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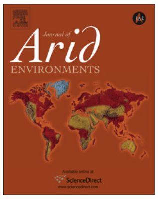

Characterising an artiodactyl family inhabiting arid habitats by its metabolism: Low metabolism and maintenance requirements in camelids

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ABSTRACT

To test whether camelids, as an artiodactyl family, are characterised by comparatively low energy expenditure, we collated literature data from experiments where at least one camelid and one ruminant species received the same diet, and literature data on camelid metabolism and energy requirements. Additionally, we measured the maintenance and resting metabolism in five alpacas, six llamas and five Bactrian camels by chamber respirometry. Irrespective of whether dry matter intake was expressed as g $kg^{-0.75}$ day^{-1}, g $kg^{-0.9}$ day^{-1}, or g $kg^{-1.0}$ day^{-1}, camelids ingested significantly less food than domestic ruminants (data available for sheep and goats). Although metabolic rates and energy requirements reported for camelids vary over a large range, they are generally below the 'average' basal mammal metabolism, and below published energy requirements for ruminants. The mean metabolic rates measured in this study were 215 ± 68, 261 ± 33 and 248 ± 51 kJ $kg^{-0.75}$ day^{-1} for alpacas, llamas and Bactrian camels, respectively. The corresponding resting metabolic rates averaged at 144 ± 64, 164 ± 38 and 192 ± 48 kJ $kg^{-0.75}$ day^{-1}. These findings confirm that camelids in general are characterised by relatively low metabolism and food intake, which might explain why this previously diverse group is currently limited to arid environments with low food resources where a reduced metabolism represents an advantage.

1. Introduction

The level of metabolism is an important characteristic of animal species. Among mammals this level is presumed to vary with ecological factors such as habitat, substrate, food habits (Lovegrove, 2000; McNab, 2008), phylogenetic affiliation (Capellini et al., 2010) or the mode of reproduction (Müller et al., 2012). Particular adaptations result in variation in metabolism even within closely related species. For example, variation in metabolism has been interpreted as adaptation to harsh environmental conditions within ruminants (Dittmann et al., 2014a), in small mammals (Lovegrove, 2003), carnivores (Careau et al., 2007), or mammals in general (Lovegrove, 2000; McNab, 2008). However, there are also cases where a whole phylogenetic lineage appears confined to a particular level of metabolism. The most typical examples among mammals are the generally low metabolic rates (MR) in the Xenarthra (Pilosa and Cingulata) or the marsupials (Enger, 1957; McNab, 2008).

Cetartiodactyla as an entity are considered a mammal group with a comparatively high level of metabolism (McNab, 2008). Yet, it has been suggested that nonruminant foregut fermenters are constrained to comparatively low MR (Clauss et al., 2010), which would, among the artiodactyls, include the peccaries and the hippopotamuses. Indeed, data from feeding experiments appear to support this hypothesis for hippos (Schwarm et al., 2006). A low MR can represent a competitive disadvantage in habitats where food supply is not limiting (chapter 13 in McNab, 2002, 2012). The physiological mechanism of rumination might liberate foregut

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fermenters from this putative metabolic constraint (Clauss et al., 2010; Matsuda et al., 2011; Schwarm et al., 2009), facilitating variable, including higher, metabolic levels among ruminant species. However, Clauss et al. (2010) suggested that camelids (Tylopoda), though functional ruminants, remain constrained to lower MR than many 'true' ruminants. They hypothesised that this may be at least partly due to a different set of morphophysiological adaptations in the forestomach required to achieve 'rumination' compared to the Ruminantia, which might limit the food intake capacity of camelids.

Several published findings support the hypothesis of a lower metabolism in camelids. In a comparative evaluation of food intake of herbivores (Meyer et al., 2010), camelids generally had lower food intakes per kg of metabolic body mass than ruminants at comparable forage fibre contents. When comparing the calculated intrauterine growth rates among different artiodactyl species (Müller et al., 2011), camelids have, due to their comparatively long gestation periods but average neonatal body mass (BM), a comparatively slow intrauterine growth. A higher metabolism might be linked to successful competition in evolutionary scenarios (chapter 13 in McNab, 2002, 2012). Even though camelids, which originate from North America and subsequently spread to both South America and Asia, had a much larger species diversity and covered a wider range of habitat niches in fossil times (Honey et al., 1998), only few extant species survived until today that appear limited to harsh environments, with other habitats apparently taken over by ruminants (e.g. Janis et al., 1994). The dromedary camel (*Camelus dromedarius*) inhabits the desert habitats of the Sahara and the Middle East (and more recently of central Australia) (Saalfeld and Edwards, 2010); the Bactrian camel (*Camelus bactrianus*) is found in the Mongolian desert (Tulgat and Schaller, 1992). The Andean highlands – home of the South American camelids (SAC) – are also of a very low food productivity, resulting in poor resource conditions that are linked, for example, to high embryonic losses in range-kept SAC (Bravo et al., 2010; Fernández-Baca et al., 1970). Finally, published maintenance energy requirements (MEm) of SAC are, at 305 kJ $kg^{-0.75}$ day^{-1} (NRC, 2007), only marginally higher than the average mammalian basal MR of 293 kJ kg $BM^{-0.75}$ d^{-1} (Kleiber, 1961). This indicates a comparatively low metabolism, because maintenance requirements are higher than basal MR (on the level of approximately 30–50%; estimate of basal metabolism of 300 kJ $kg^{-0.75}$ d^{-1} and maintenance requirements of 450–600 kJ $kg^{-0.75}$ d^{-1} in domestic ruminants (GfE, 1995, 1996; GfE, 2003; Südekum, 2002)).

Given these considerations, we aimed at systematically compiling literature data linked to the energy metabolism in camelids, and to generate own new data by measuring oxygen consumption in open chamber respirometry in camelid species. The hypothesis was that camelids generally have a lower metabolism than other mammals of their size, and in particular when compared to domestic ruminants.

2. Material and methods

2.1. Literature compilation on food intake

Direct comparisons of food intake between camelids and ruminants usually have the constraint of a difference in BM between the species. Mostly, camelids are compared to sheep or goats, which have lower BM. Therefore, a correction of the BM effect is necessary. Traditionally, food intake is either expressed as a direct proportion of BM (usually in % of BM or g kg $BM^{-1.0}$), or in relation to metabolic BM (g kg $BM^{-0.75}$) (San Martin and Bryant, 1989). The resulting difference can have a relevant effect on the result (Dulphy et al., 1998). The decision on how to present the data depends on whether intake is considered to scale allometrically or linearly with BM. Recently, it was suggested that dry matter intake (DMI) scales to $BM^{0.8-0.9}$ (Hackmann and Spain, 2010; Müller et al., 2013; Riaz et al., 2014). Therefore, literature results, from studies where voluntary daily DMI of a camelid and a ruminant species (invariably sheep and/or goats) were directly compared, were compiled using the three different expressions of g kg $BM^{-0.75}$, g kg $BM^{-0.9}$ and g kg $BM^{-1.0}$. A re-calculation of the results presented was not possible in all cases (e.g. if a source did only give one or two measures of relative food intake but not the original body mass of the animals), which led to slightly different sample sizes for the three respective data collections. For the statistical evaluation, values from camelids and domestic ruminants that had been obtained from the same experiment were compared by paired *t*-test. Additionally, we followed the approach of Dulphy et al. (1998) by testing for significant relationships between the intake of domestic ruminants and camelids under the same experimental conditions by linear regression. The relationship between dietary fibre content and DMI was tested by correlation analysis. The influence of fibre content on the intake relationship between domestic ruminants and camelids was tested by General Linear Models with ruminant DMI as the dependent, and camelid DMI and diet fibre content as the independent covariables. Analyses were performed in SPSS (21.0, SPSS Inc., Chicago, IL). Additionally, we present the data from Foose (1982) who fed similar diets to three camelid species and a large number of ruminant species.

2.2. Literature compilation on metabolism and maintenance requirements

The close scaling of energy requirements to metabolic BM (i.e. $BM^{0.75}$) is mostly unchallenged (Müller et al., 2012). Therefore, daily energy requirement data from the literature for camelids were compiled in kJ kg $BM^{-0.75}$. Data on MR were grouped according to the level of metabolism that they corresponded to, depending on the methods used in the individual studies. Thus, data were recorded as fasting metabolism (energy expenditure in respiration measurements with fasted animals), resting metabolism (with animals at rest), standing metabolism (with inactive but standing animals), general metabolism (respiration measurements over a longer period of time during which animals would stand, rest, eat, ruminate), and maintenance requirements (measured with various methods indicated when presenting the results). For comparison, published maintenance requirements for domestic ruminants were listed, including indications of the contributions of various processes to these requirements.

2.3. Own respiration chamber measurements

Oxygen consumption was measured in five alpacas kept at Zurich Zoo in December 2012, and six llamas and five Bactrian camels kept at a private camel farm in Switzerland between January and March 2013 under the Kantonal Animal Experiment Licence No. 142/2011. All animals were kept on a restricted amount (0.6, 0.8 and 1.8 kg dry matter for alpacas, llamas and camels, respectively) of pelleted lucerne (Provimi Kliba SA, Kaiseraugst, Switzerland) and had *ad libitum* access to lucerne hay (see Table S1 in online supplement for nutrient composition) for 3 weeks prior to the measurements. Water was available *ad libitum*. Animals were weighed either on a mobile scale (at the zoo) or led onto a truck scale in the vicinity of the farm. Animals were then kept, one animal at a time, separately for 24 h in respiration chambers (for alpacas, a transport box of 1.9 × 0.7 × 1.3 m; for llamas and Bactrian camels, a part of a building divided off by wooden panels of 2.9 × 1.6 × 2.4 m and 4.5 × 2.9 × 2.4 m, respectively). All 'chambers' were additionally sealed off with silicon, plastic foil and tape. In the