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Feeding biology of two functionally different foregut-fermenting mammals, the marsupial red kangaroo and the ruminant sheep: how physiological ecology can inform land management

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Abstract

Fermentative digestion in an expanded foregut region has evolved independently among Australia's marsupial kangaroos as well as among placental ruminants. However, notable differences occur in the form and function of the kangaroo and ruminant forestomachs, the main site of fermentation; kangaroos possess a tubiform forestomach, reminiscent of the horse colon, whereas ruminants possess a large vat-like structure. How these differences in gut form might influence kangaroo and sheep ecologies is uncertain. We compared diet choice, apparent digestibility (dry matter), food intake and grazing behaviour of Australia's largest kangaroo, the red kangaroo *Macropus rufus* and the ruminant sheep *Ovis aries*. Digestive efficiencies were comparable with other studies, 52% for kangaroos and 59% for sheep, but were not significantly different. Per animal, the smaller red kangaroos (body mass 24 kg) ingested less food than the larger sheep (50 kg), but both species engaged in food harvesting for the same length of time each day (c. 10 h). However, sheep spend additional time re-processing ingesta via rumination, a strategy not used by kangaroos. Kangaroos were more selective in their diet, having a narrower niche compared with sheep. The tubiform forestomach of kangaroos appears to support long foraging bouts, mainly in the evening and early morning; kangaroos rested during the hottest parts of the day. Conversely, sheep feed in short bursts, and gut-filling during feeding bouts is partly dependent on the animal freeing forestomach space by ruminating previous meals, possibly increasing water requirements of sheep through activity and thermal loads associated with more frequent feeding. Water use (L day⁻¹) by kangaroos was just 13% that of sheep, and kangaroos were able to concentrate their urine more effectively than sheep, even though the kangaroos' diet contained a high amount of high-salt chenopods, providing further support for potentially lower grazing impacts of kangaroos compared with domestic sheep in Australia's arid rangelands.

Disciplines

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Feeding biology of two functionally different foregut-fermenting mammals, the marsupial red kangaroo (*Macropus rufus*) and the ruminant sheep (*Ovis aries*): how physiological ecology can inform land management.

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Abstract

Fermentative digestion in an expanded foregut region has evolved independently among Australia's marsupial kangaroos as well as among placental ruminants. However, notable differences occur in the form and function of the kangaroo and ruminant forestomachs, the main site of fermentation; kangaroos possess a tubiform forestomach reminiscent of the horse colon, whereas ruminants possess a large vat-like structure. How these differences in gut form might influence kangaroo and sheep ecologies is uncertain. We compared diet choice, apparent digestibility (dry matter), food intake, and grazing behaviour of Australia's largest kangaroo, the red kangaroo (*Macropus rufus*) and the ruminant sheep (*Ovis aries*). Digestive efficiencies were comparable with other studies, 52% for kangaroos and 59% for sheep, but were not significantly different. Per animal, the smaller red kangaroos (body mass 24 kg) ingested less food than the larger sheep (50 kg), but both species engaged in food harvesting for the same length of time each day (ca. 10 h). However, sheep spend additional time re-

26 processing ingesta via rumination, a strategy not used by kangaroos. Kangaroos were more
27 selective in their diet, having a narrower niche compared with sheep. The tubiform
28 forestomach of kangaroos appears to support long foraging bouts, mainly in the evening and
29 early morning; kangaroos rested during the hottest parts of the day. Conversely, sheep feed in
30 short bursts, whereas gut-filling during feeding bouts is partly dependent on the animal
31 freeing forestomach space by ruminating previous meals, possibly increasing sheep water
32 requirements through activity and thermal loads associated with more frequent feeding. Water
33 use (L d^{-1}) by kangaroos was just 13% that of sheep, and kangaroos were able to concentrate
34 their urine more effectively than sheep, even though the kangaroos' diet contained a high
35 amount of high-salt chenopods, providing further support for potentially lower grazing
36 impacts of kangaroos compared with domestic sheep in Australia's arid rangelands.

37

38 **Keywords**

39 Foregut fermentation, Red kangaroo, sheep, ruminant, foraging, behaviour, saltbush, grazing

40

41

42 **Introduction**

43 Kangaroos (Family Macropodidae) are the largest of the extant marsupials (Dawson 1995).
44 Various species of kangaroos, together with their many smaller relatives, are the primary
45 native terrestrial herbivores in Australia and they occupy diverse habitats. As such, they are
46 often considered analogous to placental, ruminant ungulates on other continents (Dawson
47 1995). This comparison is accentuated by the apparent independent evolution of digestive
48 systems based on microbial fermentation of fibrous plant material in an enlarged forestomach,
49 proximal to their acid-secreting hindstomach and small intestine (Foot and Romberg 1965;
50 Hume 1974; Hume 1978; Hume and Warner 1980). While macropodids and ruminants are
51 primarily ‘foregut fermenters’, in both groups an expanded caecum in the hindgut also
52 provides supplementary fermentation (Stevens and Hume 1995).

53 Foregut fermentation as a method of food processing may afford higher levels of
54 digestive efficiency compared with hindgut-fermentation in herbivores like horses (Stevens
55 and Hume 1995). Indeed, the evolutionary success of the ruminants relative to the hindgut
56 fermenters that occurred during the Miocene has been attributed to the ruminants’ superior
57 digestive efficiencies in the face of expanding grasslands, because grasses have more hard-to-
58 digest fibre compared with browse and shrubs (Janis 1976; Illuis and Gordon 1992). A similar
59 pattern of foregut herbivore radiation occurred in Australia during the mid-Miocene and
60 Pliocene, where a major radiation of the Macropodidae is coincident with a reduced diversity
61 of equivalent-sized herbivorous, quadrupedal marsupials that were probably hindgut
62 fermenters (Clemens et al 1989; Hume 1999; Dawson 2006).

63 While foregut fermentation seems to have general advantages as a digestive strategy
64 for larger mammalian herbivores, the foregut morphology and physiology differ between the
65 kangaroos and ruminants such as sheep (Hume 1999). In form and function the tubiform
66 forestomach of kangaroos appears more like an equine colon than the vat-like structure of

67 ruminants (Stevens and Hume 1995; Hume 1999). Functionally, the large forestomach of the
68 macropodids is a modified plug-flow system, where digesta are transferred distally in rather
69 discrete boluses, with chewing only occurring at initial ingestion (Stevens and Hume 1995).
70 Ruminants, on the other hand, have a large sacculated forestomach, the ‘rumen’, which has
71 been described as a continuous-flow stirred-tank (Stevens and Hume 1995). Here, ingested
72 material is mixed and fermented continually, aided by frequent regurgitation and re-chewing
73 (rumination). Differences between the kangaroo and ruminant systems have been postulated
74 to have consequences for relative digestive efficiencies (Hume 1999; Munn et al. 2008) and,
75 presumably, also for foraging strategies.

76 Europeans introduced ruminants, mainly sheep and cattle, as domestic stock into
77 Australia some two hundred years ago. The impacts of sheep and cattle in Australia have been
78 marked, and the farming practices associated with these ruminants are seen as a major factor
79 in the decline of many native species (Fisher et al. 2003; Johnson 2006). Although laboratory
80 studies suggest that sheep are more efficient than kangaroos at digesting fibrous vegetation
81 (e.g. McIntosh 1966; Hume 1974), kangaroos persist in high numbers, especially in the semi-
82 arid rangelands, despite the intensive stocking of domestic ruminants (Dawson 1995). This
83 situation provides an avenue to assess the relative functional efficiency of herbivory in these
84 distinctive groups.

85 Initially, we demonstrated that field metabolic rates of red kangaroos (*Macropus*
86 *rufus*) were markedly lower than those of sheep (*Ovis aries*; merino breed) in a natural
87 rangeland situation (Munn et al. 2009). However, basic measures of energy and water
88 requirements only partly contribute to our understanding of herbivore ecologies or potential
89 environmental impacts. In this study we have investigated a range of factors that influence
90 kangaroo and sheep activities in a typical Australian rangeland. Specifically, do kangaroos
91 and sheep differ in their digestive efficiencies, diet choices and diet overlap, and what impacts

92 could these have on their urine electrolyte levels, urine concentrations, feeding behaviours
93 and associated energy and water needs? Together, answers to these questions provide a
94 clearer picture of how kangaroos and sheep, with their different foregut fermentation systems,
95 interact in Australia's arid and semi-arid rangelands. Moreover, our study presents a timely
96 example of how physiology can be applied to evaluate and inform large-scale management of
97 grazing systems, particularly for mitigating environmental damage associated with
98 overgrazing.

99

100 **Materials and Methods**

101 *Study site and climatic conditions*

102 The study was conducted at Fowlers Gap (31°05' S, 141°43' E), the Arid Zone Research
103 Station of the University of New South Wales, located approximately 112 km north-east of
104 the city of Broken Hill, NSW Australia. The station covers approximately 39,200 ha, with
105 vegetation dominated by low woody shrubs (< 1 m) of the family Chenopodiaceae. A
106 commercial sheep enterprise operates concurrently with research activities; also persisting on
107 the station are large uncontrolled populations of four kangaroo species; the red kangaroo (*M.*
108 *rufus*), western grey kangaroo (*M. fuliginosus*), eastern grey kangaroo (*M. giganteus*) and the
109 euro (*M. robustus erubescens*). Rainfall is variable, with a yearly average ($\pm$ SEM) of $238 \pm$
110 21 mm p.a. and a co-efficient of variation of 54% (1969-2006 inclusive; SILO Patched Point
111 Dataset, Bureau of Meteorology and NHM QLD; data patched for 1971, and February and
112 April 2000). This study was conducted during a mild autumn between the 2nd and 10th of
113 April 2007. In the six months prior to the study the research station received a total of 49.2
114 mm of rain, with the bulk occurring in January (18 mm) and March (15 mm) 2007 (Bureau of
115 Meteorology, Australia).

116

117 *Experimental design and animal enclosure*

118 The aim of this study was to compare the feeding behaviour and resource-use patterns of the
119 dominant native Australian arid-zone herbivore, the red kangaroo, with that of a major
120 domestic herbivore, the merino sheep, grazed together in a typical rangeland environment.
121 The experiment was carried out in a large (16 ha), herbivore-proof enclosure, situated on an
122 alluvial rise and naturally vegetated with chenopod shrubs (mainly saltbushes) and sparse
123 grasses; scattered small trees (*Casuarina sp.*) provided shade for the experimental animals.
124 The enclosure had not been grazed by kangaroos for over five years and had been free from
125 sheep or other herbivores (e.g. rabbit, goat, cattle) for > 20 years. At the beginning of the
126 experiment (i.e. after 3-weeks acclimation of animals) vegetation was examined by point
127 sampling along 20 randomly chosen transects (100 m). Point samples were taken every metre
128 along transects using a 5 mm diameter metal spike; a total of 2000 points was sampled. Each
129 point was categorised as bare (including litter) or belonging to the following plant groups:
130 grass, flat chenopod (saltbushes), round chenopod (bluebushes and copper burrs), forb
131 (herbaceous dicots - often annuals), malvaceous sub-shrub and trees (Dawson and Ellis
132 1994, 1996). Grass was considered dry, most plants having less than 15% green material (and
133 most were completely dry). The height of plants in transects was recorded and relative cover
134 subsequently estimated after correction for the size of the spike (5 mm diameter in our case;
135 Dawson and Ellis 1994). The biomass of each plant category was calculated using percent
136 cover and plant height (Edwards et al. 1995); total biomass was estimated to be 44 ± 30 g dry
137 matter m^{-2} . Average ($\pm$ SEM) standing plant biomass was estimated from 60 randomised
138 clipped plots of 0.25 m^2 to be 44 ± 8 g dry matter m^{-2} ; this level of biomass was markedly
139 higher than levels outside the enclosure (Pers. Obs.). Water was provided *ad libitum* via a
140 refilling trough that was used by all experimental animals. A centrally placed seven-meter
141 tower provided a platform from which behavioural observations were made.

142

143 *Study animals*

144 Wild red kangaroos (n = 7) were captured using a CO₂-powered tranquilliser rifle (darts were
145 loaded with Zoletil 100, 10 mg kg⁻¹), fitted with identifying ear tags and polyvinyl collars (2.5
146 cm wide, marked with patterns of coloured reflective tape), transferred to the experimental
147 enclosure, and allowed to acclimate for at least three weeks. Sheep (merino breed) (n = 7)
148 were introduced to the enclosure two weeks prior to data collection. All animals were mature,
149 non-reproductive (non-lactating or pregnant) females. At the beginning of the experiment
150 kangaroos and sheep had an average body mass of 23.4 ± 0.8 kg and 47.8 ± 2.8 kg,
151 respectively; sheep had five months wool and so their measured body masses were corrected
152 by subtracting 3.6 kg (Edwards et al. 1996). In a concurrent study we measured the energy
153 and water turnover of these animals over 5-9 days following the acclimation period (Munn et
154 al. 2009). At the end of the experiment animals were humanely killed (animal ethics approval,
155 UNSW ACEC 06/85A; NSW National Parks and Wildlife Scientific Licence S12054).
156 Kangaroos were killed while feeding at night by rifle shot to the head destroying the brain,
157 following the code of practice for the humane shooting of kangaroos (DEWHA 2008). Sheep
158 were first mustered to a holding pen and killed by rifle shot to the back of the head destroying
159 the brain (SCARM 1991). Blood and urine samples were immediately taken for electrolyte
160 analysis; blood was also used for field metabolic rate and water turnover measurements
161 (Munn et al. 2009). Forestomach and faecal (distal colon) samples were taken for diet analysis
162 and estimation of dry matter digestibility and dry matter intake.

163

164 *Behaviour*

165 Three days were dedicated to 24 h behavioural observations. We used a point-sampling
166 technique (Dunbar 1976) to quantify kangaroo and sheep behaviours. Scans were made every

167 10 min during the day, but every 20 min at night when observations were more difficult.
168 Night observations were made using a weak spotlight and Nikon 10x70 marine binoculars.
169 The behaviour of each species was categorised into three broad types:

170 *Foraging*: when the animal was consuming or searching for food, which included
171 eating (cropping and chewing), slow searching (i.e. the movement while feeding within a
172 patch, requiring one or two steps), and fast searching (usually walking fast between food
173 patches), interspersed with periods of cropping and chewing.

174 *Resting/ruminating*: all non-active behaviour when the animal appeared relaxed,
175 which included lying, crouching, and standing. In kangaroos, periods of lying or crouching
176 were considered ‘resting’, but for sheep sitting or lying can include bouts of rumination. We
177 were unable to measure rumination directly and periods of inactivity by sheep sitting or lying
178 must be considered as either resting or ruminating; most importantly, they do not include
179 periods of active locomotion (including standing) or foraging.

180 *Other*: Miscellaneous behaviours, which were uncommon, such as grooming,
181 drinking, and locomotion associated with drinking at the water trough (i.e. moving to and
182 from water). This included all other active non-foraging behaviours (e.g. locomotion or
183 standing alert, sometimes in response to a disturbance).

184

185 *Osmolality of blood and urine and urine electrolytes*

186 Urine samples were taken from the bladders of kangaroos (n =5) and sheep (n = 6) following
187 post-mortem evisceration; samples were unavailable from two kangaroos and one sheep (i.e.
188 bladders were empty). These were immediately stored on ice in an insulated box and were
189 frozen within one hour of collection. Urine sub-samples were later thawed and analysed for
190 osmolality, along with plasma samples from blood collected via heart puncture on deceased

191 animals. Osmolality of urine and plasma was determined using a freezing-point depression
192 osmometer (Gonotec Osmomat 030; Gallay Scientific, Melbourne).

193 Concentrations of electrolytes in urine, including sodium (Na^+), potassium (K^+),
194 chloride (Cl^-), magnesium (Mg^{++}) and calcium (Ca^{++}) were quantified using Inductively
195 Coupled Plasma Optical Emission Spectrometry (Perkin Elmer 5300DV ICP-OES; Sydney
196 Analytical Services, Seven Hills, NSW), and concentrations of Cl^- were determined using an
197 Ag/AgS Ion Specific Electrode (Sydney Analytical Services, Seven Hills, NSW). Urine sub-
198 samples were diluted for electrolyte analysis at the following ratios: 1:100 (Na^+ and K^+), 1:10
199 (Mg^{++} , Ca^{++} and sheep Cl^-) and 1:20 (kangaroo Cl^-). Electrolyte concentrations were not
200 available from blood as samples were used for labelled water analysis (see Munn et al. 2009).

201

202 *Diets*

203 At dissection samples from the kangaroo forestomach ($n = 7$) and sheep rumen ($n = 7$) were
204 collected near the oesophageal opening and were stored on ice prior to freezing (within 1 h).

205 Diet was assessed via micro-histological identification of plant fragments (Dawson and Ellis
206 1994; Edwards et al 1995). Fragments were identified as grass, flat chenopod, round

207 chenopod, forb, malvaceous sub-shrub, or tree. Samples of gut material (10 ml) were

208 washed through two sieves yielding particles greater than 500 μm and between 500 μm and

209 125 μm . Particles smaller than 125 μm were discarded because they were mostly dust and

210 microhairs. The relative volumes of the two size classes were determined by centrifugation.

211 Five sub-samples of each size class were spread on separate microscope slides. Random

212 horizontal transects were chosen and the first 20 particles on transects were identified. For

213 each size class 100 particles were examined, i.e., 200 in total per animal. Identification of

214 plant particles was made using an extensive reference collection (Dawson and Ellis 1994).

215 Total proportion of plant categories in the diet was determined according to the ratio of
216 particle size classes in each sample.

217 Diet overlap between sheep and kangaroos was determined using a Proportional
218 Similarity Index (PSI; Feinsinger et al. 1981), which compares the relative proportions of diet
219 items found in kangaroo and sheep forestomach. The dietary niche breadths of each species
220 were also determined using PSIs, with the relative proportion of each diet item in kangaroo
221 and sheep forestomach, respectively, being compared with that available in the environment
222 (i.e. % biomass; Feinsinger et al. 1981). Diet overlap PSI and niche breadths PSIs were
223 examined statistically using Mantel tests (Dawson and Ellis 1994) and software by Bonnet
224 and Van de Peer (2007; zt Version 1.1). Diet preferences of kangaroos and sheep for each
225 encountered diet item were examined using relativised electivity indices (*E), following
226 Vanderplog and Scavia (1979a,b; but see equations 6 and 7 in Lechowicz 1982).

227

228 *Diet digestibility*

229 Apparent digestibilities of dry matter (DM) from kangaroo and sheep forestomachs were
230 estimated using manganese (Mn) as a naturally occurring, indigestible marker (Nagy 1977).
231 Digestibility was estimated using Mn concentrations from forestomach samples taken
232 adjacent to the oesophageal opening and compared with that in faeces collected as formed
233 pellets from the distal colon. Digestibility was estimated according to:

$$234 \quad \text{Apparent digestibility (\%)} = \left(1 - \frac{M_d}{M_f} \right) \cdot 100 \quad (1);$$

235 where M_d = concentration of Mn in the forestomach sample (per unit DM) and M_f =
236 concentration of Mn faeces (per unit DM).

237 Forestomach (as above) and faecal (distal colon) samples (ca. 70 g) were collected at
238 dissection, immediately stored on ice, and frozen within one hour. Forestomach material and

239 faeces (ca. 20 g wet mass) were later dried at 60°C to constant mass and milled through a 1
240 mm mesh (Glen Creston c.580 micro hammer mill, Glen Creston, London). Sub-samples (0.6
241 – 1.0 g DM) of ground material were digested in nitric acid (10 mL; 70%) using a Milestone
242 Microwave Digestion System (Milestone MLS-1200 MEGA; Program 1) according to the
243 manufacturer's instructions. Digesta were weighed, diluted to 25 ml with deionized water, and
244 allowed to settle overnight. The supernatant was drawn off and analysed for Mn content using
245 an Inductively Coupled Plasma Atomic Emission Spectrometer (ICP-AES; Vista AX, Varian;
246 California, USA).

247

248 *Dry matter intakes*

249 Gross dry matter intakes (DMI) by sheep and kangaroos were estimated in relation to daily
250 energy needs (Nagy 2001). These were taken from field metabolic rates (FMR; kJ d^{-1})
251 obtained concurrently with this study (Munn et al. 2009). Gross food intakes were estimated
252 assuming that the gross energy content of sheep and kangaroo diets was 18 kJ g DM (Robbins
253 2001). Robbins (2001) reported gross energy contents of herbaceous material of 16.3 - 21.3 kJ
254 g^{-1} DM, comparable to that reported for perennial grasses and saltbushes (Corbett 1990; see
255 also Golley 1961). Thus, assuming each animal's coefficient of DM digestibility was similar
256 to energy digestibility (Moir 1961; Rittenhouse et al. 1971), we estimated that the digestible
257 energy content of whole diets ingested by kangaroos and sheep was 9.4 ± 0.7 and 10.6 ± 0.4
258 kJ g^{-1} DM, respectively. These levels of digestible energy content were similar to those
259 measured using in-vitro acid-pepsin digestions of forbs, grasses, and shrubs at our Fowlers
260 Gap study site (range of means was 9-14 kJ g^{-1} DM for all plant types from winter and
261 summer for sheep and kangaroos; McLeod, 1996).

262

263 *Statistical analysis*

264 Unless otherwise stated we used one-way ANOVAs or repeated measures ANOVAs for
265 between- and within-species comparisons. Assumptions for ANOVA were tested using the
266 Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) and Levene's test for homogeneity of
267 variances ($\alpha = 0.05$). Heteroscedastic data were $\log_{10}$ transformed (blood osmolarity, urine
268 osmolality, urine concentrations for Mg^{++} and Cl^-). When ANOVAs yielded significant
269 differences, post-hoc comparisons using Tukey's Honest Significant Differences (HSD) were
270 applied. The proportions of time that kangaroos and sheep spent engaged in different
271 behaviours over 24 h were compared using nested ANOVAs, with species nested in time. Diel
272 time-use of kangaroos and sheep was analysed using Tukey's HSD to compare patterns within
273 and between species in 20-min blocks. Proportional data were arcsine transformed. Diet
274 contents from kangaroo and sheep forestomach were not normally distributed or
275 homoscedastic. Thus, a Wilcoxon-Mann-Whitney test was used to compare the contents of
276 specific diet items between species. Within species, differences in the proportions of different
277 diet items were compared using Kruskal-Wallis tests. Of note, repeated measures ANOVAs
278 on the proportional diet contents within each species, followed by Tukey's HSD, yielded
279 identical outcomes regarding statistical significance. Results are presented as mean $\pm$ standard
280 error of the mean (SEM) and alpha was set at 0.05.

281

282 **Results**

283 *Animals*

284 Kangaroos maintained body mass throughout the experiment (% initial body mass change was
285 $0.20 \pm 0.21\% \text{ d}^{-1}$; which was not significantly different from zero; $Z = 0.97$, $P = 0.34$). Sheep
286 lost body mass on average ($\pm$ SEM) (% initial body mass change was $-0.73 \pm 0.16\% \text{ d}^{-1}$,

287 which was significantly different from zero, $Z = -3.75$, $P < 0.001$). However, this level of
288 mass loss was not considered biologically significant because sheep can drink 8-10% of their
289 body mass in a single bout (Squires 1981), and this level of body mass change was consistent
290 with that generally observed for sheep over comparable periods (Midwood et al. 1994).
291 Moreover, initial body masses for sheep were measured in the afternoon, after animals had
292 visited water, but final measurements were made in the morning, before sheep were able to
293 drink (pers. obs.).

294

295 *Behaviour*

296 The proportions of time that kangaroos and sheep foraged each day did not differ ($F_{2,46} =$
297 0.028 , $P = 0.87$). They spent on average 10.4 h d^{-1} (i.e. 43.5% of each day) engaged in
298 activities associated with food harvesting (i.e. searching and moving, cropping and chewing).
299 Similarly, sheep and kangaroo did not differ in the amount of time spent resting or
300 resting/ruminating (ca. 12 h d^{-1} ; $F_{2,46} = 0.036$, $P = 0.85$). However, in other studies sheep have
301 been found to spend 8-10 h per day ruminating, i.e. food processing by re-chewing (Hulet et
302 al. 1975), but kangaroos do not ruminate (Hume 1999).

303 The diel time-use patterns of kangaroos and sheep differed (Fig. 1A). Red kangaroos
304 spent the greater portion of each evening and early morning harvesting food, with lulls in
305 feeding between mid-night and 0400 h (Fig. 1A), with a distinct rest period between 0800
306 and 1500 h ($F_{2,46} = 5.99$, $P < 0.001$, nested ANOVA, Tukey's HSD $P < 0.05$; Fig. 1A).
307 Conversely, sheep had regular feeding bouts throughout the day, punctuated by periods of
308 rest/rumination at around 0600 h, 1000 h, and 1900-2000 h (Tukey's HSD $P < 0.05$; Fig. 1B).
309 Sheep showed a distinct rest period in the early morning between 0100 and 0300 h (Tukey's
310 HSD $P < 0.05$; Fig. 1B).

311

312 *Diets*

313 Flat-leafed chenopods comprised the most abundant food source available for kangaroos and
314 sheep and were nearly 75% of the aboveground plant biomass within the enclosure (Table 1).
315 Round-leafed chenopods were the next most abundant food source, followed by grasses and
316 then forbes and trees (Table 1). Available biomass of these plant groups was not directly
317 reflected in forestomach contents of sheep or kangaroos (Table 2), and differences were
318 apparent in sheep and kangaroos selection of plant types. Kangaroo forestomach contents
319 were dominated by round-leafed chenopods (ca. 64%) followed by equal proportions of
320 grasses and flat-leafed chenopods (ca. 15-16% for each; Table 2). Conversely, sheep
321 forestomach contents were characterised by relatively high and equal proportions of both flat-
322 and round-leafed chenopods (ca. 44-46% for each; Table 2).

323 Overall, kangaroos had a narrower dietary niche breadth than sheep; PSI (%) for
324 forestomach content relative to availability for kangaroos was $41.4 \pm 3.8\%$, and was $66.5 \pm$
325 3.1 for sheep ($F_{2,13} = 24.2$, $P < 0.001$). There was considerable overlap between kangaroo and
326 sheep diets (PSI of $66 \pm 2\%$), but Mantel's test (Mantel 1967) indicated they were
327 significantly different ($r = -0.624$, $P = 0.0001$). Dietary niche breadths indicated that neither
328 kangaroos nor sheep foraged for items in direct proportion to availability in the environment,
329 and differences in diet selection by each herbivore were apparent (i.e. electivity indices, E^* ;
330 Table 3). Specifically, the main preferred diet item for kangaroos and sheep was round-leafed
331 chenopods (Table 3). Grass was distinctly not preferred by sheep, but was apparently grazed
332 neutrally by the kangaroos. Although not statistically significant, sheep tended to have a
333 greater preference for trees/shrubs than did the kangaroos ($P=0.09$; Table 3).

334

335 *Blood and urine osmolalities and urine electrolytes*

Kangaroos produced urine that was 1.8 times more concentrated than that of sheep (Table 4). On average, osmolality of kangaroo urine was 4.6 times that of blood, as compared with sheep that had an average urine osmolality only 2.9 times that of blood (Table 4). The high concentration of kangaroo urine was associated mainly with higher contents of Na^+ and K^+ compared with sheep urine ($P \leq 0.001$, Table 4). Kangaroo urine was also high in Cl^- , about 1.7 times that of sheep, but this difference was not statistically significant ($P = 0.21$). Nonetheless, Cl^- contents of the kangaroo urine were variable, ranging between 184 and 797 mmol L^{-1} (median = 630 mmol L^{-1}) compared with the narrower sheep range of 188-370 mmol L^{-1} (median = 333 mmol L^{-1}).

Dry matter digestibility and intake

Apparent digestibility of dry matter from kangaroo and sheep forestomachs did not differ, and ranged between 52% and 59% (Table 5). From this, we estimated that kangaroos would have required only around 33% of the digestible dry matter (g d^{-1}) of sheep in order to meet their daily energy requirements (i.e. field metabolic rate, FMR kJ d^{-1} ; see Methods and Table 5). Therefore, on a per capita basis, the kangaroos in our study needed only 37 % as much food (g DM d^{-1}) as sheep in order to meet their daily energy needs (i.e. FMR; Table 5).

Discussion

Comparisons of the digestive performance of kangaroos and sheep have been limited to laboratory studies, where animals are typically restricted in movements (e.g. small pens or metabolism cages), exposed to thermoneutral conditions, and fed uniform, dried diets (McIntosh 1969; Forbes and Tribe 1970). How the digestive efficiency of sheep and kangaroos might differ under free-ranging conditions is uncertain. We found here that the digestive efficiencies of red kangaroos ($52.1 \pm 3.9\%$; Table 9) and sheep ($59.1 \pm 2.4\%$; Table

8) selecting from arid, rangeland forage in our study were not significantly different ($P = 0.13$; Table 8), but trended in the direction reported previously from feeding trials using lower fibre forages (Hume 1999). Digestibility declines by 10 – 15% when these species are fed higher fibre diets (Hume 1974; Hume 1999; Munn and Dawson 2006), implying that despite the dry environmental conditions, our kangaroos and sheep were selecting diets to maintain appropriate intakes of better quality forage (Table 2), despite differences in their diet choices. Red kangaroos were more selective, and their dietary niche breadths were narrower than those of the sheep, i.e. 41.4% versus 66.5%, respectively (see also Dawson and Ellis 1994).

The amount of raw feed that herbivores need to meet daily energy demands is largely driven by food water-content, which can vary <10% to >90%, and by digestibility that also vary widely. The pasture conditions in this study allowed us to calculate representative daily dry-matter-intake (DMI) requirements by using field metabolic rates (measured simultaneously; Munn et al. 2009). These daily DMI requirements were 994 g and 2661 g DM d⁻¹, respectively for kangaroos and sheep (Table 5). These intakes reflect the high body-mass difference between average size individuals of the two species (Table 5), as well as fundamental metabolic differences and possible differences in feeding costs. Of note, large male red kangaroos exceed sheep in body mass and can be over 90 kg body mass, and have higher absolute food requirements than mature female kangaroos, but large males are uncommon in kangaroo populations (Dawson 1995).

Information about the daily dry-food requirements of kangaroos compared with sheep has implications for the grazing management of Australia's rangelands, and highlights the importance of considering digestive efficiencies of different herbivores when considering their grazing impacts. For example, relative grazing pressures of herbivores in Australia are typically assessed against that of a 'standard' merino sheep, a core animal to Australia's rangeland industries (Dawson and Munn 2007). The energy requirements of a standard mature

386 sheep, known as a 'dry-sheep-equivalent' (DSE) are those pertaining to a 45-kg non-
387 reproductive/non-lactating (dry) ewe or wether (Dawson and Munn 2007; Munn et al 2009).
388 DSEs have become the staple measure for comparing herbivore-grazing pressures in Australia
389 (Landsberg and Stol 1996; SoE 2006; Kirkpatrick et al. 2007). Recent studies reported a DSE
390 of 0.35 for a mature, dry kangaroo of average mass (25 kg), based on direct comparisons of
391 kangaroo and sheep field metabolic rates (FMR, kJ d^{-1} ; Munn et al. 2009); that is, the
392 kangaroo uses only 35% of the energy of the sheep. Thus, if digestive efficiencies of the
393 kangaroos and sheep were the identical, then the proportional grazing impact of kangaroos
394 relative to sheep and in terms of dry feed also would be 0.35. However, differences in
395 digestive efficiency could markedly change the relative DSE of a kangaroo. If we were to
396 accept that the small difference in digestive efficiencies that we measured between kangaroos
397 and sheep was biologically relevant (i.e. 52% for kangaroos, 59% for sheep; Table 5) then we
398 would predict a kangaroo DSE of 0.42 (Table 5). Such a calculation draws attention to the
399 fact that in different regions and seasons, differences in available diets and diet qualities will
400 undoubtedly affect herbivore digestive efficiencies, and thus affect any predicted food intake
401 requirements and subsequent grazing pressures.

402 That the sheep satisfied their higher gross feed requirements by foraging for the same
403 time each day as the kangaroos is initially surprising, because the red kangaroos ingested only
404 one third as much food (dry matter). Foraging-time patterns were, however, markedly
405 different between species (Fig. 1), with the sheep using more but shorter foraging bouts. What
406 can these observations tell us about the ecology of foraging by sheep and kangaroos, and how
407 might this further influence their relative grazing pressures? Compared with kangaroos, sheep
408 appear to be less selective, bulk feeders (this study; Dawson and Ellis 1994). They have
409 proportionally bigger bites (relatively wider mouths) than those of the smaller, more slender-
410 jawed red kangaroo (Belovsky et al. 1991). Sheep feeding on chenopod shrubs have an

411 average bite size of 0.42 g dry matter as compared with only 0.16 g for red kangaroos, but
412 their rates of biting whilst cropping are comparable at 18 bites per minute (Belovsky et al.
413 1991). This focuses on the ability of sheep to harvest higher quantities of food in the same
414 period as kangaroos, but it overlooks processing the larger bite with more stem and, as such,
415 more hard-to-digest fiber.

416 The fundamental difference between kangaroos and sheep lies with the additional
417 feed-breakdown processes by sheep via rumination. Kangaroos do not ruminate and they
418 complete the oral processing of feed at time of ingestion. In sheep food processing is not
419 complete post-ingestion, and food is extensively re-processed by re-chewing and re-ingestion
420 during inter-feed bouts. Rumination offers sheep the benefits of increased mechanical
421 processing after ingestion and thus increased digestibilities, but this has a cost; it is time-
422 intensive. Rumination by sheep can comprise up to 8-10 h of resting/non-feeding bouts (Hulet
423 et al. 1975). Detailed behavioural observations confirm such estimates for sheep at our study
424 site, with free-ranging sheep ruminating for 7 h d⁻¹; this was half of the time spent 'resting'
425 (T.J. Dawson and D.M. Watson, unpublished observations). Time spent ruminating by sheep
426 should be included with time spent actively feeding to fully estimate their total temporal-
427 investment in energy acquisition. If we assume that sheep ruminate for 50% of resting time
428 then they spent 60% more time than red kangaroos in feed acquisition and processing, i.e.
429 16.5 h d⁻¹ against 10.4 h d⁻¹. Does this time ruminating have an impact on the overall daily
430 energy budget of sheep relative to that of kangaroos? This is a complex question because of
431 differences in basal metabolism, modes of locomotion as well as differences in digestive
432 strategies. However, the FMR of the kangaroos was 2.3 times their BMR whilst that of the
433 sheep was 3.8 times BMR (Munn et al. 2009). During the long period of the day that the
434 kangaroos rested they spent much time lying, apparently asleep, which contrasts with the
435 sheep and their more numerous and shorter rumination/resting periods. These different

436 patterns should contribute significantly to the overall differences FMR of kangaroos and
437 sheep.

438 One important difference between kangaroos and sheep concerns their modes of
439 locomotion. Kangaroos are exemplified by their unique bipedal hopping at higher speeds,
440 which is more energetically efficient than quadrupedal locomotion at comparable speeds
441 (Dawson and Taylor 1973), as seen in sheep. However, at lower speeds kangaroos use a
442 different, more energetically expensive form of locomotion, the pentapedal gait (Dawson and
443 Taylor 1973). Pentapedal movement uses all four limbs in addition to the tail to propel the
444 animal, and is used by kangaroos foraging within patches. It has been suggested that the
445 expense of pentapedal locomotion forces kangaroos to be highly selective feeders (Clancy and
446 Croft 1991). Sheep on the other hand may move between food patches more cheaply, and so
447 may be less selective in their diets. Nonetheless, this is probably simplistic and empirical
448 comparisons of the energy used by sheep and kangaroos during fine-scale feeding are lacking.
449 Factors like body size, phylogeny, oral and digestive morphology and vegetation structures
450 probably provide dominant impacts on feeding strategies. The complexity of this point is
451 highlighted by seasonal changes in food types and availability and the subsequent responses
452 of sheep and kangaroos. These issues are also important for understanding these herbivores'
453 role in landscape function and grazing management.

454 During seasons when grasses are available both sheep and kangaroos typically eat
455 them, but the level of selection for grasses is stronger by kangaroos (Dawson and Ellis 1994
456 Edwards et al. 1995; Edwards et al. 1996). As conditions deteriorate kangaroos largely
457 maintain their strong preference for grasses, but sheep switch to more available forage,
458 usually chenopod shrubs in the rangelands of our study (Dawson and Ellis 1994; Edwards et
459 al. 1995; Edwards et al. 1996). However, our study was conducted during an extended dry
460 period when grass (particularly green grass) was scarce (Table 1). Our kangaroos fed mainly

461 on round-leafed (bluebush) and, to a lesser extent, flat-leafed (saltbush) chenopods (Table 2).
462 High intakes of chenopods by kangaroos during dry conditions have been reported in other
463 studies (Barker and Griffiths 1966; Bailey et al. 1971; Barker 1987), but the kangaroos in our
464 study did not lose body mass throughout the experiment (Table 8). As such, adult red
465 kangaroos appear capable of meeting their maintenance needs even when their usually
466 selected diet of grasses is not available. The ability of red kangaroos to switch diets in this
467 manner may further reflect differences in how the kangaroo and ruminant foregut systems
468 operate in Australia's arid rangelands.

469 Sheep in Australia's rangelands are capable of considerable diet switching (Squires
470 1981; Dawson and Ellis 1994; Edwards et al. 1996), but they face challenges associated with
471 particle outflow from the rumen. In particular, a major consequence of the ruminant system is
472 a potential limit to food intake resulting from bulky plant material filling the gut (Stevens and
473 Hume 1995). That is, in order to free gut-space for further intake, sheep first must re-chew
474 previously harvested material to facilitate rumen emptying, only then can sheep continue
475 feeding. This was evident in our study, where sheep were observed to feed in bursts,
476 interspersed with periods of rest and rumination (Figure 1B). The ability of kangaroos to feed
477 for longer periods may be associated with the tubiform nature of their forestomach. Flow of
478 material from the tubiform forestomach of kangaroos is not restricted by particle-size as it is
479 in sheep, and numerous haustrations of the kangaroo forestomach support gut expansibility
480 (Munn et al. 2006) that probably assist kangaroos to sustain food intakes during long feeding
481 bouts. Moreover, the extensive separation of small and large particles in the kangaroo foregut
482 (Dellow 1982; Hume 1999), where finer particles are promoted more rapidly for further
483 processing in the caecum and proximal colon, may assist gut-filling during single foraging
484 bouts. This digestive arrangement offers kangaroos further advantages for their feeding
485 ecology, particularly with respect to water conservation. Because kangaroos are capable of

486 long feeding bouts (Watson and Dawson 1993; this study), they can focus on feeding when
487 thermal conditions are favourable, as was seen here. Red kangaroos generally rested under
488 shade trees during the hottest parts of the day (Figure 1A; Watson and Dawson 1993; Dawson
489 et al. 2006), a behaviour that reduces their need for evaporative cooling (Dawson and Denny
490 1969; Dawson et al 2006).

491 The kangaroos in our study used just 13% of the water of sheep (1.5 L versus 12 L d⁻¹
492 for kangaroos and sheep respectively; Munn et al. 2009). This stark difference in water usage
493 has been observed in other studies (e.g. Dawson et al. 1975). However, in all previous studies
494 the water turnover of red kangaroos has been measured in animals feeding mainly on grasses
495 (e.g. Dawson et al. 1975; Dawson et al. 2006). Unique to our study is the finding of
496 comparatively low water turnover rates for kangaroos even when ingesting high quantities of
497 chenopod shrubs (*Maireana* spp; Table 5).

498 Unlike grasses, chenopods are typically high in electrolytes, particularly Na⁺ and Cl⁻
499 (Macfarlane et al. 1967; Dawson et al. 1975). Excessive amounts of these minerals must be
500 eliminated, usually through the kidneys. On a diet of over 80% chenopods (Table 2) our red
501 kangaroos showed their considerable urine concentrating abilities (Table 4) but also had
502 comparatively low water turnover rates (Munn et al. 2009). Concentration of sheep urine
503 (mOsmol kg⁻¹) was less than half that of kangaroos and was similar to that reported for
504 merinos feeding on saltbushes (ca. 1000 mOsmol kg⁻¹; Macfarlane et al. 1967). Our data are
505 therefore consistent with conclusions that sheep grazing in Australia's chenopod shrublands
506 rely heavily on access to free water (Macfarlane 1967; Wilson 1974a,b; Dawson et al. 1975).
507 When sheep switch from low-salt grasses and forbs to high-salt chenopods their water use
508 dramatically increases from near 6 L d⁻¹ to 10-12 L d⁻¹ (Wilson 1974; Squires 1981; Munn et
509 al. 2009 and this study). Indeed, the focus of sheep grazing around watering points is a major
510 factor reducing biodiversity and increasing land degradation in these areas (James et al. 1999;

511 Fisher et al. 2003). Red kangaroos are not water-focussed in their grazing patterns (Montague-
512 Drake and Croft 2004; Fukada et al. 2009) and thus their impact on the rangelands is more
513 broadly spaced.

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A) Red Kangaroo

B) Sheep

Table 1: Mean ($\pm$ SEM) vegetation cover and biomass of available plant types found in the 16-ha experimental enclosure measured at the beginning of the field trial (i.e. after animals had acclimated in the enclosure for 2-3 weeks).

	Bare ground	Grass [†]	Flat-leafed chenopods	Round-leafed chenopods	Forbs	Malavaceous sub-shrubs*	Trees
Relative cover (%)	80.1 $\pm$ 1.4	3.5 $\pm$ 0.6	10.5 $\pm$ 1.0	2.9 $\pm$ 0.7	2.7 $\pm$ 0.4	-	0.3 $\pm$ 0.2
Biomass (g m ⁻²)	-	15.4 $\pm$ 2.9	161.7 $\pm$ 16.0	33.3 $\pm$ 8.5	6.7 $\pm$ 1.2	-	1.8 $\pm$ 1.4
Biomass %	-	7.0	73.9	15.2	3.1	-	0.8

Note: [†]Grasses were considered dry, all were < 15% green and most were completely dry (pers. Obs); *Not detected during survey, though they were observed within the enclosure.

Table 2: Mean ($\pm$ SEM) forestomach contents of red kangaroos (n = 7) and sheep (n = 7) as a proportion (%) of all identified particles.

	Grass	Flat-leafed chenopods	Round-leafed chenopods	Malavaceous sub-shrubs	Forbs	Trees
Red kangaroo	15.1 $\pm$ 3.2 ^B	16.0 $\pm$ 4.0 ^B	64.3 $\pm$ 5.0 ^A	0.6 $\pm$ 0.2 ^C	2.4 $\pm$ 0.3 ^C	1.5 $\pm$ 0.4 ^C
Sheep	2.0 $\pm$ 0.6 ^{B^C}	46.3 $\pm$ 3.1 ^A	44.8 $\pm$ 3.4 ^A	0.6 $\pm$ 0.1 ^C	2.3 $\pm$ 0.3 ^{B^C}	3.9 $\pm$ 1.0 ^B
Species effect						
<i>U</i> -statistic	77	28	72	54	56	39
<i>P</i> -value	0.002	0.022	0.015	0.89	0.71	0.10

Note: Between species effects for diet items were tested using Wilcoxon-Mann-Whitney test (*U*-statistic); Superscripts denote significant difference within species, Kruskal-Wallis (DF = 5; Kangaroo Chi-Square = 36.8, Sheep Chi-Square = 32.1, and Tukey's HSD post-hoc ^{A,B,C}*P* <0.05).

Table 3: Mean ($\pm$ SEM) electivity indices for diet items identified from the forestomach of red kangaroos (n = 7) and sheep (n = 7) grazing chenopod shrublands.

	Grass	Flat-leafed chenopods	Round-leafed chenopods	Malavceous sub-shrubs	Forbs	Trees
Red kangaroo	0.03 ± 0.07^C	-0.79 ± 0.05^A	0.38 ± 0.05^D	-	-0.41 ± 0.06^B	-0.09 ± 0.12^C
Sheep	-0.73 ± 0.09^A	-0.48 ± 0.05^A	0.22 ± 0.08^B	-	-0.42 ± 0.09^A	0.27 ± 0.16^B
Species effect						
<i>U</i> -statistic	77	31	65	-	56	37
<i>P</i> -value	0.002	0.007	0.12	-	0.70	0.06

Note: Between species effects for diet items were tested using Wilcoxon-Mann-Whitney test (*U*-statistic). Kruskal-Wallis (DF = 4; Kangaroo Chi-Square = 28.0, Sheep Chi-Square = 23.1, and Tukey's HSD post-hoc ^{A,B,C,D}*P* <0.05).

Table 4: Mean ($\pm$ SEM) urine electrolytes and urine and blood omsolality for red kangaroos (n = 5) and sheep (n = 6) grazing chenopod shrublands.

	Sodium	Potassium	Calcium	Magnesium	Chloride	Urine Osmolality (mOsmol kg ⁻¹)	[#] Blood Osmolality (mOsmol kg ⁻¹)
	(mmol L ⁻¹)	(mmol L ⁻¹)	(mmol L ⁻¹)	(mmol L ⁻¹)	(mmol L ⁻¹)		
Red Kangaroo	644 $\pm$ 41	165 $\pm$ 14	1.3 $\pm$ 0.5	27 $\pm$ 8	499 $\pm$ 120	1852 $\pm$ 204	407 $\pm$ 23
Sheep	382 $\pm$ 37	97 $\pm$ 14	1.6 $\pm$ 0.6	11 $\pm$ 1	296 $\pm$ 33	1000 $\pm$ 96	349 $\pm$ 8
Species effect							
<i>F</i> -statistic	22.3	11.8	0.13	6.17	1.86	16.1	7.1
<i>P</i> -value	0.001	0.007	0.72	0.04	0.21	0.003	0.02

Note: Species effects were tested using ANOVA; [#]sample sizes for whole blood were n = 6 for red kangaroos and n = 7 for sheep.

Table 5: Mean ($\pm$ SEM) body weights, apparent dry matter (DM) digestibility of forestomach contents, and dry feed intakes of red kangaroos (n=6) and sheep (n=5) grazing chenopod shrublands.

		Species effect	
		<i>F</i> -Statistic	<i>P</i> -value
Body weight	Red Kangaroo	23.6 $\pm$ 0.8	
	^A Sheep	50.2 $\pm$ 2.2	205
Apparent DM Digestibility (%)	Red Kangaroo	52.1 $\pm$ 3.9	
	Sheep	59.1 $\pm$ 2.4	2.5
^B Digestible DM (g d ⁻¹) required to meet daily energy requirements (FMR ^C)	Red Kangaroo	518 $\pm$ 31	
	Sheep	1572 $\pm$ 124	77.3
Gross DM (g d ⁻¹) required to meet daily energy requirements (FMR ^C)	Red Kangaroo	994 $\pm$ 60	
	Sheep	2661 $\pm$ 210	65.1
^D Gross DM (g d ⁻¹) required to meet basal metabolic energy requirements (BMR)	Red Kangaroo	437 $\pm$ 11	
	Sheep	692 $\pm$ 22	52.8
^E Gross DM (g d ⁻¹) required to meet daily energy requirements (FMR ^C) for a 'standard' animal			
	25-kg Red Kangaroo	1039	
	45-kg Sheep	2449	-

Note: ^AFleece-free weight; ^BAssuming energy digestibility is equal to dry matter digestibility; ^CFMR = field metabolic rate (kJ d⁻¹), after Munn et al. 2009, kangaroo = 4872 $\pm$ 364 (kJ d⁻¹), sheep = 16664 $\pm$ 1314 (kJ d⁻¹); ^DPredicted according to measured BMRs (kJ kg^{-0.75} d⁻¹) for mature, dry Australian merino ewes (230 kJ kg^{-0.75} d⁻¹; Marston 1948) and for mature, dry red kangaroo females (200 kJ kg^{-0.75} d⁻¹; Dawson et al. 2000); ^EEstimated using an FMR:BMR of 2.3 and 3.8 for a standard (mature, dry) 25-kg red kangaroo and a 45-kg sheep, respectively, according to Munn et al. (2009).