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## **Energy and water use by invasive goats (*Capra hircus*) in an Australian rangeland, and a caution against using broad-scale allometry to predict species-specific requirements**

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# Energy and water use by invasive goats (*Capra hircus*) in an Australian rangeland, and a caution against using broad-scale allometry to predict species-specific requirements

## Abstract

Feral goats (*Capra hircus*) are ubiquitous across much of Australia's arid and semi-arid rangelands, where they compete with domestic stock, contribute to grazing pressure on fragile ecosystems, and have been implicated in the decline of several native marsupial herbivores. Understanding the success of feral goats in Australia may provide insights into management strategies for this and other invasive herbivores. It has been suggested that frugal use of energy and water contributes to the success of feral goats in Australia, but data on the energy and water use of free-ranging animals are lacking. We measured the field metabolic rate and water turnover rate of pregnant and non-pregnant feral goats in an Australian rangeland during late summer (dry season). Field metabolic rate of pregnant goats ( $601 \pm 37 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ) was 1.3 times that of non-pregnant goats ( $456 \pm 24 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ). The water turnover rate of pregnant goats ( $228 \pm 18 \text{ mL kg}^{-0.79} \text{ d}^{-1}$ ) was also 1.3 times that of non-pregnant goats ( $173 \pm 18 \text{ kg}^{-0.79} \text{ d}^{-1}$ ), but the difference was not significant ( $P=0.07$ ). There was no significant difference in estimated dry matter digestibility between pregnant and non-pregnant goats (mean ca. 58%), blood or urine osmolality, or urine electrolyte concentrations, indicating they were probably eating similar diets and were able to maintain osmohomeostasis. Overall, the metabolic and hygric physiology of non-pregnant goats conformed statistically to the predictions for non-marine, non-reproductive placental mammals according to both conventional and phylogenetically independent analyses. That was despite the field metabolic rate and estimated dry matter intake of nonpregnant goats being only 60% of the predicted level. We suggest that general allometric analyses predict the range of adaptive possibilities for mammals, but that specific adaptations, as present in goats, result in ecologically significant departures from the average allometric curve. In the case of goats in the arid Australian rangelands, predictions from the allometric regression would overestimate their grazing pressure by about 40% with implications for the predicted impact on their local ecology.

## Keywords

Allometry, Field metabolic rate, Water turnover, Grazing, Invasive species

## Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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3 requirements.

4  
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24

## 25    **Summary**

26    Feral goats (*Capra hircus*) are ubiquitous across much of Australia's arid and semi-  
27    arid rangelands, where they compete with domestic stock, contribute to grazing  
28    pressure on fragile ecosystems, and have been implicated in the decline of several  
29    native marsupial herbivores. Understanding the success of feral goats in Australia  
30    may provide insights into management strategies for this and other invasive  
31    herbivores. It has been suggested that frugal use of energy and water contributes to the  
32    success of feral goats in Australia, but data on free-ranging animals are lacking. We  
33    measured the field metabolic rate and water turnover rate of pregnant and non-  
34    pregnant feral goats in an Australian rangeland during late summer (dry season). Field  
35    metabolic rate of pregnant goats ( $601 \pm 37 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ) was 1.3 times that of non-  
36    pregnant goats ( $456 \pm 24 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ). The water turnover rate of pregnant goats  
37    ( $228 \pm 18 \text{ mL kg}^{-0.79} \text{ d}^{-1}$ ) was also 1.3 times that of non-pregnant goats ( $173 \pm 18 \text{ kg}^{-0.79} \text{ d}^{-1}$ ), but the difference was not significant ( $P=0.07$ ). There was no significant  
38    difference in estimated dry digestibility between pregnant and non-pregnant goats  
39    (mean ca. 58%), blood or urine osmolality, or urine electrolyte concentrations,  
40    indicating they were probably eating similar diets and were able to maintain  
41    osmohomeostasis. Overall, the metabolic and hygric physiology of non-pregnant  
42    goats conformed statistically to the predictions for non-marine, non-reproductive  
43    placental mammals according to both conventional and phylogenetically independent  
44    analyses. That was despite the field metabolic rate and estimated dry matter intake of  
45    non-pregnant goats being only 60% of the predicted level. We suggest that general  
46    allometric analyses predict the range of adaptive possibilities for mammals, but that  
47    specific adaptations, as present in goats, result in ecologically significant departures  
48    from the average allometric curve. In the case of goats in the arid Australian  
49

50 rangelands, predictions from the allometric regression would overestimate their  
51 grazing pressure by about 50%, with implications for the predicted impact on their  
52 local ecology.

53  
54 Keywords: Allometry, field metabolic rate, water turnover, grazing, invasive species

55

## 56 **Introduction**

57 What makes invasive species successful? Putatively, invasive species share features  
58 that afford success in novel environments (Blackburn et al. 2009; van Kleunen et al.  
59 2010), particularly where they persist in the absence of predators (e.g. Newsome et al.  
60 2001). Features such as behavioural and physiological plasticity may further support  
61 invasive species' abilities to withstand or adapt to changes in climate (Kolar and  
62 Lodge 2001; Chown et al. 2007), or to management strategies aimed at controlling  
63 their population or impacts (e.g. manipulating water access to manage herbivores;  
64 Underhill et al., 2007; Fensham and Fairfax 2008). Information on the resource  
65 requirements of invasive species offers an opportunity to evaluate their success  
66 relative to non-invasive introduced or native species. We investigate here the field  
67 metabolic rate and water turnover rate of feral goats (*Capra hircus*) in an Australian  
68 rangeland.

69 Domestic goats were introduced to Australia with European settlement in the  
70 late 1700's (Parkes et al. 1996). Subsequently, escaped or released goats established  
71 themselves as one of the most significant invasive herbivores in Australia (Parkes et  
72 al. 1996; McLeod 2004; Coutts-Smith et al., 2007; West and Saunders 2007). Feral  
73 goats compete with domestic stock (sheep, *Ovis aries* and cattle, *Bos taurus*),  
74 contribute heavily to land degradation and overgrazing, and have been implicated in  
75 the decline of native fauna such as the yellow-footed rock wallaby (*Petrogale*

76 *xanthopus*; Wilson et al. 1976; Dawson and Ellis 1979; Harrington 1986; Lim and  
77 Giles 1987). The establishment of large and persistent populations of feral goats has  
78 been coincident with control of the dingo (*Canis lupus dingo*), which has limited  
79 predation pressure that otherwise might suppress goat populations (Newsome et al.  
80 2001). Further, a broad and flexible diet as a generalist herbivore may contribute to  
81 the goats' success (Harrington 1986; Squires 1980). Anecdotal reports suggest that  
82 goats can sustain reproductive output even during prolonged drought when forage  
83 availability and quality are poor (Parkes et al. 1996). However, fundamental  
84 information on the field energy and water requirements of feral goats in Australia is  
85 lacking. We used the doubly labelled water method to investigate the field metabolic  
86 rate (FMR) and water turnover rate (WTR) of feral goats inhabiting a typical  
87 Australian rangeland. We measured the FMR and WTR of both pregnant and non-  
88 pregnant goats. We have also examined blood and urine concentrations and urine  
89 electrolyte concentrations of goats as indicators of diet, and estimated their diet  
90 digestibility to estimate the dry matter intake (DMI) required to meet their FMR. On a  
91 broader scale, we compare the FMR, estimated DMI and WTR of non-pregnant feral  
92 goats to those of non-reproductive, terrestrial placental mammals using allometric  
93 scaling, to determine whether the energy requirements of feral goats differ from a  
94 'typical' placental mammal. We evaluate the efficacy of using allometric scaling to  
95 predict species-specific resource requirements and the implications of using this  
96 approach for predicting finer-scale, local impacts of invasive or other species.

97

98

99     **Materials and Methods**

100    *Study site and climatic conditions*

101    The study was conducted at Fowlers Gap (31°05' S, 141°43' E), the Arid Zone  
102    Research Station of the University of New South Wales, 112 km north-east of Broken  
103    Hill, New South Wales, Australia. The station covers approximately 39,200 ha and  
104    operates as a commercial sheep station. Vegetation at the study site is dominated by  
105    low woody shrubs (< 1 m), chiefly of the family Chenopodiaceae. Topography on the  
106    western half of the station includes mainly hilly regions of the Barrier Ranges (c. 300  
107    m above sea level), while flood plains (140–170 m a.s.l.) cover the remainder of the  
108    property. Rainfall at this site is variable, with a yearly average ( $\pm$  SEM) of 236.7  $\pm$   
109    20.4 mm p.a. and a co-efficient of variation of 54% (1969-2007 inclusive; SILO  
110    Patched Point Dataset, Bureau of Meteorology and NHM QLD; data patched for  
111    1971, and February and April 2000). This study was conducted during a mild late  
112    summer between the 25th February and 12<sup>th</sup> March, 2008 (Table 1).

113

114    *Study animals*

115    Free-ranging feral goats (n = 4 non-pregnant; n = 5 pregnant) were mustered between  
116    0600 h and 0800 h in the western parts of the study site. Animals were moved to  
117    purpose-built holding yards before being transferred via cage-trailer to a large (16 ha)  
118    enclosure. The enclosure had not been grazed for several years and vegetation within  
119    the enclosure was markedly higher than outside the enclosure (A. Munn et al., Pers.  
120    Obs). Water was available within the enclosure via a water trough, from which all  
121    animals were observed to drink, and abundant shade was available via scattered acacia  
122    trees and shrubs. Animals were acclimated to the enclosure for ten days prior to  
123    experimentation. The reproductive state of the goats was determined post-mortem at

124 the conclusion of the study. Of the five pregnant females, all but one carried twins,  
125 and so the combined foetal body mass was used throughout analysis. Individual foetal  
126 masses were used to estimate gestational age (McDonald et al.1988).

127

#### 128 *Measurement of FMR and WTR*

129 We measured the field metabolic rate (CO<sub>2</sub> production; L d<sup>-1</sup>) and water turnover rate  
130 (WTR; L d<sup>-1</sup>) of goats using the doubly labelled water method (Lifson and  
131 McClintock 1966; Speakman 1997). Animal numbers were limited both by the high  
132 cost of the doubly-labelled water for such large animals and the size of the enclosure.  
133 Goats were captured by muster and blood samples (ca. 4 mL) were obtained from the  
134 jugular vein for the measurement of background levels of the isotopes. Goats were  
135 then injected intraperitoneally with 0.3 g kg<sup>-1</sup> <sup>18</sup>O (> 98% enriched) and 0.15 g kg<sup>-1</sup>  
136 deuterium (<sup>2</sup>H; > 95% enriched) from separate syringes (isotopes from Rotem  
137 Industries, Israel) into the same location. The isotopes were allowed to equilibrate  
138 with body water for 6-8 h before a second blood sample (ca. 4 mL) was obtained from  
139 the jugular vein. During the equilibration period the animals were maintained in a  
140 small, shaded pen (ca. 10 m<sup>2</sup>) without access to feed or water. The goats were then  
141 released into the enclosure and allowed to range freely for 8 days, after which they  
142 were mustered and held quietly in the shaded pen until they were shot and a final  
143 blood sample obtained. Background, equilibration and final blood samples were  
144 analysed for <sup>18</sup>O and <sup>2</sup>H by isotope ratio mass spectrometry after vacuum distillation  
145 to obtain pure water (Speakman 1997; Metabolic Solutions, Nashua, NH).

146 Pool sizes ( $N_H$  or  $N_O$ ; moles) were estimated after Lifson and McClintock  
147 (1966), Speakman (1997) and Gessaman et al. (2004) as

148 
$$N_{int} = (I_{ds} - I_{dist}) * (M_{dist}/M_W) * (M_{inj} / (I_{int}-I_b)) / 18.02 \quad (1);$$



149 where  $N_{\text{int}}$  = initial intercept pool size of the isotope in the animal,  $I_{\text{ds}}$  = concentration  
 150 of isotope in isotopically-labelled water solution,  $I_{\text{dist}}$  = concentration of isotope in  
 151 water distilled from body fluid,  $M_{\text{dist}}$  = mass of distilled water,  $M_{\text{w}}$  = mass of  
 152 isotopically-labelled water used in dilution,  $M_{\text{inj}}$  = mass of isotopically-labelled water  
 153 injected into the animal,  $I_{\text{int}}$  = the intercept or equilibration concentration of isotope  
 154 ( $^{18}\text{O}$  or  $^2\text{H}$ ) and  $I_{\text{b}}$  = concentration of isotope ( $^{18}\text{O}$  or  $^2\text{H}$ ) in water distilled from the  
 155 background blood sample. Initial dilution space ratios ( $N_{\text{H}}:N_{\text{O}}$ ) were not significantly  
 156 different between pregnant and non-pregnant goats, and so a mean ( $\pm\text{SE}$ ) group ratio  
 157 of  $1.02 \pm 0.01$  was used to calculate WRT and FMR (see below). Of note, one  
 158 pregnant animal had a  $N_{\text{H}}:N_{\text{O}}$  value of 1.15, and was considered sufficiently different  
 159 to all others to exclude it from the group mean  $N_{\text{H}}:N_{\text{O}}$ ; that individual's FMR and  
 160 WTR were calculated using its specific  $N_{\text{H}}:N_{\text{O}}$ .

161 Total body water (TBW; % initial live mass) was estimated from the dilution  
 162 space ( $N$ ) for  $^{18}\text{O}$  for all goats, because  $^2\text{H}$  dilution typically overestimates body water  
 163 in ruminants (Fancy et al. 1986). Because of the potential for body water content to  
 164 change throughout the experiment, particularly in pregnant animals (McDonald et al.  
 165 1988), we estimated WTR ( $r_{\text{H}_2\text{O}}$ ;  $\text{mol d}^{-1}$ ) for linearly changing body water contents  
 166 according to:

$$167 \quad r_{\text{H}_2\text{O}} = (k_{\text{H}} * \bar{N}_{\text{H}} / \text{R-displace}) / (f_1) + (1 - X) \quad (2);$$

168 where,  $k_{\text{H}}$  =  $^2\text{H}$  flux (turnover rate) during the experiment (see Equation 3),  $\bar{N}_{\text{H}}$  = the  
 169 mean isotope pool size calculated from  $^2\text{H}$  dilution and for linearly changing body  
 170 water (see equations 4, 5 and 6 below), R-displace = mean group displacement ratio  
 171 for body water pools, estimated from initial pool sizes for  $^2\text{H}$  and  $^{18}\text{O}$  (i.e.  $N_{\text{H}}:N_{\text{O}}$ ;  
 172 Midwood et al. 1994),  $f_1$  = fractionation constant for  $^2\text{H}_2\text{O}$  vapour relative to  $^2\text{H}_2\text{O}$   
 173 liquid (assumed to be 0.93; Lifson and McClintock, 1966; Nagy and Costa 1980;

174 Speakman 1997),  $X$  = estimate of the proportion of total water loss that is fractionated  
175 (assumed = 0.25; Speakman 1997).

176

177 Deuterium flux during the experiment ( $k_H$ ) was estimated as:

178 
$$k_H = (\ln H_{\text{int}} - \ln H_{\text{final}}) / t \quad (3);$$

179 where  $\ln$  = natural log of initial ( $H_{\text{int}}$ ) and final ( $H_{\text{final}}$ ) concentrations (ppm) of  $^2\text{H}$  in

180 body water after correction for background levels, and  $t$  = time (days).

181

182 The mean isotopic pool size ( $\bar{N}$ ) for  $^{18}\text{O}$  and  $^2\text{H}$  was calculated for a linearly

183 changing body water pool according to:

184 
$$N_1 = M_{B1} * N_{\text{int}} / M_{B1} \quad (4),$$

185 
$$N_2 = M_{B2} * N_{\text{int}} / M_{B1} \quad (5),$$

186 
$$\bar{N} = (N_1 + N_2) / 2 \quad (6);$$

187 where  $N_1$  and  $N_2$  are the initial and final isotopic pool sizes (i.e. for  $^{18}\text{O}$  or  $^2\text{H}$ ),  $M_{B1}$  and

188  $M_{B2}$  = body mass at the beginning and end of the experiment,  $N_{\text{int}}$  = initial isotope

189 pool size ( $^{18}\text{O}$  or  $^2\text{H}$ ), assuming that body water content remained a constant fraction

190 of body mass (i.e.  $N_{\text{int}} / M_{B1}$ ) for each animal (Nagy and Costa 1980; Gessaman et al.

191 2004).

192 The production of  $\text{CO}_2$  ( $r_{\text{CO}_2}$ ;  $\text{mol d}^{-1}$ ) was estimated using equations validated

193 for ruminants after Midwood et al. (1994) as:

194 
$$r_{\text{CO}_2} = ( (k_O * \bar{N}_O) - [(r_{\text{H}_2\text{O}} * X * f_2) + (1 - X) * r_{\text{H}_2\text{O}}] ) / 2f_3 \quad (7);$$

195 where  $k_O$  =  $^{18}\text{O}$  flux (turnover rate) during the experiment (see equation 3, substituting

196  $^2\text{H}$  for  $^{18}\text{O}$ ),  $\bar{N}_O$  = the mean isotope pool size calculated from  $^{18}\text{O}$  dilution and for

197 linearly changing body water (equations 4 - 6),  $r_{\text{H}_2\text{O}}$  = as per equation 2,  $X$  = estimate

198 of the proportion of total water loss that is fractionated (assumed = 0.25; Speakman  
199 1997),  $f_2$  = fractionation constant for  $\text{H}_2^{18}\text{O}$  vapour relative to  $\text{H}_2^{18}\text{O}$  liquid (assumed  
200 to be 0.99; Speakman 1997), and  $f_3$  = the fractionation constant for  $\text{H}_2^{18}\text{O}_2$  gas  
201 relative to  $\text{H}_2^{18}\text{O}$  liquid (assumed to be 1.039; Lifson and McLintock 1966; Speakman  
202 1997). Carbon dioxide production was then converted to a field metabolic rate (FMR;  
203  $\text{kJ d}^{-1}$ ) assuming energy equivalents of  $21.7 \text{ kJ L}^{-1} \text{ CO}_2$  (Nagy et al. 1999).

204

#### 205 *Potential errors of DLW method in ruminants*

206 The use of the doubly labelled water method in ruminants may be complicated by the  
207 large amount of vegetative material in the gut, which provides a substrate for  
208 deuterium exchange with plant fibre and subsequent faecal loss, in addition to the  
209 incorporation of deuterium as methane during methanogenic fermentation (Fancy et  
210 al. 1986; Midwood et al. 1989, 1993, 1994). Therefore, some of the deuterium  
211 introduced as labelled water may be lost via avenues other than water, possibly  
212 elevating the estimation of the deuterium flux and thus water flux ( $r_{\text{H}_2\text{O}}$ ), and therefore  
213 underestimating the  $\text{CO}_2$  production via the difference between  $^{18}\text{O}$  and  $^2\text{H}$  fluxes  
214 (Fancy et al. 1986; Midwood et al. 1989, 1993, 1994). Because of these avenues  $\text{CO}_2$   
215 production can be underestimated by between 3% and 12% from non-growing (stable  
216 body mass) ruminants (Fancy et al. 1986; Midwood et al. 1989, 1993, 1994).

217 However, more recent validation of the use of deuterium-labelled water to measure  
218 WTR of sheep and goats found no significant differences between isotope-kinetic  
219 predictions and those estimated from water intake (combined with preformed sources;  
220 Al-Ramamneh et al. 2010; see also Junghans et al. 1997). Moreover, errors of the  
221 DLW method described by the earlier validations in ruminants (e.g. Midwood et al.  
222 1989, 1993, 1994; Fancy et al. 1986) were within the ranges reported from validation

223 trials with non-ruminants (e.g. Sparling et al. 2008). Correcting for deuterium losses  
224 in faeces and methane in free-ranging ruminants is difficult and rarely attempted (but  
225 see Williams et al. 2001). We could not measure methane or faecal output from our  
226 goats, and so have presented unadjusted values for WTR and FMR. We later discuss  
227 the likely impacts of deuterium loss through faeces and CH<sub>4</sub> on our results, based on  
228 data for other ruminants (Midwood et al. 1993, 1994).

229

#### 230 *Osmolality of blood and urine and urine electrolytes*

231 Urine samples were taken from the goat bladders immediately following post-mortem  
232 evisceration. These samples were immediately stored on ice in an insulated box and were  
233 frozen within one hour of collection. Urine sub-samples were later thawed and analysed for  
234 osmolality, along with whole-blood samples collected via heart puncture of deceased animals.  
235 The osmolality of urine and blood was determined using a freezing-point depression  
236 osmometer (Gonotec Osmomat 030; Gallay Scientific, Melbourne). Concentrations of  
237 electrolytes in urine, including sodium (Na<sup>+</sup>), potassium (K<sup>+</sup>), magnesium (Mg<sup>++</sup>) and calcium  
238 (Ca<sup>++</sup>) were quantified using Inductively Coupled Plasma Optical Emission Spectrometry  
239 (Perkin Elmer 5300DV ICP-OES; Sydney Analytical Services, Seven Hills, NSW), and  
240 concentrations of Cl<sup>-</sup> were determined using an Ag/AgS Ion Specific Electrode (Sydney  
241 Analytical Services, Seven Hills, NSW). Electrolyte concentrations were not available for  
242 blood as the samples were used for labelled water analysis.

243

#### 244 *Diet digestibility*

245 Apparent digestibilities of dry matter (DM) from the rumen were estimated using manganese  
246 (Mn) as a naturally occurring indigestible marker (Nagy 1977; Bersényi et al. 2002; see also  
247 Fadely et al. 1990 and references therein). Absorption and secretion of Mn in the gut of  
248 vertebrates is negligible and it has been used as a digestibility marker for numerous species

(e.g. Nagy 1977). Because the amount of Mn should not change along the gut, the digestibility of the diet was estimated using Mn concentrations from forestomach samples taken adjacent to the oesophageal opening at the cardia and compared with that in faeces collected as formed pellets from the distal colon. Digestibility was estimated according to:

$$\text{Apparent digestibility (\%)} = \left(1 - \frac{M_d}{M_f}\right) \cdot 100 \quad (2);$$

where  $M_d$  = concentration of Mn in the forestomach sample (per unit DM) and  $M_f$  = concentration of Mn faeces (per unit DM). Rumen (as above) and faecal (distal colon) sub-samples (ca. 70 g wet mass) were collected at dissection then immediately stored on ice and frozen within one hour. Forestomach material and faeces (ca. 70 g wet mass) were later dried at 60°C to constant mass and then milled through a 1 mm mesh (Glen Creston c.580 micro hammer mill, Glen Creston, London). Sub-samples (0.6 – 1.0 g DM) of ground material were then digested in nitric acid (10 mL; 70%) using a Milestone Microwave Digestion System (Milestone MLS-1200 MEGA; Program 1) according to the manufacturer's instructions. Digesta were then weighed, diluted to 25 ml with deionized water, allowed to settle overnight, then the supernatant was drawn off and analysed for Mn content using an Inductively Coupled Plasma Atomic Emission Spectrometer (ICP-AES; Vista AX, Varian; California, USA).

#### *Dry matter intakes*

Daily DMI (g d<sup>-1</sup>) was estimated as the amount of dry material needed to satisfy an animal's FMR (kJ d<sup>-1</sup>) according to the metabolisable energy content of that animal's diet ( $E_{\text{met}}$ ; kJ g<sup>-1</sup> DM), as  $\text{FMR}/E_{\text{met}}$  (Nagy et al. 1999). For herbivores diets the gross energy content of herbaceous material generally ranges from 16.3 - 21.3 kJ g<sup>-1</sup> DM (Robbins 2001), which is comparable to that reported for perennial grasses and saltbushes typical of our study site (Corbett 1990; see also Golley 1961). Using our estimates of the dry matter digestibility of

273 goat rumen material (ca. 58%), we predicted the digestible energy content of the goat's diet to  
274 be  $12.2 \pm 0.4 \text{ kJ g}^{-1} \text{ DM}$  (assuming a gross energy content of 21 kJ and that energy  
275 digestibility was comparable to dry matter digestibility). Other studies at the same field site  
276 found comparable digestibility coefficients using in-vitro acid-pepsin digestions of forbs,  
277 grasses and shrubs (range of means was 9-14  $\text{kJ g}^{-1} \text{ DM}$  for all plant types from winter and  
278 summer; McLeod 1996). However, neither our estimate of digestible energy content nor the  
279 in-vitro estimates of energy digestibility (McLeod 1996) account for energy losses as urine or  
280 methane, which were unknown for our goats. Therefore, we have assumed that the  
281 metabolisable energy content of our goats' diets ( $E_{\text{met}}$ ) was  $11.5 \text{ kJ g}^{-1} \text{ DM}$  (Nagy et al. 1999),  
282 consistent with other investigations of ruminant metabolisable energy content for forage  
283 (Nagy et al. 1999).

284

#### 285 *Allometry of FMR, DMI and WTR*

286 The FMR and WTR of non-pregnant goats were compared with other adult, non-  
287 marine, non-reproductive (i.e. non-lactating/non-pregnant) placental mammals ( $n = 64$   
288 species for FMR and  $n=37$  species WTR respectively; Appendix A1). These data  
289 include species covering four orders of magnitude of body mass. Data for WTR was  
290 used only from species for which FMR was simultaneously measured (Table 4).  
291 When data were available from more than one season, we selected the lowest values  
292 for FMR and WTR, typically using data collected during the dry season; FMRs  
293 reported during other seasons, or following rainfall, were generally higher (e.g. Mutze  
294 et al. 1991; Nagy and Gruchacz 1994; Covell et al. 1996; Degen et al. 1991, 1997;  
295 Williams et al. 1997, 2001; see Appendix). Importantly, all previous allometric  
296 analyses of mammalian FMR (e.g. Anderson and Jetz 2005; Capellini et al. 2010;  
297 Speakman and Król 2010) have included data from animals that were pregnant and/or

lactating, were growing juveniles, or were otherwise confounded (see Appendix A2). We have therefore collated the most conservative dataset for placental mammal FMR and WTR, using minimal seasonal values where known, which should provide a reasonable estimate of the minimum free-range resource requirements of placental mammals generally.

Resource requirements of our goats were further compared with those of eutherian mammals by converting our FMR dataset to gross DMIs, according to each species' diet and respective metabolisable energy contents (i.e.  $E_{\text{met}}$ ; Nagy et al. 1999; Appendix A1). While the metabolisable energy content of dry food probably varies considerably, broad patterns may be attributable to mammalian dietary guilds according to whether the species is an insectivore ( $E_{\text{met}} = 18.7 \text{ kJ g}^{-1} \text{ DM}$ ), a nectarivore ( $20.6 \text{ kJ g}^{-1} \text{ DM}$ ), a carnivore ( $16.8 \text{ kJ g}^{-1} \text{ DM}$ ), a frugivore ( $6.6 \text{ kJ g}^{-1} \text{ DM}$ ), a granivore ( $16.9 \text{ kJ g}^{-1} \text{ DM}$ ), a hindgut fermenting herbivore ( $10 \text{ kJ g}^{-1} \text{ DM}$ ), a foregut fermenting herbivore (mainly ruminants;  $11.5 \text{ kJ g}^{-1} \text{ DM}$ ), or an omnivore ( $14 \text{ kJ g}^{-1} \text{ DM}$ ); after Nagy et al. 1999 (see Appendix A1). To investigate the potential impact of aridity on FMR, WTR and DMI, we further classed animals as either desert or non-desert species (Nagy et al. 1999; Appendix 1).

The allometry of FMR, WTR and DMI was examined using conventional and phylogenetically independent linear regression of  $\log_{10}$ -transformed physiological data and body mass. Allometric relationships for desert or non-desert species were compared by ANCOVA. Allometrically-predicted FMR, WTR and DMI were determined from the conventional regressions using the maximum variance unbiased estimate (MVUE) of Hayes and Shonkwiler (2006, 2007), and conformity to conventional and phylogenetically-independent allometric relationships was assessed using the 95% prediction limits for the regression (Cooper and Withers 2006). For

323 phylogenetically-independent analyses, data were rendered independent of phylogeny  
324 by autoregression (Cheverud and Dow 1985; Rohlf 2001) using the mammalian  
325 phylogenetic tree of Bininda-Emonds et al. (2007). A phylogenetic distance matrix  
326 was obtained from the original Nexus file published by Binidna-Emondas et al. (2007)  
327 using the APE module for the package R. The species in our dataset were extracted  
328 from this distance matrix. The nexus file (and distance matrix generated from this)  
329 provides branch lengths. We are unaware of any polytomies in the database. Of note,  
330 our program for phylogenetic analysis required the phylogenetic tree to be in the  
331 format of a distance matrix, rather than the Newick format presented by Bininda-  
332 Emonds et al. (2007), so it was necessary to convert the Nexus file to a distance  
333 matrix. Extracting species required for this study from the overall mammal distance  
334 matrix was done using custom-written Visual Basic (V6) programs (P.C. Withers).  
335 The strength ( $K^*$ ) and significance ( $P$ ) of the phylogenetic signal for each  
336 phylogenetic variable, and for body mass, was determined after Blomberg et al.  
337 (2003) and Withers et al. (2006).

338

### 339 *Statistical analysis*

340 For between-group comparisons of pregnant and non-pregnant goats we used  
341 ANOVA, unless otherwise stated. Assumptions for ANOVA were tested using the  
342 Kolmogorov-Smirnov test for normality ( $\alpha = 0.05$ ) and Levene's test for homogeneity  
343 of variances ( $\alpha = 0.05$ ). Proportional data were arcsine transformed for analysis. Urine  
344 electrolyte concentrations ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Cl}^-$  and  $\text{Ca}^{++}$ ) were  $\log_{10}$  transformed to normalise  
345 their distribution. Arid and non-arid allometric relationships and those for FMR and  
346 DMI were compared using ANCOVA. Diet effects were examined using ANOVA on  
347 the residuals of the allometric relationship for each physiological variable. For those



variables with a significant diet effect, the allometric residual for goats was compared to those of other herbivores with a one-sample t-test. The significance of phylogenetic correction on the allometric relationships for FMR, DMI and WTR was determined using an F-test comparing the mean square error (MSE) for the conventional allometric regression with the MSE for the phylogenetically corrected regression, after Withers et al. (2006). Statistical analyses were performed using Minitab 15 and StatistiXL V1.8. Autocorrelation (autoregression), sub-sampling of the distance matrix of Bininda-Emonds et al. (2007), calculation of the MVUE and determination of  $K^*$  and the significance of phylogenetic signals were achieved using custom-written Visual Basic (V6) programs (P.C. Withers). Values are presented as mean  $\pm$  standard error unless stated otherwise.

## **Results**

Pregnant ( $42.7 \pm 2$  kg) goats were 50% heavier than the non-pregnant goats ( $28.8 \pm 1.5$  kg; Table 2). There was no significant difference in the average body mass change during the experiment (mean change  $+1.1\% d^{-1}$ ; Table 2). Four of the five pregnant goats carried twins. The youngest twin-pair weighed 400 g and 480 g, respectively, and were approximately 95 days old (animal G2), approaching the latter stages of the second trimester (i.e. 51 – 100 days; McDonald et al. 1988). The remaining foetuses ranged in ages from 120 to 127 days (mass range 1000 – 1300 g), estimated to be mid-way through their third trimester (i.e. 101 – 150 days; McDonald et al. 1988).

Equilibration blood samples ( $\sim 8$  hours after injection) indicated that goat body fluids were enriched above background levels to  $388 \pm 12$  ppm for  $^{18}O$  and  $192 \pm 10$  ppm for  $^2H$ . Final blood samples (approximately eight days following equilibrium) had concentrations of  $^{18}O$  and  $^2H$  substantially above background levels

for all goats (range 65-111 ppm above background for  $^{18}\text{O}$ , and 39-92 ppm for  $^2\text{H}$ ).

The dilution space ratio and the kinetics of the labelled isotopes in the body water of

our goats were within ranges acceptable to establish field metabolic and water

turnover rates (Table 2; Speakman 1997).

The FMR of pregnant goats was significantly higher (approximately 1.3 times)

than the FMR of non-pregnant goats (Table 2), even after accounting for the

difference in their body masses by allometry (i.e.  $\text{kJ kg}^{-0.73} \text{d}^{-1}$ ; Table 2). Similarly, the

WTR of the pregnant goats was 1.3 times that of non-pregnant goats after accounting

for body mass differences (i.e.  $\text{mL H}_2\text{O kg}^{-0.79} \text{d}^{-1}$ ), though this difference was not

statistically significant ( $P = 0.066$ ; Table 3). Total body water content (61.5% of body

mass) was not different between the pregnant and non-pregnant goats (Table 3). It is

important to note that there is potential for incorporation of labelled isotopes,

particularly deuterium, into growing fetuses and as uterine water. However, amniotic

fluid volume remains constant in natal goats between 110 and 130 days of pregnancy,

and allantoic fluid increases only by around  $10\text{g d}^{-1}$  over the same period (McDonald

et al.1988). Thus, changes in uterine water content during our 10-day trial are unlikely

to have had a large effect on the results (mean body mass change of the animals was

$+1.2 \pm 0.3\% \text{d}^{-1}$  of initial body mass, and was not significantly different between the

pregnant and non-pregnant animals, Table 2).

The apparent digestibility of dry matter from pregnant and non-pregnant goat rumens

was not significantly different, averaging 58.2% (Table 3). Therefore, consistent with their

higher FMR, the pregnant goats in our study had daily DMIs that were significantly higher

than those on non-pregnant animals after accounting for body mass differences via allometry

(i.e.  $\text{g DM kg}^{-0.76} \text{d}^{-1}$ ; Table 3). There were no significant differences between the pregnant

397 and non-pregnant goats with respect to blood or urine osmolality or urine electrolyte  
398 concentrations (Table 4).

399         The conventional allometric relationship for FMR for non-marine placental  
400 mammals was highly significant ( $R^2 = 0.948$ ;  $F_{1,62} = 1121$ ,  $P < 0.001$ ), with a scaling  
401 exponent of 0.73. The FMR of non-pregnant goats was 60% of predicted, but it  
402 conformed statistically to the relationship, being well within the 95% prediction limits  
403 for a further datum (Figure 1). The significant allometric relationship for FMR  
404 remained ( $R^2 = 0.883$ ;  $F_{1,62} = 468$ ,  $P < 0.001$ ) after accounting for the significant and  
405 exaggerated phylogenetic signal in both body mass ( $K^* = 1.31$ ,  $P < 0.001$ ) and FMR  
406 ( $K^* = 1.21$ ,  $P < 0.001$ ), and the goats still conformed to this relationship. Accounting  
407 for phylogeny did not reduce the variability in the allometric relationship for FMR  
408 (MSE conventional regression = 0.044, MSE for phylogenetically independent  
409 regression = 0.047,  $F_{62,62} = 0.948$ ,  $P = 0.583$ ).

410         Dry matter intakes by non-marine placental mammals scaled similarly to  
411 FMR, with a DMI scaling exponent of 0.76 (slope comparison with FMR,  $F_{1,124} =$   
412  $0.846$ ,  $P = 0.360$ ). The DMIs of our goats conformed to the allometric relationship  
413 derived for non-marine placental-mammals (conventional analysis;  $R^2 = 0.947$ ;  $F_{1,62} =$   
414  $1098$ ,  $P < 0.001$ ), being well within the 95% prediction limits for a further datum  
415 (Figure 1), despite these non-pregnant goats having a DMI just 62% of that predicted.  
416 The significant allometric relationship for DMI for non-marine placental mammals  
417 remained after accounting for the significant and exaggerated phylogenetic signal in  
418 DMI ( $R^2 = 0.882$ ;  $F_{1,62} = 463$ ,  $P < 0.001$ ;  $K^* = 1.14$ ,  $P < 0.001$ ), and our goats still  
419 conformed to this relationship. Accounting for phylogeny did not reduce the  
420 variability in the allometric relationship for DMI (MSE conventional regression =

0.049, MSE for phylogenetically independent regression = 0.054,  $F_{62,62} = 0.911$ ,  $P = 0.642$ ).

The WTRs of all goats conformed statistically to the general placental-mammal allometric relationship ( $R^2 = 0.866$ ;  $F_{1,36} = 232$ ,  $P < 0.001$ ), being well within the 95% prediction limits for a further datum (Figure 1). Goat WTR was 94% of that the allometrically predicted value. After accounting for a significant phylogenetic signal in WTR ( $K^* = 1.06$ ,  $P < 0.001$ ), the statistically significant allometric relationship for scaling WTR with body mass remained ( $R^2 = 0.707$ ;  $F_{1,36} = 87$ ,  $P < 0.001$ ), and goats conformed to this relationship (Figure 1C). Accounting for phylogeny did not significantly reduce the variability in the allometric relationship for WTR (MSE conventional regression = 0.178, MSE for phylogenetically independent regression = 0.146,  $F_{35,35} = 1.226$ ,  $P = 0.275$ ).

There was a significant difference in the slope of the conventional allometric relationship for FMR between desert ( $0.77 \pm 0.03$ ) and non-desert ( $0.69 \pm 0.03$ ) placental mammals ( $F_{1,60} = 4.72$ ,  $P = 0.034$ ; Table 5), precluding examination for an elevation difference. The FMR of non-pregnant goats conformed equally well to both the desert and non-desert datasets. When the data for FMR were phylogenetically corrected there was no significant difference in the allometric slope between desert and non-desert placental mammals (common slope = 0.70;  $F_{1,60} = 2.63$ ,  $P = 0.11$ ) but the intercepts differed ( $F_{1,61} = 5.44$ ,  $P = 0.023$ ) with the desert species having a lower phylogenetically-independent FMR than non-desert species. Our goats conformed more closely to the desert-mammal line than the non-desert line (Figure 1).

Desert mammals had a lower DMI than those from more mesic environments, with the regressions for desert and non-desert species having the same slope ( $F_{1,60} = 3.0$ ,  $P = 0.09$ ), but with the intercept for desert species being significantly lower ( $F_{1,61}$

446 = 14.8,  $P < 0.001$ ). The DMI of non-pregnant goats was 66% of that predicted for a  
447 desert species, and 62% of that predicted for a non-desert species. The significant  
448 difference between desert and non-desert mammals' intercepts for DMI remained  
449 when the data were subject to phylogenetically-independent analysis ( $F_{1,61} = 8.95$ ,  $P =$   
450 0.004).

451 The allometric relationships for conventional analysis of WTR for desert and  
452 non-desert mammals were not significantly different with regard to slope ( $F_{1,34} = 0.61$   
453  $P = 0.420$ ) or intercept ( $F_{1,35} = 0.32$ ,  $P = 0.576$ ). However, the slope of the regression  
454 for phylogenetically-independent analysis for the desert and non-desert mammal  
455 WTRs were significantly different (slope =  $0.82 \pm 0.08$  for desert species, and  $0.50 \pm$   
456  $0.11$  for non-desert species;  $F_{1,33} = 6.18$ ,  $P = 0.018$ ), which precluded an analysis for  
457 differences in intercept.

458 Diet had no statistically significant effect on the FMR or WTR of non-marine  
459 placental mammals, either before or after phylogenetic analysis. However, we found a  
460 statistically significant effect of diet on the DMI of non-marine placental mammals,  
461 both before ( $F_{6,57} = 2.85$ ,  $P = 0.017$ ) and after accounting for phylogenetic history  
462 ( $F_{6,57} = 2.47$ ,  $P = 0.034$ ). Notably, the DMI of our goats were significantly lower than  
463 that predicted for other herbivores by both conventional ( $T_{19} = 4.9$ ,  $P < 0.001$ ) and  
464 phylogenetically independent analyses ( $T_{19} = 2.3$ ,  $P = 0.032$ ).

465

## 466 **Discussion**

467 The success of feral goats surviving, indeed thriving, in arid and semi-arid Australia  
468 does not seem to be related to a remarkable water economy, at least when surface  
469 water is freely available as it was in this study. The WTR we measured for non-  
470 pregnant goats was as predicted for a non-desert species, and similar WTRs have been

471 reported for goats at the same study site (Dawson et al. 1975). It was suggested  
472 therefore that goats do not generally exhibit the physiological specialisations for water  
473 economy of some African desert ungulates (Dawson et al. 1975),. However, daily  
474 water turnover is dependent on many factors, including the availability of free water,  
475 the distance to water from foraging sites, forage mineral content, forage water content,  
476 and thermal challenges that may increase an animal's water requirements, and urine  
477 concentration ability (Silanikove 2000; Cain et al. 2006). Consequently, evaluating  
478 the daily water turnover of desert animals under non-water-stressed conditions is not  
479 likely to provide much insight for evaluating the benefits of adaptations related to  
480 water use. For example, ability to withstand dehydration appears to be a key  
481 adaptation of large desert mammals (Cain et al. 2006) and studies on water-restricted,  
482 free-range animals would be useful. Nonetheless, we did identify a significant  
483 difference in the allometric slope for WTR between desert and non-desert mammals,  
484 indicating that smaller ( $< 100$  g), but not the larger, desert species exhibited lower  
485 daily WTRs compared with non-desert species. It must be noted however that larger  
486 desert species are overly represented in the data set available. Further data on  
487 comparably sized mesic-zone mammals are required to provide a truly 'general' data  
488 set for comparison with our goats or other species.

489         Daily energy and food (dry matter) requirement of our goats was typical of  
490 desert-adapted animals, and importantly that was significantly lower than those found  
491 in non-desert species. Feral goats are descended from the bezoar, *Capra aegagrus*  
492 (Naderi et al. 2009), which is naturally found in arid habitats in the Middle East  
493 (Weinberg et al. 2008). Overall, reduced energy and therefore food requirements  
494 appear to be a general feature of desert species, including goats, presumably aiding  
495 their survival in low productivity habitats (Silanikove 2000). Therefore, the success of

496 feral goats in the Australian arid zone is probably attributable to a combination of  
497 features that support their low energy and food requirements, including flexible  
498 feeding behaviours, and their ability to select the most nutritious and digestible plant  
499 parts from a variety of forages (e.g. buds, leaves, fruits and flowers; Hoppe et al.  
500 1977; Huston 1978; Warren et al. 1984; Harrington 1986; Lu 1988).

501       Our data on apparent dry matter digestibility of rumen material (ca. 58%)  
502 suggest that the goats were selecting good quality diets, and achieved digestibility  
503 comparable with high-quality diets fed in captivity (Freudenberger and Hume 1992).  
504 Similarities in blood and urine osmolality and urine electrolyte concentrations of our  
505 goats to values reported for free-range goats at the same study site (Dawson et al.  
506 1975; Dawson and Ellis 1996), suggest that the vegetation eaten by our goats was of  
507 similar composition to that ingested by truly free-range animals. Both the free range  
508 goats of Dawson et al. (1975) and those from our study were capable of maintaining  
509 osmo-homeostasis. Our data for the WTR, FMR and DMI of feral goats are therefore  
510 likely to be broadly applicable to goats throughout the rangelands, where they subsist  
511 mainly on trees and shrubs, and to a lesser extent flat- and round-leaf chenopods  
512 (Dawson et al. 1975; Dawson and Ellis 1996).

513       As mixed-feeders, feral goats can adapt readily to seasonal and geographical  
514 variation in diet availability (Lu 1988), and their tolerance of bitter plants (Bell 1959)  
515 enables them to feed on vegetation that is unpalatable to other herbivores. Moreover,  
516 the proliferation of artificial watering points (Fensham and Fairfax 2008) and the  
517 removal of dingoes (Newsome et al. 2001) from much of Australia's arid and semi-  
518 arid regions, thereby supporting and protecting pastoral stock, may have released  
519 goats from water limitation and predation pressure, respectively. It is likely that a

520 combination of all of these factors explains the feral goat's success as an invasive  
521 species in the Australian rangelands.

522         While the FMR and DMI we measured in non-pregnant goats were only ca.  
523 60% of those predicted for a placental mammal (conventional analysis), they were not  
524 statistically lower than predicted by allometry (Figure 1). Such an outcome raises  
525 issues about the utility of using the allometry of placental FMR for making ecological  
526 predictions. For example, using the general placental FMR-allometry to predict the  
527 energy and food requirements of feral goats in an Australian rangeland would  
528 overestimate their local grazing pressure. This has major implications for using  
529 allometric datasets to infer or predict micro-ecological phenomena from a macro-  
530 ecological perspective (see also conclusions of Capellini et al. 2010). Interestingly,  
531 accounting for phylogeny did not improve the predictive power of our allometric  
532 relationships, despite significant phylogenetic signals in body mass and physiological  
533 parameters. This suggests that the phylogenetic signal in body mass and physiological  
534 traits has a similar pattern. Accounting for phylogeny for allometric relationships for a  
535 range of physiological variables (basal metabolic rate, body temperature, thermal  
536 conductance and evaporative water loss) for marsupials also failed to reduce the  
537 variability of these relationships (Withers et al 2006). In these examples, predictions  
538 from conventional allometric analyses are at least as robust as those from allometric  
539 analyses that account for phylogenetic history.

540         While we constrained our analysis to the most conservative data available, our  
541 FMRs, DMIs and WTRs were collated for species from a broad range of habitats and  
542 circumstances. Notably, these include many animals from extreme habitats (e.g.  
543 desert-dwelling Arabian oryx *Oryx leucoryx*, Williams et al. 2001) and/or with  
544 extreme lifestyles (e.g. three-toed sloth *Bradypus variegates*, Nagy and Montgemory



1980; namib desert golden mole *Eremitalpa granti namibensis*, Seymour et al. 1998). Consequently, the prediction limits described by the allometry of FMR and DMI (and to a lesser extent WTR) may well represent boundaries for what is physiologically or ecologically possible for non-reproductive placental mammals. If that is indeed the case, then fundamentally no species will statistically be different from the allometric regressions (see Cooper and Withers 2006). It may not be possible for any species differ statistically from the current dataset.

Because the full dataset represents the range of physiology that is possible, it then becomes informative to determine the basis of the variability making up those possibilities. A more meaningful comparison is revealed by the separate allometries for desert and non-desert species. The different scaling exponents for FMR between the desert and non-desert species hampers conventional comparisons of their allometry, but when the influence of phylogenetic history is removed, desert-adapted species have FMRs significantly lower than non-desert species (Figure 1). Further, the FMR that we measured in goats resident in the arid rangelands conformed better to the desert relationship than the non-desert relationship. These data suggest that feral goats in Australia are similar to desert-adapted placentals generally with regards to their energy requirements. However, comparisons of resource use by feral goats with different but sympatric species under comparable environmental conditions will likely provide better insights for predicting and managing local herbivore grazing pressures on Australia's rangelands.

The field metabolic rate of our non-pregnant goats ( $456 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ; Table 3) was comparable with that reported for other goat breeds under free-range or near free-range conditions (c.f.  $455 - 550 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ; Animut et al. 2005; Lachica and Aguilera 2003, 2005). This level of daily energy use was less than half that measured

570 in domestic Merino sheep ( $956 \text{ kJ kg}^{-0.73} \text{ d}^{-1}$ ) grazed at the same location and under  
571 comparable environmental conditions (Munn et al. 2009). Sheep grazing for wool and  
572 meat production is the dominant industry in Australia's rangelands. Our data suggest  
573 that the grazing pressures imposed by sheep are considerably higher than those by  
574 feral goats, but the reasons for this are unclear. The higher energy turnover of the  
575 Merino sheep compared with our goats could be related to differences in their  
576 minimal or maintenance metabolic rates, differences in their activity levels or the  
577 energetic costs for activity, or to differences in their productivity state. Merino sheep  
578 are bred for wool production, which is an energy cost not imposed on the feral goats.  
579 Further studies comparing goats with Merino sheep under more stringent dietary  
580 intakes (e.g. at maintenance rations) would help distinguish how these species  
581 partition energy turnover and how this related to their free-range FMRs and WTRs.

582       It is noted that the FMR of Merino sheep measured by Munn et al. (2009)  
583 were adjusted for deuterium losses in  $\text{CH}_4$ , assuming productions of  $0.422 \text{ L CH}_4 \text{ kg}^{-1}$   
584 body mass  $\text{d}^{-1}$  (Midwood et al. 1989) and by reducing WTR by  $1.02 \text{ g d}^{-1}$  for each litre  
585 of  $\text{CH}_4$  produced (Midwood et al. 1989). Similar adjustment would have increased the  
586 FMR of our non-pregnant goats by just 3%, comparable with  $\text{CH}_4$ -related errors  
587 reported for other ruminants (Fancy et al. 1986; Midwood et al. 1993, 1994).  
588 Nonetheless,  $\text{CH}_4$  output is heavily dependent on diet composition, which was  
589 unknown for our goats, and the 1.03 correction factor (i.e. + 3%) could lead to an  
590 overestimate of goat FMR if the  $\text{CH}_4$  production of goats was less than sheep. Trees  
591 and shrubs (Dawson et al. 1975) typically contain more tannin than commercial  
592 concentrates or legume forages (as used in the validation studies on sheep by  
593 Midwood et al. 1989), and tannins reduce  $\text{CH}_4$  output from goats (Puchala et al.

2005). However, even when using a 1.03 correction factor, the FMR of our goats was within the range of data from other arid-adapted ungulates, (Figure 1A).

Deuterium losses via fecal solids can also complicate comparisons of ruminant FMR (Midwood et al. 1989, 1993, 1994; Williams et al. 2001). For ruminants, fecal-deuterium losses derived from isotope exchanges with bulky vegetable matter (mainly in the rumen) may lead to overestimates of water flux by a further 3-5% above those associated with CH<sub>4</sub>. The range of errors quantified via respirometry validations are from < 1% to ca. 15% (Fancy et al. 1986; Midwood et al. 1993, 1994). Therefore, assuming that the combined losses of CH<sub>4</sub> and fecal-deuterium resulted in an underestimation of our reported CO<sub>2</sub> production by a liberal value of 10% (i.e. 5% for CH<sub>4</sub> and a further 5% for faecal losses; Fancy et al., 1986; Midwood et al. 1989; 1993, 1994), then the FMR for our non-pregnant feral goats may have been as high as 502 kJ kg<sup>-0.73</sup> d<sup>-1</sup>. This value is still within the range of other goat breeds, and is just 52% of the FMR of domestic Merino sheep FMR grazed at the same site (Munn et al. 2009). Thus, even allowing for the maximum errors in the technique, it remains that goats have an energy requirement typical of desert-adapted placentals.

The daily water turnover rates (WTR) of our goats were comparable with those measured in free-ranging goats at the same study site and under similar environmental conditions (i.e. ca. 3.0 L d<sup>-1</sup>; Dawson et al. 1975). Further, the WTR of our non-pregnant goats was comparable with that predicted for a general placental mammal of equivalent body mass (Figure 1B). More striking was that the WTR of our non-pregnant goats (173 mL kg<sup>-0.79</sup> d<sup>-1</sup>) was just 33% of the WTR of non-pregnant Merino sheep grazed at the same site under comparable environmental conditions (Munn et al. 2009). Differences between the water use of our non-reproductive feral goats and Merino sheep are further accentuated if their WTRs are adjusted using

619 crude corrections for CH<sub>4</sub>- and fecal-deuterium losses, assuming that the raw WTRs  
620 for these animals are overestimated by up to 10% (errors from validations studies  
621 range from 2% – 10%; Midwood et al. 1989, 1993, 1994; Haggarty et al. 1998).  
622 Therefore, assuming a water-flux correction factor of 0.9 (to correct an overestimate  
623 of 10%), the WTR of our non-pregnant goats would be 156 mL kg<sup>-0.79</sup> d<sup>-1</sup>, around  
624 84% that predicted for a general placental and just 30% that of Merino sheep grazed at  
625 the same site (i.e. sheep = 521 L kg<sup>-0.79</sup> d<sup>-1</sup>, after Munn et al. 2009).

626         While analysis of dry-goats provides an insight into adaptations that might  
627 enhance frugal resource-use to support the persistence of invasive species, that  
628 persistence requires population stabilisation or expansion and the energy and water  
629 requirements of these animals under more intense life history stages, such as during  
630 reproduction, will better quantify their environmental impact. Anecdotal reports  
631 indicate that in Australia's arid rangelands, feral goats maintain breeding even during  
632 prolonged drought (Parkes et al. 1996; see also Silanikove 2000). Such an observation  
633 suggests that goats have lower energy and / or water requirements for reproduction  
634 compared with other species. However, we found that the additional energy  
635 requirement of pregnant goats relative to non-pregnant goats was comparable to the  
636 difference reported for other species (i.e. 1.2 – 1.3 times higher in pregnant animals,  
637 Robbins 2001; Table 2). The pregnant goats in our study were mostly carrying 3<sup>rd</sup>  
638 trimester twins, and the 3<sup>rd</sup> trimester is the peak of energy expenditure during  
639 pregnancy in placental mammals (e.g. Goldberg et al. 1993; Pekins et al. 1998). The  
640 higher energy requirements of pregnant mothers at that stage is associated with  
641 numerous factors, including foetal growth, elevated basal metabolic rates, elevated  
642 maintenance costs for placental and uterine tissues, and increased activity costs  
643 associated with carrying additional mass (Gittleman and Thompson 1988; Schoeller

and Fijeld 1991; Goldberg et al. 1993; Robbins 2001). Moreover, data on the FMR and WTR of lactating goats would be useful in appreciating the costs of reproduction in feral goats and how this might influence their population dynamics and survival in Australia's rangelands.

## **Conclusions**

We caution against using broad-scale allometry of FMR to predict local-scale species-specific impacts or requirements. This approach has been used in other studies, for example to predict the impacts of feral cats on seabirds (Keitt et al. 2002), to infer prey community dynamics as driven by predicted wolf FMRs (Gazzola et al. 2007), to evaluate the ecology of restoration for mammalian assemblages (Gorman 2007), and to assess macroecological phenomena such as the energy equivalence rule in birds (Russo et al. 2003). Because allometry averages a broad range of adaptive possibilities, using allometry to make species-specific predictions is unlikely to be biologically or ecologically relevant, at least with regard to local phenomena. In our case the potential grazing pressure of feral goats would have been overestimated by 40% if we relied on allometric predictions of their energy and food requirements. Consequently, broad-scale allometries of animal resource use may not be an appropriate tool for evaluating adaptive management protocols, either for invasive species or for other situations such as recovery programs for endangered species. We further question the usefulness of broad-scale allometry for predicting species-specific responses to climate changes or imposed animal management strategies (e.g. water-point closure). In short, there is no substitute for comparative, on-ground studies.

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Table 1: Body mass, doubly labelled water kinetics, and field metabolic rate (FMR) of non-pregnant (n = 4) and pregnant (n = 5) feral goats grazed together in rangeland in arid Australia.

	<sup>#</sup> Body mass (kg)	Body mass change (% d <sup>-1</sup> )	<i>K</i> <sup>18</sup> O/ <sup>2</sup> H	Dilution space ratio ( <i>N<sub>H</sub>:N<sub>O</sub></i> ) <sup>‡</sup>	FMR (kJ d <sup>-1</sup> )	FMR (kJ kg <sup>-0.73</sup> d <sup>-1</sup> ) <sup>†</sup>
Non-Pregnant	28.8 ± 2.0	0.99 ± 0.32	1.18 ± 0.03	1.01 ± 0.02	5278 ± 343	455.9 ± 24.2
Pregnant	42.7 ± 1.5 (40.8 ± 1.4)	1.16 ± 0.26	1.20 ± 0.03	1.04 ± 0.01	9225 ± 595	600.9 ± 36.6 (615.5 ± 36.5)
<i>F</i>	31.2 (25.8)	0.2	0.2	1.5	26.2	9.7 (11.7)
<i>P</i>	<b>0.001</b>	0.68	0.648	0.270	<b>0.001</b>	<b>0.017</b> <b>(0.01)</b>
Mean (±SE)	-	1.10 ± 0.2	1.19 ± 0.03	1.02 ± 0.01	-	-

Note: <sup>#</sup>Average of initial and final body masses, including fetal mass for pregnant animals (average fetal mass = 1.9 ± 0.3 kg); <sup>‡</sup>A sample size of n=4 was used here for pregnant animals as one individual had a *N<sub>H</sub>:N<sub>O</sub>* value markedly higher than all others (see methods text for details).

<sup>†</sup>Values in parenthesis are relative to foetus-free body mass.



Table 2: Total body water content (TBW; %), rate of water turnover (WTR) of non-pregnant (n = 4) and pregnant (n = 5) feral goats grazing together in rangeland in arid Australia.

	TBW (%)	WTR (L d <sup>-1</sup> )	WTR (mL kg <sup>-0.75</sup> d <sup>-1</sup> ) <sup>†</sup>
Non-Pregnant	60.7 ± 0.7	2.42 ± 0.17	173.0 ± 17.5
Pregnant	62.0 ± 1.1	4.43 ± 0.39	228.1 ± 17.7 (236.5 ± 19.3)
<i>F</i>	0.9	18.6	4.7 ( <b>5.6</b> )
<i>P</i>	0.367	<b>0.004</b>	0.066 <b>(0.049)</b>
Mean (±SE)	61.5 ± 0.7	-	-

<sup>†</sup>Values in parenthesis are relative to foetus-free body mass.

Table 3: Apparent digestibility of rumen dry matter (DM) and dry matter intakes (DMI)<sup>†</sup> estimated for non-pregnant (n = 4) and pregnant (n = 5) feral goats grazing together in rangeland in arid Australia.

	Apparent DM	DMI	DMI
	digestibility (%)	(g d <sup>-1</sup> )	(g kg <sup>-0.76</sup> d <sup>-1</sup> ) <sup>#</sup>
Non-Pregnant	54.4 ± 2.9	459 ± 30	35.9 ± 1.9
Pregnant	61.2 ± 2.3	802 ± 52	46.4 ± 2.9
			(47.9 ± 2.8)
<i>F</i>	3.32	29	8.7
			(10.8)
<i>P</i>	0.111	<b>0.001</b>	<b>0.03</b>
			<b>(0.01)</b>
Mean (±SE)	58.2 ± 2.1	-	-

<sup>†</sup> Estimated DMI needed to meet daily FMR, assuming metabolisable energy content of forage of 11.5kJ g<sup>-1</sup> DM (see text). <sup>#</sup>Values in parenthesis are relative to foetus-free body mass.

Table 4: Mean ( $\pm$  SEM) urine electrolytes and urine and blood osmolality for non-pregnant (n = 4) and pregnant (n = 5) feral goats grazing together in rangeland in arid Australia.

						Urine	Blood
	Sodium	Potassium	Calcium	Magnesium	Chloride	Osmolality	Osmolality
	(mmol L <sup>-1</sup> )	(mmol L <sup>-1</sup> )	(mmol L <sup>-1</sup> )	(mmol L <sup>-1</sup> )	(mmol L <sup>-1</sup> )	(mOsmol kg <sup>-1</sup> )	(mOsmol kg <sup>-1</sup> )
Non-Pregnant	82 $\pm$ 11	20 $\pm$ 5	0.52 $\pm$ 0.20	5.8 $\pm$ 1.3	47 $\pm$ 17	476 $\pm$ 83	337 $\pm$ 4
Pregnant	196 $\pm$ 77	36 $\pm$ 13	0.88 $\pm$ 0.3	6.2 $\pm$ 1.0	87 $\pm$ 32	751 $\pm$ 132	333 $\pm$ 5
<i>F</i>	2.88	1.57	1.12	0.1	1.33	1.78	0.00
<i>P</i>	0.13	0.25	0.25	0.81	0.29	0.224	0.95
Mean ( $\pm$ SE)	144 $\pm$ 45	29 $\pm$ 8	0.72 $\pm$ 02	6.0 $\pm$ 0.8	70 $\pm$ 20	629 $\pm$ 107	335 $\pm$ 4

1 Table 5: Allometric regressions for field metabolic rate (FMR), dry matter intake  
2 (DMI) and water turnover rate (WTR) for non-marine, non-reproductive placental  
3 mammals, by conventional and phylogenetically independent methods. All regression  
4 were statistically significant ( $P < 0.001$ )

		Slope	Intercept	R <sup>2</sup>
<b>Conventional</b>				
FMR	All (64)	$0.73 \pm 0.022$	$0.65 \pm 0.057$	0.95
	Arid (30)	$0.77 \pm 0.029$	$0.46 \pm 0.078$	0.96
	Non-arid (32)	$0.69 \pm 0.027$	$0.81 \pm 0.068$	0.96
DMI	All (64)	$0.76 \pm 0.023$	$-0.56 \pm 0.060$	0.95
	Arid (30)	$0.80 \pm 0.03$	$-0.75 \pm 0.08$	0.96
	Non-arid (32)	$0.73 \pm 0.03$	$-0.40 \pm 0.070$	0.96
WTR	All (37)	$0.79 \pm 0.05$	$-0.30 \pm 0.14$	0.86
	Arid (22)	$0.90 \pm 0.04$	$-0.75 \pm 0.11$	0.96
	Non-arid (15)	$0.66 \pm 0.08$	$0.24 \pm 0.22$	0.83
<b>Phylogenetically independent</b>				
FMR	All (64)	$0.69 \pm 0.032$	$0.002 \pm 0.027$	0.88
	Arid (30)	$0.74 \pm 0.046$	$-0.064 \pm 0.040$	0.90
	Non-arid (32)	$0.65 \pm 0.041$	$0.052 \pm 0.034$	0.89
DMI	All (64)	$0.73 \pm 0.034$	$0.004 \pm 0.029$	0.88
	Arid (30)	$0.79 \pm 0.050$	$-0.082 \pm 0.044$	0.90
	Non-arid (32)	$0.70 \pm 0.041$	$0.077 \pm 0.034$	0.91
WTR	All (37)	$0.65 \pm 0.071$	$0.052 \pm 0.063$	0.71
	Arid (22)	$0.82 \pm 0.077$	$-0.072 \pm 0.068$	0.85
	Non-arid (15)	$0.50 \pm 0.106$	$0.168 \pm 0.099$	0.63

5 Values are  $\pm$  standard error, with sample sizes (N) in parenthesis.

6

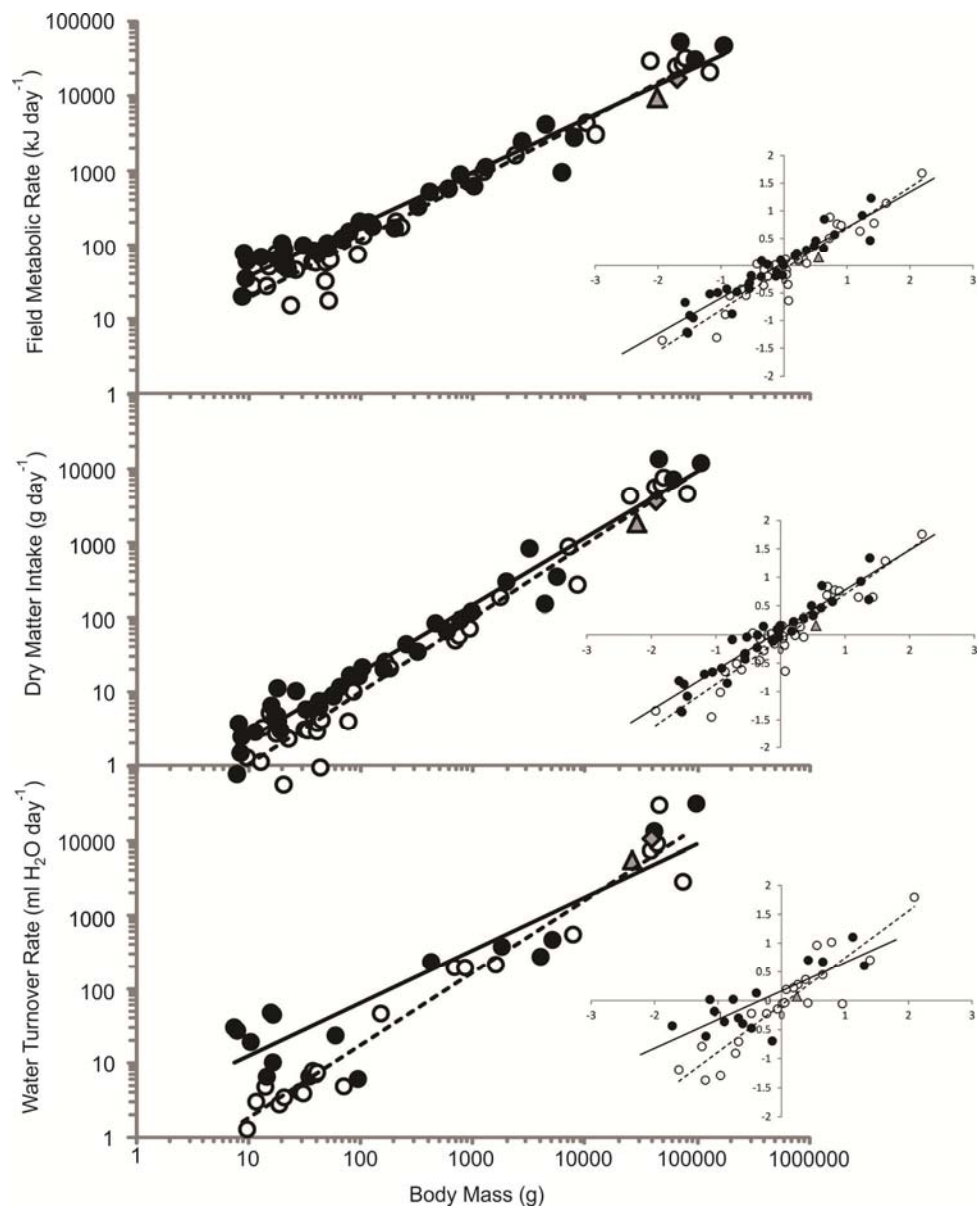
7

8    Figure Captions

9

10    Figure 1: Conventional (main) and phylogenetically independent (insets) allometric  
11    relationships for field metabolic rate, water turnover rate and dry matter intake for  
12    non-marine, non-reproductive placental mammals (see Appendix for raw data): open  
13    circles = arid zone species, black circles are non-arid zone species; grey triangle =  
14    non-pregnant goat, grey diamond = pregnant goat; dashed line = arid regression, solid  
15    line = non-arid regression; insets are phylogenetically independent residuals with  
16    symbols as for the conventional regression.

17



18 Figure 1

19

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Appendix A1: Body mass (BM; g), field metabolic rate (FMR;  $\text{kJ d}^{-1}$ ), dry matter intake (DMI;  $\text{g d}^{-1}$ ), water turnover rate (WTR;  $\text{mL d}^{-1}$ ), diet (I = insectivore, N = nectarivore, C = carnivore, F = frugivore, G = granivore, H = hindgut fermenting herbivore, H (R) = foregut fermenting herbivore, and O = omnivore), and habitat (D = desert, ND = non-desert) for non-marine placental mammals, collated from non-reproductive animals under free-range or near free-range conditions; the most conservative seasonal data for FMRs and WTRs were used when available.

<i>Genus species</i>	Common name	BM (g)	FMR ( $\text{kJ d}^{-1}$ )	DMI ( $\text{g d}^{-1}$ )	WTR ( $\text{mL d}^{-1}$ )	Diet	Habitat	Reference
<i>Saccopteryx bilineata</i>	Sac-winged bat	7.9	16.2	0.9		I	ND	Voigt et al., 2001
<i>Sorex araneus</i>	Common shrew	8.19	58.1	3.1	20.24	I	ND	Ochocińska and Taylor, 2005
<i>Plecotus auritus</i>	Brown long-eared bat	8.5	27.6	1.5		I	ND	Speakman and Racey, 1987
<i>Glossophaga commissarisi</i>	Commissaris's long-tongued bat	8.7	45.7	2.2	18.5	N	ND	Voigt et al., 2006
<i>Gerbillus henleyi</i>	Pygmy gerbil	9.7	22.2	1.3	1.1	G	D	Degen et al., 1997
<i>Anoura caudifer</i>	Flower-visiting bat	11.5	51.9	2.5	13.4	N	ND	von Helversen and Reyer, 1984
<i>Macrotus californicus</i>	California leaf-nosed bat (Big eared bat)	12.9	22.1	1.2	2.46	I	D	Bell et al., 1986
<i>Peromyscus crinitus</i>	Canyon mouse	13.4	39.3	2.8		O	D	Mullen, 1971a
<i>Mus domesticus (musculus)</i>	Wild house mouse	15.5	57.1	4.1	3.74	O	D	Mutze et al., 1991
<i>Clethrionomys rutilus</i>	Northern red-backed vole	16	48.96	4.9	5	H	ND	Holleman et al., 1982
<i>Syconycteris australis</i>	Southern blossom bat	17.36	76.87	3.7	30.91	N	ND	Geiser and Coburn, 1999
<i>Perognathus formosus</i>	Pocket mouse	17.7	40.5	2.4		G	D	Mullen and Chew, 1973
<i>Apodemus sylvaticus</i>	Wood mice	18.1	64.4	3.8	7.5	G	ND	Corp et al., 1999
<i>Carollia brevicauda</i>	Silky short-tailed bat	18.2	50	7.6	29.1	F	ND	Voigt et al., 2006

<i>Peromyscus maniculatus</i>	Deer mouse	18.4	46.3	3.3		O	D	Hayes, 1989
<i>Peromyscus leucopus</i>	White-footed deer mouse	19.4	36.5	2.6		O	ND	Randolph, 1980
<i>Eremitalpa granti</i> ( <i>namibensis</i> )	Namib desert golden mole	20.67	12.46	0.7	2.27	I	D	Seymour et al., 1998
<i>Gerbillus allenbyi</i>	Allenby's gerbil	22.8	35.6	2.1	2.78	G	D	Degen et al., 1992
<i>Microtus agrestis</i>	Field vole	26.5	72.7	7.1		H	ND	Meerlo et al., 1997
<i>Gerbillus pyramidum</i>	Greater egyptian gerbil	31.8	45.2	2.7	3.24	G	D	Degen et al., 1992
<i>Pseudomys albocinereus</i>	Ash-gray mouse	32.6	62.2	4.4		O	ND	Nagy, 1987 (after Nagy and Morris, Pers. Obs.)
<i>Dipodomys merriami</i>	Desert-dwelling kangaroo rat	33.9	44.0	2.6	3.1	G	D	Nagy and Gruchacz, 1994
<i>Acomys cahirinus</i>	Common spiny mouse	38.27	51.7	3.7	5.04	O	D	Degen et al., 1986
<i>Pseudomys nanus</i>	Barrow Island mouse	40.9	25.5	2.6	5.27	H	D	Bradshaw et al., 1994#
<i>Sekeetamys calurus</i>	Bushy-tailed jird	41.23	44	3.1	5.89	O	D	Degen et al., 1986
<i>Microgale dobsoni</i>	Dobson's shrew tenrec	42.6	77.1	5.5		I	ND	Stephenson et al., 1994
<i>Microgale talazaci</i>	Talazac's shrew tenrec	42.8	66.5	4.8		I	ND	Stephenson et al., 1994
<i>Zyzomys argurus</i>	Rock rats	43.78	14.3	1.0	5.4	O	D	Bradshaw et al., 1994#
<i>Acomys russatus</i>	Golden spiny mouse	45.04	47.8	3.4	5.65	O	D	Degen et al., 1986
<i>Dipodomys microps</i>	Chisel-toothed kangaroo rat	56.96	89.2	6.4		O	D	Mullen, 1971b
<i>Praeomys natalensis</i>	Multi-mammate mouse	57.3	86.6	6.2		O	ND	Green and Rowe-Rowe, 1987
<i>Microcebus murinus</i>	Grey mouse lemur	65.6	109.2	7.8	16.2	O	ND	Schmid and Speakman, 2000
<i>Meriones crassus</i>	Sundevall's Jird	77.6	55.7	3.3	3.81	G	D	Degen et al., 1997
<i>Phyllostomus hastatus</i>	Greater spear-nosed bat	80.8	146	10.428 57143		O	ND	Kunz et al., 1998
<i>Ammospermophilus</i>	White-tailed antelope squirrel	86.25	97.5	7.0		O	D	Karasov, 1981



<i>leucurus</i>								
<i>Tamias striatus</i>	Eastern chipmunk	96.3	143	10.2		O	ND	Randolph, 1980
<i>Thomomys bottae</i>	Botta's pocket gopher	103.8	127.4	12.7	4.67	H	ND	Gettinger, 1984
<i>Heliophobius argenteocinereus</i>	Silvery mole rat	161	121.8	12.18		H	ND	Zelova et al., 2011
<i>Psammomys obesus</i>	Fat sand rat	165.6	146.3	14.6	30.2	H	D	Degen et al., 1991
<i>Octodon degus</i>	Degus	182.2	125	12.5		H	D	Bozinovic et al., 2003
<i>Spermophilus saturatus</i>	Cascade golden-mantled ground squirrel	256	226.5	22.7		H	ND	Kenagy et al., 1989
<i>Tamiasciurus hudsonicus</i>	Red Squirrel	322	347	18.9		G	ND	Bryce et al., 2001
<i>Cavia magna</i>	Greater guinea pig	466	381.6	38.2	132.4	H	ND	Künkele et al., 2005
<i>Sciurus carolinensis</i>	Eastern gray squirrel	588	574	31.2		G	ND	Bryce et al., 2001
<i>Suricata suricatta</i>	Meerkat	697	468	25.0		I	D	Scantlebury et al., 2002
<i>Bassariscus astutus</i>	Ringtailed cat	752	472	28.1	113.3	C	D	Chevalier, 1989
<i>Lepilemur ruficaudatus</i>	Red-tailed sportive lemur	774.2	411.5	41.2		H	ND	Drack et al., 1999
<i>Vulpes cana</i>	Blanford's fox	936.5	627.5	33.6	112.4	I	D	Geffen et al., 1992
<i>Martes americana</i>	American Martin	975	709	50.6		O	ND	Gilbert et al., 2009#
<i>Vulpes rueppelli</i>	Rüppell's fox	1750	1014.7	72.5	123	O	D	Williams et al., 2002
<i>Vulpes velox</i>	Swift fox	1990	1488	106.3	205	O	ND	Covell et al., 1996
<i>Marmota flaviventris</i>	Yellow bellied marmot	3190	2434	243.4		H	ND	Salsbury and Armitage, 1994
<i>Bradypus variegatus</i>	Three-toed sloth	4385	611.9	61.2	154	H	ND	Nagy and Montgomery, 1980
<i>Vulpes vulpes</i>	Red fox	5597	1681	120.1	251	O	ND	Winstanley et al., 2003
<i>Alouatta palliata</i>	Mantled howler monkey	7116	2542	254.2		H	D	Nagy and Milton, 1979
<i>Proteles cristata</i>	Aardwolf	8543	1845	98.7	292	I	D	Williams et al., 1997

<i>Lycaon pictus</i>	African wild dog	25170	15300	910.7		C	D	Gorman et al., 1998
<i>Antidorcas marsupialis</i>	Antelope Springbok	42100	13100	1139.1	3180	H (R)	D	Nagy and Knight, 1994
<i>Odocoileus hemionus</i>	Mule deer	45400	26700	2321.7	5500	H (R)	ND	Nagy, 1987 (after Nagy and Jacobson, Pers. Obs.); see also Nagy et al. 1990
<i>Lama pacos</i>	Alpaca	48000	14050	1221.7	3850	H (R)	D	Riek et al., 2007
<i>Ovis aries</i>	Sheep	50200	16664	1449.0	11500	H (R)	D	Munn et al., 2009
<i>Rangifer tarandus</i>	Reindeer	61000	15980	1389.6		H (R)	ND	Gotaas et al., 2000
<i>Oryx leucoryx</i>	Arabian oryx	81500	11081	963.6	1310	H (R)	D	Williams et al., 2001
<i>Cervus elaphus</i>	Red deer	107300	24050	2091.3	11963	H (R)	ND	Haggarty et al., 1998

26 Appendix A2: Published reports for field metabolic and water turnover rates for marine and non-marine placental mammals omitted from our  
27 allometric analyses and *a priori* justifications for their omission.

<b>Genus species</b>	<b>Common name</b>	<b>Habitat</b>	<b>Omission justification</b>	<b>Reference</b>
<i>Pipistrellus pipistrellus</i>	Pipistrelle	ND	Pregnant or lactating	Racey and Speakman, 1987; Speakman, 1997
<i>Myotis lucifugus</i>	Little brown bat	ND	Pregnant or lactating	Kurta et al., 1987
<i>Eptesicus fuscus</i>	Big brown bat	ND	Pregnant or lactating	Kurta et al., 1990
<i>Mus domesticas</i>	feral house mouse	ND	Body mass not specified	Rowe-Rowe et al., 1989
<i>Microtus pennsylvanicus</i>	Meadow vole	ND	Not free range, 25 m <sup>2</sup> enclosure, high density; home range = 400-800 m <sup>2</sup> (Getz, 1961)	Bertraux et al., 1996
<i>Lemmus trimucronatus</i>	Brown lemming	ND	n= 1 male, n=2 females, likely pregnant and each carrying transmitter – not validated for load	Peterson et al., 1976
<i>Arvicola terrestris</i>	Water vole	ND	Authors caution that re-breathing of isotopes may have occurred	Grenot et al., 1984
<i>Vulpes macrotis</i>	Kit fox	ND	Mixed sexes and reproductive states, specific body masses not available	Girard, 2001
<i>Lepus californicus</i>	Black-tailed jackrabbit	D	Authors note DLW results were not comparable with measured feed intakes, may not be sufficiently free-range in a 300 m <sup>2</sup> enclosure, home ranges =1-3 km <sup>2</sup> (Smith, 1990)	Shoemaker et al., 1976
<i>Arctocephalus gazella</i>	Antarctic fur seal	M	Lactating	Costa et al., 1989; Costa et al., 1985; Costa and Trillmich, 1988
<i>Arctocephalus galapagoensis</i>	Galapagos fur seal	M	Lactating	Costa and Trillmich, 1988
<i>Callorhinus ursinus</i>	Northern fur seal	M	Lactating and pups	Costa et al., 1985; Costa and Gentry, 1986

<i>Neophoca cinerea</i>	Australian sea lion	M	Lactating	Costa and Gales, 2003
<i>Zalophus californicus</i>	California sea lion	M	Lactating	Costa et al., 1985
<i>Phocartos hookeri</i>	New Zealand sea lion	M	Lactating	Costa and Gales, 2000
<i>Mirounga angustirostris</i>	Northern elephant seal	M	Pups	Kretzmann et al., 1993
<i>Phoca vitulina</i>	Harbour seal (common seal)	M	N=1 adult male <sup>#</sup>	Reilly and Fedak, 1991
<i>Odobenus rosmarus</i>	Walrus	M	N=2 adult males <sup>#</sup>	Acquarone et al., 2006

<sup>#</sup>We have omitted these data because there is no evidence that males of such large species are representative of both sexes, and because the scaling of FMR in marine and terrestrial mammals may differ (Speakman and Król, 2010).

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