

## The effects of lactation on the feeding behaviour and activity patterns of free-ranging female koalas (*Phascolarctos cinereus* Goldfuss)

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### Abstract

The free-ranging feeding behaviour and activity patterns of three lactating and two non-lactating female koalas (*Phascolarctos cinereus*) were investigated using acoustically sensitive radio-telemetry. Lactating females were found to consume more leaf material, masticate more per leaf and at a greater rate, and perform more ingestive and merycism mastications per 24 h than non-lactating females. Results suggest that female koalas are 'income breeders' that compensate for the higher energetic demands of lactation by increasing intake and, to a lesser degree, investing more in each mouthful so as to produce a shift in digesta particle size distribution in favour of more finer particles. Compared with non-lactating females, lactating female koalas were also found to spend more time moving within trees, feeding per 24 h and per bout, and less time resting and sleeping per 24 h, although the proportion of active time spent feeding was similar (~80%). This implies that female koalas adopt a 'time minimizing' strategy whereby activity budgets respond to current requirements. Lactation-compensation mechanisms are compared with those reported for koalas with high tooth wear, and the capacity of aging female koalas to compensate for lactation are discussed.

### Introduction

For most mammals, lactation results in large increases in energy requirements (Gittleman and Thompson 1988) and is not only considered the most costly component of reproduction, it is also regarded as the most energetically expensive life-history event (Thompson 1992). Furthermore, other concurrent nonlactational consequences of dependency such as infant care, transportation and thermoregulation can impose additional costs (Price 1992; McLean and Speakman 1997; Sanchez *et al.* 1999).

Female mammals have been found to compensate for these increased energetic and nutrient requirements through a combination of physiological and behavioural mechanisms. Most commonly, the extra requirements of lactation are met by increased food intake (e.g. ruminants: Weston 1988; non-ruminating foregut fermenters: Cork 1991; marsupial carnivores: Green *et al.* 1988; omnivorous primates: Nievergelt and Martin 1999). However, a reduction in levels of activity and metabolism (Racey and Speakman 1987; Mellish *et al.* 2000) and the utilisation of previously stored energy reserves (Oftedal 1993; Bowen *et al.* 2001) have also been identified as important mechanisms in some animals. Depending on the degree to which the maternal investment strategy emphasises either short-term adjustment of food intake or fat reserve utilisation, mammals are considered respectively as either 'income' or 'capital' breeders (Stearns 1989).

Koalas (*Phascolarctos cinereus*), are small-medium sized (>15 kg) arboreal folivores that feed almost exclusively on a eucalyptus diet (Pratt 1937) that is high in fibre and low in available nutrients and energy (Cork and Sanson 1990). The poor quality of this diet, compounded with the allometric constraints of small body size (Demment and Van Soest

1985) are likely to affect and even limit the amount of energy available for reproduction in koalas. Although the total metabolisable energy requirements for reproduction are similar to those of other mammals, the mass-specific daily rate of energy transfer to the young is the lowest recorded in a mammal and the lactation period over which energy is transferred is 58% longer than is predicted for a mammal of their mass (Krockenberger *et al.* 1998).

Koalas are inactive animals, spending most (80–85%) of the time resting and sleeping (Nagy and Martin 1985; Mitchell 1990; Logan and Sanson 2002a). Inactivity and low metabolic requirements are thought to allow koalas to conserve energy and contribute substantially to their ability to utilise such a poor-quality diet (Cork and Sanson 1990). Moreover, male koalas spend most (65–85%) of their active time feeding (Logan and Sanson 2002a), and female koalas are considered to be even less active than males (Mitchell 1990). Consequently, it is unlikely that female koalas could offset the increased energy costs of lactation by reducing the levels and the costs of other non-feeding activities. In addition, koalas do not carry substantial fat reserves (Degabriele *et al.* 1978; Ellis and Carrick 1992) and are therefore likely to adopt an 'income' strategy, whereby the extra energetic costs associated with lactation are met largely by increases in food consumption, feeding effort and time allocation to feeding.

The aim of this study was to investigate the effects of lactation and juvenile dependency on the feeding behaviour and activity patterns of free-ranging female koalas.

## Methods

### *Study site*

The 25-ha study site was located in coastal manna gum woodland on the south-west side of Raymond Island, approximately 300 km east of Melbourne, Australia (38°55'S, 147°45'E). The low, open vegetation was dominated by coastal manna gum (*Eucalyptus pryoriana*) with a thick understorey of bracken fern (*Pteridium esculentum*). *Banksia serrata*, *B. integrifolia*, *Acacia longifolia* and *Exocarpos cupressiformis* were also present, and, although rarely consumed, they provide more shade than manna gums and were frequently used on hot days.

The investigation took place during November 2000, in which the average minimum and maximum temperatures were 16°C and 31°C respectively. As a result of a dry winter and spring, the flush of new leaves did not occur until late December 2000, and thus only mature manna gum foliage was available. The breeding season of Victorian koalas usually begins in October and extends through to late February. Young are born from November to March and they emerge from pouches from June to November (McNally 1957; Martin and Handasyde 1990). November was selected as the time in which females with relatively small back-young (those that breed late the previous season), and thus in peak lactation (Krockenberger *et al.* 1998), as well as females that had not yet mated in this season, could be readily encountered. Furthermore, the weather conditions during October (high winds and heavy rains) would be considered unfavorable for acoustic telemetry.

Three female koalas accompanied by small back-young and two unaccompanied adult female koalas were captured using the methods described by Lee and Martin (1988). Upon capture, each individual was weighed (adult females to  $\pm 50$  g, back-young to  $\pm 10$  g). The two non-lactating and three lactating females weighed 9.4, 8.3, 8.7, 8.0 and 9.5 kg respectively. Back-young weighed 1.3 kg ( $\pm 0.3$ , s.d.) and were estimated (based on Martin 1985) to be ~250–300 days old, the age at which Krockenberger *et al.* (1998) associated the greatest lactation load. The degree of tooth wear of adults was also assessed (following the descriptions of Martin (1981) and Lanyon and Sanson (1986)) to ensure that all females had the same level of wear (Wear Class 2) after Logan and Sanson (2002a, 2002b) found that tooth wear had the potential to affect the feeding behaviour and activity patterns of koalas. Each adult was fitted with a collar containing an acoustically sensitive audio-transmitter (Greager *et al.* 1979; Lentle *et al.* 1998; Logan and Sanson 2002b) before being released back into the tree from which it had been captured. Pouch inspections suggested that the two non-lactating females had previously bred, and both were subsequently found to have back-young in November 2001. Krockenberger *et al.* (1998) noted that females that had the longest lactation periods failed to breed in the following season. Regular trips to Raymond Island from 1999 to 2001 revealed that many females still had back-young well into February (perhaps attributable to the extended dry period).

Microphone transmissions were initially monitored using a Uniden Bearcat (66–512 MHz, 1k) scanner and hand-held Yagi antenna. Animals were released within 10 min of capture, and their recovery and wellbeing periodically monitored for 72 h thereafter. During this time, the various sounds transmitted by the collar were calibrated against behavioural activities of the koalas. Thereafter, each individual was randomly allocated to 2 of the next 10 days, during which the sounds that it made over a continuous 24-h period (commencing at 17:00 hours) were recorded onto the audio channel of three sequential, 5-h stereo HiFi BASF video-cassette tapes (to enable extensive recording periods – up to 10 h), using a long-play, Panasonic stereo HiFi VCR via a Uniden Bearcat (66–512 MHz, 1k) scanner attached to a Discone wide-band, omni-directional antenna raised to 5 m. A concurrent video time-stamp was provided by an IR CCD camera focused on a small stopwatch. The VCR, camera and scanner were powered by one of three Century 86T deep-cycle batteries in a charge/discharge rotational cycle, via a 140-W inverter. Daily (24-h) recording sessions in which the maximum ambient temperature exceeded 30°C or that contained either rain or high winds were abandoned and further postponed for an additional day because Watson and Dawson (1993) and Lentle *et al.* (1998) highlighted the influences of weather conditions on the feeding behaviour of free-ranging herbivores. Initially, three lactating and three non-lactating female koalas were collared; however, equipment failure prevented sound transmission from one of the non-lactating females and thus reduced the sample size of the controls to two.

At the conclusion of the investigation, individuals were recaptured, weighed and the collar removed. All individuals and young had either maintained or slightly gained weight.

The VCR tapes were played back in real time through an AV amplifying monitor. In-house software (written by M. Logan), synchronised to the playback, permitted each audibly recognisable event (such as an ingestive mastication) to be digitally flagged, along with the exact time and date at which the event occurred. Ingestive and merycism mastications were distinguished following the descriptions of Logan (2001).

#### *Feeding behaviour*

The resulting digital data were subsequently manipulated to calculate the following feeding parameters per animal per day (24 h): number of leaves consumed, ingestive mastications per bite, total number of ingestive mastications, ingestive mastication rate, total number of merycism mastications, merycism mastication rate and the leaf-consumption rate. Observations indicated that koalas ingested only one leaf at a time. Hence, the total number of leaves consumed per animal per 24 h was calculated as the number of biting (excising) sounds detected. Likewise, the total number of ingestive mastications per animal per 24 h was calculated as the number of ingestive mastication sounds detected for that period. The number of ingestive mastications per leaf was calculated by dividing the number of biting sounds per animal per day by the total number of ingestive mastications for that period. Mastication rates (ingestive and merycism) were determined by first calculating the time elapsed (in milliseconds) between the start of two consecutive mastication events. The mastication rate (mastications  $s^{-1}$ ) for each 24-h session was then calculated by taking the reciprocal of the average of each of the individual intra-mastication intervals over that period, excluding those intervals that exceed 5000 milliseconds in duration. Finally, the average mastication rate (mastications  $s^{-1}$ ) per animal per 24 h was calculated. Leaf-consumption time was defined as the time (in seconds) that elapsed between two consecutive bite events that were no more than 60 s apart. The average leaf-consumption time was hence calculated for each individual per 24 h. Each of the feeding performance parameters was subsequently expressed as an average for the two 24-h recording sessions for each animal.

#### *Activity patterns*

Events were divided into five activity categories: feeding (defined by chewing, biting and other food-procurement sounds); moving within a tree (defined by climbing sounds), walking on the ground between trees (defined by walking, running sounds), resting (defined by the presence of regular wakeful sounds such as head/limb movements, scratching, vocalising) and sleeping (defined by the presence of breathing sounds and absence of all other major wakeful sounds for a period of at least 5 min). An additional category, 'inactive', which combined resting and sleeping was subsequently added.

The start and finish of categories were marked by the presence of defining sounds and the absence of defining sounds for a period of more than 5 min respectively. Hence the timing and duration of each activity was recorded. In the event that two or more categories co-occurred, the category recorded was determined on the basis of a rarity hierarchy (walking–moving–feeding–inactive–sleeping), in which walking was the rarest and was given highest priority.

A feeding bout was defined as a continuous block of feeding sounds that were not interrupted by more than 5 min of either resting or sleeping sounds, and thus feeding-bout lengths were calculated as the number of minutes elapsed within each feeding bout for each 24-h period. Feeding-bout lengths, as well as the amount of time spent feeding, inactive and sleeping were then expressed as the average amounts of time (in hours) spent per 24 h for each of the two continuous, non-consecutive 24-h recording sessions for each individual. The amounts of time spent moving and walking were expressed as the average amount of time (in minutes) spent per 24 h for each of the two continuous, non-consecutive 24-h recording sessions for each individual.

#### *Home range*

Throughout the 18-day period, the five koalas (and three back-young) were routinely located by orienting a hand-held Yagi antenna towards the direction of greatest signal strength and progressively de-tuning a Uniden Bearcat (66–512 MHz, 1k) scanning receiver on approach. All individuals were located once per day between 08:00 and 09:00 hours for 18 consecutive days for home-range analysis. Animal locations were determined by estimating the position ( $\pm 5$  m) within a 1000  $\times$  1000 m reference grid with 50-m increments. To determine tree use, individuals were also relocated when the sound signals indicated a change of tree.

#### *Data analysis*

Separate or pooled variance *t*-tests were performed as appropriate to determine the effect of lactation and juvenile dependency on the (scaled to metabolic weights) mean number of ingestive mastications, mean number of leaves consumed, mean number of ingestive mastications per bite, mean ingestive mastication rate (mastications  $s^{-1}$ ), mean number of merycism mastications, mean merycism mastication rate (mastications  $s^{-1}$ ) per 24 h, and mean amount of time spent on each activity per 24-h period. All analyses were carried out using R (Ihaka and Gentleman 1996) and at a significance level (*P* value) of 0.05. Home ranges were calculated using a 95% minimum convex polygons (CALHOME software: Kie *et al.* 1994). Incremental area analysis confirmed that the number of fixes (18) were adequate to describe the home ranges of each of the female koalas.

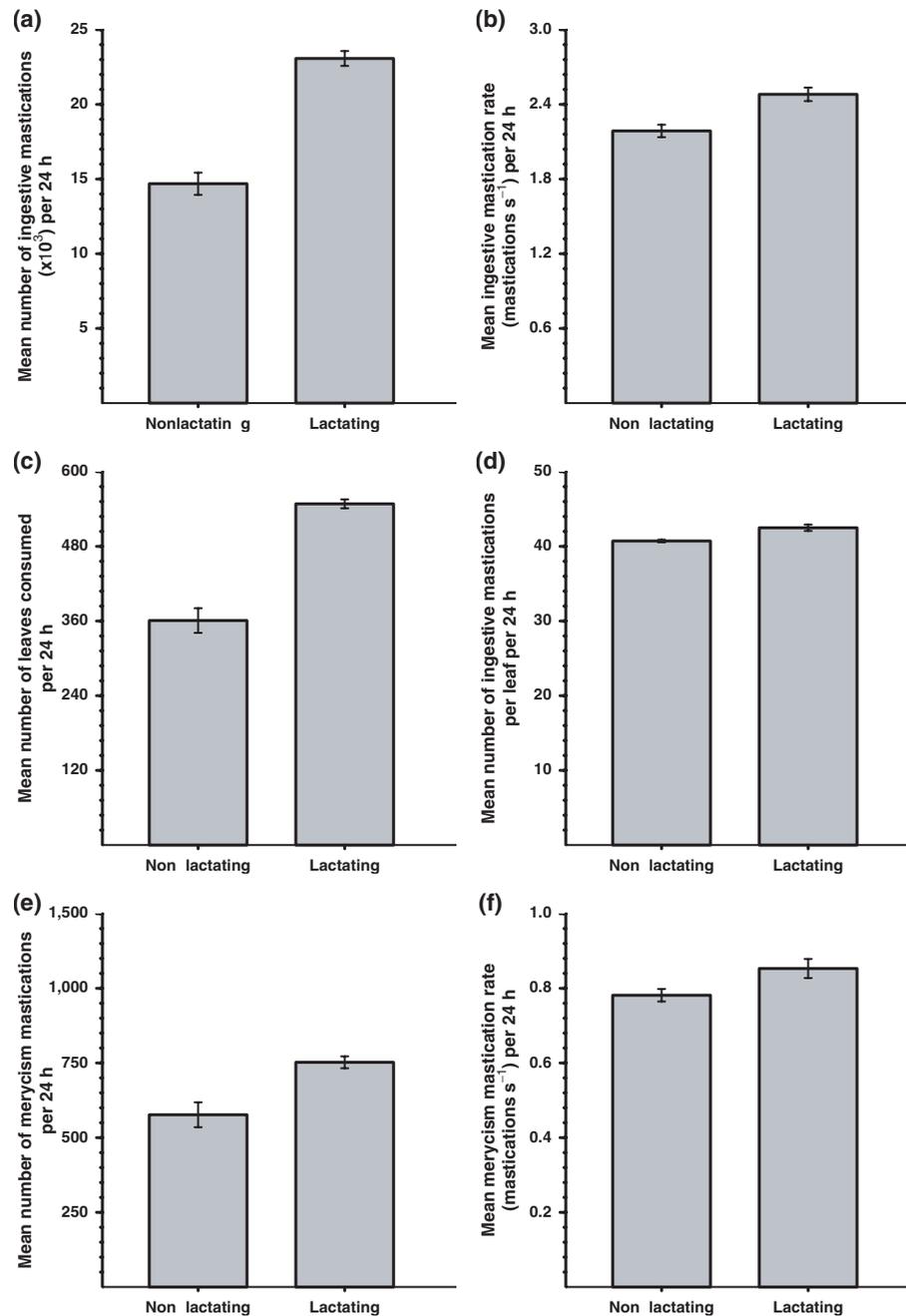
### **Results**

Females with a dependent young were found to consume 51% more leaves per 24 h ( $t_3 = 8.92$ ,  $P = 0.011$ ), masticate 4.5% more per leaf ( $t_3 = 3.19$ ,  $P = 0.047$ ), perform 57% more ingestive mastications per 24 h ( $t_3 = 10.26$ ,  $P = 0.002$ ) and at a 13.4% greater rate ( $t_3 = 3.72$ ,  $P = 0.034$ ) than females without a dependent young (Fig. 1*a–d*). They were also found to perform 30.4% more merycism mastications per 24 h ( $t_3 = 6.86$ ,  $P = 0.006$ ) than those females without young (Fig. 1*e*); however, no significant differences were found between the rate (mastications  $s^{-1}$ ) at which females with and without dependent young performed the merycism mastications ( $t_3 = 2.03$ ,  $P = 0.1356$ ) (see Fig. 1*f*). The ratio of ingestive mastications to merycism mastications was found to be significantly higher in lactating females than in non-lactating females ( $t_{2,81} = 4.31$ ,  $P = 0.026$ ), indicating that the increase in the number of merycism mastications associated with lactation was proportionally lower than the increase in the number of ingestive mastication.

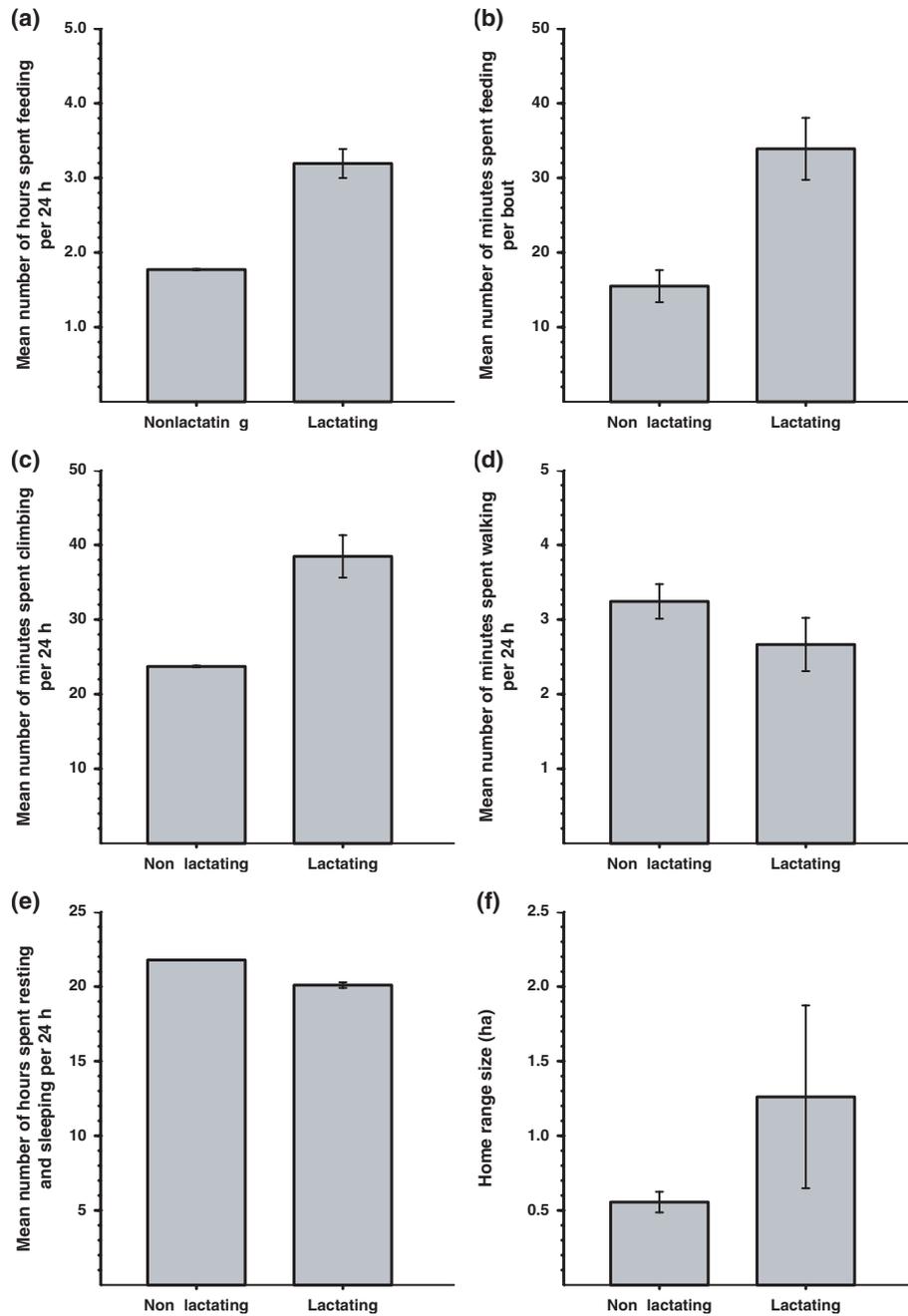
Lactating females were found to spend 80.2% more time feeding per 24 h ( $t_{2,26} = 4.85$ ,  $P = 0.031$ ), 118.8% more time feeding per feeding bout ( $t_{2,82} = 3.93$ ,  $P = 0.032$ ), 62.2% more time climbing within trees per 24 h ( $t_{2,01} = 5.19$ ,  $P = 0.035$ ), and 8.37% less time resting and sleeping per 24 h ( $t_{2,01} = 8.92$ ,  $P = 0.012$ ) than non-lactating females (Fig. 2*a–d*). The amount of time spent walking on the ground and range sizes were not found to differ significantly between lactating and non-lactating females (Fig. 2*e, f*).

### **Discussion**

Herbivores derive most of their energy from plant material either through the endogenous breakdown of cell contents (Keys *et al.* 1969) or via the microbial fermentation of cell walls (Prins and Kreulen 1990). Before the cell contents can be utilised, they must first be



**Fig. 1.** The effect of lactation on the mean ( $\pm$ s.e.) (a) number of ingestive mastications per 24 h, (b) ingestive mastication rate (mastications per second) per 24 h, (c) number of leaves consumed per 24 h, (d) number of ingestive mastications per ingestive leaf per 24 h, (e) number of merycism mastications per 24 h, and (f) merycism mastication rate (mastications  $s^{-1}$ ) per 24 h. Means were calculated from the mean feeding parameters of two continuous, non-consecutive 24-h recording sessions for each of the three lactating and two non-lactating females.



**Fig. 2.** The effect of lactation on the mean ( $\pm$ s.e.) (a) number of hours spent feeding per 24 h, (b) number of minutes spent feeding per bout of feeding per 24 h, (c) number of minutes spent climbing within trees per 24 h, (d) number of minutes spent traveling on the ground between trees (walking) per 24 h, (e) number of hours spent resting while awake and sleeping per 24 h, and (f) home-range size (ha). For (a)–(e) means were calculated from the mean parameter timings of two continuous, non-consecutive 24-h recording sessions for each of the three lactating and two non-lactating females.

released from the obstructive cell wall. In hindgut fermenters, in which digestion takes place before the cells have been exposed to extensive fermentation, the cells must be ruptured through mastication. Likewise, in both hindgut and foregut fermenters, the rates of cellulose fermentation depend on the size and degree of damage (and thus extent of mastication) of the food particles presented to the gut microflora (Pearce and Moir 1964; McLeod and Minson 1969; Latham *et al.* 1978). Koalas are hindgut fermenters and therefore derive most of their energy from the cell contents. However, koalas have an extraordinarily complex and capacious hindgut (caecum and proximal colon) in which fine particles are selectively retained relative to the larger (space-filling), less fermentable particles that pass through more quickly (Cork and Warner 1983). This degree of hindgut specialisation is thought to contribute to the koala's ability to bend the allometric rules and utilise a diet that is high in fibre despite its small body size. In addition, Logan (2001) suggested that the occurrence of merycism (the action of regurgitating, remasticating and reswallowing preingested food material) may assist in the preparation of food material and thus contribute to an increase in the rate and extent of cell content digestion and cell wall fermentation.

#### *Food processing*

As expected, lactating females were found to consume significantly more leaf material than non-lactating females (Fig. 1c). Higher intake and ingestive processing might also be expected to increase the number of cells ruptured during mastication and therefore increase the intake of digestible energy from cell contents within the small intestine. Similarly, increased food intake could increase energy uptake from fermentation of cell wall. The 51% increase in food consumption observed here is similar to Krockenberger's (2003) estimated increase of 41% derived from isotopic measures of water intake, and therefore confirms his suggestion that the increased intake of koalas during lactation represented one of the lowest increases recorded in a mammal. Krockenberger (2003) argued that a low increase in energy intake is probably facilitated by the koala's very low peak milk output (Krockenberger *et al.* 1998). Whilst these two are undoubtedly correlated, the direction of causality is arguably more likely to be driven from the nutritional constraints rather than from the lactational strategies.

Weston (1988) found that lactating ewes consumed more roughage, had a greater rate of consumption, maintained higher levels of digesta throughout the gut, cleared a particulate marker more rapidly, and ruminated more than non-lactating ewes; however, there was no detectable difference in digesta particle size distributions. In ruminants, the passage of particles through the gut is regulated by the reticulo-omasal orifice, whereby only particles below a critical size can pass out of the reticulum and into the omasum. Mastication (ingestive and rumination) functions to maintain a constant production of particles just below a threshold size that will fit through this 'gastric sieve'. This, in turn, maintains a balance between particle retention, passage and fermentation (Cork 1994) and is critical for controlled fermentation. If the fermentation rate is too low, the host starves. On the other hand, since the bacteria have access to cell nutrients before the host, very high fermentation rates can also be deadly due to the over-production of gas. Hence a dramatic shift in particle size distribution could upset the fermentation process. It appears that compensation is achieved by increasing intake, gut capacity and passage rate (perhaps via a slight relaxation of the reticulo-omasal sieve rather than a shift in particle size distribution) so as to produce a greater volume of appropriately fermentable particles. In contrast, selective retention of particles within the caecum and proximal colon of koalas is more likely to represent a

gradational (rather than threshold) selector, whereby the finer the particle, the greater the probability of retention. If so, increasing intake and gut passage rate is likely to result in a shift in the caecal particle size distribution towards more finer particles. This could increase the rate and extent of fermentation by the nutrient-starved hindgut bacteria and thus increase the energy available for the lactating koala.

Wei *et al.* (1999) found that although dry-matter intake of lactating and non-lactating female red pandas was similar, lactating females had significantly higher dry matter digested and digestibility. They suggested that lactating females may have achieved higher digestibilities by masticating the bamboo leaves more extensively, a suggestion that was partly supported by a greater proportion of fine particles (<1 mm) in the faecal pellets of lactating females than in those of non-lactating females. This implies that more extensive mastication can also bring about a shift in the particle size distribution of ingested food. In the present study, lactating female koalas were found to have a higher number of ingestive mastications per mouthful than non-lactating females (Fig. 1*d*). This slight increase is likely to result in a greater proportion of cells being ruptured as well as in the production of a greater proportion of fine particles, and thus a further shift in the caecal particle size distribution. An increase in the amount of released cell contents and a shift in gastric and caecal particle size distributions, would increase the rate and extent of digestion of cell contents and cell wall fermentation respectively, thereby potentially compensating (at least in part) for the extra energy and nutrient requirements of lactation.

Whether the rates and extents of both digestion and fermentation increase proportionally to one another during lactation is unknown and perhaps the question of most interest. Despite the extreme degree of hindgut development, cell wall fermentation within the hindgut of koalas contributes only an estimated 9% of the daily digestible energy intake (Cork and Hume 1983). This puzzled Cork and Hume (1983), who concluded that the hindgut of koalas made only a minor energetic contribution and therefore must fulfill an important alternative function to have persisted in such a developed state. Nitrogen recycling (Cork 1986), water balance (Cork and Sanson 1990) as well as cytoplasm detanning (O'Brien *et al.* 1986) to increase protein availability have all been proposed as alternative functions. However, this disparity might itself emphasise both the importance of the contribution made by the hindgut fermentation towards enabling koalas to utilise a diet high in fibre and low in nutrients, as well as the relative difficulty in extracting energy from cell wall fermentation compared with cell content digestion. The disproportionately high degree of hindgut specialisation may also facilitate shifts in the relative energy contributions of the hindgut and foregut processes under different levels of energetic and/or nutrient stress. It would be interesting to see whether the proportions of energy derived from cell wall fermentation and cell contents extraction that were reported by Cork and Hume (1983) are altered under the energetic stresses of lactation.

Lactating female koalas performed 30.4% more merycism mastications per 24 h than did non-lactating females (Fig. 1*e*). This increase may be due to the higher food intake that results in a greater quantity of ingesta available or requiring preprocessing. Interestingly, the higher ratio of ingestive mastications to merycism mastications in lactating versus non-lactating females indicates that the relative difference in merycism mastications between lactating and non-lactating females was less than that of ingestive mastications and thus suggests a relative reduction in merycism effort. Furthermore, whilst lactating females had significantly higher ingestive mastication rates than non-lactating females (Fig. 1*b*), there was no difference in merycism mastication rates (Fig. 1*f*). Logan and Sanson (2002*b*) speculated that altered mastication rates could alter the fracture properties of the food

material, whereby teeth occluding at greater velocity could promote a greater degree of food reduction.

A smaller response in merycism behaviour than ingestive behaviour may reflect the disproportionate efforts required to further reduce particles of different sizes. Shipley *et al.* (1994) and Perez-Barberia and Gordon (1998) indicate that there is an exponential relationship between the initial size of food particles and the number of mastications required to bring about a certain rate of particle reduction. Therefore, whilst a little extra effort during initial ingestive mastication (e.g. faster mastications and more mastications per unit of ingested food) may reduce some relatively large particles into many smaller particles, a disproportionately large amount of effort may be required to further reduce the size of already small particles. Hence a more substantial increase in merycism effort may not achieve substantial energetic returns. Furthermore, increased ingestive mastication may reduce the relative need to more extensive merycism.

Alternatively, the lesser extents of merycism may be due to temporal constraints. A faster ingestive mastication rate may simply decrease the amount of time required to masticate more leaves more thoroughly, whilst altering the time required to remasticate the small quantities of regurgitated food is potentially of less value. In fact, the substantially slower merycism mastication rate compared with ingestive mastication rate (Logan 2001) does imply different functionality anyway. Logan (2001) noted that merycism was performed at frequent, yet irregular, intervals while the koalas were awake and resting and suggested that the lack of any obvious body movements prior to remastication could indicate that regurgitated food material accumulates gradually in the mouth, rather than being heaved up as a large bolus. In the present study, lactating female koalas were not found to spend any more time resting while awake than were non-lactating females ( $P > 0.5$ ). It is possible that the time required to accumulate enough material to stimulate a bout of remastication prohibits substantially more frequent bouts of merycism and thus the lactating females may not have had the opportunity to remasticate a more substantial quality of food material. The possibility that the behaviours interpreted and measured as merycism in koalas actually represent the mastication of food material stored within the mouth following a bout of feeding cannot be discounted. However, the frequency and prolonged occurrence of merycism bouts following the cessation of feeding suggest that more food is being processed than can be stored in a koala's mouth. Furthermore, oral food storage is usually observed only in species that utilise patchy food sources or transport food – neither of which apply to koalas. Therefore, it is unlikely that the patterns observed are the result of processing oral food stores.

#### *Activity patterns*

To accommodate the acquisition and comminution of more food material, lactating female koalas invested 80.2% more time in feeding than did non-lactating females (Fig. 2a). Barclay (1989) suggested that the degree to which female hoary bats (*Lasiurus cinereus*) increase the time spent foraging throughout lactation (to a peak of at least 73% greater than during early lactation), despite a constant abundance of food, implies that hoary bats restrict the amount of foraging time to just what was necessary to meet their current energy demands, and thus act as 'time minimisers'. So, too, the optimal foraging strategy for koalas appears to be that of a 'time minimiser'. Clearly, the non-lactating females in this study could have foraged for longer and stored the excess energy in fat reserves. However, koalas do not appear to utilise fat stores and it may be less efficient to store and later catabolise fat reserves than it is to adjust the current feeding behaviour to meet the current energy

demands. Moreover, in the long term, excess foraging is likely to accelerate the rate of tooth wear and the effects thereof (Logan and Sanson 2002b).

Lactating females were found to spend 118.8% more time feeding per bout (Fig. 2b). Masticating food to a greater extent (and increased gut passage rate) may require a greater volume of food material to be ingested (necessitating greater time for ingestion) before satiety is reached and a bout of feeding is complete. Alternatively, the increased bout duration associated with lactation may relate to the preference for more stable and capacious roosts (see below). Given the extra effort invested in travelling from a roost to the leaves and back again, it might be more efficient to feed in fewer, yet longer, bouts.

Gedir and Hudson (2000) investigated the feeding behaviour and activity patterns of captive wapiti hinds (*Cervus elaphus canadensis*) on two pastoral grazing regimes (light and heavy) during four phases of the reproductive cycle (early gestation, late gestation, peak lactation and late lactation). Wapiti hinds were found to graze longest during late lactation, when they also spent a greater proportion of their active time foraging and restricted foraging to fewer, yet longer, feeding bouts. Interestingly (and in contrast to the wapiti hinds), despite spending a significantly greater amount of time feeding per 24 h, lactating female koalas did not spend a significantly greater proportion of their active time feeding (81.7% v. 79.7%). Instead, they spent 8.37% less time resting and sleeping (Fig. 2e), presumably to the detriment of energy conservation.

For the remaining 20% of active time, lactating females were found to spend 62.2% more time moving around (climbing) within trees than were non-lactating females (Fig. 2c). This is perhaps even more significant when considering the potential costs of infant carrying (Price 1992; Sanchez *et al.* 1999). Concurrent observations revealed that lactating females appeared to prefer roosts that provided some protection from the summer sun. On days that exceeded 30°C, females with dependents (not just those recorded) were usually found sheltering in shadier trees (e.g. *Banksia*, *Acacia* and *Exocarpus*). Lactating female koalas also tended to roost in more spacious and stable parts of the trees (such as forks in the main trunk). This may be a precaution for the added weight and unpredictable shifts in balance caused by an adherent, yet at times acrobatic, dependent. Due to the sparse and distal nature of coastal manna gum foliage, stable and sheltered roosts tend to be further away from the leaves than those used by non-lactating females. This may also provide an alternative explanation for why feeding-bout durations were greater in lactating than non-lactating females. Given the extra effort invested in traveling from a roost to the leaves and back again, it might be more efficient to feed in fewer, yet longer, bouts.

Lactating females also appeared to utilise larger trees in which distances between roosts and leaves, as well as between different leaf-bearing branches, were greater. However, such trees are likely to provide a greater variety as well as quantity of roosts and leaves thereby reducing the necessity for more frequent tree swapping. The ranges of lactating females were highly variable and appeared to be related to the density of larger trees. While the size of the areas used by these animals ranged from 0.49 to 2.4 ha the number of trees used remained relatively constant (1.67 per 24 h). In contrast, the two non-lactating females had small ranges and utilised more trees (3.0 per 24 h).

#### *Comparison with tooth wear compensations*

Logan and Sanson (2002b), and Logan (2003) investigated the effects of tooth wear on the ingestive feeding behaviour, and merycism (rumination-like) behaviour respectively of free-ranging male koalas. Although the techniques and equipment used in both studies were comparable to the present study, the lactating females used in the present study were

estimated to be at peak lactation (and thus represent an extreme with respect to energy and nutrient requirements), whereas the individuals investigated by Logan and Sanson (2002*b*), and Logan (2003) did not necessarily represent the extremes of high and low tooth wear. Furthermore, since this study was conducted in a different year and different time of year, it is possible that the leaves consumed had different biochemical and/or physical properties. Nevertheless, it is interesting to compare the relative contributions of the feeding compensations used to offset the two different nutritional stresses (tooth wear and lactation).

Logan and Sanson (2002*b*) found that the koala with the highest degree of tooth wear consumed 41% more leaf material per 24 h and masticated leaves 25% more than the individual with the lowest degree of tooth wear. This resulted in a 116% increase in total ingestive mastications per 24 h. By comparison, the results of this study suggest that lactation leads to a relatively higher increase in leaf consumption (51%), yet a substantially lower increase in the number of mastications per leaf (4.5% cf. 25%), and thus lower increase in total ingestive mastications per 24 h.

Individuals with high degrees of tooth wear do not necessarily have higher energy requirements than individuals with lower degrees of tooth wear; rather, they have difficulty maintaining energy intake due to the ineffectiveness of the teeth. Compensating for tooth wear is likely to emphasise the maintenance of gastric and caecal particle size distribution so as to maintain energy intake. This is achieved by processing food material to a greater extent. In contrast, lactational compensations emphasise the shift in particle size distributions towards the finer particles so as to increase energy intake. Due to the negative exponential relationship between masticatory effort and particle breakdown, this may be achieved most efficiently through greater food intake and gut passage rate as well as the selective retention of fine particles.

#### *Ecological implications*

Despite these differences, the strategies for compensating for lactation and tooth wear are very similar. Therefore the ability of a female koala to compensate for lactation (meet the extra energetic demands of milk production) may depend on the extent to which it is already compensating for tooth wear. Martin (1981) and Martin and Handasyde (1990) present age-specific fecundity data from a number of Victorian koala populations. Whilst it is obvious that fecundity is lower in populations infected with *Chlamydia*, the data (particularly from the *Chlamydia*-free French Island population) also indicate that fecundity declines with age (actually degree of tooth wear). Hence, by reducing the capacity to compensate for the extra costs of lactation, tooth wear, the major aging effect (P. Mitchell, pers. comm), could ultimately define the reproductive lifespan of female koalas.

Although it is acknowledged that the above conclusions are based on only a small number of individuals, the enormous investment of time required to obtain this quantity and quality of data per individual per 24 h currently prohibits large sample sizes. The results presented are consistent with the literature and provide further understanding of the mechanisms by which female koalas compensate for the extra energy demands imposed by lactation and juvenile dependency.

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## References

- Barclay, R. M. R. (1989). The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behavioral Ecology and Sociobiology* **24**, 31–38.
- Bowen, W. D., Inverson, S. J., Boness, D. J., and Oftedal, O. T. (2001). Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* **15**, 325–334.
- Cork, S. J. (1986). Foliage of *Eucalyptus punctata* and the maintenance nitrogen requirements of koalas *Phascolarctos cinereus*. *Australian Journal of Zoology* **34**, 17–24.
- Cork, S. J. (1991). Meeting the energy requirements for lactation in a macropodid marsupial: current nutrition versus stored body reserves. *Journal of Zoology (London)* **225**, 567–576.
- Cork, S. J. (1994). Digestive constraints on dietary scope in small and moderately small mammals: how much do we really understand?. In 'The Digestive System in Mammals: Food, Form, and Function'. (Eds D. J. Chivers and P. Langer.) pp. 370–390. (Cambridge University Press: Cambridge.)
- Cork, S. J., and Hume, I. D. (1983). Microbial digestion in the koala (*Phascolarctos cinereus*, Marsupialia), an arboreal folivore. *Journal of Comparative Physiology B* **152**, 131–135.
- Cork, S. J., and Sanson, G. D. (1990). Digestion and nutrition in the koala: a review. In 'The Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 129–144. (Surrey Beatty: Sydney.)
- Cork, S. J., and Warner, A. C. I. (1983). The passage of digesta markers through the gut of a folivorous marsupial, the koala *Phascolarctos cinereus*. *Journal of Comparative Physiology B* **152**, 43–51.
- Degabriele, R., Harrop, C. J. F., and Dawson, T. J. (1978). Water metabolism of the koala (*Phascolarctos cinereus*). In 'The Ecology of the Arboreal Folivores'. (Ed. G. G. Montgomery.) pp. 163–172. (Smithsonian Institution Press: Washington, DC.)
- Demment, M. W., and Van Soest, P. J. (1985). A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125**, 641–672.
- Ellis, W. A. H., and Carrick, F. N. (1992). Total body water and estimation of fat in the koala (*Phascolarctos cinereus*). *Australian Veterinary Journal* **69**, 229–231.
- Gedir, J. V., and Hudson, R. J. (2000). Seasonal foraging behavioural compensation in reproductive wapiti hinds *Cervus elaphus canadensis*. *Applied Animal Behaviour Science* **67**, 137–150.
- Gittleman, J. L., and Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist* **28**, 863–875.
- Greager, D. C., Jenness, C. A., and Ward, G. D. (1979). An acoustically sensitive transmitter for telemetering the activities of wild animals. *Journal of Wildlife Management* **43**, 1001–1007.
- Green, B., Merchant, J., and Newgrain, K. (1988). Lactational energetics of a marsupial carnivore, the eastern quoll (*Dasyurus viverrinus*). *Australian Journal of Zoology* **45**, 295–306.
- Ihaka, R., and Gentleman, R. (1996). R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* **5**, 299–314.
- Keys, J. E., Van Soest, P. J., and Young, E. P. (1969). Comparative study of the digestibility of forage cellulose and hemicellulose in ruminants and nonruminants. *Journal of Animal Science* **38**, 559–564.
- Kie, J. G., Baldwin, A. B., and Evans, C. J. (1994). CALHOME: homerange analysis program; electronic user's manual. U. S. Forest Service, Pacific Southwest Research Station, Fresno, California.
- Krockenberger, A. K. (2003). Meeting the energetic demands of reproduction in female koalas, *Phascolarctos cinereus*: evidence for energetic compensation. *Journal of Comparative Physiology B* **173**, 531–540.
- Krockenberger, A. K., Hume, I. D., and Cork, S. J. (1998). Production of milk and nutrition of the dependent young of free-ranging koalas (*Phascolarctos cinereus*). *Physiological Zoology* **71**, 45–56.
- Lanyon, J. M., and Sanson, G. D. (1986). Koala (*Phascolarctos cinereus*) dentition and nutrition: I. Morphology and occlusion of cheekteeth. *Journal of Zoology (London)* **209**, 155–168.

- Latham, M. J., Brooker, B. E., Pettipher, G. L., and Harris, P. J. (1978). Adhesion of *Bacteroides succinogenes* in pure culture and in the presence of *Ruminococcus*. *Applied Environmental Microbiology* **35**, 1166–1173.
- Lee, A. K., and Martin, R. W. (1988). Translocation of the koala to a new habitat. In 'Translocations of Wild Animals'. (Eds L. Nielson and R. D. Brown.) pp. 152–190. (Wisconsin Humane Society: Milwaukee.)
- Lentle, R. G., Potter, M. A., Stafford, K. J., Springett, B. P., and Haslett, S. (1998). The temporal characteristics of feeding activity in free-ranging tamar wallabies (*Macropus eugenii* Desmarest). *Australian Journal of Zoology* **46**, 601–615.
- Logan, M. (2001). Evidence for the occurrence of rumination-like behaviour, or merycism in koalas (*Phascolarctos cinereus*, Goldfuss). *Journal of Zoology (London)* **255**, 83–87.
- Logan, M. (2003). The effect of tooth wear on the rumination-like behavior, or merycism, of free-ranging male koalas (*Phascolarctos cinereus*). *Journal of Mammalogy* **84**, 897–902.
- Logan, M., and Sanson, G. D. (2002a). The effect of tooth wear on the activity patterns of free-ranging koalas (*Phascolarctos cinereus* Goldfuss). *Australian Journal of Zoology* **50**, 281–292.
- Logan, M., and Sanson, G. D. (2002b). The effect of tooth wear on the feeding behaviour of free-ranging koalas (*Phascolarctos cinereus*, Goldfuss). *Journal of Zoology (London)* **256**, 63–69.
- Martin, R. W. (1981). Age-specific fertility in three populations of koala, *Phascolarctos cinereus* (Goldfuss), in Victoria. *Australian Wildlife Research* **8**, 275–283.
- Martin, R. W. (1985). Overbrowsing, and decline of a population of the koala, *Phascolarctos cinereus*, in Victoria. 2. Population condition. *Australian Wildlife Research* **12**, 367–375.
- Martin, R. W., and Handasyde, K. A. (1990). Population dynamics of the koala (*Phascolarctos cinereus*) in southeastern Australia. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 75–84. (Surrey Beatty: Sydney.)
- McLean, J. A., and Speakman, J. R. (1997). Non-nutritional maternal support in the brown long-eared bat. *Animal Behaviour* **54**, 1193–1204.
- McLeod, M. N., and Minson, D. J. (1969). Sources of variation in the *in vitro* digestibility of tropical grasses. *Journal of the British Grassland Society* **24**, 244–249.
- McNally, J. (1957). A field survey of a koala population. *Proceedings of the Linnean Society of New South Wales* **May**, 18–27.
- Mellish, J. E., Iverson, S. J., and Bowen, W. D. (2000). Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. *Proceedings of the Royal Society of London Series B* **267**, 1245–1251.
- Mitchell, P. (1990). The home ranges and social activity of koalas – a quantitative analysis. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 171–187. (Surrey Beatty: Sydney.)
- Nagy, K. A., and Martin, R. W. (1985). Field metabolism rate, water flux, food consumption and time budget of koalas, *Phascolarctos cinereus* (Marsupialia: Phascolarctidae) in Victoria (Australia). *Australian Journal of Zoology* **33**, 655–666.
- Nievergelt, C., and Martin, R. (1999). Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Physiology and Behavior* **65**, 849–854.
- O'Brien, T. P., Lomdahl, A., and Sanson, G. D. (1986). Preliminary microscopic investigations of the digesta derived from foliage of *Eucalyptus ovata* in the digestive tract of the common ringtail possum (*Pseudocheirus peregrinus*, Marsupialia). *Australian Journal of Zoology* **34**, 157–176.
- Oftedal, O. T. (1993). The adaptation of milk secretion to the constraints of fasting in bears, seals and baleen whales. *Journal of Dairy Science* **76**, 3234–3246.
- Pearce, G. R., and Moir, R. J. (1964). Rumination in sheep. 1. The influence of rumination and grinding upon the passage and digestion. *Australian Journal of Agricultural Research* **15**, 635–644.
- Perez-Barberia, F. J., and Gordon, I. J. (1998). Factors affecting food comminution during chewing in ruminants: a review. *Biological Journal of the Linnean Society* **63**, 233–256.
- Pratt, A. (1937). 'The Call of the Koala.' (Robertson and Mullens: Melbourne.)
- Price, E. C. (1992). The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology* **26**, 23–33.
- Prins, R. A., and Kreulen, D. A. (1990). Comparison of plant cell wall digestion in mammals. In 'The Rumen Ecosystem: The Microbial Metabolism and its Regulation'. (Eds S. Hoshino, H. Minato and H. Itabashi.) pp. 109–120. (Scientific Societies Press: Tokyo.)
- Racey, P. A., and Speakman, J. R. (1987). The energy costs of pregnancy and lactation in heterothermic bats. *Symposia of the Zoological Society of London* **83**, 635–638.

- Sanchez, S., Pelaez, F., Gil-Burmann, C., and Kaumanns, W. (1999). Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology* **48**, 99–111.
- Shiple, L. A., Gross, J. E., Spalinger, D. E., Hobbs, N. T., and Wunder, B. A. (1994). The scaling of intake rate in mammalian herbivores. *American Naturalist* **143**, 1055–1082.
- Stearns, S. C. (1989). Trade-offs in life history evolution. *Functional Ecology* **3**, 329–351.
- Thompson, S. D. (1992). Gestation and lactation in small mammals: basal metabolic rate and the limits to energy use. In 'Mammalian Energetics. Interdisciplinary Views of Metabolism and Reproduction'. (Eds T. E. Tomasi and T. H. Horton.) pp. 213–260. (Comstock: Ithaca, NY.)
- Watson, D. M., and Dawson, T. J. (1993). The effects of age, sex, reproductive status and temporal factors on the time-use of free-ranging red kangaroos (*Macropus rufus*) in western New South Wales. *Wildlife Research* **20**, 785–801.
- Wei, F., Feng, Z., Wang, Z., Zhou, A., and Hu, J. (1999). Nutrient and energy requirements of red panda (*Ailurus fulgens*) during lactation. *Mammalia* **63**, 3–10.
- Weston, R. H. (1988). Factors limiting the intake of feed by sheep: XII. Digesta load and chewing activities in relation to lactation and its attendant increase in voluntary roughage consumption. *Australian Journal of Agricultural Research* **39**, 671–678.

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