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ORIGINAL PAPER

A. J. Munn · T. J. Dawson

Energy requirements of the red kangaroo (*Macropus rufus*): impacts of age, growth and body size in a large desert-dwelling herbivore

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Abstract Generally, young growing mammals have resting metabolic rates (RMRs) that are proportionally greater than those of adult animals. This is seen in the red kangaroo (*Macropus rufus*), a large (>20 kg) herbivorous marsupial common to arid and semi-arid inland Australia. Juvenile red kangaroos have RMRs 1.5–1.6 times those expected for adult marsupials of an equivalent body mass. When fed high-quality chopped lucerne hay, young-at-foot (YAF) kangaroos, which have permanently left the mother's pouch but are still sucking, and recently weaned red kangaroos had digestible energy intakes of 641±27 kJ $kg^{-0.75}day^{-1}$ and 677±26 kJ $kg^{-0.75}day^{-1}$, respectively, significantly higher than the 385±37 kJ $kg^{-0.75}day^{-1}$ ingested by mature, non-lactating females. However, YAF and weaned red kangaroos had maintenance energy requirements (MERs) that were not significantly higher than those of mature, non-lactating females, the values ranging between 384 kJ $kg^{-0.75}day^{-1}$ and 390 kJ $kg^{-0.75}day^{-1}$ digestible energy. Importantly, the MER of mature female red kangaroos was 84% of that previously reported for similarly sized, but still growing, male red kangaroos. Growth was the main factor affecting the proportionally higher energy requirements of the juvenile red kangaroos relative to non-reproductive mature females. On a good quality diet, juvenile red kangaroos from permanent pouch exit until shortly after weaning (ca. 220–400 days) had average growth rates of 55 g body mass day^{-1}. At this level of growth, juveniles had total daily digestible energy requirements (i.e. MER plus growth energy requirements) that were 1.7–1.8 times the MER of mature, non-reproductive females. Our data suggest that the proportionally higher RMR of juvenile red kangaroos is largely explained by the additional energy needed for growth. Energy contents of the tissue gained by the YAF and weaned red kangaroos during growth were estimated to be 5.3 kJ g^{-1}, within the range found for most young growing mammals.

Keywords Kangaroos · Juvenile · Basal metabolism · Maintenance energy requirement · Growth

Abbreviations *BMR* basal metabolic rate · *DEI* digestible energy intake · *MER* maintenance energy requirement · MER_g maintenance plus growth energy requirement · *PPE* permanent pouch exit · *RMR* resting metabolic rate · *YAF* young-at-foot

Introduction

The impact of body size on the basal metabolic rate (BMR) of adult mammals is well appreciated; between-species body size is the single universal factor affecting the metabolic rate of animals (Brody 1945; Kleiber 1975; Schmidt-Nielsen 1984; Heusner 1991; West et al. 1997; Dodds et al. 2001). Generally, inter-specific BMR varies allometrically with body mass, usually body mass raised to the power of 0.75 (Kleiber 1975; Schmidt-Nielsen 1984). Phylogenetic influences, however, are seen, as in the case of marsupials (Dawson and Hulbert 1970). Marsupials have BMRs around 70% of those of comparable eutherians, though diet, habitat and other factors may also have an impact on basal metabolism (McNab 1986; Lovegrove 2000). Within-species affects of body size on metabolism are less well understood (Hayssen and Lacy 1985; Heusner 1991), particularly with reference to juvenile animals.

In young growing mammals, BMR cannot be measured directly. BMR is defined as the minimal resting metabolism of mature (i.e. not growing),

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A. J. Munn (✉) · T. J. Dawson
School of Biological Earth and Environmental Sciences,
University of New South Wales,
2052 Sydney, NSW, Australia
E-mail: ; a.munn@unsw.edu.au
Tel.: +61-2-93852123
Fax: +61-2-93851558

non-reproductive, post-absorptive, non-stressed, wakeful animals in a thermoneutral environment and with minimal activity (Withers 1992). However, because of their growth-related metabolism, the closest analogue to BMR in young animals is resting metabolic rate (RMR). In this context, the RMR of juvenile animals is comparable to the BMR of adults, each representing the minimal energy metabolism needed to maintain proper functioning and, in the case of juveniles, growth.

Generally, young growing mammals have minimal RMRs that are relatively greater than the BMRs of adult animals (Brody 1945; Robbins 1993). In marsupials, the pattern of growth and development of metabolism is complex (for reviews see Tyndale-Biscoe and Janssens 1988; Janssens et al. 1997). For example, in macropodoid marsupials (kangaroos, rat-kangaroos and wallabies; superfamily Macropodoidea), metabolism is low and thermoregulatory ability is limited during the early stages of pouch life. However, as the age of permanent-pouch-exit (PPE) approaches, metabolic rate increases and thermoregulation matures (Hulbert 1988; Janssens et al. 1997). This pattern of development is seen in the red kangaroo, a large (>20 kg) herbivorous macropodid common to the arid and semi-arid regions of inland Australia (Dawson 1995).

Like all marsupials, red kangaroos are 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 around 190 days old, weighing around 2 kg, the young is fully furred and ventures out of the pouch for short periods. By 230–250 days, the young red kangaroo permanently exits the mother's pouch, becoming a "young-at-foot" (YAF; mass 4–5 kg). YAF kangaroos forage in association with their mothers, but also continue to suck from the mother's pouch, accessing the same teat that they used during pouch life. This occurs even though another young may occupy the pouch. Red kangaroos are fully weaned at around 1 year old and 10–12 kg (Sharman et al. 1964).

Like other juvenile mammals, YAF and weaned red kangaroos have mass-specific (W kg^{-1}) and allometrically related (W kg$^{-0.75}$) RMRs markedly higher than the BMRs of non-reproductive adult females (Munn and Dawson 2001). Overall, the RMR of YAF and weaned red kangaroos was 1.5–1.6 times that expected for adult marsupials of equivalent body size (Dawson and Hulbert 1970; Hayssen and Lacy 1985; Hinds et al. 1993). In other words, with respect to minimal metabolic rates, juvenile red kangaroos are not just 'small adults'. Is the relatively higher RMR of juvenile red kangaroos a function of their smaller body size and growth or are other factors involved?

Using a series of feeding trials the maintenance energy requirements (MERs) of juvenile red kangaroos (YAF and weaned) were compared with those of non-reproductive adult females. In this case, MER was determined as that level of energy intake needed to maintain body mass (i.e. the body-balance method). Allometrically related comparisons of MER were made using a body-mass exponent of 0.75 (Dawson and Hulbert 1970; Kleiber 1975; West et al. 1997), though sufficient data is provided to afford alternative treatments. Thus it was possible to compare the energy requirements of the different kangaroo age classes and to evaluate juveniles as if they were just small adults.

The energetic costs of growth in juvenile red kangaroos after pouch exit were also quantified. Interestingly, red kangaroos reach PPE and are fully weaned around 6 months earlier than the young of some other large kangaroo species, including the eastern (*Macropus giganteus*) and western (*Macropus fuliginosus*) grey kangaroos (Frith and Sharman 1964; Poole 1975). Red kangaroos typically reach PPE and are fully weaned 20% earlier than expected for a macropodid marsupial of their body size (Russell 1982). The mechanisms behind the accelerated development of red kangaroos are unknown, but may be important for their survival in arid environments. In such environments drought is frequent and kangaroos must be able to take full advantage of high quality forage when available.

Materials and methods

Experimental animals

Juveniles

Six juvenile kangaroos (four females, two males) were taken from their mothers shortly before PPE. These animals were aged from foot and tail length (Sharman et al. 1964) and treated for parasites (internal and external) using Ivermectin (0.2 mg kg^{-1}; Large Animal Ivomec, Merck, Sharpe and Dohme, Granville). They were hand-reared using artificial pouches (Williams and Williams 1999) until they reached the age of PPE at approximately 250 days (Sharman et al. 1964). Five weeks prior to experimentation the animals were transferred to our laboratory animal house and maintained in pens (4300×1200×2500 mm) under a 12 h light/dark cycle (12L : 12D). The now YAF kangaroos were weighed at the beginning of each week (±0.05 kg). Feed [Gordon's Rabbit Pellets (Gordon's Specialty Stock Feeds, Yanderra), Kangaroo Cubes (Doust and Rabbidge, Forbes), and a lucerne/bran mix (Kensington Produce, Sydney)] and water were available ad libitum. This diet was supplemented with Digestelact (Digestelact Low Lactose, Sharpe Laboratories, Sydney), a low-lactose milk powder commonly used for hand-rearing orphaned marsupials (Williams and Williams 1999), made to full strength (125 g per 900 ml H_2O). During non-experimental periods a daily supplement of 100 ml of Digestelact was offered to the YAF. Milk intakes by red kangaroo young have not been reported, but on this intake of Digestelact, plus forage and pellets, the YAF red kangaroos maintained growth rates comparable to those previously reported by Sharman et al. (1964).

Milk was withheld from the YAF red kangaroos according to the specific diet treatments described below. Milk intake was reduced over time until it was eliminated at normal weaning age, ca. 360 days. During the rearing process, juveniles were exposed to fresh grass and soil, and to the faeces of adult red kangaroos, to facilitate infection by the microbes needed for the proper functioning of the kangaroo stomach.

Feeding trials were carried out when the average age (±SEM) of the YAF red kangaroos was 302±6 days and the average body mass was 6.4±0.2 kg. Trials were repeated using the same kangaroos after they had been fully weaned and were approximately 394 ± 7 days and had a body mass of 10.9 ± 0.3 kg.

Adults

Six non-lactating adult female red kangaroos were used. These were tame animals from a captive colony and were maintained under housing conditions identical to those of the juveniles. Feed [Kangaroo Cubes (Doust and Rabbidge, Forbes), and a lucerne/bran mix (Kensington Produce, Sydney)] and water were available ad libitum. Five of the adult females were known to be at least 5 years old; the other was 4 years old. Average body mass of the adult females during the experiments was 25.8 ± 1.6 kg.

Diet and diet regimens

Two forages of different fibre levels were used in the feeding trials. Chopped lucerne (alfalfa) (*Medicago sativa*) hay was considered "high" quality forage, being comparatively low in fibre (neutral detergent fibre) and high in nitrogen. Chopped oaten (*Avena sativa)* hay was considered "poor" quality forage, being higher in fibre and low in nitrogen content (Table 1). Apparent dry matter digestibility of lucerne and oaten hays by adult red kangaroos was ca. 55% and 45%, respectively (McIntosh 1966; Hume 1974). Some animals initially refused the chopped oaten hay. Subsequently, the diet was always lightly sprayed ($<5\%$ v/w) with unsweetened apple juice (Golden Circle, Sydney) to increase palatability. The contribution of the juice to energy and nitrogen intakes was assessed as negligible.

In preliminary trials, YAF red kangaroos offered only chopped oaten hay (i.e. without a milk supplement) eventually did not eat. This treatment was, therefore, omitted from the main trials. Only by using a milk supplement (Digestelact) were we able to assess the YAF red kangaroos' capabilities when fed chopped oaten hay. On this diet YAF red kangaroos received a milk supplement of 80 ml day^{-1} of full strength Digestelact. Milk was fed at 0900 hours and 1800 hours at 40 ml per feed. This level of milk intake was used to mimic that likely to be faced by YAF red kangaroos subject to harsh environmental conditions. A detailed study of the importance of the milk supplement to the digestion of forage by YAF red kangaroos was reported by Munn and Dawson (2003).

Diet order was established by randomly allocating three YAF red kangaroos to a starting diet of chopped lucerne or oaten hay (with milk). YAF were then assigned a fixed regimen of lucerne, followed by chopped oaten hay with milk or vice-versa. After weaning, feeding trials were repeated using the same red kangaroos, maintaining the diet order initially established. Importantly, weaned red kangaroos did not receive any milk supplement. Similarly, three adult female red kangaroos were randomly assigned to a starting diet of chopped lucerne followed by oaten hay, the order being reversed for the remaining adults. This fixed, counter-balanced design was used to minimise carry-over affects caused by diet order or animal age (Zar 1999).

Table 1 Composition of the chopped lucerne and oaten hays and Digestelact milk powder. Results are means ± SEM

	Lucerne hay	Oaten hay	Digestelact
Dry matter (% initial mass)	92.2 ± 0.6	92.4 ± 0.4	99.0 ± 0.0
Ash (% dry matter)	9.6 ± 0.3	5.8 ± 0.1	4.84 ± 0.0
Organic matter (% dry matter)	90.4 ± 0.3	94.2 ± 0.1	95.2 ± 0.0
Energy (kJ g^{-1}) (kJ ml^{-1}milk)	18.5 ± 0.2	16.7 ± 0.4	21.9 ± 0.2 (2.74 ± 0.03)†
Nitrogen (%) (g l^{-1} milk)	3.2 ± 0.07	0.94 ± 0.09	4.74 ± 0.01 (5.6 ± 0.01)†
Neutral detergent fibre (%)	44 ± 1	68 ± 1	–
Acid detergent fibre (%)	31 ± 1	36 ± 1	–
Lignin (%)	6 ± 0.2	4 ± 0.3	–

†Values in *parenthesis* are for Digestelact at normal (125 g 900 ml^{-1}H_2O) dilution

Experimental procedure

Feeding trials were conducted in a temperature-controlled room (25 °C) on a 12L : 12D cycle, with lights on at 0600 hours. Adult and juvenile kangaroos were housed individually in metabolism cages (1245×960×1670 mm) with mesh floors. Faeces and urine passed to a collection tray beneath each cage. Collection trays consisted of a fine mesh wire on which faeces and any spilt feed were trapped, allowing urine to flow to the tray bottom where it drained continuously into polyethylene volumetric flasks. Feed and water containers were attached to the outside of each cage to minimise feed spillage. Feed and water containers and waste collection trays were cleaned daily with demineralised water.

YAF and weaned kangaroos were allowed 5 days to acclimate to their metabolism cage before a preliminary trial commenced. Preliminary trials were conducted for at least 5 days or until feed intake was stable, after which time a 5-day feeding trial commenced. During each trial, feed refusals and faeces produced were collected quantitatively and bulked over the 5 days and stored frozen. YAF and weaned kangaroos were weighed (± 0.05 kg) at the same time each day throughout the preliminary and feeding trials. At the end of each trial, animals were allowed at least 10 days to recover, during which time they received their usual diet (i.e. water, kangaroo cubes, rabbit pellets, lucerne/bran mix) ad libitum; YAF also received 100 ml Digestelact day^{-1}.

Adult red kangaroos were allowed at least 10 days to acclimate to their experimental diet and metabolism cage (i.e. preliminary trial). After feed intake had stabilised a 5-day feeding trial commenced. Adult kangaroos were weighed (± 0.05 kg) at the beginning of the preliminary and experimental trials and again at the end of the experimental trial. After each experimental trial adult kangaroos were allowed at least 10 days to recover, during which time they received their usual diet (water, kangaroo cubes, lucerne/bran mix) ad libitum.

During the preliminary and feeding trials herbage was offered to the YAF, weaned and adult red kangaroos at twice the previous day's level of voluntary feed intake. Also, some kangaroos showed considerable feed sorting and the gross intakes of dietary energy by YAF, weaned and adult red kangaroos were calculated as:

Energy Intake = (Energy in FO×Mass FO) − (Energy in FR×Mass FR);

where *FO* = feed offered, *FR* = feed refused, energy content is in kJ g^{-1} organic matter and mass is in grams.

Analysis of samples

Samples of the feed offered and bulked feed refusals and faeces were thawed and sub-samples (20%) prepared for analysis by drying in a forced-draft convection oven at 50 °C (to prevent the formation of artefact lignin by the Maillard reaction; Robertson and Van Soest 1981) for 48 h or until constant mass. As a check, further sub-samples were dried at 90 °C for a further 24 h, but there was no change in dry matter content. Dried samples were ground through a 1 mm mesh using a Wiley Mill (Arthur Thomas, Scientific Apparatus, Philadelphia, USA). Ash contents of dried, ground feedstuffs (including Digestelact milk powder) and faeces were determined in duplicate by dry-ashing 0.5-g samples at 550 °C overnight in a Thermolyne Muffle Furnace (Model 62700; Dubuque, Iowa, USA). Results are presented on an organic matter basis (i.e. dry matter−ash content).

Neutral detergent fibre (largely cellulose, hemicellulose and lignin/cutin), acid detergent fibre (largely cellulose and lignin/cutin) and lignin/cutin contents of feeds were determined in duplicate on 0.5-g samples using a sequential filter-bag technique and an ANKOM Fibre Analyser (Model 220, ANKOM Technology, Fairport New York, USA). The reagents and general procedures used for fibre analysis were as for Goering and Van Soest (1970), modified according Van Soest et al. (1991). This sequential filter-bag technique ensured no loss of sample throughout treatment. Nitrogen content of lucerne and oaten hays was determined in duplicate by total combustion of approximately 0.2-g samples in a Leco CHN-1000 elemental analyser (Leco St. Joseph, Mich., USA). Energy contents of dried ground feedstuffs and faeces were determined by combusting duplicate sub-samples of 0.7 g in a ballistic bomb calorimeter (Gallenkamp, Model CB-375; Gallenkamp, UK), using a benzoic acid standard for calibration every 25 samples.

Data analysis

Apparent energy digestibility was calculated as:

$$\frac{\text{Energy Intake} - \text{Fecal Energy Output}}{\text{Energy Intake}} \cdot 100$$

and used to estimate digestible energy intakes (DEI).

Repeated measures ANOVAs were used to compare within- and between-group data from YAF, weaned and adult red kangaroos. Non-independence of the YAF and weaned kangaroos prevented their combined analysis with adult data (Zar 1999). Therefore, YAF and weaned kangaroos were compared using two-way repeated measures ANOVAs with two levels of within group factors (diet and age). YAF and weaned data were then compared separately to those of adult red kangaroos using two-way repeated measures ANOVA. Statistical outcomes for the within-YAF, -weaned and -adult red kangaroo data were identical across all statistical treatments. Therefore, although tested independently, results are presented as if they were one data set.

Assumptions for ANOVA were tested using the Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) and Levene's test for homogeneity of variances ($\alpha = 0.05$). To achieve normality, log (+1) transformations were applied to the following data sets: energy intake (kJ day^{-1}; YAF vs. adults; weaned vs. adults) and DEI (kJ day^{-1}; YAF vs. weaned; YAF vs. adult). Data for apparent energy digestibility (YAF vs. adult; weaned vs. adult) and DEI (kJ kg$^{-0.75}$day^{-1}; YAF vs. weaned; YAF vs. adult; weaned vs. adult), however, could not be normalised ($P < 0.05$) and were compared using a Friedman's test (a non-parametric ANOVA for repeated measures; Zar 1999). Significant differences detected by ANOVA were further investigated using a Tukey's Honest Significant Differences (HSD) post-hoc test. Significant differences detected by Friedman's test were investigated using Eqn. 11.3 from Zar (1999) and SE was adjusted for repeated measures (Zar 1999). Regression analyses were performed using the least-squares method (Zar 1999). ANOVAs and Tukey's HSD tests were performed using Minitab for Windows 12.1 (1998; Minitab, Pa., USA). All data are presented as means ± SEM. Duplicate samples in all cases were repeated if replicates differed by more than 5%.

Results

Growth and body mass change

Growth of the juvenile red kangaroos between 200 days and 450 days followed a sigmoidal pattern (Fig. 1), common to most forms of ontogenetic growth (Brody 1945; Zullinger et al. 1984; West et al. 2001). However, from PPE to shortly after weaning age, logistic and linear models explained 94% and 92%, respectively, of the variation in growth by the juvenile red kangaroos. A linear growth rate has been found previously for a range of marsupial species between these ages (Maynes 1976; Russell 1982). Therefore, the linear model was accepted here for simplicity. Of note, red kangaroos continue to grow well after weaning age. Adult female red kangaroos attain a maximum body mass of 25–35 kg by 5 years and males may take 10–15 years to reach their maximum body mass of 70–80 kg (Dawson 1995).

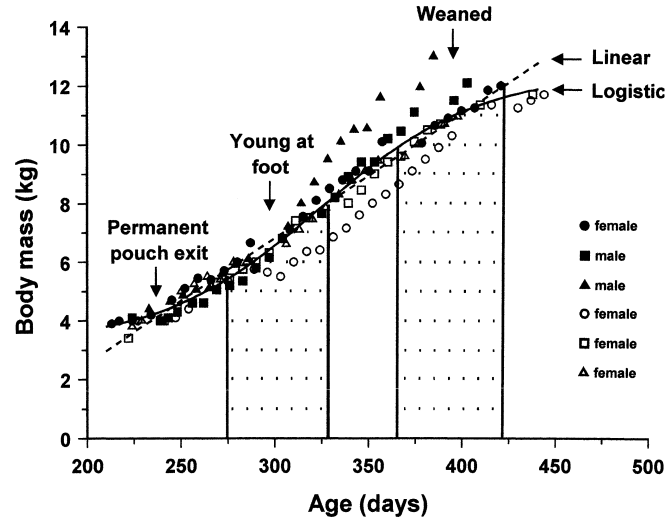

Fig. 1 Growth of juvenile red kangaroos from permanent pouch exit to young-at-foot and weaning stages. *Shaded areas* indicate the intervals at which feeding trials were conducted. Data from chopped oaten hay trials omitted. Logistic model ($y = \text{min} + (\text{max}-\text{min})/1 + \exp(\text{-K}^*(x - x_{50}))$; where $min = 3.2 \pm 0.3$, $max = 12.5 \pm 0.3$, $x_{50} = 324 \pm 3$ and $K = 0.024 \pm 0.0023$; *Sum Squares* = 110, $DF = 260$, $r^2 = 0.94$), linear model ($y = 0.0427x - 5.99$, where y = mass (kg) and x = time (day since birth), $r^2 = 0.92$, $F = 1558$, $DF = 131$, $P < 0.001$)

When fed the high-quality chopped lucerne hay, both YAF and weaned red kangaroos gained 43–55 g body mass day^{-1} (Table 2), rates that were comparable with the overall growth rate of 55 g day^{-1}estimated from the linear model for the young kangaroos aged between 250 days and 400 days (Fig. 1). Overall, the YAF and weaned red kangaroos fed chopped lucerne hay gained 3.3 ± 0.7% and 2.6 ± 0.5% of their initial body mass, respectively, over the 5-day trial, values that were not significantly different. In contrast, changes in body mass by the non-reproductive adult female red kangaroos fed chopped lucerne hay were essentially zero (Table 2).

When fed chopped oaten hay, YAF and weaned red kangaroos lost 32–33 g body mass day^{-1}, equivalent to between 1% and 3% of their initial body mass over the 5-day trial (Table 2). Body mass changes by the adult female kangaroos fed chopped oaten hay were variable (Table 2) but not significantly different from the adults fed chopped lucerne hay.

Energy intake and digestibility

Apparent digestibility of energy from chopped lucerne hay by the YAF, weaned and adult red kangaroos did

Table 2 Changes in body mass by young-at-foot (*YAF*), weaned and adult red kangaroos fed chopped lucerne and oaten hays

	YAF	Weaned	Adult
Initial body mass (kg)			
Lucerne hay	$6.4 \pm 0.5^{\mathrm{Z}}$	$10.8 \pm 0.3^{\mathrm{Y}}$	$25.8 \pm 1.5^{\mathrm{X}}$
Oaten hay	$6.1 \pm 0.3^{\mathrm{Z}}$	$10.9 \pm 0.5^{\mathrm{Y}}$	$25.7 \pm 1.6^{\mathrm{X}}$
Mass change (g day^{-1})			
Lucerne hay	$43 \pm 9^{\mathrm{X}}$***	$55 \pm 11^{\mathrm{X}}$***	$0.0 \pm 16^{\mathrm{X}}$
Oaten hay	$-32 \pm 14^{\mathrm{X}}$	$-33 \pm 14^{\mathrm{X}}$	$-61 \pm 30^{\mathrm{X}}$
Mass change (%initial)			
Lucerne hay	$3.3 \pm 0.67^{\mathrm{A}}$***	$2.6 \pm 0.47^{\mathrm{A}}$**	$0.1 \pm 0.31^{\mathrm{B}}$
Oaten hay	$-2.3 \pm 0.96^{\mathrm{A}}$	$-1.5 \pm 0.65^{\mathrm{A}}$	$-1.2 \pm 0.54^{\mathrm{A}}$

$^{\mathrm{A,B}}P < 0.05$; $^{\mathrm{X,Y,Z}}P < 0.01$; within a row, means ± SEM bearing different superscripts differ significantly
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; asterisks indicate significant differences between diets within ages

not differ significantly, ranging between 59% and 62%. When fed chopped lucerne hay, the gross energy intake by YAF red kangaroos was 4354 ± 422 kJ day^{-1}, 59% of that by adult females. By the time of weaning, gross energy intakes by juveniles on this diet approached those of adults and were not significantly different (Table 3). In allometric terms (i.e. kJ kg$^{-0.75}$day^{-1}), DEI by the YAF and weaned red kangaroos were not significantly different, but were 1.7 times and 1.8 times, respectively, that of the adult females.

When fed chopped oaten hay, gross energy intakes (kJ day^{-1}) by the YAF and weaned red kangaroos were only 42% and 46%, respectively, of their intakes on chopped lucerne hay (Table 3). In contrast, gross energy intake by adult female kangaroos was not affected by diet (Table 3). The apparent digestibilities of energy from chopped oaten hay by the YAF, weaned and adult red kangaroos ranged between 46% and 48% and were not significantly different. Importantly though, the YAF fed chopped oaten hay also received a milk supplement. Assuming that milk-energy had a digestibility of 95%, as has been found for comparable eutherian herbivores (Penning et al. 1977; Roy 1980; Ternouth et al. 1985a, 1985b), the apparent digestibility of energy from the chopped oaten hay alone by the YAF was just 40 ± 3%, significantly lower than that by the adult red kangaroos but not the weaned animals (Table 3). Allometrically, the DEI (kJ kg$^{-0.75}$day^{-1}) from chopped oaten hay alone (i.e. excluding digestible milk-energy intake) of the YAF was also significantly lower than those of the weaned and adult females.

Energy requirements for maintenance and growth

There were significant positive relationships between change in body mass (g day^{-1}) and DEI (kJ day^{-1}) by the YAF, weaned and adult red kangaroos (Fig. 2). Regression slopes from these data were not significantly different (YAF vs. weaned $t_{(2)} = 0.76$, YAF vs. adult $t_{(2)} = 0.85$, and weaned vs. adult $t_{(2)} = 1.8$; $DF = 20$, $P > 0.05$). The y-intercept indicates the digestible energy required for maintaining body mass (i.e. MER) by the YAF, weaned and adult red kangaroos. YAF red kangaroos had a MER of 1,575 kJ day^{-1}, significantly lower than those by weaned or adult red kangaroos, their values being 2,345 kJ day^{-1} ($t_{(2)} = 2.3$, $DF = 21$, $P < 0.05$) and 4,240 kJ day^{-1} ($t_{(2)} = 4.9$, $DF = 21$, $P < 0.001$), respectively. Weaned red kangaroos also had a significantly lower MER than did adult females ($t_{(2)} = 3.7$, $DF = 21$, $P < 0.01$). Overall, the MER of the YAF and weaned red kangaroos was 37% and 55%, respectively, of that of adult females.

However, when growth is taken into account the picture changes. From the regression equations outlined in Fig. 2 and assuming that the YAF red kangaroos were growing at 55 g day^{-1} (Fig. 1), their total daily digestible energy requirements for maintenance plus

Table 3 Energy intake, faecal output and apparent digestibility by YAF, weaned and adult red kangaroos fed chopped lucerne and oaten hays. *DEI* digestible energy intake

	YAF	Weaned	Adult
Gross energy intake (kJ day^{-1})			
Lucerne hay	$4354 \pm 422^{\mathrm{A}}$***	$6475 \pm 170^{\mathrm{B}}$***	$7387 \pm 721^{\mathrm{B}}$
Oaten hay	$1815 \pm 204^{\mathrm{A}}$	$3009 \pm 435^{\mathrm{A}}$	$6098 \pm 837^{\mathrm{B}}$
Faecal energy output (kJ day^{-1})			
Lucerne hay	$1750 \pm 186^{\mathrm{A}}$	$2466 \pm 169^{\mathrm{AB}}$	$3062 \pm 424^{\mathrm{B}}$
Oaten hay	$987 \pm 155^{\mathrm{A}}$	$1648 \pm 261^{\mathrm{A}}$	$3190 \pm 448^{\mathrm{B}}$
Apparent energy digestibility (%)			
Lucerne hay	$60 \pm 0.8^{\mathrm{A}}$*(**)	$62 \pm 2^{\mathrm{A}}$**	$59 \pm 2^{\mathrm{A}}$**
Oaten hay (from forage†)	$47 \pm 3^{\mathrm{AB}}$ ($40 \pm 3^{\mathrm{A}}$)	$46 \pm 2^{\mathrm{AB}}$	$48 \pm 0.3^{\mathrm{B}}$
DEI (kJ day^{-1})			
Lucerne hay	$2603 \pm 244^{\mathrm{A}}$***(***)	$4009 \pm 123^{\mathrm{B}}$***	$4324 \pm 304^{\mathrm{B}}$
Oaten hay (from forage†)	$837 \pm 67^{\mathrm{Z}}$($629 \pm 67^{\mathrm{Z}}$)	$1360 \pm 203^{\mathrm{Y}}$	$2908 \pm 387^{\mathrm{X}}$
DEI (kJ kg$^{-0.75}$day$^{-1)}$			
Lucerne hay	$641 \pm 27^{\mathrm{X}}$***(***)	$677 \pm 26^{\mathrm{X}}$***	$385 \pm 37^{\mathrm{Y}}$**
Oaten hay (from forage†)	$214 \pm 12^{\mathrm{X}}$($160 \pm 12^{\mathrm{Z}}$)	$226 \pm 30^{\mathrm{X}}$	$260 \pm 40^{\mathrm{Y}}$

$^{\mathrm{A,B}}P < 0.05$; $^{\mathrm{X,Y,Z}}P < 0.01$; within a row, means ± SEM bearing different superscripts differ significantly
*$P <$ 0.05, **$P <$ 0.01, ***$P <$ 0.001; asterisks indicate significant differences between diets within ages
†Apparent energy digestibility and DEI from forage was estimated assuming a milk-energy digestibility of 95% (see text)

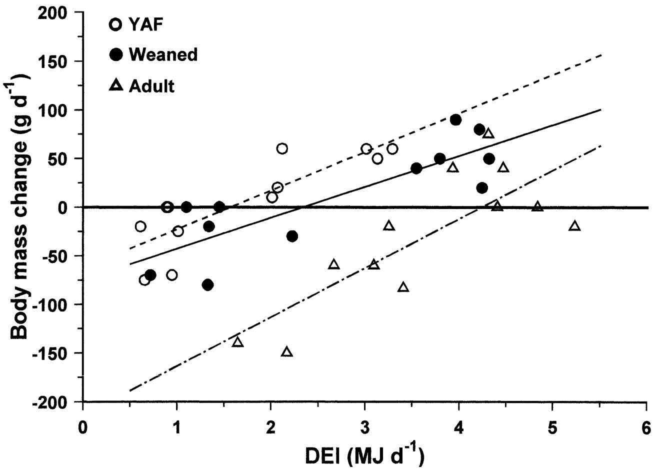

Fig. 2 Body mass change (g day^{-1}) as a function of digestible energy intake (DEI; MJ day^{-1}) by YAF, weaned and adult red kangaroos. *Dashed line* = YAF, $y=39.8x-62.7$ (±15.6), $r^2=0.72$, $F=25$, $DF=11$, $P<0.001$. *Solid line* = weaned, $y=31.9x-74.8$ (±19.5), $r^2=0.71$; $F=24$, $DF=11$, $P<0.001$. *Dash–dot–dash line* = adult, $y=50.5x-214.1$ (±46.2), $r^2=0.63$; $F=17$, $DF=11$, $P<0.001$

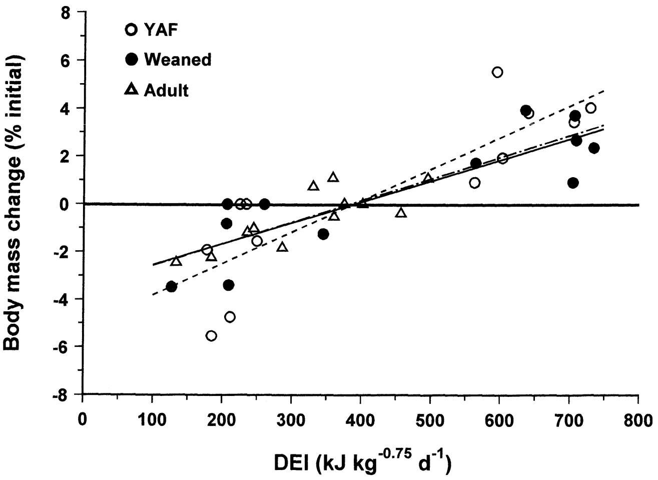

Fig. 3 Proportional change in body mass (% initial) as a function of allometrically related DEI (kJ kg$^{-0.75}$day^{-1}) by YAF, weaned and adult red kangaroos. *Dashed line* = YAF, $y=0.0132x-5.13$ (±1.19), $r^2=0.74$, $F=28$, $DF=11$, $P<0.001$. *Solid line* = weaned, $y=0.0088x-3.43$ (±0.84), $r^2=0.74$; $F=28$, $DF=11$, $P<0.001$. *Dash–dot–dash line* = adult, $y=0.0091x-3.49$ (±0.71), $r^2=0.65$; $F=19$, $DF=11$, $P<0.001$

growth (MER$_g$) were estimated as 2,957 kJ day^{-1}, some 70% of the MER of mature females. Moreover, weaned red kangaroos growing at 55 g day^{-1} would require 4,069 kJ digestible energy day^{-1}, or more than 95% of the MER of mature females. Therefore, the energy required for these growth rates (i.e. MER$_g$–MER) was 1,382 kJ and 1,724 kJ digestible energy day^{-1} for YAF and weaned red kangaroos, respectively, in addition to their MER. These requirements for growth are equivalent to 47% and 42%, respectively, of their total daily energy requirements (i.e. MER$_g$).

The allometrically related MER (kJ kg$^{-0.75}$day^{-1}) of YAF, weaned and adult female red kangaroos are compared in Fig. 3. Regression slopes relating proportional body mass changes (percent initial mass) as a function of DEI (kJ kg$^{-0.75}$day^{-1}) were not significantly different among the YAF, weaned and adult red kangaroos (YAF vs. weaned $t_{(2)}=1.5$, YAF vs. adult $t_{(2)}=1.3$, adult vs. weaned $t_{(2)}=0.1$; $DF=20$, $P>0.05$). No significant difference was found between the MER by YAF, weaned and adult kangaroos (YAF vs. weaned $t_{(2)}=0.3$, YAF vs. adult $t_{(2)}=0.2$, adult vs. weaned $t_{(2)}=0.1$; $DF=21$, $P>0.05$), the values being 389 kJ, 390 kJ and 384 kJ digestible energy kg$^{-0.75}$day^{-1}, respectively (Fig. 3). However, when growing on the chopped lucerne hay diets, the total daily MER$_g$ by the YAF and weaned red kangaroos were 639 kJ and 685 kJ digestible energy kg$^{-0.75}$day^{-1}, respectively; these values being 1.7–1.8 times the MER of the non-reproductive adult female kangaroos.

Discussion

Growth by the juvenile red kangaroos in this study was comparable to that previously reported for this species. Between the ages of 220 days and 400 days the juveniles accrued an average of 55 g body mass day^{-1}(Fig. 1), comparable with the 60 g day^{-1} growth rate reported for similarly aged red kangaroos under ideal conditions (Sharman et al. 1964; Frith and Calaby 1969). This study indicates that the energetic cost of growth may be the major reason for the higher RMR of juvenile red kangaroos compared with non-lactating adult females (Munn and Dawson 2001).

The daily energy budget of adult red kangaroos is largely unaffected by growth, although adults have daily costs associated with homeostasis and the maintenance of body mass. The MER (digestible energy) of the adult female red kangaroos in this study (384 kJ kg$^{-0.75}$day^{-1}) was 1.9 times their BMR (Dawson et al. 2000) and 16% lower than that previously reported for similarly sized male red kangaroos (456 kJ kg$^{-0.75}$day^{-1}, body mass 27–33 kg; Hume 1974). Male red kangaroos, however, continue to grow throughout most of their life, attaining maximum body masses of 70–80 kg by 15 years of age (Edwards 1990; Dawson 1995). Furthermore, Hume (1974) estimated MER indirectly, assuming zero energy balance was equivalent to zero nitrogen balance. This is likely the case in adult animals, but may lead to overestimates of MER in animals that are still growing. Hume's (1974) males were at a stage equal to a period of high growth (Dawson 1995) and consequently their MERs may have been overestimated. Our estimates of the MER of adult red kangaroos are applicable to fully grown non-lactating females. Notably, mature females are the predominant age/size class among red kangaroo populations (Dawson 1995) and our data are important for assessing the competitive grazing impacts of red kangaroos with other herbivores in Australia's arid rangelands.

The MERs (kJ day^{-1}) of the YAF and weaned red kangaroos were significantly lower than those by adult females, consistent with the juveniles' smaller absolute body sizes. However, the total daily MER_gs of the YAF and weaned red kangaroos were substantially increased above MER. For example, a 6-kg YAF growing at 55 g day^{-1} would need some 70% of the digestible energy needed by a 27-kg adult female at maintenance. By the time of final weaning, an 11-kg red kangaroo growing at the same rate would require as much as 95% of the MER of an adult female. In the YAF and weaned red kangaroos these energy requirements for growth amounted to 53% and 43%, respectively, of their DEI (kJ day^{-1}) on the chopped lucerne hay diets. Importantly, their growth-energy requirement of 25–31 kJ g^{-1} of body mass gain are not only due to the energy deposited as live tissue, but also an indication of the total energetic cost of growth by the young red kangaroos at a stage when growth rate is at its peak (Sharman et al. 1964).

The net energy deposited per unit of tissue can be assessed depending on the composition of the accumulated matter (Reeds et al. 1982; Robbins 1993). Water and ash, for example, contain no available chemical energy, but protein and fat average 23 kJ g^{-1} and 38 kJ g^{-1}, respectively (Withers 1992). Tribe and Peel (1963) estimated the body composition of nine red kangaroos, two of which were of an age/size comparable to the YAF red kangaroos studied here. Body composition of the two young red kangaroos (body masses 8.3 kg and 9.2 kg) was not very different from that of adult red kangaroos (body masses 18–72 kg), consisting of around 76% water, 1.6% ash, 21% protein and 1.3% fat (Tribe and Peel 1963). From the standard energy coefficients for protein and fat (Withers 1992), we estimate that YAF and weaned red kangaroos growing at 43 g day^{-1} and 55 g day^{-1}, respectively (Table 2), would have incorporated 228 kJ day^{-1} and 292 kJ day^{-1}, respectively. This is equivalent to an energy deposit of 5.3 kJ g^{-1} of increase in body mass, which is within the range found for most young growing mammals (4–13 kJ g^{-1}; Robbins 1993). This is also equivalent to a crude energy efficiency of growth (i.e. converted energy/DEI×100; Brody 1945) of 11.4% and 7.3% for the YAF and weaned red kangaroos, respectively, fed chopped lucerne hay. Green et al. (1988) reported that young tammar wallabies (*Macropus eugenii*) prior to permanently leaving the mother's pouch converted milk-energy into body tissue with efficiencies ranging between 23% and 36%, but lack of data on the energetic efficiency of growth in marsupials beyond pouch exit prevents comparisons with similarly sized kangaroos. Also, our estimates of crude energy efficiencies of growth are for caged animals under laboratory conditions and, as such, they are likely to be greater than those of wild juvenile kangaroos faced with additional thermoregulatory and locomotor costs. For comparison, the crude energy efficiencies of growth by domestic cattle range from 37% at 1 month to 9% by 10 months, by which time they are fully weaned (Brody 1945).

Our results show that the energetic cost of growth is the major factor contributing to the proportionally higher energy requirements of juvenile red kangaroos than of mature females, because the MERs (kJ digestible energy $\text{kg}^{-0.75}\text{day}^{-1}$) of YAF, weaned and adult female red kangaroos were not significantly different (Fig. 3). Therefore, exclusive of the energetic cost of growth, the minimal daily digestible energy requirements of juvenile red kangaroos were no higher, or lower, than expected for an adult marsupial of equivalent body mass. In this sense, juvenile red kangaroos could be considered as small adults, but ones that require considerable extra energy if they are to grow optimally.

That the allometrically related MERs (kJ $\text{kg}^{-0.75}$ day^{-1}) of the YAF and weaned red kangaroos were no different from those of adult females is contrary to the findings on minimal RMRs by Munn and Dawson (2001). Munn and Dawson (2001) reported that the RMR of YAF and weaned red kangaroos (body mass 6.6–10.8 kg) was 1.5–1.6 times that predicted for an adult marsupial of equivalent body mass. Given that there were no significant differences in the MER (kJ $\text{kg}^{-0.75}\text{day}^{-1}$) of the YAF, weaned and adult red kangaroos, these data indicate that the higher RMR of juvenile red kangaroos (relative to the BMR of adults) could be explained largely by an up-regulation of metabolism associated with growth. The time-scale for such adjustments is unclear, but our data suggest that it occurs within a week. After the YAF red kangaroos had completed their oaten hay trials and were returned to their normal ad libitum diet, they required 7–10 days to return to normal growth rates. Therefore, in the absence of tissue growth, the juveniles' metabolic rate is similar to that expected for an adult of their body size.

Clearly, the cost of growth plays an important role in the energy relations of juvenile red kangaroos. However, when faced with poor-quality, high-fibre forage (e.g. chopped oaten hay), growth by the YAF and weaned red kangaroos was compromised (Table 2) by low DEI (kJ day^{-1}) (Table 3). Given their higher energetic demands, the potential for nutritional stress to affect juvenile and adult red kangaroos differently during harsh environmental conditions is easy to appreciate. Also, the digestibility of fibrous forage is typically lower among small herbivores (Demment and Van Soest 1985; Cork 1994), further compounding the problems faced by juvenile red kangaroo when such low-quality vegetation predominates.

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