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Mechanistic explanations for juvenile kangaroo mortalities: broad implications for the population dynamics of large herbivores during climate change

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Mechanistic Explanations for Juvenile Kangaroo Mortalities: Broad Implications for the Population Dynamics of Large Herbivores During Climate Change

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Summary

Why do juvenile kangaroos die during drought? Answering this question is important because juvenile mortality typically drives whole population dynamics of large herbivores. To clarify reasons for the vulnerability of juveniles we investigated the ecophysiology of young red kangaroos (Macroopus rufus), Australia's largest marsupial herbivore. Compared with adults, juveniles had higher energy and water needs; these were related to requirements for growth and thermoregulation. Most importantly, juveniles could not maintain growth on poorer quality (high fibre) forage due to an inability to expand gut-fill. Adults could adjust gut-fill to compensate, thereby increasing their survivability in dry conditions when easily digestible, low-fibre forage is scarce. We have provided a specific mechanism linking juvenile kangaroo mortalities with food quality, which is in turn driven by rainfall and hence climate change impacts.

Introduction

The population dynamics large mammalian herbivores appear tightly linked with environmental factors, mediated largely through juvenile survival and recruitment [1-5]. Across a wide range of ungulates, for example, survivorship among "prime-aged" females (i.e. the main source of population fecundity) is generally high and stable, but
Energy and the cost of growth

An animal’s basal metabolic rate (BMR) describes its minimal energy requirements and is defined as the minimal resting metabolism of mature (i.e., not growing), non-reproductive, post-absorptive, non-stressed, wakeful animals in a thermoneutral environment and with minimal activity [12]. In common with most marsupials, adult red kangaroos have basal metabolic rates around 70% of those of comparable eutherians [13,14]. To some extent, the low BMR of marsupials may contribute to lower field-energy requirements, and this has been suggested as a reason for the ability of these mammals to inhabit Australia’s dry interior [15,16]. However, unlike adults, juvenile animals have additional energy demands associated with growth; how these additional demands may impact juvenile kangaroo survivorship is unclear.

In red kangaroos, growth rate peaks between the times when the young permanently leaves the mother’s pouch (ca. 250 days since birth) through until shortly after weaning (ca. 700 days). The focus of juvenile growth lies in energy growth has ongoing and unceasing. The closest available resting metabolic rate (RMR) with juvenile RMI is 50-60 g days of food was measured. The RMR of YA W 685 kJ-kg^{-0.75} 0.75, d^{-1} for marsupials, as close to 50-60 g-day, with 1% growth rate (Fig.

The burden of food required within their traditional energy intake allows the juveniles to maintain optimal body condition, a social and adult in the same time period. By the time the young permanently leaves the mother’s pouch, they are expected to be half of the initial body mass.
Weaning (ca. 360 days old). This stage of being a young-at-foot (YAF) is also the focus of juvenile mortality in red kangaroos during dry conditions. However, because of the growth-related metabolism of juveniles, it is difficult to determine their underlying energy needs compared with those of adults, or to quantify the impact that growth has on their daily energy/food requirements and its ecological consequences. The closest analogue to BMR in young mammals is a fasted resting metabolic rate (RMR) within a thermoneutral environment. Therefore, recent studies have examined juvenile RMRs per unit of body mass^{0.75}; a body mass exponent of 0.75 was chosen to evaluate these young herbivores as if they were small adults. On this basis, the RMR of YAF red kangaroos was measured as 1.5 times that expected for an adult marsupial of equivalent body mass [13; 17-19]. That is, an adult kangaroo of the same body mass as a YAF (7.4 kg) is predicted to have a RMR of approximately 200 kJ kg^{-0.75} d^{-1} [17-19], but YAF and weaned red kangaroos each had RMRs of near 300 kJ kg^{-0.75} d^{-1} [17].

Interestingly, the higher RMR of juvenile red kangaroos, relative to adults, does not translate into higher maintenance energy requirements (MER). An animal's MER refers to the daily energy intake needed simply to maintain body mass and, contrary to findings for RMR, there were no significant differences in the MERs of YAF, weaned and adult red kangaroos [20]. MER of all cohorts varied within the narrow range of 384-390 kJ kg^{-0.75} d^{-1}, but these estimates necessarily omitted the contribution of growth to daily energy requirements or intakes. When the cost of growth was taken into account, juveniles did indeed have higher food requirements (Fig. 2), compared with adults, in order to maintain ideal growth rates [20]. To sustain ideal growth rates of 50-60 g day^{-1} [20-22] the YAF and weaned red kangaroos had daily energy requirements that were 1.7-1.8 times the MER of mature, non-lactating females (639 kJ and 685 kJ kg^{-0.75} d^{-1}, respectively, for YAF and weaned kangaroos, as against 384 kJ kg^{-0.75} d^{-1} for mature females). Therefore, because there was no difference in the MERs of YAF, weaned and adult red kangaroos, the higher resting metabolic requirements of the juveniles can be explained largely by their additional energy requirements for growth (Fig. 1).

The burden of growth for juvenile red kangaroos has a major impact on their daily food requirements and hence their ecology. For example, to sustain ideal growth rates within their thermoneutral zone, YAF red kangaroos would require total daily digestible energy intakes (kJ d^{-1}) approaching 70% of that required by mature, non-lactating females, despite being only 20-25% of the adult's body mass. Moreover, during dry conditions, and especially drought, the mother's lactation usually declines, rendering the juveniles more dependent on forage. By weaning, the young red kangaroos require as much as 95% of the daily energy intake (kJ d^{-1}) of mature females if they are to maintain optimal growth, though they are still only half the body mass of mature females [20].

Additional to energy needs for RMR and growth are those associated with free living, which must also be taken into account when comparing the ecology of juvenile and adult animals. In particular, the energetic costs for thermoregulation may be expected to be higher for the smaller juvenile red kangaroos as compared with adults. By the time the young kangaroo exits the mothers pouch permanently it is less than 1/3 of the mature female body mass, but it must contend with the same environmental
conditions experienced by larger, adult animals. A small body size has distinct disadvantages with regard to thermoregulation because of a higher surface area to volume ratio. In short, smaller animals lose relatively more heat to the environment under cold conditions, and also potentially suffer greater external heat loads at ambient temperatures above deep body temperature.

Could water be limiting juvenile survival?

In their arid environment, red kangaroos routinely experience environmental temperatures in excess of their deep body temperatures. Adult animals are known to adjust their behaviour accordingly at high environmental temperatures as a means of reducing water requirements for thermoregulation. For example, red kangaroos are largely nocturnal, foraging at night and at dusk and dawn [23]. By limiting activity during the day red kangaroos minimise their overall water use during dry conditions. This is also seen among juvenile kangaroos [24]. Despite these behavioural adjustments, juvenile red kangaroos may be expected to have a greater water debt during dry conditions compared with adults. Under warm conditions for example, when ambient temperatures approach deep body temperature (ca. $T_d$ 33°C), both YAF and weaned require water as seen in their $T_d$ range 25°C to 37°C. Under very hot conditions, licking the ventral body surface to cool down, increase water loss levels (range: 1-2 mmol·kg$^{-1}$·day$^{-1}$) [25]. Despite the high $T_d$ 45°C, both adult and weaned kangaroos appear to cope well with the very hot conditions, having abilities to maintain core body temperatures.
weaned red kangaroos are unable to maintain their body temperature at basal levels as seen in adults [17]; juveniles' \( T_b \) increased from basal levels of 36.9 ± 0.2°C at \( T_a \) 25°C to 37.7 ± 0.2°C at \( T_a \) 33°C. To prevent further overheating under these warm conditions, YAF and kangaroos evaporated around 14 mL H\(_2\)O-h\(^{-1}\) by panting and/or licking the body surface (mainly the forelimbs, legs, belly, and tail). Under similarly hot conditions, adult kangaroos on the other hand were able to maintain \( T_b \) at basal levels (range 36.3 ± 0.2°C to 36.5 ± 0.2°C) and evaporated around 25 mL H\(_2\)O-h\(^{-1}\). This level of water loss by adults was only around 1.8 times more than that of juveniles, despite the adults being more than three times larger than YAF. Under hot conditions, \( T_a \) 45°C, such as are routinely experienced by kangaroos in arid regions, both YAF and weaned red kangaroos evaporated an amount of water similar to that of adults, with the values ranging between 79 mL and 84 mL H\(_2\)O-h\(^{-1}\). This level of thermoregulatory water loss by the juvenile kangaroos could have profound implications for their abilities to survive during dry conditions.
Adult red kangaroos drink infrequently and even during summer median return to water is about a week [24-25]. However, being smaller than adults, juvenile kangaroos have smaller absolute body-water reserves and under hot conditions they should need to drink more frequently than adults, especially in light of their high water use for thermoregulation. While still suckling, the water in their mother’s milk could ameliorate water losses by YAF kangaroos, but lactation is declining at this time and even may be prematurely shutdown during drought [26-28]. This means that YAF and weaned red kangaroos may be more dependent on water points, where predators focus and food is sparse. Notably, in one study, 97% of the red kangaroos killed by dingos around watering holes were juveniles [29]. Although adult red kangaroos, and presumably YAF, do not show water focussed grazing, they must travel to and from water sources from their distant home ranges [30] and thus if juveniles access water more frequently than adults they may incur high travelling costs (e.g. [31]).

Food limitation and nutrition: quantity or quality?

Primarily grass-eaters, adult kangaroos are able to utilise fibrous vegetation by fermentative digestion in a large forestomach, in a manner analogous to digestion in ruminants [32-38]. However, in form and function, the tubiform foregut of kangaroos is more like that of the equine colon rather than the vat-like structure of ruminants [37]. It has been suggested that the tubiform foregut in kangaroos contributes to their ability to persist on relatively fibrous grasses compared with ruminants [37-38], but red kangaroos do prefer fresh green growth and focus foraging on this when possible [39]. Moreover, recent work suggest that the ability of adult red kangaroos to persist better on poor-quality forage as compared with sheep may be related more to the kangaroos’ lower overall energy requirements [40]. The extent to which the relatively higher daily energy requirements (kJ.kg⁻⁰.⁷5.d⁻¹) of juvenile kangaroos might impact on their body condition in the face of decreased food quality is uncertain, but they certainly perform better (e.g. sustain ideal growth) on more nutritious forage [20].

Young, fresh plant growth is generally more nutritious than mature, dry forage. Young plant growth contains higher proportions of easily digestible cell contents relative to the less digestible structural carbohydrates of cellulose and hemicellulose, i.e. fibre [41-42]. Fresh plant growth is also higher in protein (nitrogen) compared with mature forage. Juvenile red kangaroos appear particularly reliant on fresh, high-quality forage [43]. For example, measured as an index of plant “greeness”, and hence age [43], or directly as nitrogen or fibre content [11], forage quality was found to be the best predictor of body condition in red kangaroos in arid regions of western NSW. This was especially so for juvenile red kangaroos and particularly for young males. During dry conditions production of fresh green herbage declines and is quickly eaten out. In drought mature fibrous grasses can make up over 90% of the adult red kangaroos’ diet [39]. The limited extent to which juvenile red kangaroos appear able to utilise fibrous grasses suggests that food quality, and not just quantity is important (e.g. [44]).

Forage quality is typically discussed in terms of the level of plant fibre because mammalian enzymes cannot readily break down these fibre fractions. The digestion of fibre requires fermentation by specialised microbes, usually in expanded regions of
an return to the kangaroos should need ater use forild ameliora- and even YAF and diators focus d by dingos nos, and pre- o and from access water 1).

vegetation by digestion in f kangaroos f ruminants ates to their 37-38], but en possible os to persist to the a relatively t impact on, a, but they rage [20]. dry forage. ) contents ul-cellulose, ) compared fresh, high-ness", and was found of western for young d is quickly d adult red appear able s important we because e digestion l regions of the fore- or hind-gut [45]. Small herbivores, however, have smaller absolute gut sizes relative to their metabolic needs and necessarily have faster rates of feed passage [46-48]. Compared with larger animals, material ingested by smaller herbivores is exposed to microbial action for a shorter period, thereby lowering digestive efficiency (i.e. nutrient extracted per unit feed ingested). Consequently, fibre digestion is believed to be less efficient among smaller herbivores [48]. It has been suggested that the smaller body/gut size and comparatively fast food passage might explain the lesser ability of juvenile red kangaroos to cope with the fibrous forage available during droughts. However, using the most reliable inert markers to measure food passage in juvenile and adult kangaroos [49], the situation was found to be more complex.

When offered high-quality forage of chopped lucerne hay containing about 44% neutral-detergent fibre (NDF; see [49]), overall food passage rates were similar for YAF, weaned and mature female kangaroos (Fig. 2). The mean retention time (MRT) of particles in the gastrointestinal tract, for example, varied between 25 h and 22 h for YAF and weaned kangaroos, respectively, and 29 h for mature females [49]. As expected, digestion of NDF (% digestibility) was lowest for the smaller YAF (27%), followed by weaned (34%) and then mature female (40%) kangaroos, but total dry matter (DM) digestion of chopped lucerne was similar for all age classes, varying within the narrow range of 55-59%. Notably, this level of DM digestion was comparable to that seen in mature male red kangaroos fed similar forage [34]. Moreover, on high-quality forage the YAF and weaned kangaroos showed food passage rates comparable to those of larger adults. Notably, the YAF were capable of maintaining ideal growth rates when offered high-quality lucerne even when they did not receive any milk, which they would normally be still taking at this stage of development. However, on a poor-quality diet of chopped oaten hay (Avena sativa) containing ca.

<table>
<thead>
<tr>
<th>Gut-fill (g DM)</th>
<th>YAF</th>
<th>Weaned</th>
<th>Adult</th>
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<tbody>
<tr>
<td>Lucerne hay</td>
<td>121.6 ± 20.8B</td>
<td>158.6 ± 23.6B</td>
<td>264.0 ± 23.7A*</td>
</tr>
<tr>
<td>Oaten hay</td>
<td>113.9 ± 22.9B</td>
<td>150.7 ± 43.3B</td>
<td>426.5 ± 25.5A</td>
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<th>Gut-fill (g DM kg⁻¹)</th>
<th>YAF</th>
<th>Weaned</th>
<th>Adult</th>
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</thead>
<tbody>
<tr>
<td>Lucerne hay</td>
<td>18.4 ± 2.8B</td>
<td>14.8 ± 2.0B</td>
<td>10.6 ± 1.5A</td>
</tr>
<tr>
<td>Oaten hay</td>
<td>18.0 ± 3.4A</td>
<td>13.5 ± 3.2A</td>
<td>16.8 ± 0.8A</td>
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<tr>
<th>Gut-fill (g DM kg⁻0.75)</th>
<th>YAF</th>
<th>Weaned</th>
<th>Adult</th>
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<tbody>
<tr>
<td>Lucerne hay</td>
<td>29.4 ± 4.5A</td>
<td>26.7 ± 3.7A</td>
<td>23.7 ± 2.8A</td>
</tr>
<tr>
<td>Oaten hay</td>
<td>28.5 ± 5.4A</td>
<td>24.6 ± 6.2A</td>
<td>37.7 ± 1.5A</td>
</tr>
</tbody>
</table>

Means ± SEM bearing different superscripts are significantly different within diets between ages (A,B,C p < 0.05). Stars (*) associated with lucerne hay diets indicate significant differences between diets within ages (p < 0.01). After [49].
68% NDF, the situation was very different.

On chopped oat hay neither the YAF nor weaned kangaroos could maintain growth, and both age classes lost body mass on this fibrous forage. The smaller YAF kangaroos were least capable of digesting NDF from oat hay, at only ca. 18%, followed by the weaned (23%) and mature female (27%) kangaroos. Overall, the digestibility of DM from the oat hay was lowest for the YAF, which digested only 34% DM, significantly less than the 42% digested by weaned and mature female kangaroos. That the weaned kangaroos were capable of digesting the fibrous oat hay with as much efficacy as that of mature females is important because it indicates that overall extraction of nutrients (using DM as proxy) by the smaller juveniles is comparable that of adults despite large differences in their body masses; weaned kangaroos being around 10-12 kg compared with mature females of 25-30 kg and males of 60-70 kg. This result is somewhat contrary to that expected based on the smaller body size and apparently faster rates of feed passage in smaller herbivores. Indeed, on the chopped oat hay forage the MRTs of particles in YAF, weaned and mature female kangaroos were not significantly different from one another, and ranged from 30 h to 35 h (Fig. 2). The question arises then, why then do the recently weaned animals (as well as YAF whose milk will likely have been cut off) still show high mortalities during drought? The answer lies with total gastrointestinal capacity, or gut-fill.

Using calculations of DM gut-fill based on forage digestibility and particle MRTs [50], the smaller juveniles were found to be limited in their capacity to expand the gut to accommodate poorer quality forage [49]. On both poor (oat hay) and high (chopped lucerne) quality forages YAF and weaned kangaroos had levels of gut-fill of around 25 – 30 g DM kg\(^{-0.75}\) (Table 1). This level of fill was similar to that of mature females on chopped lucerne hay at 24 g DM kg\(^{-0.75}\). However, on the poor quality forage the mature female kangaroos were capable of expanding total gut fill by 1.6 times (g DM-kg \(^{0.75}\); Table 1). Adult female red kangaroos, therefore, were able to respond to the decline in forage quality simply by increasing the total nutrient load within in the gut. Juveniles, on the other hand, appeared limited by their absolute gut capacity. Even on high quality forages the juvenile red kangaroos apparently maximised gut fill in order to extract sufficient nutrients to maintain growth. This is particularly important in light of the fact that in order to sustain growth the juvenile red kangaroos required around 1.8 times as much energy each day per unit body mass\(^{0.75}\) as did mature females. Notably, even on the poor-quality forage the mature female kangaroos were able to maintain their body mass.

At the scale of the individual, juvenile red kangaroos therefore may be expected to employ different foraging strategies from adults. At the least, juvenile red kangaroos require forage with less than 40–50% fibre (NDF) to sustain growth. Under good environmental conditions this may not be a problem. Juveniles could satisfy their requirements by feeding on highly nutritious, fresh plant growth. However, during dry conditions, when feed quantity and quality are reduced, juveniles may be required to spend more time foraging, searching out high-quality feed and thereby increasing predation and thermal risks. It is not immediately known whether YAF and adult red kangaroos differ in their behavioural responses to changes in vegetation, but such differences could be important for understanding the vulnerability of juveniles during drought.

Dealing with Drought

For example, red kangaroos may be viewed as very adaptable and flexible feeding in the environment to ensure survival, but are there ecologic or management implications for improving the survival of this species?

The most immediate adaptations of red kangaroos to the environment are their feeding habits, their ability to reduce body weight during drought, and their high reproductive rate. All these adaptations are reflected in the current population dynamics of red kangaroos, which are dominated by high juvenile survival rates in the absence of food or water. This suggests that the current population is not limited by the availability of food or water, but by the ability of juveniles to survive and grow into adults.

This knowledge can be used to improve the management of red kangaroos, both in the wild and in managed environments. For example, the use of supplementary feed can help to maintain the population during times of drought, but this should be done in a way that does not encourage the population to rely on human-provided food sources. This can be done by providing food in a manner that mimics natural foraging behavior, such as by providing food in natural habitats or by using meat that is less palatable to the animals.

Reference

For example, sub-adult red kangaroos spend more time searching for feed and less time chewing than mature males or females [24]. Nonetheless, the inability of the small, young animals to further expand gut-fill as forage quality declined appears to be the main difference in the capacity of juveniles and adult kangaroos to utilise fibrous forage. In this sense, juvenile red kangaroos appear limited not by how well they can process poor quality forage, as predicted from theory [48], but by how much they can process.

Dealing with climate change: a mechanistic approach

The most likely immediate causes of juvenile kangaroo mortalities during drought are dehydration and malnutrition [51]. The findings presented here have provided specific information about how juvenile kangaroos’ physiology interrelates with their environment to affect their survival; especially with regards to rainfall and its affect on food quality. However, recent work indicates that the rainfall-population dynamic in red kangaroos is more complex than originally thought [52-53]. Clearly, a mechanistic explanation for the survival or mortality of juvenile red kangaroos is essential for improving our understanding of kangaroo population dynamics, particularly in the face of environmental changes. Extensive literature cites the importance of juveniles in the ecology of large herbivore species (see reviews by [3-5]), but practical application of this information relevant to climate change is largely lacking. More information is needed to fully appreciate how juvenile mortality among large herbivores is influenced by environmental conditions (but see also [54]). Even with the extensive red kangaroo dataset presented here, the picture is far from complete. For example, what are the costs of juvenile locomotion relative to adults? How well can juveniles manage short-term water restriction? Even simple information on water turnover and field metabolic rate are lacking for juveniles of most large mammalian herbivores. This knowledge gap must be narrowed if we are to properly assess and predict the potential impacts of climate change on large mammalian herbivores, many of which are ecologically, culturally and economically important worldwide [55-56].

References


young, tooth eruption and age determination in the red kangaroo, _Megaleia rufa_.


