Biochemical adaptation of camelids during periods where feed is withheld

J. Wensvoort1, D. J. Kyle2, E. R. Ørskov3 & D. A. Bourke2

1 P.O. Box 9220, Dubai, UAE.
2 Rowett Research Institute, Greenburn Road, Bucksburn, Aberdeen AB21 9SB, UK.
3 Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, UK (b.orskov@raluri.sari.ac.uk).
* corresponding author.

Abstract: Biochemical changes during fasting or the withholding of feed for 5 day were studied in serum of camelids (dromedary camel, llama) and ruminants (sheep, steers). Camels maintained low levels of 13-hydroxybutyrate (BHB) and high levels of glucose but showed some increased levels of non-esterified fatty acid (NEFA) and urea when fasting. Sheep and steers showed a rise in serum BHB and much higher increases of NEFA than camels and llamas. Sheep showed decreased serum glucose. The llama showed some increase in BHB but NEFA was lower than the other three species. The results indicate that camelids have a unique ability to control lipolytic and gluconeogenic activity to prevent or postpone the state of ketosis. Understanding and manipulation of these metabolic mechanisms in cattle and sheep could have great benefit to the livestock industry.

Key words: camels, cattle, glucose requirement, ketosis, reindeer, sheep.

Introduction

Through evolution, camelids i.e. camels (Camelus spp.) and South American camelids (llamas, alpacas, guanacos and vicuna), have specifically adapted to dry arid environments. Camels are known to be able to starve for long periods and to use dietary energy very efficiently. Their maintenance energy requirement is as low as 314 kJ/kg0.75 (Guerouali & Filali, 1992). This is approximately two thirds of the requirement of beef cattle (Bos taurus) (NRC, 1985). Similarly, the maintenance requirement of digestible energy in the llama (Llama glama) was reported to be 37% lower than in sheep (Johnson, 1989).

The efficiency and fasting ability of camelids can be explained in part by behavioural and physiological characteristics (Wilson, 1984) but biochemical mechanisms may also contribute. In ruminants when food is unavailable, a breakdown of body tissue is induced and generally causes a shift in the main energy producing pathway (Trichloroacetic acid cycle, TCA-cycle) towards increased formation of ketone bodies (β-hydroxybutyrate (BHB) and acetoacetate) as a result of insufficient supply of oxaloacetate precursors. During fasting camelids may be able to utilise free fatty acid and ketone bodies more effectively and not need to rely fully on classical ruminant biochemical pathways for their energy and glucose requirement. This study describes the changes in blood biochemistry observed during fasting in two camelid species (dromedary
camel and llama) in comparison with sheep and cattle.

**Material and methods**

Three adult camels (*C. dromedarius*), three sheep (*Ovis aries*), three steers (*B. taurus*) and one llama (*L. glama*) were used in this study. The camels were kept at the Central Veterinary Research Laboratory in Dubai and the three steers, sheep and llama at the Rowett Research Institute in Aberdeen. Prior to the study all the animals were fed diets which were adequate for maintenance.

The camels, steers and sheep had food withheld for five consecutive days on one occasion. The llama had food withheld for five days on three occasions with six weeks between periods. Drinking water was always available. Blood samples were obtained once each day by jugular venepuncture from three days prior to fasting until five days after fasting. The serum was separated, centrifuged and stored at -20°C until analysis.

**Biochemistry studies**

BHB, glucose, non-esterified fatty acids (NEFA) and urea were determined with a Kone dynamic selective chemistry analyzer. The urea using the method of March *et al.* (1965), glucose by the method of Trinder (1969), NEFA by the method of Matsubara *et al.* (1983) and BHB by the method of Li *et al.* (1980).

**Data analysis studies**

Analysis of variance and Student's *t*-test were used to compare biochemical values with each species (except llama) before and during the fast-
ing periods. As only one llama was used in these studies, the data obtained from this animal was not used for statistical analysis but for comparison with the other species. Data are presented as mean values in figs. 1-4.

Results

Withholding of food did not cause any significant change in the serum concentration of BHB in camels, whereas marked increases ($P < 0.05$) were found in the sheep and steers (Fig. 1). In all species NEFA increased ($P < 0.05$) with fasting but the increases were much larger in the sheep and steers than in the camels (Fig. 2). In camels, serum glucose was maintained during the period where food was withheld and increased after feeding commenced again. Glucose concentrations decreased ($P < 0.05$) in sheep during fasting but did not change significantly in steers. After feeding there was no significant change in glucose concentrations in sheep or steers (Fig. 3). The data collected from the llama indicated similar changes in glucose, NEFA and urea to those observed in the camels. Blood urea concentration increased in all species during fasting (Fig. 4). This could be due to increase in amino acid oxidation to supply glucose precursors or to changes in glomerular filtration rate.

Discussion

In camels, the plasma concentration of ketone bodies has been previously reported to increase (Uro, 1987) or remain unchanged (Mirgani, 1982) during fasting, as observed in this study. It has been suggested that ketones have a very low entry rate in camels (Chandrasena et al., 1979) and kinetic studies would be required to confirm this. The low levels of BHB observed in these studies during fasting, may indicate that camels can supply sufficient 4 carbon (C4) metabolites for maintenance of the TCA-cycle or alternatively that they require fewer C4 metabolites or use different metabolites than other species of ruminants. Other factors which may contribute to maintaining the TCA-cycle and/or the high blood glucose levels in fasting ruminants include conversion of monocarboxylic fatty acids, mobilised from depot fats, to dicarboxylic acids by β-oxidation yielding succinic acid (4-carbon unit) through β-oxidation; oxidation of acetoacetate and BHB by 3-ketoacid-CoA transferase activity to produce succinate; acetoacetyl-CoA thiolase activity to produce acetyl-CoA; conversion of acetone to pyruvate or enzyme activity which provides NADPH i.e. acetyl-CoA carboxylase in the isocitrate dehydrogenase pathway. The increased level of urea during starvation indicates increased amino acid breakdown with supply of oxaloacetate precursors and possible gluconeogenesis. However the serum concentration of urea provides no indication of the extent of lean tissue degradation and gluconeogenesis and studies of nitrogen excretion in fasting camelids are required to confirm these observations.

In camelids the lower rates of increase in serum NEFA during starvation and the higher serum glucose levels which are maintained throughout starvation are probably of major importance in preventing elevation of ketone bodies during starvation in comparison with sheep and cattle. Camelids and camels in particular seem to have a special ability to control their lipolytic and gluconeogenic rates to prevent or postpone a pathological state of ketosis.

Ørskov & Ryle (1990) recommended that sheep and cattle should be fed about one third of maintenance during the dry or cold season to reduce BHB to normal levels and avoid excessive degradation of lean tissue for the provision of glucose precursors based on observations of glucose infusions to reduce BHB to normal levels. It is quite possible that indigenous ruminants adapted to severe fluctuations in nutrient supply have evolved similar mechanisms to reduce their glucose requirement. Soveri et al. (1992) reported BHB values of 0.4 mmol/l in undernourished reindeer calves which compare with 4 mmol/l in starved cattle (Ørskov et al., 1999). There is a great need to understand better the mechanisms by which indigenous species of ruminants withstand prolonged periods when the amount or availability of forage is much reduced, as shown for the camelids here. While a state of pathological ketosis may be difficult to define reducing the BHB from 4 to 1 mmol/l by infusions of small amounts of glucose or feeding them one-third of maintenance decreased fasting N excretion by 40% and also decreased heat production as measured in respiration chambers (Chowdhury & Ørskov, 1994; Ørskov et al., 1999).
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References

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