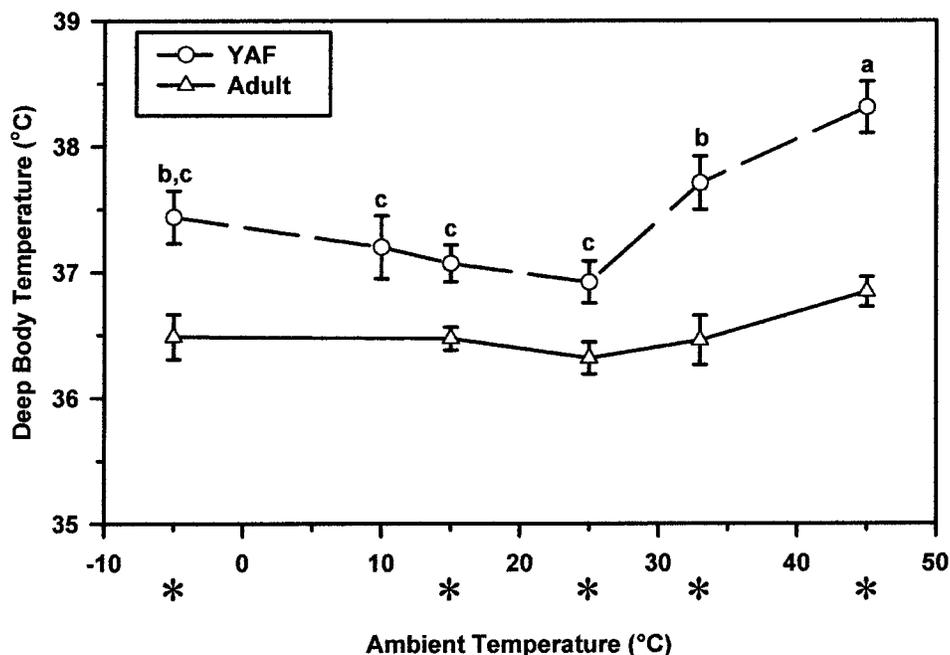


Figure 1. Deep body temperature ($^{\circ}\text{C}$) of adult and young-at-foot (YAF) red kangaroos at a range of ambient temperatures ($^{\circ}\text{C}$). Values are means \pm SEM. Letters denote differences within groups, and asterisks on the X-axis denote differences between juvenile and adult means (Student-Newman-Keuls, $P < 0.05$). Adult data from Dawson et al. (2000a).

kangaroo populations is tightly linked with the survival of juvenile kangaroos from just after PPE until shortly after weaning.

This study examines the importance of thermal conditions to the potential survival of YAF red kangaroos. We have determined their resting energy, water requirements, and thermoregulatory responses to a wide range of environmental temperatures. The data for YAF red kangaroos are compared with information from adult red kangaroos (Dawson et al. 2000a) to determine their relative resource requirements when faced with thermal extremes. We also examined the question, can we predict the resource requirements of juvenile kangaroos as if they were just small adults?

Material and Methods

Experimental Animals

Seven juvenile red kangaroos (five females and two males) were hand reared using artificial pouches until they reached PPE age (Williams and Williams 1999). Four weeks before experimentation, the animals were transferred to our laboratory animal house and kept under conditions comparable to those of the adult red kangaroos in the study of Dawson et al. (2000a). During this time, animals were familiarised with the experimental procedure and implanted intraperitoneally with temperature-sensitive radio transmitters ($\pm 0.1^{\circ}\text{C}$; Sirtrack, Havlock North, New Zealand), which were calibrated against a

certified mercury-in-glass thermometer (National Testing Authorities, Sandringham, Victoria). The diet of YAF kangaroos (Gordons rabbit pellets [Gordon's Specialty Stock Feeds, Yanderra], Kangaroo cubes [Doust and Rabbidge, Forbes], and Lucerne/Bran mix [Kensington Stock Feeds, Sydney] was supplemented with a ration of low-lactose milk (Digestelact, Sharpe Laboratories, Sydney), which was reduced over time until it was eliminated at normal weaning age. Food was withheld for 24 h before experimentation.

Age was estimated from foot and tail length (Sharman et al. 1964), and the major part of this study was carried out when animals were an average (\pm SEM) age of 313 ± 5 d old, with a mass of 8.6 ± 0.3 kg. Data were also obtained for four animals after weaning age (age = 374 ± 26 d old, mass = 11.55 ± 0.6 kg) and compared with that obtained from the same animals shortly after PPE (age = 307 ± 1.0 d old, mass = 7.4 ± 0.3 kg).

Experimental Procedure

Animals were weighed to the nearest 0.1 kg and placed in an open-circuit metabolism chamber ($695 \times 450 \times 580$ mm) within a temperature-controlled room. T_a was regulated to $\pm 0.5^{\circ}\text{C}$ of a set point, and each animal was tested at T_a 's of -5° , 10° , 15° , 25° , 33° , and 45°C . T_a ($\pm 0.1^{\circ}\text{C}$) was measured using a thermocouple placed in the excurrent port of the cham-

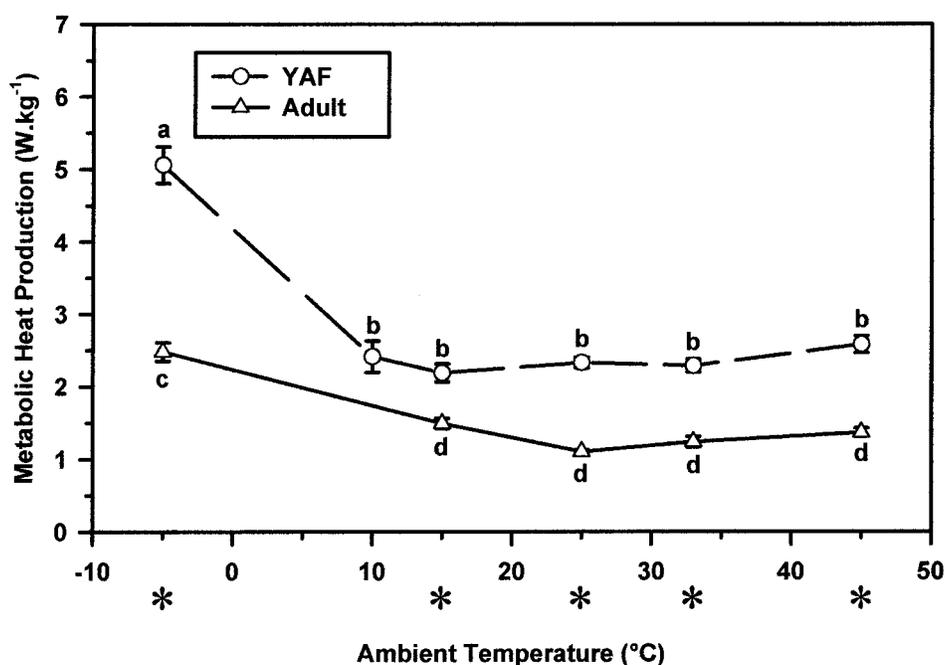


Figure 2. Mass-specific metabolism ($W\ kg^{-1}$) of adult and young-at-foot (YAF) red kangaroos at a range of ambient temperatures ($^{\circ}C$). Values are means \pm SEM. Letters denote differences within groups, and asterisks on the X-axis denote differences between juvenile and adult means (Student-Newman-Keuls, $P < 0.05$). Adult data from Dawson et al. (2000a).

ber. The metabolism chamber consisted of a mesh floor above a bath of vegetable oil to trap excreta, and the walls of the metabolism chamber were painted flat black to reduce radiation reflection (Porter 1969; Maloney and Dawson 1994a). Experiments were performed between 0800 and 1600 hours, corresponding to the resting phase of adult red kangaroo circadian rhythm (Watson and Dawson 1993). Animals were monitored throughout each experiment via a low-light CCD camera (Oatley Electronics, Sydney) mounted inside the chamber.

At least 3 h was allowed for equilibration at any given temperature; data collection commenced when the animal's body temperature had stabilised. Flow rate (FR) of dry air through

the metabolism chamber was measured upstream using a Hastings mass flowmeter (model HFM-201, John Morris Scientific, Sydney) and adjusted to prevent water vapour inside the chamber from exceeding 15 mmHg. A subsample of air ($125\ mL\ min^{-1}$) was drawn from the excurrent port using a flow controller (Applied Electrochemistry R2 flow controller, Ametek, Pittsburgh) and passed through a capacitance-type relative humidity sensor ($\%RH\ [\pm 0.1\%]$; CHK Engineering, Sydney), which was calibrated regularly using saturated solutions of lithium chloride, sodium chloride, and magnesium chloride (Winston and Bates 1960). After leaving the humidity sensor, the excurrent air was dried with Drierite and split into two gas

Table 1: Total metabolic heat production (TMHP) and evaporative heat loss (TEHL) of young-at-foot (YAF) and adult red kangaroos at a range of ambient temperatures ($^{\circ}C$)

| | $-5.5 \pm .3$ | $10.3 \pm .2$ | $15.2 \pm .1$ | $25.7 \pm .3$ | $33.3 \pm .1$ | $45.5 \pm .1$ |
|-----------|------------------------|--------------------|------------------------|------------------------|------------------------|------------------------|
| TMHP (W): | | | | | | |
| YAF | $39.34 \pm 4.29^{A,*}$ | 19.91 ± 2.30^B | $16.82 \pm 1.86^{B,*}$ | $15.20 \pm 1.82^{B,*}$ | $17.22 \pm 2.11^{B,*}$ | $19.67 \pm 2.80^{B,*}$ |
| Adult | 58.31 ± 4.77^A | ... | 35.06 ± 1.58^B | 25.98 ± 1.29^C | 30.18 ± 2.91^{BC} | 32.52 ± 2.34^{BC} |
| TEHL (W): | | | | | | |
| YAF | $3.15 \pm .60^C$ | $3.22 \pm .71^C$ | $3.00 \pm .43^C$ | $3.87 \pm .40^C$ | $9.54 \pm 1.35^{B,*}$ | 52.53 ± 4.67^A |
| Adult | $4.06 \pm .75^B$ | ... | $5.74 \pm .60^B$ | 7.97 ± 1.04^B | 16.76 ± 1.19^B | 56.57 ± 4.56^A |

Note. Values are means \pm SEM. Letters denote differences within rows (Student-Newman-Keuls [SNK], $P < 0.05$). Adult data from Dawson et al. (2000a). See text for explanations of abbreviations.

* Denotes differences between YAF and adult kangaroos (SNK, $P < 0.05$).

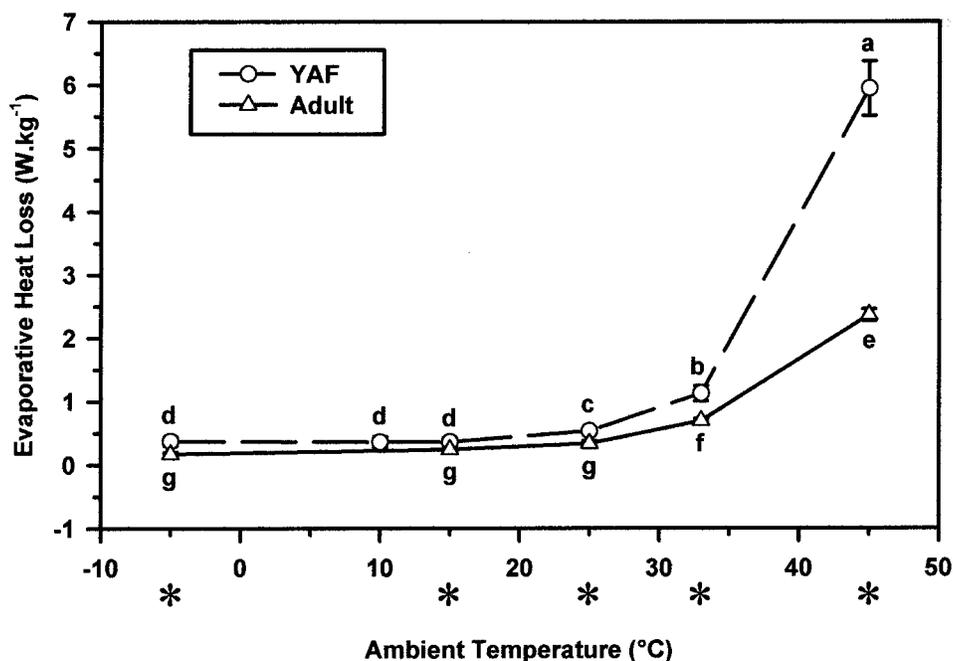


Figure 3. Mass-specific evaporative heat loss (W kg^{-1}) of adult and young-at-foot (YAF) red kangaroos at a range of ambient temperatures ($^{\circ}\text{C}$). Values are means \pm SEM. Letters denote differences within groups, and asterisks on the X-axis denote differences between juvenile and adult means (Student-Newman-Keuls, $P < 0.05$). Adult data from Dawson et al. (2000a).

lines. The first line was passed through a carbon dioxide analyser (Uras 10E, Hartmann and Braun, Frankfurt), and the second was scrubbed of CO_2 with Ascarite and redried before passing through an oxygen analyser (Applied Electrochemistry S3A-III, Ametek, Pittsburgh).

Sensor outputs (FR, %RH, $\%\text{O}_2$, and $\%\text{CO}_2$) were logged on a personal computer at 5-s intervals using Warthog Lab-helper software (Chappell 1995) via a CB-50 connector block (National Instruments, Ringwood, Victoria) and a 12-bit analog/digital (A/D) converter (National Instruments Lab-NB card, Ringwood, Victoria). This system averaged approximately 120 readings for each recorded value and gave a maximum resolution of 0.006% for $\%\text{O}_2$ and 0.002% for $\%\text{CO}_2$. The whole

system was calibrated regularly using the iron-burn method of Young et al. (1984). Body temperature (intraperitoneal temperature; T_b) was logged continuously on a personal computer using an AR8000 receiver and CU8232 remote control interface (AOR, Tokyo).

At the end of each experiment, while the animal was still inside the temperature-controlled room, expired air temperature (T_{ex}) was measured using a 0.25-mm thermocouple placed just inside the nares. Once stable, readings were logged at 0.1-s intervals on a personal computer via a 12-bit A/D converter (Sable Systems, Henderson, Nev.). All temperature-measuring devices used were calibrated to $\pm 0.1^{\circ}\text{C}$ using a certified mercury-in-glass thermometer (National Testing Authorities, Australia).

Table 2: Respiratory variables of young-at-foot (YAF) and adult red kangaroos at a range of ambient temperatures ($^{\circ}\text{C}$)

| | -5.5 \pm .3 | 10.3 \pm .2 | 15.2 \pm .1 | 25.7 \pm .3 | 33.3 \pm .1 | 45.5 \pm .1 |
|-------|------------------|------------------|------------------|-----------------|---------------------------------|-----------------------------------|
| fr: | | | | | | |
| YAF | 14.94 \pm 1.35 | 12.55 \pm 1.90 | 11.92 \pm .68 | 9.32 \pm 1.30 | 83.35 \pm 9.99 ^{B,*} | 323.16 \pm 13.56 ^{A,*} |
| Adult | 11.0 \pm .97 | ... | 10.58 \pm 1.09 | 8.91 \pm 1.19 | 34.88 \pm 10.88 | 146.03 \pm 17.53 ^A |
| RQ: | | | | | | |
| YAF | .82 \pm .04 | .81 \pm .01 | .83 \pm .02 | .83 \pm .01 | .93 \pm .04 ^B | 1.09 \pm .04 ^A |

Note. fr, respiratory rate (breaths min^{-1}); RQ, respiratory quotient. Values are means \pm SEM. Letters denote differences within rows (Student-Newman-Keuls [SNK], $P < 0.001$). Adult data from Dawson et al. (2000a). RQs were not available for adult red kangaroos.

* Differences between YAF and adult kangaroos (SNK, $P < 0.001$).

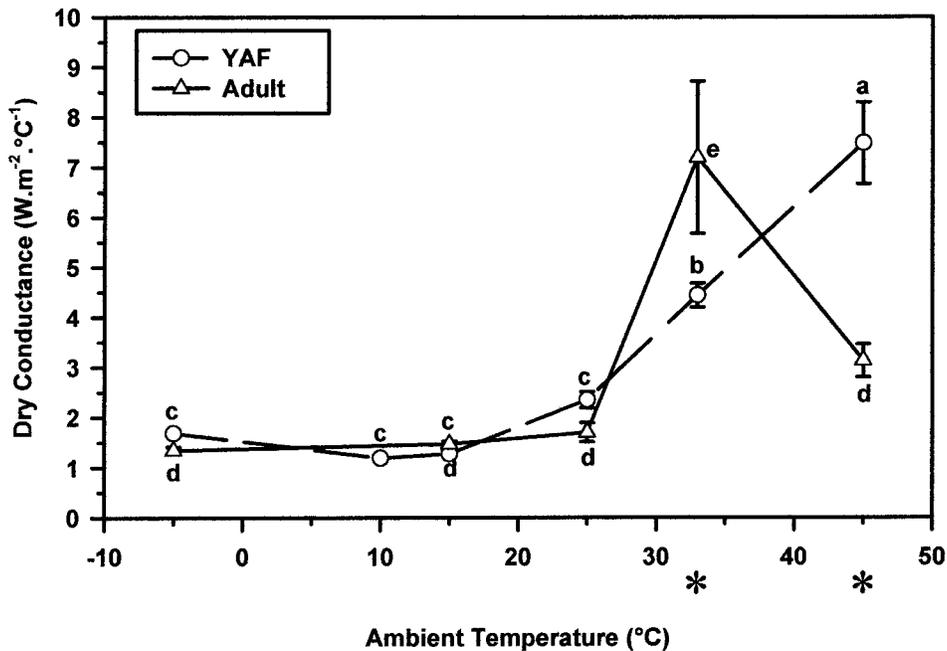


Figure 4. Dry conductance ($\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$) of adult and young-at-foot (YAF) red kangaroos at a range of ambient temperatures ($^\circ\text{C}$). Values are means \pm SEM. Letters denote differences within groups, and asterisks on the X-axis denote differences between juvenile and adult means (Student-Newman-Keuls, $P < 0.05$). Adult data from Dawson et al. (2000a).

The fur surface areas (SA) of six YAF red kangaroos, weighing 6.8 ± 0.5 kg, were measured using the technique of Dawson et al. (2000a). From estimates of total SA, a Meeh factor (see Dawson and Hulbert 1970) was calculated as

$$\text{SA} = 13.2 \pm 0.25 \text{ mass}(\text{g})^{0.667}$$

and used to estimate the SA for all animals.

Data Analysis

Oxygen consumption ($\dot{V}\text{O}_2$; mL min^{-1}), carbon dioxide production ($\dot{V}\text{CO}_2$; mL min^{-1}), and evaporative water loss (EWL; g min^{-1}) were measured by open-circuit respirometry using the equations summarised by Maloney and Dawson (1994a) after Hill (1972) and Withers (1977; see also Depocas and Hart 1957). A minimum 20 min of $\dot{V}\text{O}_2$ and EWL during an exposure were used to estimate metabolic heat production (MHP; W kg^{-1}) and evaporative heat loss (EHL; W kg^{-1}), respectively, assuming heat equivalents of $20.08 \text{ kJ L}^{-1} \text{ O}_2$ and $2.43 \text{ kJ g}^{-1} \text{ H}_2\text{O}$.

The metabolism chamber also acted as a whole-body plethysmograph (see Malan 1973), allowing estimates of respiratory rate (fr ; breaths min^{-1}) and tidal volume calculated for a related study. Maloney and Dawson (1994b) have discussed in detail the potential errors of plethysmography, and the methods

used here were essentially identical to those of Dawson et al. (2000b). Respiratory evaporative heat loss (REHL) was then calculated as the difference in water content of inspired and expired air, assuming air was inhaled at chamber temperature and humidity and expired saturated at T_{ex} and assuming a heat equivalent of $2.43 \text{ kJ g}^{-1} \text{ H}_2\text{O}$. Cutaneous evaporative heat loss (CEHL) was determined as the difference between EHL and REHL.

At each T_a , the rate of dry heat flow at the body surface, or dry conductance (C_{dry} ; $\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$), was estimated as (Dawson and Schmidt-Nielsen 1966)

$$C_{\text{dry}} = \frac{(\text{MHP} - \text{EHL})}{(T_b - T_a) \times \text{SA}}$$

where MHP, EHL, T_b , and T_a are as above and SA is in square meters. Heat storage was omitted from this equation, since T_b was constant throughout the measurement period.

Data for juveniles were compared with that for adult red kangaroos obtained from Dawson et al. (2000a; $n = 7$). Average mass (\pm SEM) of the adults was 23.5 ± 1.1 kg. Data were only available for adults at T_a 's of -5° , 15° , 25° , 33° , and 45°C .

Data for YAF and adult red kangaroos were compared using two-way repeated-measures ANOVA for experiments at T_a 's of -5° , 15° , 25° , 33° , and 45°C . One-way repeated-measures ANOVA was used to analyse data for the YAF kangaroos, in-

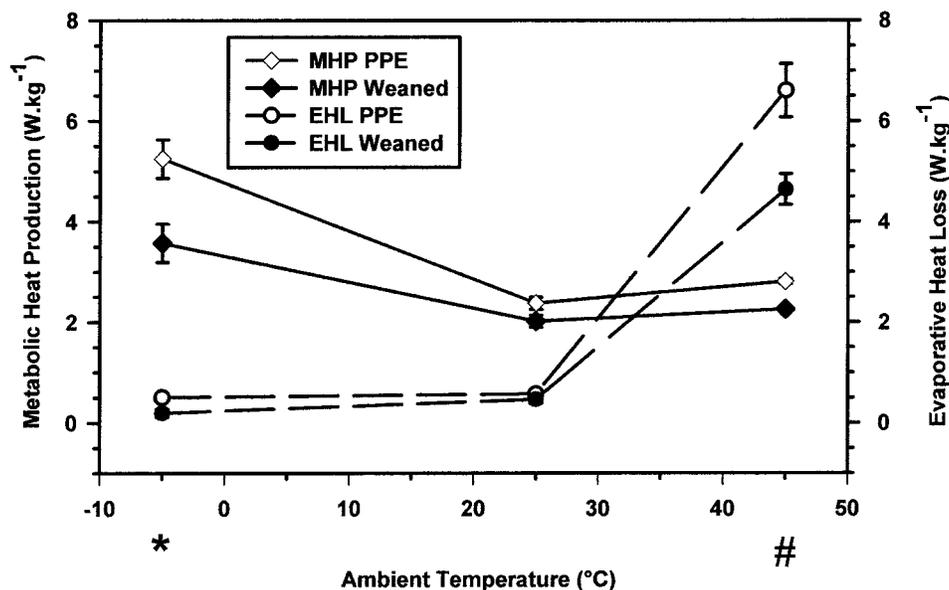


Figure 5. Mass-specific metabolism (MHP ; $W\ kg^{-1}$) and evaporative heat loss (EHL ; $W\ kg^{-1}$) of permanent pouch exit (PPE) and weaned red kangaroos at a range of ambient temperatures ($^{\circ}C$). Values are means \pm SEM. For within-group significant differences, refer to the text. The asterisk and hatch mark on the X-axis denote differences between PPE and weaned means for MHP and EHL, respectively (Student-Newman-Keuls, $P < 0.05$).

cluding results from experiments at T_a $10^{\circ}C$. A repeated-measures ANOVA, with two levels of within-group factors (age and temperature), was also used to compare the data from four YAF red kangaroos soon after PPE and again after weaning age. When ANOVAs yielded significant differences, a Student-Newman-Keuls test was performed. In all cases, the results for significance within YAF red kangaroo data were the same for the one-way and two-way ANOVAs and post hoc tests (i.e., for tests with and without measurements from the T_a $10^{\circ}C$ experiments). All statistical analyses were performed using Statistica 4.1 for Macintosh (Statsoft 1991) and results are presented as mean \pm SEM.

Results

YAF versus Adult Kangaroos

The T_b of YAF red kangaroos was significantly higher (0.6° – $1.5^{\circ}C$) and more labile than that of adult red kangaroos over the range of T_a studied ($P < 0.05$; Fig. 1). A minimum value of $36.9^{\circ} \pm 0.2^{\circ}C$ was obtained at T_a near $25^{\circ}C$. Unlike that of adults, the T_b of YAF red kangaroos increased significantly at T_a $33^{\circ}C$ and again at $45^{\circ}C$ ($P < 0.05$). There was also a significant incremental increase in the T_b of YAF as T_a decreased to $-5^{\circ}C$ ($P < 0.05$; Fig. 1).

The mass-specific MHP ($W\ kg^{-1}$) of YAF red kangaroos was approximately twice that of adults at all T_a ($P < 0.0001$; Fig. 2). As with adults, MHP only increased in the cold. At T_a $-5^{\circ}C$,

MHP similarly increased from thermoneutral levels by 2.3- and 2.2-fold in adult and YAF kangaroos, respectively ($P < 0.01$; Fig. 2). In whole-animal terms, YAF had a total metabolic heat production 60%–70% that of adults at all T_a 's ($P < 0.01$; Table 1).

The mass-specific EHL ($W\ kg^{-1}$) of YAF red kangaroos was significantly higher than that of adults at all T_a ($P < 0.05$; Fig. 3). Under warm conditions, at T_a $33^{\circ}C$, the relative increase from thermoneutral EHL was similar in both adult and YAF kangaroos, with the EHL of juveniles being 60% higher. However, at T_a $45^{\circ}C$, considerably higher than T_b , the YAF EHL was 11.5 times higher than that seen at T_a $25^{\circ}C$ and more than 2.5 times greater than that of adults. In whole-animal terms, the total evaporative heat loss (TEHL) of YAF kangaroos was not significantly different from that of adults at most T_a ; only at T_a $33^{\circ}C$ did adults have a slight but significantly greater TEHL ($P < 0.05$; Table 1).

The respiratory quotient (RQ; $\dot{V}_{CO_2}/\dot{V}_{O_2}$) for YAF red kangaroos ranged between 0.81 ± 0.01 and 0.83 ± 0.01 at T_a 's from -5° to $25^{\circ}C$, increasing significantly at T_a $33^{\circ}C$ and again at $45^{\circ}C$ ($P < 0.001$; Table 2). This was correlated with significant increases in the fr of YAF kangaroos at both T_a 33° and $45^{\circ}C$, by around nine and 35 times, respectively, that of thermoneutral fr's (at T_a $25^{\circ}C$; $P < 0.001$; Table 2). At T_a 33° and $45^{\circ}C$, the fr's of YAF red kangaroos were significantly higher than those of adult red kangaroos, by around 2.4 and 2.2 times, respectively ($P < 0.05$; Table 2). At thermoneutral T_a 's and below, however,

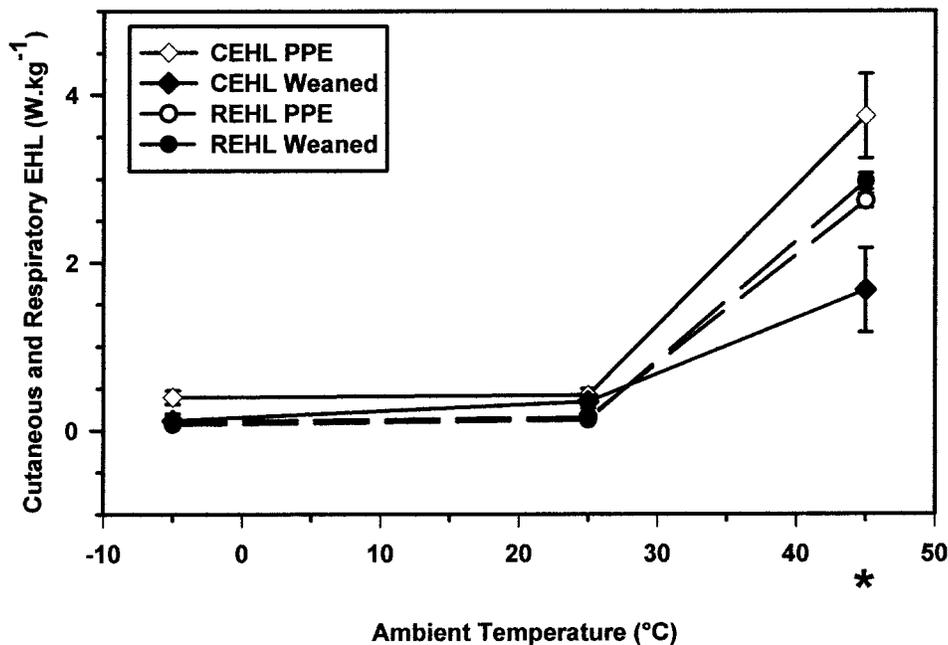


Figure 6. Mass-specific respiratory (*REHL*) and cutaneous evaporative heat loss (*CEHL*; W kg^{-1}) of permanent pouch exit (*PPE*) and weaned red kangaroos at a range of ambient temperatures ($^{\circ}\text{C}$). Values are means \pm SEM. For within-group significant differences, refer to the text. The asterisk on the X-axis denotes a difference between *PPE* and weaned means for *CEHL* (Student-Newman-Keuls, $P < 0.05$).

there were no differences between YAF and adult red kangaroo fr's ($P > 0.05$; Table 2).

YAF and adult red kangaroos showed similar patterns in C_{dry} from $T_a -5^{\circ}$ to 33°C (Fig. 4). In both groups, C_{dry} was not different at $T_a 25^{\circ}\text{C}$ and below. At $T_a 33^{\circ}\text{C}$, both groups showed a significant increase in C_{dry} , with that of adults being 1.6 times higher ($P < 0.01$; Fig. 4). However, as T_a exceeded T_b ($T_a 45^{\circ}\text{C}$), the pattern of C_{dry} in adult and YAF kangaroos differed. While the C_{dry} of adults decreased to levels that were not significantly different from those seen at $T_a 25^{\circ}\text{C}$ ($P > 0.05$), the C_{dry} of juveniles continued to increase, reaching levels 3.2 times higher than those seen under thermoneutral conditions ($P < 0.001$; Fig. 4).

YAF versus Weaned Kangaroos

The T_b of young red kangaroos was unchanged from *PPE* to weaning age, ranging between $36.8^{\circ} \pm 0.2^{\circ}\text{C}$ and $36.9^{\circ} \pm 0.4^{\circ}\text{C}$, respectively, at $T_a 25^{\circ}\text{C}$ ($P > 0.05$). Both age groups showed significant increases in T_b from thermoneutral levels ($P < 0.05$) at $T_a 45^{\circ}\text{C}$ but were not in themselves significantly different ($P > 0.05$); the values being $37.8^{\circ} \pm 0.4^{\circ}\text{C}$ and $38.4^{\circ} \pm 0.3^{\circ}\text{C}$ for the YAF and weaned kangaroos, respectively. Under thermoneutral conditions ($T_a 25^{\circ}\text{C}$), there was also no difference between the two age groups with respect to *MHP* or *EHL* (Fig. 5). At $T_a 45^{\circ}\text{C}$, there was also no difference in the heat

loss (or *MHP* since T_b was constant) from young kangaroos after *PPE* or after weaning age. However, under cold conditions ($T_a -5^{\circ}\text{C}$), the *MHP* of weaned kangaroos was 32% lower than that of YAF shortly after *PPE* ($P < 0.001$; Fig. 5). Weaned kangaroos also had a significantly lower *EHL* at $T_a 45^{\circ}\text{C}$, which was 30% lower than that at *PPE* age ($P < 0.001$; Fig. 5). At high T_a , the lower *EHL* of weaned kangaroos was primarily as a reduction in *CEHL* because there was no significant difference in *REHL* from *PPE* or weaned kangaroos at any T_a (Fig. 6). Correlated with the reduction in *EHL* at high T_a 's, the C_{dry} of weaned red kangaroos at $T_a 45^{\circ}\text{C}$ was 33% lower than that of kangaroos just after *PPE* ($P < 0.01$; Fig. 7). There were no differences between *PPE* and weaned red kangaroos with respect to *RQ* or *fr* at any T_a ($P > 0.05$; Table 3), although both *RQ* and *fr* were significantly increased within each group at $T_a 45^{\circ}\text{C}$ ($P < 0.001$; Table 3).

Discussion

Recently, long-term studies on large, herbivorous mammals have uncovered a consistent pattern of high juvenile mortality relative to the rates of adult survival (Sæther 1997; Gaillard et al. 1998). Red kangaroos also show this pattern (Newsome et al. 1967; Newsome 1977; Robertson 1986; Shepherd 1987). However, few studies have compared the physiological differences between juveniles and adults or considered how such

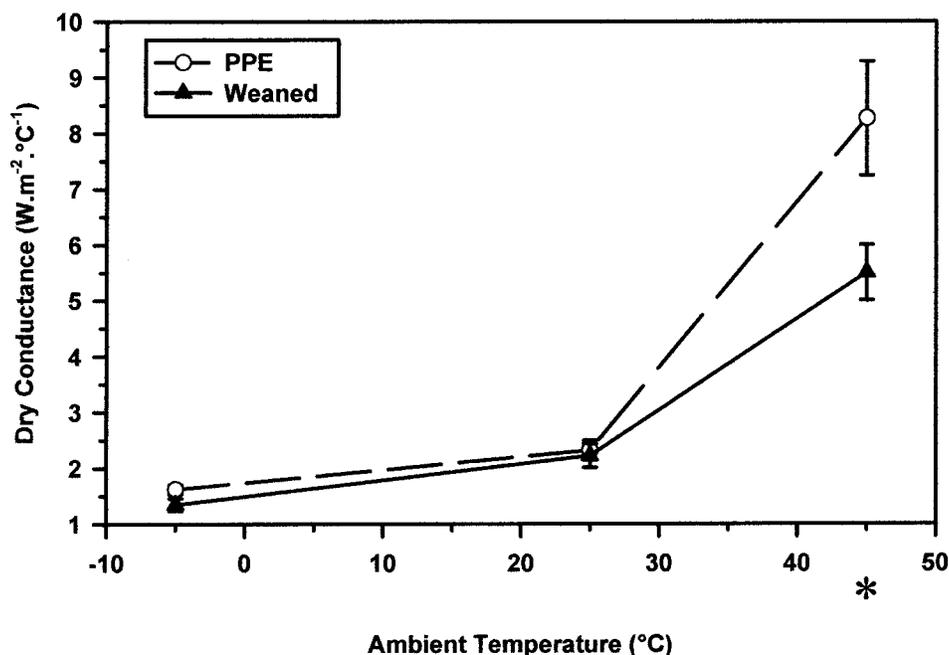


Figure 7. Dry conductance ($\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$) of permanent pouch exit (PPE) and weaned red kangaroos at a range of ambient temperatures ($^\circ\text{C}$). Values are means \pm SEM. For within-group significant differences, refer to the text. The asterisk on the X-axis denotes a difference between PPE and weaned means (Student-Newman-Keuls, $P < 0.05$).

differences could relate to survivorship. Our results indicate that there are major differences in the energy needs and basic thermoregulatory physiology of juvenile kangaroos as compared with adults. These differences cannot be adequately explained by the usual allometric variation associated with body size among adults. From the allometric equations for marsupials in general (Dawson and Hulbert 1969; Hayssen and Lacy 1985; Hinds et al. 1993), the resting metabolism of an adult kangaroo of the same mass as a YAF kangaroo (7.2 kg) is predicted to be $2.3 \text{ W kg}^{-0.75}$, as compared with our measured value of $3.5 \text{ W kg}^{-0.75}$. This is 1.5 times higher than predicted, indicating that YAF kangaroos have a resting metabolism considerably greater than would be expected for an adult marsupial of their size. This not only has implications for the general ecology of young kangaroos but must also influence how these animals maintain T_b under thermal extremes.

The more labile T_b of YAF red kangaroos over a range of T_a are consistent with findings for many young mammals (Janssens et al. 1997; Holloway and Geiser 2000). In the newborn marsupial, T_b is unregulated and thermoregulation is not well developed until shortly before PPE (Hulbert 1988; Holloway and Geiser 2000). Our results indicate that after PPE the T_b 's of YAF red kangaroos are somewhat higher than that of adults, by around $0.6^\circ\text{--}1.5^\circ\text{C}$ (Fig. 1). Gemmel and Cepon (1993) and Janssens et al. (1997) have discussed similar findings for a number of marsupials. For the pouched kangaroo, a higher T_b cre-

ates a gradient for heat loss to the mother, allowing the young to dump the considerable metabolic heat produced during active growth. In the weeks surrounding PPE, growth rate in red kangaroos is at its peak (Sharman et al. 1964), and the continued higher T_b of young kangaroos may be a legacy of a high metabolism at this stage.

The relatively higher metabolism of YAF kangaroos in this study, as compared with adults (Fig. 2), is consistent with that seen in most young mammals (Brody 1945; Thompson et al. 1987; Janssens et al. 1997; Holloway and Geiser 2000). Overall, the YAF red kangaroos had double the metabolic intensity of adults. Consequently, a YAF at 7 kg had a total energy requirement approaching 70% of that of a mature female weighing 25 kg (Table 1). Such levels of metabolism have important ecological implications for these arid zone herbivores. While YAF red kangaroos at 300 d old still get some milk from their mothers, milk intake declines rapidly from PPE, and dependence on forage becomes total at about 360 d old (Sharman et al. 1964; Merchant 1989). Of note, the high metabolism of juveniles was not significantly diminished by weaning age, although their metabolic needs in response to cold were reduced by this stage (Fig. 5).

Our metabolic data suggest that juvenile kangaroos would require proportionally higher forage intakes than adults, perhaps necessitating longer foraging times. Also, because digestibility of fibrous vegetation is less efficient in smaller herbivores

Table 3: Respiratory variables of permanent pouch exit (PPE) and weaned red kangaroos at a range of ambient temperatures (°C)

| | -5.6 ± .6 | 25.7 ± .3 | 45.4 ± .3 |
|--------|--------------|-------------|-----------------------------|
| fr: | | | |
| PPE | 13.60 ± 1.70 | 7.69 ± 1.13 | 317.51 ± 14.24 ^A |
| Weaned | 11.97 ± 1.72 | 8.32 ± .46 | 295.32 ± 12.19 ^A |
| RQ: | | | |
| PPE | .86 ± .05 | .83 ± .01 | 1.10 ± .05 ^A |
| Weaned | .76 ± .03 | .86 ± .02 | 1.05 ± .06 ^A |

Note. fr, respiratory rate (breaths min⁻¹); RQ, respiratory quotient. Values are means ± SEM. Letters denote differences within rows (Student-Newman-Keuls, $P < 0.001$).

(Demment and Van Soest 1985), juveniles should require better-quality forage than can be handled by adult red kangaroos. Given such a pattern, the potential nutritional stresses on juvenile red kangaroos in their unpredictable habitat are easy to appreciate.

Consistent with a higher metabolism, the mass-specific EHL of the YAF kangaroos was higher than that of adults at all T_a . Therefore, despite the YAF kangaroos being three times smaller, the TEHL from YAF and adult kangaroos was actually similar (Table 1). At higher T_a , thermoregulatory EHL comes into play and by T_a 33°C the mass-specific EHL from adult and YAF kangaroos was increased, proportionally more so in the YAF (Fig. 3). At even higher T_a (45°C), the mass-specific EHL from YAF kangaroos was 2.5 times that of adults (Fig. 3), and their TEHL remained similar (Table 1).

At the higher T_a 's of 33° and 45°C, the YAF kangaroos accommodated their high EWLs through both cutaneous and respiratory means. In the YAF, licking of the body surface (legs, feet, forearms, belly, and tail; A. J. Munn and T. J. Dawson, personal observation) appeared to be the major route of CEHL, although sweating cannot be ruled out, as adult red kangaroos are known to sweat in response to exercise (Dawson et al. 1974). Both adult and YAF red kangaroos used panting to increase REHL in response to higher T_a 's, with YAF kangaroos panting considerably faster than adults at T_a 33° and 45°C (Table 2). The relatively high water use by the YAF kangaroos in general has obvious ecological implications. Adult red kangaroos water infrequently, even in summer (Dawson et al. 1975), but juveniles could be constrained to remain near water holes where feed is sparse and predators focus.

The high water losses from YAF red kangaroos at T_a 45°C appear to be due to several factors. First, a higher metabolism means a higher internal heat load, which must be lost in addition to the heat that flowed into the body (external heat load) since T_a well exceeded T_b . This external heat load was much elevated in the YAF kangaroos, as indicated by their considerably higher C_{dry} at T_a 45°C. Being smaller, the YAF kangaroos would have a relatively higher SA to volume ratio as compared

with adults, no doubt contributing to a higher external heat load. More importantly, the YAF kangaroos did not show the drop in C_{dry} at T_a 45°C observed in the adult kangaroos. This feature of adult red kangaroos is associated with peripheral vasoconstriction, a mechanism for reducing external heat loads, thereby conserving water (Dawson et al. 2000a). In the YAF kangaroos, this mechanism does not appear to be well developed and is still not fully developed at weaning (Fig. 7), although the C_{dry} at T_a 45°C was significantly reduced by weaning age (Fig. 7). This was correlated with a significantly lower level of CEHL from the weaned kangaroos (Fig. 6). Compared with adult and weaned kangaroos, the greater reliance of YAF kangaroos on cutaneous evaporation, and its impact on C_{dry} , warrants further investigation.

Compared with the younger red kangaroos, the reduced energy and water requirements of weaned kangaroos at extremes of T_a (Fig. 5) suggest that survival may be highly dependent on growth rate. For weaned and subadult kangaroos, reduced thermoregulatory constraints mean they could forage further from water points and are more likely to encounter patches of high-quality feed.

In terms of understanding the population dynamics of red kangaroos, as well as other species of large herbivores, it seems apparent that the physiology of juvenile animals plays a critical role in shaping future populations. In young red kangaroos, survival is probably linked with feed and water availability, which, in turn, are influenced by environmental factors. Compared with adults, the high energy and water demands of young kangaroos would imply that juveniles should be considered as ecologically distinct units of the population whose resource requirements cannot be predicted from the allometric relationships described for adult animals.

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