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Modelling digestive constraints in non-ruminant and ruminant foregut-fermenting mammals

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Abstract

It has been suggested that large foregut-fermenting marsupial herbivores, the kangaroos and their relatives, may be less constrained by food intake limitations as compared with ruminants, due mainly to differences in their digestive morphology and management of ingesta particles through the gut. In particular, as the quality of forage declines with increasing contents of plant fibre (cellulose, hemicelluloses and lignin; measured as neutral-detergent fibre, NDF), the tubiform foregut of kangaroos may allow these animals to maintain food intakes more so than ruminants like sheep, which appear to be limited by fibrous bulk filling the foregut and truncating further ingestion. Using available data on dry matter intake (DMI, g kg^{-0.75} d⁻¹), ingesta mean retention time (MRT, h), and apparent digestibility, we modelled digestible dry matter intake (DDMI) and digestible energy intake (DEI) by ruminant sheep (*Ovis aries*) and by the largest marsupial herbivore, the red kangaroo (*Macropus rufus*). Sheep achieved higher MRTs on similar DMIs, and hence sheep achieved higher DDIMs for any given level of DMI as compared with kangaroos. Interestingly, MRT declined in response to increasing DMI in a similar pattern for both species, and the association between DMI and plant NDF contents did not support the hypothesis that kangaroos are less affected by increasing fibre relative to sheep. However, when DEI was modelled according to DDIMs and dietary energy contents, we show that the kangaroos could meet their daily maintenance energy requirements (MER) at lower levels of DMI and on diets with higher fibre contents compared with sheep, due largely to the kangaroos' lower absolute maintenance and basal energy metabolisms compared with eutherians. These results suggest that differences in the metabolic set-point of different species can have profound effects on their nutritional niche, even when their digestive constraints are similar, as was the case for these ruminant and non-ruminant foregut fermenters.

Keywords

Kangaroos, Marsupials, Foregut, Hindgut, Herbivore, Nutrition, Ruminant, Non-ruminant

Disciplines

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1 Modelling digestive constraints in non-ruminant and ruminant foregut-fermenting mammals

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13 Keywords: Kangaroos; marsupials; foregut; hindgut; herbivore; nutrition; ruminant; non-
14 ruminant.

Abstract

It has been suggested that large foregut-fermenting marsupial herbivores, the kangaroos and their relatives, may be less constrained by food intake limitations as compared with ruminants, due mainly to differences in their digestive morphology and management of ingesta particles through the gut. In particular, as the quality of forage declines with increasing contents of plant fibre (cellulose, hemicelluloses and lignin; measured as neutral detergent fibre, NDF), the tubiform foregut of kangaroos may allow these animals to maintain food intakes more so than ruminants like sheep, which appear to be limited by fibrous bulk filling the foregut and truncating further ingestion. Using available data on dry matter intake (DMI, $\text{g kg}^{-0.75} \text{ d}^{-1}$), ingesta mean retention time (MRT, h), and apparent digestibility, we modelled digestible dry matter intake (DDMI) and digestible energy intake (DEI) by ruminant sheep (*Ovis aries*) and by the largest marsupial herbivore, the red kangaroo (*Macropus rufus*). Sheep achieved higher MRTs on similar DMIs, and hence sheep achieved higher DDMIs for any given level of DMI as compared with kangaroos. Interestingly, MRT declined in response to increasing DMI in a similar pattern for both species, and the association between DMI and plant NDF contents did not support the hypothesis that kangaroos are less affected by increasing fibre relative to sheep. However, when DEI was modelled according to DDMIs and dietary energy contents, we show that the kangaroos could meet their daily maintenance energy requirements (MER) at lower levels of DMI and on diets with higher fibre contents compared with sheep, due largely to the kangaroos' lower absolute maintenance and basal energy metabolisms compared with eutherians. These results suggest that differences in the metabolic set-point of different species can have profound effects on their nutritional niche, even when their digestive constraints are similar, as was the case for these ruminant and non-ruminant foregut fermenters.

43 **Introduction**

44 Mammalian herbivores cannot breakdown plant fibre auto-enzymatically, and they rely on the
45 fermentation of fibrous components by intestinal microbes, which yield the short-chain fatty
46 acids that are absorbed and metabolised by the host (Stevens and Hume 1998). However,
47 fermentation takes time (Hummel et al. 2006) and mammalian herbivores have evolved
48 specialised gut compartments that assist the retention of fibrous materials for efficient
49 digestion. There are two broad morphophysiological types of mammalian herbivores, defined
50 according to where fermentation takes place along the gastro-intestine; i.e. in the forestomach
51 anterior to the acid-stomach (as in ruminant and non-ruminant foregut fermenters), or in the
52 hindgut distal to the acid-stomach (as in colon and caecum fermenters). Foregut and hindgut
53 fermentation systems each have their own benefits and drawbacks with regard to digestive
54 efficiency, and these are discussed in detail elsewhere (e.g. Stevens and Hume 1995).
55 However, for both types of herbivore, body size is thought to play a key role in their ecology
56 and evolution, principally via its impacts of energy/nutrient requirements and gut capacity
57 (Demment and Van Soest 1985; Illius and Gordon 1992).

58 Gut capacity is thought to limit food residence time in gut, constraining the intensity of
59 fermentation and subsequent assimilation of digestible nutrients. However, in a recent
60 analysis, Clauss et al. (2007a, 2008) argued that for mammalian herbivores gut-residence time
61 of food is less impacted by body size than previously thought, suggesting that oft-cited
62 models defining herbivore constraints (e.g. Parra 1978; Demment and Van Soest 1985; Illius
63 and Gordon 1992; Cork 1996) may be inappropriate for large mammalian herbivores. Instead,
64 interactions between food intake (rather than body mass) and food residence time (i.e. mean
65 retention time; MRT), may be more important for understanding the evolution and ecology of
66 large herbivores and, ultimately, for predicting the cost-benefit boundaries that define their
67 nutritional niches.

68 Herbivores can differ in the way they respond to different levels of feed intake,
69 depending primarily upon food quality and on their ingestive and digestive
70 morphophysiology. In particular, changes in food intake levels can have different effects on
71 the MRT and digestibility (fermentation) of ingested particles. On the one hand, an increase in
72 food intake (measured as dry matter intake; DMI, $\text{g kg}^{-0.75} \text{ d}^{-1}$) can lead to shorter ingesta
73 MRT (h) and subsequently lower digestive efficiency (i.e. nutrient extracted per unit of
74 material ingested). Consequently, reduced MRTs associated with increasing DMIs can
75 impose an intrinsic limit on the amount of feed the animal can ingest, thus limiting digestible
76 dry matter intake (DDMI, $\text{g kg}^{-0.75} \text{ d}^{-1}$). For example, Clauss et al. (2007b) found a
77 particularly steep negative relationship between MRT and DMI in ruminant (sheep and cattle)
78 and non-ruminant (hippopotamus) foregut fermenters, which truncated their DDMIs at
79 increasing levels DMI.

80 Alternatively, increasing levels DMI may have only a mild influence on MRT and
81 digestive efficiencies, as seen in the hindgut-fermenting equids (horse and donkey) and
82 elephants. Horses and elephants, for example, achieve nearly constant MRTs over a wide
83 range of DMIs (e.g. Fig. 1). As such, these hindgut fermenters can sustain digestive
84 efficiencies and hence DDMIs over a broader range of food intake levels as compared with
85 ruminants and other foregut fermenters (Clauss et al. 2007b). Recently, another hindgut
86 fermenter, the marsupial koala (*Phascolarctos cinereus*) was shown to have a MRT similarly
87 unaffected by increased food intake (Krockenberger and Hume 2007). For these species, the
88 apparent uncoupling of MRT from DMI suggests that other factors may dominate their
89 feeding patterns and diet selections, such as activity budgets, mechanical or anti-nutritive
90 constraints.

91 Clauss et al. (2007b) focussed comparisons of the MRT-DMI patterns on non-ruminant
92 foregut (hippo) *versus* hindgut (elephant) fermenters, and speculated that their findings
93 supported the so called “Bell/Janis/Foose” model of niche separation between two other

major herbivore groups, the foregut fermenting ruminants and the colon/large intestine fermenting equids. The Bell/Janis/Foose model predicts that equids can more easily compensate for reductions in forage quality (increased fibre) as compared to ruminants (Bell 1971; Janis 1976; Foose 1982; Duncan et al. 1990). This is probably because ruminants must reduce ingesta particle sizes via regurgitation and re-chewing before material can flow from the rumen-reticulum (via the omasum) to the lower gut. Thus, for ruminants coarse fibrous diets can impair DMIs as bulky material fills the gut. On the other hand, the colon-fermenting equids may not be as limited by fibrous bulk, which passes from the gut more quickly, freeing space for further DMI. However, it is uncertain whether differences in the cost/benefit structure of fore- *versus* hind-gut fermentation systems (see Stevens and Hume 1998) or differences in how ruminants and horses manage ingesta particles may dominate their niche partitioning. Therefore, in this contribution we have examined the DMI-MRT patterns in two distinctly different types of foregut fermenting herbivore, the ruminant sheep (*Ovis aries*) and the macropodid marsupial the red kangaroo (*Macropus rufus*).

Kangaroos and their relatives possess a foregut fermentaion set-up that has been compared with that of ruminants (e.g. Kinnear et al. 1979). However, in form and function the tubiform foregut of kangaroos is more like the hindgut of the colon-fermenting horse (Fig. 2; Hume 1999). Like the horse colon, the kangaroo foregut is typified by numerous haustrations that likely provide elastic support for flexibility in DMIs under different nutritrional circumstances (Munn and Dawson 2006). Most notably, kangaroos differ from sheep in that, like equids, they are not limited by the particle-size restrictions that control the flow of material from the foregut (see Hume 1999), and they do not exhibit the regurgetation/re-chewing behaviours that typify ruminant feeding. Additionally, when compared directly to sheep, red kangaroos are able to maintain body condition for longer during drought conditions when mainly poor-quality, high fibre forages dominate (Edwards et al. 1996), reminiscent of differences between cattle and horses; unquantified observations indicate that when diet

quality is very low cattle lose body condition, but sympatric horses are less affected (Abaturov 2005; Koene 2006). As such, we speculated that the relationship between DMI and MRT in kangaroos may be expected to resemble that of equids (Fig. 1), with concomitant implications for their ecology and niche specialisations.

Methods

We collated data on DMI, MRT and digestibility in sheep and macropods to model the interactions between these parameters and impacts on DDMI. Additionally, we evaluated the relationship between dietary fibre content (neutral-detergent-fibre, NDF) and forage intake (DMI) by sheep and kangaroos. We collated data on DMI and particle MRT from feeding trial experiments with domestic sheep (Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970; Udén et al. 1982; Udén and Van Soest 1982; Cherney et al. 1990; Cherney et al. 1991; Kennedy et al. 1992; Bartocci et al. 1997) and captive red kangaroos (*Macropus rufus*) (Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970; individual data on adult and weaned juveniles from Munn and Dawson 2006). The red kangaroo was the only macropodid for which a reasonable number of DMI and MRT measurements were available in the literature. Differences in slope and intercept of the DMI-MRT regression were tested with ANCOVA using SPSS 12.0 (SPSS Inc., Chicago, IL, USA).

Data on MRT and apparent digestibility (aD) of dry matter (DM) was available for sheep and kangaroos for two diets, chopped lucerne hay (*Medicago sativa*) and chopped oat hay or straw (*Avena sativa*), from three comparative studies that fed these forages to *M. rufus* and sheep under comparable conditions (Foot and Romberg 1965; McIntosh 1966; Forbes and Tribe 1970). There is a systematic difference in nutrient composition between lucerne and oaten hay, and therefore these forages were evaluated separately for their potential impacts on DMI-MRT coupling. The relationship between aD of DM and MRT was characterized for each forage type using an exponential function typical of fermentation rates (Blümmel and

Ørskov 1993). In theory, a simple linear regression could have been applied to the data to describe the relationship of MRT and aD DM. However, as linear equations could be extrapolated to digestibility coefficients above 100 %, the exponential function is more biologically meaningful because digestibility cannot be optimized endlessly (Blümmel and Ørskov 1993). Subsequently, the associations between DMI and MRT, and between MRT and aD of DM, were used to model the influence of DMI on each species' digestible dry matter intake (DDMI). The DDMIs modeled for sheep and kangaroos were then converted to digestible energy intakes (DEI; kJ) according to standardized gross energy contents of 18.4 kJ g⁻¹ DM for plant forage (ARC 1980; SCA 1990; Ostrowski-Meissner 1987), and assuming that the digestibility of gross energy was equivalent to that for dry matter (Robbins 1993; Munn and Dawson 2003; Munn and Dawson 2006). To evaluate the potential energetic limitations of the MRT-DMI continuum we used maintenance energy requirements (MER) for each species according to published data derived from feeding trials using diets comparable those described here; red kangaroos MER = 390 kJ digestible energy (DE) kg^{-0.75} d⁻¹ (Munn and Dawson 2003), sheep MER = 569 kJ DE kg^{-0.75} d⁻¹ (Hume 1974).

To investigate the potential for forage quality (fibre content) to effect DMI patterns, we compared data for sheep taken from Van Soest (1965) who, using a dataset from 83 intake trials, found a correlation between DMI (VDMI; g kg^{-0.75} d⁻¹) and dietary NDF (%DM) of

$$\text{DMI} = 110.4 - 1716 / (100 - \text{NDF}) \quad (1)$$

Similar descriptions for DMI-NDF interactions do not exist for kangaroos. Therefore, we collated data from feeding trials from a range of macropodid species offered a variety of forages *ad libitum*. However, several of these studies pre-dated modern fibre analysis methods (see Van Soest *et al.* 1991) and so did not report on NDF contents specifically, but they did include values for crude fibre (CF); others only presented data for acid detergent fibre (ADF). For trials that gave only CF values, an ADF value was assumed by choosing forage of the same botanical composition and similar CF and crude protein value from Australian feed

composition tables (Ostrowski-Meissner 1987), which was then converted to a NDF content estimated using the following equations (NRC 2001):

$$\text{Grass forage (oaten hay): NDF} = 2.0 \cdot \text{ADF} - 13.78 \quad (2)$$

$$\text{Legume forage (lucerne hay): NDF} = 1.2 \cdot \text{ADF} + 0.89 \quad (3)$$

Results

There was no difference in the slope of the DMI-MRT relationship between sheep and red kangaroos (Fig. 3; ANCOVA, $P = 0.632$). For any given level of DMI, sheep had longer MRTs than the kangaroos ($P < 0.001$).

There was no significant relationship between MRT and aD of DM for either the lucerne or oaten hay forages by sheep and red kangaroos (Fig. 4). Nonetheless, these curves describe the relationships between aD of DM and MRT that are directly applicable to our models for DDMI (i.e. Fig. 5). Due to the shortage of data, we did not consider the digestive efficiency of sheep and kangaroos separately, but our procedure is in accord with the assumption that time available for digestion is the major determinant of forage digestion if the sequence of fermentation and auto-enzymatic digestion is similar. Because both sheep and kangaroos are foregut fermenters, this condition was met.

The relationship between DMI and DDMI (Fig. 5) was modelled for oaten and lucerne hays using the equations derived from Fig. 3 and Fig. 4. Theoretically, sheep could achieve higher DDMIs at any level of DMI as compared with red kangaroos (Fig. 5). However, because DDMI is also dependent on the content of hard-to-digest, fibrous material in a given diet, we compared kangaroo and sheep DMIs relative to forage NDF content (Fig. 6). Overall, it was apparent that the potential for increasing forage NDF (%DM) to limit DMI was similar in both sheep and kangaroos (Fig. 6), and the kangaroos did not show a marked advantage

196 compared with sheep. In other words, feed intake was depressed by NDF (%DM) in a similar
197 fashion and to a similar extent in both the ruminant and the kangaroos.

198 While differences were not apparent in the MRT-DMI coupling or the impact of diet
199 NDF on DMIs between sheep and kangaroos, differences in their potential to satisfy daily
200 energy requirements (for maintenance; MER) on a given diet were detected. On either the
201 lucerne (Fig. 7a) or oaten (Fig. 7b) hay diets, we found that kangaroos could, theoretically,
202 satisfy their MER at intake levels lower than those required by sheep. Moreover, for both
203 lucerne and oaten hay models, the kangaroos could, theoretically, satisfy their MERs at NDF
204 contents (%DM) in excess of those that would limit sheep intakes. For example, in the lucerne
205 hay model, kangaroos could satisfy MERs even when NDF was in excess of ca. 80% DM, but
206 sheep would fail to acquire sufficient energy at NDF contents of around 70% DM. This
207 difference was more pronounced for the oaten hay model, where kangaroos could meet MER
208 at diets containing as much as 67% NDF, but sheep would require a diet with less than 54%
209 NDF (Fig. 7).

211 **Discussion**

212 The tubiform foregut of kangaroos is comparable in form and function to the haustrated
213 equine colon, and as such we predicted that the slope of the MRT-DMI curve for red
214 kangaroos would be more like that of horses (Fig. 2) rather than sheep. This was not the case
215 and there was little difference in the food-intake patterns between sheep and macropodid
216 kangaroos generally. The slope of the DMI-MRT-relationship for sheep and the red kangaroo
217 were not significantly different (Fig. 3). Consequently, our data did not support the suggestion
218 that kangaroos could maintain high intake levels with a lesser reduction in digestive
219 efficiency as compared with sheep. Moreover, our data suggest that there is little difference
220 between the sheep and kangaroos in their ingestive responses to diet NDF contents (Fig. 6); in
221 other words there did not appear to be any fundamental difference in the intake limitations of

sheep and kangaroos due to dietary NDF content, despite sheep possessing the particle-size limitations on digesta flow unique to ruminants. Therefore, factors other than differences in the particle-flow mechanisms of ruminants and kangaroos must affect their DMI-MRT slope. Like the hindgut fermenting equids, kangaroos are less restricted by particle-size dependent flow of ingesta, but their DMI-MRT slope resembles that of the ruminants.

An important factor that determines the slope of the DMI-MRT-relationship is the spare capacity available in the gastrointestinal tract. For elephants and horses, the potential for the abdominal cavity to expand (“swell”) has been cited as a major facilitator in increasing gut capacity where MRT is kept more or less constant. Similarly, an increase in forestomach volume with higher DMIs has been reported in ruminants (reviewed in Clauss et al. 2007b), though the magnitude of “swelling” is probably less so than in hindgut fermenters, echoing suggestions that the magnitude of ‘spare capacity’ in the gut of different herbivore groups probably plays a key role in niche partitioning (Karasov and McWilliams 2005). Complex intestinal haustrae, for example, are considered an adaptation for gut volume expansion (Langer and Takács 2004), and occur in both equids and macropods (Fig. 2). However, if the gastrointestinal tract and abdominal cavity of macropods was more suitable for compensatory distension, we would expect the slope of the DMI-MRT relationship of macropods to be shallower than that for sheep. While mature red kangaroos are known to increase gut-fill in response to low-quality (high fibre) diets (Munn and Dawson 2006), the degree to which their abdominal cavity can accommodate such increases is unknown, but is probably much less than that seen in horses. The small body size and tight abdominal musculature (necessary for the hopping gait), and the additional rigidity provided to the abdominal wall by the epipubic bones of kangaroos (Dawson et al. 1989), probably limit potential for gut-distension, leading to their MRT-DMI curve resembling that of sheep (Fig 3.) rather than equids (Fig. 1). Interestingly, complex haustrae are not seen in the foregut of hippopotamus (Langer 1975; Langer 1976), which also exhibit a steep MRT-DMI curve comparable to sheep and

kangaroos (Clauss et al. 2007b). Overall, our models suggest that differences in the ability of herbivore types to expand gut-fill in response to diet quality (fibre content) plays a key role in defining their food intake limitation.

Based solely on DMI, MRT and the aD of DM, our model predicts maximum forage intakes by red kangaroo of $70\text{--}80 \text{ g kg}^{-0.75} \text{ d}^{-1}$ (Fig. 5), which are comparable to reported maximum DMIs of $62\text{--}66 \text{ g kg}^{-0.75} \text{ d}^{-1}$ for red kangaroos feeding on pasture in experimental yards (Short 1985; Short 1986). For other free-ranging macropods, maximum DMIs of $85\text{--}87 \text{ g kg}^{-0.75} \text{ d}^{-1}$ have been documented (Prince 1976; Short 1986), and the intake of roughages measured in feeding trial with captive animals does not exceed $70 \text{ g kg}^{-0.75} \text{ d}^{-1}$ (Fig. 5). Thus, the DMI-DDMI model presented here for the red kangaroo appears to reflect the maximum DMI in this species, similar to the calculation for hippopotamuses (Clauss et al. 2007b).

Our model predicted that sheep should have an upper limit to DMI of $110\text{--}120 \text{ g kg}^{-0.75} \text{ d}^{-1}$, regardless of forage type (Fig. 5); yet, in the data presented by Van Soest (1965), maximum intakes of only ca. $90 \text{ g kg}^{-0.75} \text{ d}^{-1}$ were observed (Fig. 6). Furthermore, free-ranging sheep feeding on pasture had maximum DMIs as low as $61 \text{ g kg}^{-0.75} \text{ d}^{-1}$ (Short 1985). That our model predicts higher intakes by sheep than are actually observed suggests that factors additional to DMI, MRT and aD of DM must determine their intake limitations, at least under some circumstances. It is generally accepted that the intake limitations of ruminants like sheep revolve around the need to reduce ingesta particle sizes before material can flow from the foregut to free-up space for further ingestion, and this is harder to achieve on high-fibre diets (Lechner-Doll et al. 1991; Jung and Allen 1995; Allen 1996).

The selective retention of particles as a function of their density and size is considered a peculiarity of the ruminant forestomach (Shaver et al. 1986; Welch 1986; Shaver et al. 1988; Lechner-Doll et al. 1991, Schwarm et al. 2008), and it has been shown that the grinding of forages can greatly enhance their intake (Minson 1967; Laredo and Minson 1975). In contrast to ruminants, no mechanical outflow limitation has so far been demonstrated in any other

herbivore. Indeed, the absence of a mechanical intake limit is considered an important characteristic of both hindgut fermentation systems (Janis 1976; Hume and Sakaguchi 1991) and, to some extent, of the kangaroo foregut (Hume 1999). Nonetheless, intake limitations related to increasing NDF have been demonstrated in kangaroos (McIntosh 1966; Hume 1974; Hollis 1984) and horses (Lawrence et al. 2001). Whereas the limitation by rumen fill due to NDF-rich forages appears reasonably understood (see Allen 1996), no concept has been proposed for that would explain the limiting effect of NDF on intake in herbivores that are presumably not constrained in the same mechanical way as ruminants (i.e. particle-size/density limiting outflow from the foregut). However, such a mechanical constraints simply may have not been demonstrated, and indeed, grinding and pelleting food (i.e. relaxing the particle-size restrictions) increases food intake not only in sheep, but also in kangaroos (Freudenberger and Hume 1992) and horses (Haenlein et al. 1966; Schurg et al. 1978). Nonetheless, how such mechanical constraints or limitations might operate within each the different herbivore groups, or if they reflect common mechanism, remains to be investigated. Our results do not support the suggestion that on high-fibre forages intake is less reduced in kangaroos and their relatives than it is in ruminants (see Hume 1999, p. 250). For that, further studies using forages of higher fibre content than those cited here would need to be conducted to fully appreciate differences in the responses of sheep and kangaroos at extreme limits to their digestive capabilities. Results from studies in which sheep and macropods were directly compared are not unanimous. For example, food intake by macropods decreased less so than in sheep with decreasing forage quality (Foot and Romberg 1965; Hollis 1984). Intakes of straw-based forages of increasing fibre content decreased in a similar way in macropods and goats when the forages were fed chopped, but macropods could maintain comparatively higher intakes when these forages were offered in pelleted form (Freudenberger and Hume 1992). Other studies have found that reductions in food intake of non-pelleted forages in response to increasing NDF (%DM) were comparable for ruminants and kangaroos (McIntosh

1966; Forbes and Tribe 1970; Hume 1974). Clearly, further research is required to fully appreciate differences in the limitations of the sheep and kangaroo digestive system, but we did predict that red kangaroos should be able to maintain body condition for longer than sheep or other ruminates if offered diets particularly high in fibre.

Our model suggests that the lower energy requirement of the marsupial kangaroos (Dawson and Hulbert 1970; Munn and Dawson 2001) presents them with advantages over sheep as diet quality declines. Specifically, on an energetic basis, kangaroos are predicted to meet their maintenance energy requirements at higher forage NDF levels than sheep, even though they apparently share the sheep's intake limitation linked to NDF content (Fig. 6). This is due to the comparatively lower energetic requirements of the kangaroos (Munn and Dawson 2003) relative to sheep (Hume 1974). Other factors that contribute to the 'low-energy' lifestyle of kangaroos include their energetically-economical hopping gait, which affords them long distance movements (Dawson and Taylor 1973; Baudinette et al. 1992) to food and water, lower protein requirements (Hume 1974; Munn et al. 2006), and low daily water turnovers (Dawson et al. 1975). Thus, the major point from our study is that despite similar digestive constraints with regard to MRT-DMI and intake limits related to forage fibre content, variations in the metabolic energy requirements of kangaroos and sheep is probably the primary factor influencing their nutritional niche.

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Figure Legends

Figure 1. Relationship between dry matter intake (DMI, $\text{g/kg}^{0.75}/\text{d}$) and particle mean retention time (MRT, h) in the total gastrointestinal tract of two ruminant and two equid species. From Clauss et al. (2007), note the less drastic decrease in MRT with increasing DMI in equids.

Figure 2. Gastrointestinal tract of a typical large macropodid marsupial, the eastern grey kangaroo (*Macropus giganteus*), and an equid, the pony (*Equus caballus*). From Stevens and Hume (1995).

Fig. 3. Relationship between the relative dry matter intake (DMI in $\text{g/kg}^{0.75}/\text{d}$) and the particle mean retention time (MRT in h) in the total gastrointestinal tract in sheep and red kangaroos (*Macropus rufus*) collated from different sources (see Methods). Note the parallelity of the slopes.

Fig. 4. Relationships between the particle mean retention time (MRT, h) and the apparent digestibility (aD of DM, %) of dry matter (DM) for a) lucerne hay (LH) and b) oaten straw (OS) in sheep and kangaroos used for the model calculation in Figure 5.

Fig. 5. Relationships between dry matter intake (DMI in $\text{g/kg}^{0.75}/\text{d}$) and digestible dry matter intake (DDMI in $\text{g/kg}^{0.75}/\text{d}$) modelled according to the equations from Figs. 3 and 4 for a) lucerne hay and b) oaten straw in sheep and kangaroos. The interrupted lines indicate the extrapolated range. Filled and open symbols represent the values actually measured in digestion trials (see Methods for sources).

531

532 Fig. 6. Relationship between forage cell wall content (measured as NDF in dry matter) and
533 the food intake (DMI) in sheep (Van Soest 1965) and different macropodid species (Foot and
534 Romberg 1965; McIntosh 1966; Forbes and Tribe 1970; Hume 1974; Dellow 1982; Dellow
535 and Hume 1982; Hollis 1984; Munn and Dawson 2006).

536

537 Fig. 7. Theoretical digestible energy intake (DEI) limit at different levels of dietary fibre
538 contents (neutral-detergent fibre; NDF) levels, using information from Figure 5 for kangaroos
539 and sheep feeding on a) lucerne hay or b) oaten hay. (MR = daily metabolic energy needed to
540 maintain body mass)

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Fig 1

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