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Comparative Biochemistry and Physiology, Part A 143 (2006) 504–507
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Feed intake, forestomach fluid volume, dilution rate and mean retention of fluid in the forestomach during water deprivation and rehydration in camels (*Camelus* sp.)

W. von Engelhardt *, P. Haarmeyer, M. Lechner-Doll

Department of Physiology, School of Veterinary Medicine, Bischhofsholer Damm 15/102, D-30173 Hannover, Germany

Received 31 May 2005; received in revised form 10 January 2006; accepted 11 January 2006
Available online 21 February 2006

Abstract

Camels were deprived of water for 11 days. Before and during water deprivation and during rehydration changes in body weight, feed and water intake were measured. Using the liquid marker Cr-EDTA forestomach fluid volume, mean fluid retention and fluid dilution in the forestomach were estimated. At the eleventh day of water deprivation hay intake had decreased to only 9.6% of controls, dilution rates had decreased to 31%, mean retention time of fluid in the forestomach had increased to 189%. At the end of dehydration flow of saliva of 2 l/h mainly contributed to the still rather high dilution rates. Thereby buffering capacity and flow of fluid into the forestomach for microbial digestion as well as the outflow from the forestomach were maintained. At the beginning of rehydration camels drank 97 l within a few minutes, and animals thereby replaced all the water lost. Following this first huge water intake water is rapidly absorbed from the forestomach, and forestomach volume decreased again to dehydration values. At the third day of rehydration control values were reached again. Although feed intake decreased dramatically during water deprivation, functions of the forestomach can be maintained sufficiently mainly due to saliva inflow. This explains the mostly rapid recovery of camels when water is available again.

Keywords: Camel; Dehydration; Forestomach; Rehydration; Retention time; Saliva; Water absorption

1. Introduction

Camels have the exceptional ability to withstand long periods of dehydration, and they are able to replenish in a relative short period of time the water lost. Whereas changes of water metabolism, body fluid and its regulation, body temperature, kidney function, appetite and hormonal aspects during dehydration have been studied in the past (MacFarlane et al., 1963; Schmidt-Nielsen, 1964; Wilson, 1989; Robertshaw and Zine-Filali, 1995), little is known on functions of the forestomach in camels during severe periods of withdrawal of water. It was the aim of our study to get information on fluid volume, dilution rates and retention time of fluid in the forestomach of camels before and during withdrawal of drinking water and during the early phase of rehydration. We hypothesized that even at the end of severe dehydration due to a continuing saliva secretion a satisfactory requisite for microbial digestion in the forestomach and a continuing reduced outflow of digesta from the forestomach persists.

2. Materials and methods

2.1. Experimental animals

We used two Bactrian camels *Camelus bactrianus* and two tulus — a cross breed between one-humped camel *Camelus dromedarius* and Bactrian camel *C. bactrianus* (Table 1). Prior to the studies all animals were fitted with a fistula in the dorsal–caudal section of compartment 1 (C1) of the forestomach.

2.2. Feed and water intake

Prior to water deprivation feed intake of the individual camels was measured for six weeks. For 4 h each day animals could move

* Corresponding author. Tel.: +49 511 8567272; fax: +49 511 8567687.
E-mail address: wolfgang.von.engelhardt@tiho-hannover.de (W. von Engelhardt).

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doi:10.1016/j.cbpa.2006.01.021

Table 1
Experimental animals

Name	Breed	Gender	Age [years]	Mean mass [kg]
Ro	Cross breed (tulu)	Female	5	510
Sei	Cross breed (tulu)	Female	12	770
Em	*Camelus bactrianus*	Male (castrated)	7	600
Su	*Camelus bactrianus*	Male (castrated)	18	740

A tulu is a cross breeding between one-humped camel *Camelus dromedarius* and Bactrian camel *Camelus bactrianus*.

freely in a runout, during the rest of the day they were tethered indoor using a halter. Hay and water were offered ad libitum, and the camels received daily 2 kg dried sugar pulp shred soaked in 0.5 l water.

2.3. Fluid volume of the forestomach, dilution rate, mean retention time of fluid

Chromium-ethylenediaminetetraacetic acid (Cr-EDTA 1%, Binnerts et al., 1968) was used as fluid marker. 100 ml of the Cr-EDTA solution was added as a single injection via the fistula deep into forestomach contents of C1. Details of experimental steps, analysis and estimations had been given earlier (Lechner-Doll et al., 1990). *Forestomach fluid* volume in C1 and C2 (V_0) is $V_0 = M_0 / C_0$, where M_0 is the amount of Cr-EDTA injected (mg), and C_0 is the marker concentration at the moment when the 1% Cr-EDTA solution was added (time zero)(mg/l). *Dilution rate* (f) in compartments C1 and C2 is fluid volume times rate constant ($f = V_0 \cdot k$), where the rate constant (k) (transfer from the pool in terms of fraction of total marker moving per unit of time, also referred as elimination rate) is $k = (\ln C_0 - \ln C_t) / t$, where C_t is the marker concentration at time t (mg/l), and t is the time of sampling in hours after addition of the marker into C1. *Mean retention time* of fluid in C1 and C2 ($\overline{R}$) is the reciprocal value of rate constant, $\overline{R} = 1 / k$.

2.4. Statistics

Results were expressed as means and standard deviations. Differences between means were checked for significance ($p < 0.05$) by one factorial Analysis of Variance.

3. Results

3.1. Feed intake, water intake and body weight before, during and after withdrawal of drinking water

Camels were deprived of drinking water for 11 days. Mean water intake before deprivation was 22.3±2.3 l per day (Fig. 1A). When water was offered again the camels drank 97.3±24.1 l water within approximately 1 h, that is nearly 4 1/2 times the earlier daily water intake. During the dehydration period hay intake decreased from 8.3±0.79 to 0.8±0.5 kg dry matter per day (decrease of hay intake to 9.6%) (Fig. 1B). At the first day of rehydration feed intake increased to 4.7±0.6 kg dry matter. During dehydration camels lost 9.95% of the body weight (72.5±17.9 kg).

3.2. Fluid volume, dilution rate and mean retention time of fluid in compartments 1 and 2

The *fluid volume* of C1 and C2 (Fig. 2, first graph) decreased during the deprivation period from 69.7±4.3 to 36.4±5.8 l, which is a decrease to 52.2%. After water was offered again fluid volume reached 90.4±9.2 l, which is 129.7% of the volume prior to dehydration. However, 24 h after the beginning of rehydration forestomach fluid volume was again as low as at the eighth day of dehydration. At the second day of rehydration forestomach fluid volume had reached again the starting values before dehydration. Changes of mean forestomach fluid volumes estimated between days 6 and 13 were significantly different from the days prior to that.

The *dilution rate* in C1 and C2 (Fig. 2, second graph) decreased from 5.8±0.9 l/h before dehydration to 1.8±0.4 l/h at the 11th day without drinking water, which is a decreased to 31%. In the first hour of rehydration the camels drank 97 l water, but at the same time dilution rates increased to only 74% of the starting value before water deprivation. It is interesting to note that on the day after the start of rehydration dilution rates were still nearly as low as at the end of the dehydration period. Two days later dilution rate had returned to the original values. Changes of mean dilution rates estimated between days 6 and 8 and between days 11 and 13 were significantly different from the means up to day 6.

The *mean retention time of fluid* in C1 and C2 (Fig. 2, final graph) was 12.1±1.6 h before and 22.9±0.3 h at the end of water deprivation, that is an increase to 189.3%. After rehydration mean retention time had returned back to the original values

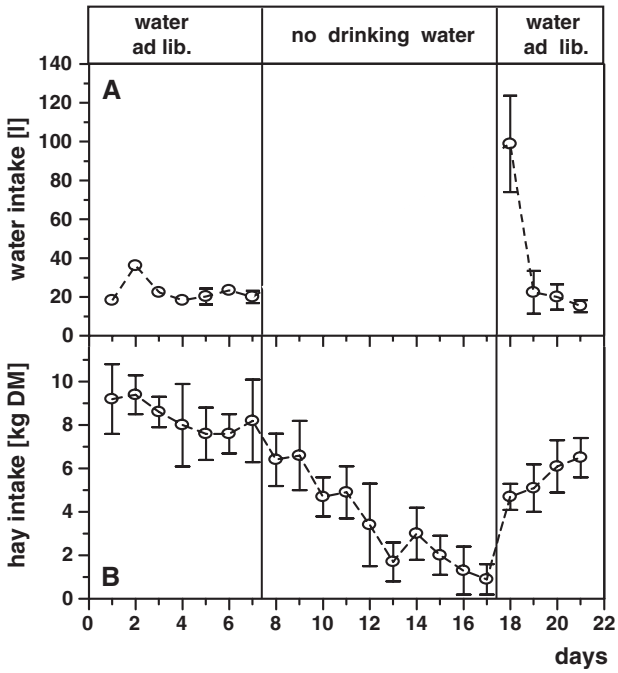

Fig. 1. Daily intake of drinking water (A) and daily hay intake (B) in four camels when water was available ad libitum for seven days, when no drinking water was given for 11 days (water deprivation period), and when water was again available ad libitum during four days of rehydration. Means and standard deviations are given for each day.

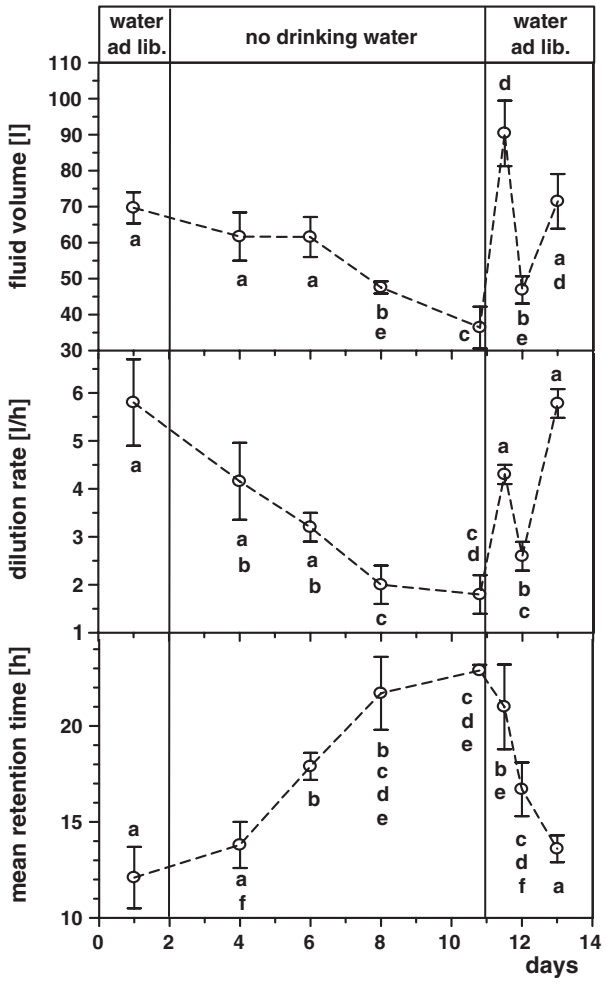

Fig. 2. Mean fluid volume of the forestomach (C1 and C2) in four camels (upper graph), dilution rates of forestomach fluid (second graph) and mean retention time of forestomach fluid (lower graph) one day before water was withheld, during the water deprivation period (11 days), and during the rehydration period (3 days) when water was offered again ad libitum. Means and standard deviations are given. Different letters below the means indicate significance ($p<0.05$) between means within each of the three panels.

within two days. Mean retention times estimated between days 4 and 13 were significantly higher than on days 1, 4 and 13.

4. Discussion

In the four camels forestomach fluid volumes before dehydration (controls, Fig. 1) were comparable with findings of earlier studies (Heller et al., 1986; Lechner-Doll et al., 1990, 1994). In younger and smaller camels (200–250 kg; Heller et al., 1986) fed fresh Lucerne forestomach fluid volumes as a percentage of body weight had been higher. Forestomach fluid volume of 10.6 l/100 kg body weight in our camels before the water deprivation period (Fig. 2) is similar to that estimated in camels, indigenous cattle, sheep and goats grazing a thornbush savannah pasture in Kenya (Lechner-Doll et al., 1990). In these four species in the studies in Kenya forestomach fluid volume was higher in animals during the dry compared to the green season. In the earlier studies, after only 7 days of water deprivation forestomach fluid volume in camels had reduced to 66% (Lechner-Doll et al., 1994) (Table 2).

During the 11 days of water deprivation hay intake decreased to only 10% of the control values (Table 2). Due to markedly lower energy requirements for maintenance of camelids compared with domestic ruminants (dromedary: Guerouali and Zine-Filali, 1992; llama: Schneider et al., 1974) this extremely low feed intake in camels for several days (Fig. 1) may have less serious consequences than in ruminates. In llamas it has been observed that diminished feed intake even decreased maintenance energy requirements further to values below these already low requirements (Schneider et al., 1974). Both, camels and llamas are camelids (*Tylopoda*). *Tylopoda* and *Ruminantia* represent two distinct suborders of *Artiodactyla,* and forestomachs and forestomach fermentation developed independently during evolution.

Only at a constant fluid forestomach volume the dilution rate of forestomach fluid reflects water intake and flow of saliva, on one hand, and this is identical to fluid passage rate out of the forestomach and water absorption from the forestomach under steady state conditions. However, in the foregoing water deprivation study forestomach volume had decreased when water was withheld, and therefore in our studies the dilution rate is not totally equal to the fluid passage rate. Yet, the estimated dilution rates in our experiments are valuable parameters for estimation of salivary flow at the end of the water deprivation period. Flow of saliva into the forestomach would have been 2 l/h provided that (1) we neglect a presumable very low or not existing water absorption from C1 and C2 at the end of water deprivation, and (2) we consider a diminution of forestomach fluid volume of 0.2 l/h, and we (3) take into account the dilution rate of 1.8 l/h. This flow of saliva achieves a continuous addition of an isotonic fluid of high buffering capacity into the forestomach and an appreciable forestomach fluid

Table 2
Comparison of forestomach fluid volume, dilution rate and mean retention time of fluid in C1 and C2 before dehydration (controls), at the end of water deprivation and during early rehydration in camels

	Present findings	Lechner-Doll et al. (1994)
Days of dehydration	11	7
Hay intake at end of dehydration [% of control]	9.7%	20%
Forestomach fluid volume at end of dehydration [% of control]	52.2%	66%
Dilution rate of forestomach fluid at end of dehydration [% of control]	31%	60%
Loss of body weight during dehydration	72.5±17.9 kg 9.95%±2.8% of BW	App. 10% of BW
Drinking water immediately after dehydration	97 l	90 l
Osmolarity of forestomach fluid		
End of dehydration	–	312±20.5 mOsm/l
After first water intake	–	138±20.2 mOsm/l

BW = body mass.

volume even after 11 days without drinking water. Thereby a sufficient microbial activity in forestomach contents could have been maintained, and at the end of water deprivation microbial breakdown of feed particles in the forestomach could have been still satisfactory. This is confirmed by observations that camels can utilize low-quality roughages favourably during severe dehydration (Mousa et al., 1983). The long retention time of fluid at the end of the dehydration period (Fig. 2) may be interpreted as an improved digestibility of the small amount of hay eaten.

Immediately after the end of water deprivation our camels drank 97 l water and thereby replaced their water deficit within a few minutes. In other studies it had been estimated that at rehydration camels actually imbibe even more water than they have lost (Robertshaw and Zine-Filali, 1995). The entire amount ingested is retained in the first instance in C1 and C2. Thereby forestomach contents get very hypotonic, and a large osmotic gradient created between forestomach and systemic fluid (Table 2). This results in a rapid absorption of water from C1 and C2. This is expressed in our study by the extensive drop of forestomach fluid volume from 90.4 l immediately after water intake to 46.9 l within 12 h, and many litres of water are absorbed rapidly from the hypotonic forestomach. Camels can overcome a rapid absorption of a hypotonic fluid due to the resistance of erythrocytes to haemolysis, camel erythrocytes have a low osmotic fragility (Perk, 1963). Lipid composition of the erythrocyte membrane (Al-Qarawi and Mousa, 2004) and also the haemoglobin sequences of camelids (Bogner et al., 1998) may be part of a natural selection process aimed at protecting camels against osmotic destruction of their erythrocytes during rapid rehydration.

We conclude that in camels after 11 days of water deprivation due to a still continuous flow of saliva isotonic fluid and buffering capacity reaches the forestomach to maintain about 50% of the control fluid volume and a sufficient microbial digestion in forestomach contents. This assists in a rapid recovery of camels after severe dehydration when water and feed is available again. About 50% of the huge amount of water camels drink in a very short time at the beginning of rehydration is rapidly absorbed. During evolution camel erythrocytes have developed mechanisms that prevent severe damage due to absorption of the large quantity of hypotonic fluid.

Acknowledgement

We thank Prof. B. Schröder for his assistance in preparing the illustrations and the electronic version of the manuscript.

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