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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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±37 kJ kg$^{-0.73}$ d$^{-1}$) was 1.3 times that of non-pregnant goats (456±24 kJ kg$^{-0.73}$ d$^{-1}$). The water turnover rate of pregnant goats (228±18 mL kg$^{-0.79}$ d$^{-1}$) was also 1.3 times that of non-pregnant goats (173±18 mL kg$^{-0.79}$ 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

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Summary

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 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 ± 37 kJ kg^{-0.73} d^{-1}) was 1.3 times that of non-pregnant goats (456 ± 24 kJ kg^{-0.73} d^{-1}). The water turnover rate of pregnant goats (228 ± 18 mL kg^{-0.79} d^{-1}) was also 1.3 times that of non-pregnant goats (173 ± 18 kg^{-0.79} d^{-1}), but the difference was not significant (*P*=0.07). There was no significant difference in estimated dry 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 non-pregnant 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 50%, with implications for the predicted impact on their
local ecology.

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

Introduction

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

Domestic goats were introduced to Australia with European settlement in the
late 1700’s (Parkes et al. 1996). Subsequently, escaped or released goats established
themselves as one of the most significant invasive herbivores in Australia (Parkes et
al. 1996; McLeod 2004; Coutts-Smith et al., 2007; West and Saunders 2007). Feral
goats compete with domestic stock (sheep, Ovis aries and cattle, Bos taurus),
contribute heavily to land degradation and overgrazing, and have been implicated in
the decline of native fauna such as the yellow-footed rock wallaby (Petrogale
The establishment of large and persistent populations of feral goats has been coincident with control of the dingo (*Canis lupus dingo*), which has limited predation pressure that otherwise might suppress goat populations (Newsome et al. 2001). Further, a broad and flexible diet as a generalist herbivore may contribute to the goats’ success (Harrington 1986; Squires 1980). Anecdotal reports suggest that goats can sustain reproductive output even during prolonged drought when forage availability and quality are poor (Parkes et al. 1996). However, fundamental information on the field energy and water requirements of feral goats in Australia is lacking. We used the doubly labelled water method to investigate the field metabolic rate (FMR) and water turnover rate (WTR) of feral goats inhabiting a typical Australian rangeland. We measured the FMR and WTR of both pregnant and non-pregnant goats. We have also examined blood and urine concentrations and urine electrolyte concentrations of goats as indicators of diet, and estimated their diet digestibility to estimate the dry matter intake (DMI) required to meet their FMR. On a broader scale, we compare the FMR, estimated DMI and WTR of non-pregnant feral goats to those of non-reproductive, terrestrial placental mammals using allometric scaling, to determine whether the energy requirements of feral goats differ from a ‘typical’ placental mammal. We evaluate the efficacy of using allometric scaling to predict species-specific resource requirements and the implications of using this approach for predicting finer-scale, local impacts of invasive or other species.
Materials and Methods

Study site and climatic conditions

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

Study animals

Free-ranging feral goats (n = 4 non-pregnant; n = 5 pregnant) were mustered between 0600 h and 0800 h in the western parts of the study site. Animals were moved to purpose-built holding yards before being transferred via cage-trailer to a large (16 ha) enclosure. The enclosure had not been grazed for several years and vegetation within the enclosure was markedly higher than outside the enclosure (A. Munn et al., Pers. Obs). Water was available within the enclosure via a water trough, from which all animals were observed to drink, and abundant shade was available via scattered acacia trees and shrubs. Animals were acclimated to the enclosure for ten days prior to experimentation. The reproductive state of the goats was determined post-mortem at
the conclusion of the study. Of the five pregnant females, all but one carried twins, and so the combined foetal body mass was used throughout analysis. Individual foetal masses were used to estimate gestational age (McDonald et al. 1988).

Measurement of FMR and WTR

We measured the field metabolic rate (CO₂ production; L d⁻¹) and water turnover rate (WTR; L d⁻¹) of goats using the doubly labelled water method (Lifson and McClintock 1966; Speakman 1997). Animal numbers were limited both by the high cost of the doubly-labelled water for such large animals and the size of the enclosure. Goats were captured by muster and blood samples (ca. 4 mL) were obtained from the jugular vein for the measurement of background levels of the isotopes. Goats were then injected intraperitoneally with 0.3 g kg⁻¹ ¹⁸O (> 98% enriched) and 0.15 g kg⁻¹ deuterium (²H; > 95% enriched) from separate syringes (isotopes from Rotem Industries, Israel) into the same location. The isotopes were allowed to equilibrate with body water for 6-8 h before a second blood sample (ca. 4 mL) was obtained from the jugular vein. During the equilibration period the animals were maintained in a small, shaded pen (ca. 10 m²) without access to feed or water. The goats were then released into the enclosure and allowed to range freely for 8 days, after which they were mustered and held quietly in the shaded pen until they were shot and a final blood sample obtained. Background, equilibration and final blood samples were analysed for ¹⁸O and ²H by isotope ratio mass spectrometry after vacuum distillation to obtain pure water (Speakman 1997; Metabolic Solutions, Nashua, NH).

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

\[ N_{\text{int}} = (I_{\text{ds}} - I_{\text{dist}}) \times (M_{\text{dist}} / M_W) \times (M_{\text{inj}} / (I_{\text{int}} - I_b)) / 18.02 \]  

(1)
where $N_{\text{int}}$ = initial intercept pool size of the isotope in the animal, $I_{\text{ds}}$ = concentration of isotope in isotopically-labelled water solution, $I_{\text{dist}}$ = concentration of isotope in water distilled from body fluid, $M_{\text{dist}}$ = mass of distilled water, $M_W$ = mass of isotopically-labelled water used in dilution, $M_{\text{inj}}$ = mass of isotopically-labelled water injected into the animal, $I_{\text{int}}$ = the intercept or equilibration concentration of isotope ($^{18}\text{O}$ or $^2\text{H}$) and $I_b$ = concentration of isotope ($^{18}\text{O}$ or $^2\text{H}$) in water distilled from the background blood sample. Initial dilution space ratios ($N_{\text{H}}:N_{\text{O}}$) were not significantly different between pregnant and non-pregnant goats, and so a mean ($\pm$SE) group ratio of 1.02 $\pm$ 0.01 was used to calculate WRT and FMR (see below). Of note, one pregnant animal had a $N_{\text{H}}:N_{\text{O}}$ value of 1.15, and was considered sufficiently different to all others to exclude it from the group mean $N_{\text{H}}:N_{\text{O}}$; that individual’s FMR and WTR were calculated using its specific $N_{\text{H}}:N_{\text{O}}$.

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

$$r_{\text{H}_2\text{O}} = (k_h * \bar{N}_{\text{H}}/ R\text{-displace})/(f_1 + (1-\lambda))$$

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

$$k_{H} = \frac{(\ln H_{\text{int}} - \ln H_{\text{final}})}{t}$$  \hspace{1cm} (3);

where $\ln$ = natural log of initial ($H_{\text{int}}$) and final ($H_{\text{final}}$) concentrations (ppm) of $^2$H in body water after correction for background levels, and $t$ = time (days).

The mean isotopic pool size ($\overline{N}$) for $^{18}$O and $^2$H was calculated for a linearly changing body water pool according to:

$$N_1 = \frac{M_{B1} \cdot N_{\text{int}}}{M_{B1}}$$  \hspace{1cm} (4),

$$N_2 = \frac{M_{B2} \cdot N_{\text{int}}}{M_{B1}}$$  \hspace{1cm} (5),

$$\overline{N} = \frac{(N_1 + N_2)}{2}$$  \hspace{1cm} (6);

where $N_1$ and $N_2$ are the initial and final isotopic pool sizes (i.e. for $^{18}$O or $^2$H), $M_{B1}$ and $M_{B2}$ = body mass at the beginning and end of the experiment, $N_{\text{int}}$ = initial isotope pool size ($^{18}$O or $^2$H), assuming that body water content remained a constant fraction of body mass (i.e. $N_{\text{int}} / M_{B1}$) for each animal (Nagy and Costa 1980; Gessaman et al. 2004).

The production of CO$_2$ ($r_{CO_2}$; mol d$^{-1}$) was estimated using equations validated for ruminants after Midwood et al. (1994) as:

$$r_{CO_2} = \left( (k_{O} \cdot \overline{N}_{O}) - \left[ (r_{H_2O} \cdot X \cdot f_2) + (1-X) \cdot r_{H_2O} \right] \right) / 2f_3$$  \hspace{1cm} (7);
of the proportion of total water loss that is fractionated (assumed = 0.25; Speakman 1997), $f_2 = \text{fractionation constant for } H_2^{18}O \text{ vapour relative to } H_2^{18}O \text{ liquid }$ (assumed to be 0.99; Speakman 1997), and $f_3 = \text{the fractionation constant for } H_2^{18}O_2 \text{ gas relative to } H_2^{18}O \text{ liquid }$ (assumed to be 1.039; Lifson and McLintock 1966; Speakman 1997). Carbon dioxide production was then converted to a field metabolic rate (FMR; kJ d$^{-1}$) assuming energy equivalents of 21.7 kJ L$^{-1}$ CO$_2$ (Nagy et al. 1999).

**Potential errors of DLW method in ruminants**

The use of the doubly labelled water method in ruminants may be complicated by the large amount of vegetative material in the gut, which provides a substrate for deuterium exchange with plant fibre and subsequent faecal loss, in addition to the incorporation of deuterium as methane during methanogenic fermentation (Fancy et al. 1986; Midwood et al. 1989, 1993, 1994). Therefore, some of the deuterium introduced as labelled water may be lost via avenues other than water, possibly elevating the estimation of the deuterium flux and thus water flux ($r_{H_2O}$), and therefore underestimating the CO$_2$ production via the difference between $^{18}$O and $^2$H fluxes (Fancy et al. 1986; Midwood et al. 1989, 1993, 1994). Because of these avenues CO$_2$ production can be underestimated by between 3% and 12% from non-growing (stable body mass) ruminants (Fancy et al. 1986; Midwood et al. 1989, 1993, 1994). However, more recent validation of the use of deuterium-labelled water to measure WTR of sheep and goats found no significant differences between isotope-kinetic predictions and those estimated from water intake (combined with preformed sources; Al-Ramamneh et al. 2010; see also Junghans et al. 1997). Moreover, errors of the DLW method described by the earlier validations in ruminants (e.g. Midwood et al. 1989, 1993, 1994; Fancy et al. 1986) were within the ranges reported from validation
trials with non-ruminants (e.g. Sparling et al. 2008). Correcting for deuterium losses in faeces and methane in free-ranging ruminants is difficult and rarely attempted (but see Williams et al. 2001). We could not measure methane or faecal output from our goats, and so have presented unadjusted values for WTR and FMR. We later discuss the likely impacts of deuterium loss through faeces and CH$_4$ on our results, based on data for other ruminants (Midwood et al. 1993, 1994).

Osmolalities of blood and urine and urine electrolytes

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

Diet digestibility

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

\[
\text{Apparent digestibility} \% = \left(1 - \frac{M_d}{M_f}\right) \times 100
\]

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

Allometry of FMR, DMI and WTR

The FMR and WTR of non-pregnant goats were compared with other adult, non-marine, non-reproductive (i.e. non-lactating/non-pregnant) placental mammals ($n = 64$ species for FMR and $n=37$ species WTR respectively; Appendix A1). These data include species covering four orders of magnitude of body mass. Data for WTR was used only from species for which FMR was simultaneously measured (Table 4). When data were available from more than one season, we selected the lowest values for FMR and WTR, typically using data collected during the dry season; FMRs reported during other seasons, or following rainfall, were generally higher (e.g. Mutze et al. 1991; Nagy and Gruchacz 1994; Covell et al. 1996; Degen et al. 1991, 1997; Williams et al. 1997, 2001; see Appendix). Importantly, all previous allometric analyses of mammalian FMR (e.g. Anderson and Jetz 2005; Capellini et al. 2010; 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 kJ g\(^{-1}\) DM), a carnivore (16.8 kJ g\(^{-1}\) DM), a frugivore (6.6 kJ g\(^{-1}\) DM), a granivore (16.9 kJ g\(^{-1}\) DM), a hindgut fermenting herbivore (10 kJ g\(^{-1}\) DM), a foregut fermenting herbivore (mainly ruminants; 11.5 kJ g\(^{-1}\) DM), or an omnivore (14 kJ g\(^{-1}\) 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
phylogenetically-independent analyses, data were rendered independent of phylogeny by autoregression (Cheverud and Dow 1985; Rohlf 2001) using the mammalian phylogenetic tree of Bininda-Emonds et al. (2007). A phylogenetic distance matrix was obtained from the original Nexus file published by Binidna-Emondas et al. (2007) using the APE module for the package R. The species in our dataset were extracted from this distance matrix. The nexus file (and distance matrix generated from this) provides branch lengths. We are unaware of any polytomies in the database. Of note, our program for phylogenetic analysis required the phylogenetic tree to be in the format of a distance matrix, rather than the Newick format presented by Bininda-Emonds et al. (2007), so it was necessary to convert the Nexus file to a distance matrix. Extracting species required for this study from the overall mammal distance matrix was done using custom-written Visual Basic (V6) programs (P.C. Withers). The strength ($K^*$) and significance ($P$) of the phylogenetic signal for each phylogenetic variable, and for body mass, was determined after Blomberg et al. (2003) and Withers et al. (2006).

**Statistical analysis**

For between-group comparisons of pregnant and non-pregnant goats we used ANOVA, unless otherwise stated. Assumptions for ANOVA were tested using the Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) and Levene’s test for homogeneity of variances ($\alpha = 0.05$). Proportional data were arcsine transformed for analysis. Urine electrolyte concentrations ($Na^+$, $K^+$, $Cl^-$ and $Ca^{++}$) were $log_{10}$ transformed to normalise their distribution. Arid and non-arid allometric relationships and those for FMR and DMI were compared using ANCOVA. Diet effects were examined using ANOVA on 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 ± standard error unless stated otherwise.

**Results**

Pregnant (42.7 ± 2 kg) goats were 50% heavier than the non-pregnant goats (28.8 ± 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 (~ 8 hours after injection) indicated that goat body fluids were enriched above background levels to 388 ± 12 ppm for $^{18}$O and 192 ± 10 ppm for $^2$H. Final blood samples (approximately eight days following equilibrium) had concentrations of $^{18}$O and $^2$H substantially above background levels
for all goats (range 65-111 ppm above background for $^{18}$O, and 39-92 ppm for $^2$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. kJ kg$^{-0.73}$ 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. mL H$_2$O kg$^{-0.79}$ 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 10g 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 $+1.2 \pm 0.3$% 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. g DM kg$^{-0.76}$ d$^{-1}$; Table 3). There were no significant differences between the pregnant
and non-pregnant goats with respect to blood or urine osmolality or urine electrolyte concentrations (Table 4).

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

Dry matter intakes by non-marine placental mammals scaled similarly to FMR, with a DMI scaling exponent of 0.76 (slope comparison with FMR, $F_{1,124} = 0.846, P = 0.360$). The DMIs of our goats conformed to the allometric relationship derived for non-marine placental-mammals (conventional analysis; $R^2 = 0.947; F_{1,62} = 1098, P <0.001$), being well within the 95% prediction limits for a further datum (Figure 1), despite these non-pregnant goats having a DMI just 62% of that predicted. The significant allometric relationship for DMI for non-marine placental mammals remained after accounting for the significant and exaggerated phylogenetic signal in DMI ($R^2 = 0.882; F_{1,62} = 463, P < 0.001; K^* = 1.14, P < 0.001$), and our goats still conformed to this relationship. Accounting for phylogeny did not reduce the 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 allometricaly 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 ± 0.03) and non-desert (0.69 ± 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}
The DMI of non-pregnant goats was 66% of that predicted for a desert species, and 62% of that predicted for a non-desert species. The significant difference between desert and non-desert mammals’ intercepts for DMI remained when the data were subject to phylogenetically-independent analysis ($F_{1,61} = 8.95, P = 0.004$).

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

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

**Discussion**

The success of feral goats surviving, indeed thriving, in arid and semi-arid Australia does not seem to be related to a remarkable water economy, at least when surface water is freely available as it was in this study. The WTR we measured for non-pregnant goats was as predicted for a non-desert species, and similar WTRs have been
reported for goats at the same study site (Dawson et al. 1975). It was suggested therefore that goats do not generally exhibit the physiological specialisations for water economy of some African desert ungulates (Dawson et al. 1975). However, daily water turnover is dependent on many factors, including the availability of free water, the distance to water from foraging sites, forage mineral content, forage water content, and thermal challenges that may increase an animal’s water requirements, and urine concentration ability (Silanikove 2000; Cain et al. 2006). Consequently, evaluating the daily water turnover of desert animals under non-water-stressed conditions is not likely to provide much insight for evaluating the benefits of adaptations related to water use. For example, ability to withstand dehydration appears to be a key adaptation of large desert mammals (Cain et al. 2006) and studies on water-restricted, free-range animals would be useful. Nonetheless, we did identify a significant difference in the allometric slope for WTR between desert and non-desert mammals, indicating that smaller (< 100 g), but not the larger, desert species exhibited lower daily WTRs compared with non-desert species. It must be noted however that larger desert species are overly represented in the data set available. Further data on comparably sized mesic-zone mammals are required to provide a truly ‘general’ data set for comparison with our goats or other species.

Daily energy and food (dry matter) requirement of our goats was typical of desert-adapted animals, and importantly that was significantly lower than those found in non-desert species. Feral goats are descended from the bezoar, *Capra aegagrus* (Naderi et al. 2009), which is naturally found in arid habitats in the Middle East (Weinberg et al. 2008). Overall, reduced energy and therefore food requirements appear to be a general feature of desert species, including goats, presumably aiding their survival in low productivity habitats (Silanikove 2000). Therefore, the success of
Feral goats in the Australian arid zone is probably attributable to a combination of features that support their low energy and food requirements, including flexible feeding behaviours, and their ability to select the most nutritious and digestible plant parts from a variety of forages (e.g. buds, leaves, fruits and flowers; Hoppe et al. 1977; Huston 1978; Warren et al. 1984; Harrington 1986; Lu 1988).

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

As mixed-feeders, feral goats can adapt readily to seasonal and geographical variation in diet availability (Lu 1988), and their tolerance of bitter plants (Bell 1959) enables them to feed on vegetation that is unpalatable to other herbivores. Moreover, the proliferation of artificial watering points (Fensham and Fairfax 2008) and the removal of dingoes (Newsome et al. 2001) from much of Australia’s arid and semi-arid regions, thereby supporting and protecting pastoral stock, may have released goats from water limitation and predation pressure, respectively. It is likely that a
combination of all of these factors explains the feral goat’s success as an invasive
species in the Australian rangelands.

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

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

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 kJ kg$^{-0.73}$ 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 kJ kg$^{-0.73}$ d$^{-1}$; Animut et al. 2005; Lachica and Aguilera 2003, 2005). This level of daily energy use was less than half that measured
in domestic Merino sheep (956 kJ kg\(^{-0.73}\) d\(^{-1}\)) grazed at the same location and under comparable environmental conditions (Munn et al. 2009). Sheep grazing for wool and meat production is the dominant industry in Australia’s rangelands. Our data suggest that the grazing pressures imposed by sheep are considerably higher than those by feral goats, but the reasons for this are unclear. The higher energy turnover of the Merino sheep compared with our goats could be related to differences in their minimal or maintenance metabolic rates, differences in their activity levels or the energetic costs for activity, or to differences in their productivity state. Merino sheep are bred for wool production, which is an energy cost not imposed on the feral goats. Further studies comparing goats with Merino sheep under more stringent dietary intakes (e.g. at maintenance rations) would help distinguish how these species partition energy turnover and how this related to their free-range FMRs and WTRs. It is noted that the FMR of Merino sheep measured by Munn et al. (2009) were adjusted for deuterium losses in CH\(_4\), assuming productions of 0.422 L CH\(_4\) kg\(^{-1}\) body mass d\(^{-1}\) (Midwood et al. 1989) and by reducing WTR by 1.02 g d\(^{-1}\) for each litre of CH\(_4\) produced (Midwood et al. 1989). Similar adjustment would have increased the FMR of our non-pregnant goats by just 3%, comparable with CH\(_4\)-related errors reported for other ruminants (Fancy et al. 1986; Midwood et al. 1993, 1994). Nonetheless, CH\(_4\) output is heavily dependent on diet composition, which was unknown for our goats, and the 1.03 correction factor (i.e. + 3%) could lead to an overestimate of goat FMR if the CH\(_4\) production of goats was less than sheep. Trees and shrubs (Dawson et al. 1975) typically contain more tannin than commercial concentrates or legume forages (as used in the validation studies on sheep by Midwood et al. 1989), and tannins reduce CH\(_4\) output from goats (Puchala et al.
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 CH₄. 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 CH₄ and fecal-deuterium resulted in an underestimation of our reported CO₂ production by a liberal value of 10% (i.e. 5% for CH₄ 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⁻⁰.⁷³ d⁻¹. 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⁻¹; 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⁻⁰.⁷⁹ d⁻¹) 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
crude corrections for CH$_4$- and fecal-deuterium losses, assuming that the raw WTRs for these animals are overestimated by up to 10% (errors from validations studies range from 2% – 10%; Midwood et al. 1989, 1993, 1994; Haggarty et al. 1998). Therefore, assuming a water-flux correction factor of 0.9 (to correct an overestimate of 10%), the WTR of our non-pregnant goats would be 156 mL kg$^{-0.79}$ d$^{-1}$, around 84% that predicted for a general placental and just 30% that of Merino sheep grazed at the same site (i.e. sheep = 521 L kg$^{-0.79}$ d$^{-1}$, after Munn et al. 2009).

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


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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.

<table>
<thead>
<tr>
<th></th>
<th>Body mass (kg)</th>
<th>Body mass change (% d⁻¹)</th>
<th>$K^{18}O/^{2}H$</th>
<th>Dilution space ratio ($N_{H}:N_{O}$)‡</th>
<th>FMR (kJ d⁻¹)</th>
<th>FMR (kJ kg⁻⁰.⁷³ d⁻¹)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Pregnant</td>
<td>28.8 ± 2.0</td>
<td>0.99 ± 0.32</td>
<td>1.18 ± 0.03</td>
<td>1.01 ± 0.02</td>
<td>5278 ± 343</td>
<td>455.9 ± 24.2</td>
</tr>
<tr>
<td>Pregnant</td>
<td>42.7 ± 1.5</td>
<td>1.16 ± 0.26</td>
<td>1.20 ± 0.03</td>
<td>1.04 ± 0.01</td>
<td>9225 ± 595</td>
<td>600.9 ± 36.6</td>
</tr>
</tbody>
</table>
<pre><code>              | (40.8 ± 1.4)  |                          |                 |                                      |              | (615.5 ± 36.5)       |
</code></pre>
<p>| $F$              | 31.2 (25.8)   | 0.2                      | 0.2             | 1.5                                  | 26.2         | 9.7 (11.7)           |
| $P$              | <strong>0.001</strong>     | 0.68                     | 0.648           | 0.270                                | <strong>0.001</strong>    | <strong>0.017</strong>            |
|               |                          |                 |                                      |              | (0.01)               |
| Mean (±SE)       | -             | 1.10 ± 0.2               | 1.19 ± 0.03     | 1.02 ± 0.01                          | -            | -                    |</p>

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

<table>
<thead>
<tr>
<th></th>
<th>TBW (%)</th>
<th>WTR (L d⁻¹)</th>
<th>WTR (mL kg⁻⁰.⁷⁹ d⁻¹)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Pregnant</td>
<td>60.7 ± 0.7</td>
<td>2.42 ± 0.17</td>
<td>173.0 ± 17.5</td>
</tr>
<tr>
<td>Pregnant</td>
<td>62.0 ± 1.1</td>
<td>4.43 ± 0.39</td>
<td>228.1 ± 17.7 (236.5 ± 19.3)</td>
</tr>
<tr>
<td>F</td>
<td>0.9</td>
<td>18.6</td>
<td>4.7 (5.6)</td>
</tr>
<tr>
<td>P</td>
<td>0.367</td>
<td><strong>0.004</strong></td>
<td>0.066 (0.049)</td>
</tr>
<tr>
<td>Mean (±SE)</td>
<td>61.5 ± 0.7</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

†Values in parenthesis are relative to foetus-free body mass.
Table 3: Apparent digestibility of rumen dry matter (DM) and dry matter intakes (DMI)† estimated for non-pregnant (n = 4) and pregnant (n = 5) feral goats grazing together in rangeland in arid Australia.

<table>
<thead>
<tr>
<th></th>
<th>Apparent DM digestibility (%)</th>
<th>DMI (g d⁻¹)</th>
<th>DMI (g kg⁻⁰.⁷⁶ d⁻¹)#</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Pregnant</td>
<td>54.4 ± 2.9</td>
<td>459 ± 30</td>
<td>35.9 ± 1.9</td>
</tr>
<tr>
<td>Pregnant</td>
<td>61.2 ± 2.3</td>
<td>802 ± 52</td>
<td>46.4 ± 2.9</td>
</tr>
</tbody>
</table>

|    | 3.32 | 29   | 8.7  |
|    |      |      | (10.8) |

|    | 0.111 | 0.001 | 0.03  |
|    |       |       | (0.01) |

Mean (±SE) 58.2 ± 2.1 - -

†Estimated DMI needed to meet daily FMR, assuming metabolisable energy content of forage of 11.5kJ g⁻¹ DM (see text). #Values in parenthesis are relative to foetus-free body mass.
Table 4: Mean (± 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.

<table>
<thead>
<tr>
<th></th>
<th>Sodium (mmol L⁻¹)</th>
<th>Potassium (mmol L⁻¹)</th>
<th>Calcium (mmol L⁻¹)</th>
<th>Magnesium (mmol L⁻¹)</th>
<th>Chloride (mmol L⁻¹)</th>
<th>Urine Osmolality (mOsmol kg⁻¹)</th>
<th>Blood Osmolality (mOsmol kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Pregnant</td>
<td>82 ± 11</td>
<td>20 ± 5</td>
<td>0.52 ± 0.20</td>
<td>5.8 ± 1.3</td>
<td>47 ± 17</td>
<td>476 ± 83</td>
<td>337 ± 4</td>
</tr>
<tr>
<td>Pregnant</td>
<td>196 ± 77</td>
<td>36 ± 13</td>
<td>0.88 ± 0.3</td>
<td>6.2 ± 1.0</td>
<td>87 ± 32</td>
<td>751 ± 132</td>
<td>333 ± 5</td>
</tr>
<tr>
<td>F</td>
<td>2.88</td>
<td>1.57</td>
<td>1.12</td>
<td>0.1</td>
<td>1.33</td>
<td>1.78</td>
<td>0.00</td>
</tr>
<tr>
<td>P</td>
<td>0.13</td>
<td>0.25</td>
<td>0.25</td>
<td>0.81</td>
<td>0.29</td>
<td>0.224</td>
<td>0.95</td>
</tr>
<tr>
<td>Mean (±SE)</td>
<td>144 ± 45</td>
<td>29 ± 8</td>
<td>0.72 ± 02</td>
<td>6.0 ± 0.8</td>
<td>70 ± 20</td>
<td>629 ± 107</td>
<td>335 ± 4</td>
</tr>
</tbody>
</table>
Table 5: Allometric regressions for field metabolic rate (FMR), dry matter intake (DMI) and water turnover rate (WTR) for non-marine, non-reproductive placental mammals, by conventional and phylogenetically independent methods. All regression were statistically significant \((P < 0.001)\)

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

Values are ± standard error, with sample sizes (N) in parenthesis.
Figure 1: Conventional (main) and phylogenetically independent (insets) allometric relationships for field metabolic rate, water turnover rate and dry matter intake for non-marine, non-reproductive placental mammals (see Appendix for raw data): open circles = arid zone species, black circles are non-arid zone species; grey triangle = non-pregnant goat, grey diamond = pregnant goat; dashed line = arid regression, solid line = non-arid regression; insets are phylogenetically independent residuals with symbols as for the conventional regression.
Figure 1
Appendix A1: Body mass (BM; g), field metabolic rate (FMR; kJ d⁻¹), dry matter intake (DMI; g d⁻¹), water turnover rate (WTR; 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.

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<tr>
<th>Genus species</th>
<th>Common name</th>
<th>BM (g)</th>
<th>FMR (kJ d⁻¹)</th>
<th>DMI (g d⁻¹)</th>
<th>WTR (mL d⁻¹)</th>
<th>Diet</th>
<th>Habitat</th>
<th>Reference</th>
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<td>Saccopteryx bilineata</td>
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<td>58.1</td>
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<td>I</td>
<td>ND</td>
<td>Ochocinski and Taylor, 2005</td>
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<td>ND</td>
<td>Speakman and Racey, 1987</td>
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<td>Commissaris’s long-tongued bat</td>
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<td>45.7</td>
<td>2.2</td>
<td>18.5</td>
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<td>ND</td>
<td>Voigt et al., 2006</td>
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<td>Pygmy gerbil</td>
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<td>22.2</td>
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<td>1.1</td>
<td>G</td>
<td>D</td>
<td>Degen et al., 1997</td>
</tr>
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<td>51.9</td>
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<td>ND</td>
<td>von Helversen and Reyer, 1984</td>
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<td>22.1</td>
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<td>Bell et al., 1986</td>
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<td>39.3</td>
<td>2.8</td>
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<td>O</td>
<td>D</td>
<td>Mullen, 1971a</td>
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<td>Wild house mouse</td>
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<td>Mullen et al., 1991</td>
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<td>30.91</td>
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<td>40.5</td>
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<td>G</td>
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<td>64.4</td>
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<td>7.5</td>
<td>G</td>
<td>ND</td>
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<td>50</td>
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<td>29.1</td>
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<td>ND</td>
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<td>Carcass Mass (g)</td>
<td>Fat Mass (g)</td>
<td>Sex</td>
<td>Reference</td>
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<td>O</td>
<td>Hayes, 1989</td>
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<td>19.4</td>
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<td>O</td>
<td>Randolph, 1980</td>
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<td>G</td>
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<td>G</td>
<td>Degen et al., 1992</td>
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<td>62.2</td>
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<td>O</td>
<td>Nagy, 1987 (after Nagy and Morris, Pers. Obs.)</td>
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<td>G</td>
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<td>ND</td>
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<td>468</td>
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<td>113.3</td>
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<td>D</td>
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<td>Lepilemur ruficaudatus</td>
<td>Red-tailed sportive lemur</td>
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<td>H</td>
<td>ND</td>
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<td>975</td>
<td>709</td>
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<td>ND</td>
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<td>1488</td>
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<td>Covell et al., 1996</td>
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<tr>
<td>Marmota flaviventris</td>
<td>Yellow bellied marmot</td>
<td>3190</td>
<td>2434</td>
<td>243.4</td>
<td>H</td>
<td>ND</td>
<td>Salsbury and Armitage, 1994</td>
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<tr>
<td>Bradypus variegatus</td>
<td>Three-toed sloth</td>
<td>4385</td>
<td>611.9</td>
<td>61.2</td>
<td>154</td>
<td>H</td>
<td>ND</td>
<td>Nagy and Montgomery, 1980</td>
</tr>
<tr>
<td>Vulpes vulpes</td>
<td>Red fox</td>
<td>5597</td>
<td>1681</td>
<td>120.1</td>
<td>251</td>
<td>O</td>
<td>ND</td>
<td>Winstanley et al., 2003</td>
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<tr>
<td>Alouatta palliata</td>
<td>Mantled howler monkey</td>
<td>7116</td>
<td>2542</td>
<td>254.2</td>
<td>H</td>
<td>D</td>
<td>Nagy and Milton, 1979</td>
<td></td>
</tr>
<tr>
<td>Proteles cristata</td>
<td>Aardwolf</td>
<td>8543</td>
<td>1845</td>
<td>98.7</td>
<td>292</td>
<td>I</td>
<td>D</td>
<td>Williams et al., 1997</td>
</tr>
<tr>
<td>Species</td>
<td>Common Name</td>
<td>Mass 1</td>
<td>Mass 2</td>
<td>Mass 3</td>
<td>Method</td>
<td>Location</td>
<td>Reference</td>
<td></td>
</tr>
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<td>----------------------------</td>
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<tr>
<td>Lycaon pictus</td>
<td>African wild dog</td>
<td>25170</td>
<td>15300</td>
<td>910.7</td>
<td>C</td>
<td>D</td>
<td>Gorman et al., 1998</td>
<td></td>
</tr>
</tbody>
</table>
| Antidorcas marsupialis  | Antelope Springbok | 42100   | 13100   | 1139.1  | 3180   | H (R)    | D                          | Nagy and Knight, 1994
| Odocoileus hemionus     | Mule deer        | 45400   | 26700   | 2321.7  | 5500   | H (R)    | ND                        | Nagy, 1987 (after Nagy and Jacobson, Pers. Obs.); see also Nagy et al. 1990
| Lama pacos              | Alpaca           | 48000   | 14050   | 1221.7  | 3850   | H (R)    | D                          | Riek et al., 2007
| Ovis aries              | Sheep            | 50200   | 16664   | 1449.0  | 11500  | H (R)    | D                          | Munn et al., 2009
| Rangifer tarandus       | Reindeer         | 61000   | 15980   | 1389.6  | 11500  | H (R)    | ND                        | Gotaas et al., 2000
| Oryx leucoryx           | Arabian oryx     | 81500   | 11081   | 963.6   | 1310   | H (R)    | D                          | Williams et al., 2001
| Cervus elaphus          | Red deer         | 107300  | 24050   | 2091.3  | 11963  | H (R)    | ND                        | Haggarty et al., 1998
Appendix A2: Published reports for field metabolic and water turnover rates for marine and non-marine placental mammals omitted from our allometric analyses and *a priori* justifications for their omission.

<table>
<thead>
<tr>
<th>Genus species</th>
<th>Common name</th>
<th>Habitat</th>
<th>Omission justification</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pipistrellus pipistrellus</em></td>
<td>Pipistrelle</td>
<td>ND</td>
<td>Pregnant or lactating</td>
<td>Racey and Speakman, 1987; Speakman, 1997</td>
</tr>
<tr>
<td><em>Myotis lucifugus</em></td>
<td>Little brown bat</td>
<td>ND</td>
<td>Pregnant or lactating</td>
<td>Kurta et al., 1987</td>
</tr>
<tr>
<td><em>Eptesicus fuscus</em></td>
<td>Big brown bat</td>
<td>ND</td>
<td>Pregnant or lactating</td>
<td>Kurta et al., 1990</td>
</tr>
<tr>
<td><em>Mus domesticas</em></td>
<td>feral house mouse</td>
<td>ND</td>
<td>Body mass not specified</td>
<td>Rowe-Rowe et al., 1989</td>
</tr>
<tr>
<td><em>Microtus pennsylvanicus</em></td>
<td>Meadow vole</td>
<td>ND</td>
<td>Not free range, 25 m² enclosure, high density; home range = 400-800 m² (Getz, 1961)</td>
<td>Bertraux et al., 1996</td>
</tr>
<tr>
<td><em>Lemmus trimucronatus</em></td>
<td>Brown lemming</td>
<td>ND</td>
<td>n= 1 male, n=2 females, likely pregnant and each carrying transmitter – not validated for load</td>
<td>Peterson et al., 1976</td>
</tr>
<tr>
<td><em>Arvicola terrestris</em></td>
<td>Water vole</td>
<td>ND</td>
<td>Authors caution that re-breathing of isotopes may have occurred</td>
<td>Grenot et al., 1984</td>
</tr>
<tr>
<td><em>Vulpes macrotis</em></td>
<td>Kit fix</td>
<td>ND</td>
<td>Mixed sexes and reproductive states, specific body masses not available</td>
<td>Girard, 2001</td>
</tr>
<tr>
<td><em>Lepus californicus</em></td>
<td>Black-tailed jackrabbit</td>
<td>D</td>
<td>Authors note DLW results were not comparable with measured feed intakes, may not be sufficiently free-range in a 300 m² enclosure, home ranges =1-3 km² (Smith, 1990)</td>
<td>Shoemaker et al., 1976</td>
</tr>
<tr>
<td><em>Arctocephalus gazella</em></td>
<td>Antarctic fur seal</td>
<td>M</td>
<td>Lactating</td>
<td>Costa et al., 1989; Costa et al., 1985; Costa and Trillmich, 1988</td>
</tr>
<tr>
<td><em>Arctocephalus galapagoensis</em></td>
<td>Galapagos fur seal</td>
<td>M</td>
<td>Lactating</td>
<td>Costa and Trillmich, 1988</td>
</tr>
<tr>
<td><em>Callorhinus ursinus</em></td>
<td>Northern fur seal</td>
<td>M</td>
<td>Lactating and pups</td>
<td>Costa et al., 1985; Costa and Gentry, 1986</td>
</tr>
<tr>
<td><strong>Neophoca cinerea</strong></td>
<td>Australian sea lion</td>
<td>M</td>
<td>Lactating</td>
<td>Costa and Gales, 2003</td>
</tr>
<tr>
<td>----------------------</td>
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<tr>
<td><strong>Zalophus californicus</strong></td>
<td>California sea lion</td>
<td>M</td>
<td>Lactating</td>
<td>Costa et al., 1985</td>
</tr>
<tr>
<td><strong>Phocarctos hookeri</strong></td>
<td>New Zealand sea lion</td>
<td>M</td>
<td>Lactating</td>
<td>Costa and Gales, 2000</td>
</tr>
<tr>
<td><strong>Mirounga angustirostris</strong></td>
<td>Northern elephant seal</td>
<td>M</td>
<td>Pups</td>
<td>Kretzmann et al., 1993</td>
</tr>
<tr>
<td><strong>Phoca vitulina</strong></td>
<td>Harbour seal (common seal)</td>
<td>M</td>
<td>N=1 adult male#</td>
<td>Reilly and Fedak, 1991</td>
</tr>
<tr>
<td><strong>Odobenus rosmarus</strong></td>
<td>Warlrus</td>
<td>M</td>
<td>N=2 adult males#</td>
<td>Acquarone et al., 2006</td>
</tr>
</tbody>
</table>

#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).
Appendix A1 and A2 References


Speakman J.R. and Racey P.A. 1987. The equilibrium concentration of oxygen-18 in body water: implications for the accuracy of the doubly-labelled water


