HOMEOSTATIC RESPONSES TO WATER DEPRIVATION OR HEMORRHAGE IN LACTATING AND NON-LACTATING BEDOUIN GOATS

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(Received 23 February 1983)

Abstract — 1. Three lactating and three non-lactating black Bedouin goats were subjected to four days of water deprivation or to hemorrhage.
2. Four days of water deprivation caused body wt losses of 32 and 23%, and plasma volume losses of 30 and 34% in lactating and non-lactating goats respectively.
3. Plasma osmolality increased 17 and 15% in lactating and non-lactating goats. Plasma arginine vasopressin concentration rose from about 5 pg/ml to a mean of 36 pg/ml. Plasma renin activity increased from about 0.7 ng/ml/hr to a mean of 3.45 ng/ml/hr in lactating and to 3.15 ng/ml/hr in non-lactating goats.
4. At 4.5 hr post-rehydration plasma osmolality and plasma arginine vasopressin concentration were back to normal in non-lactating, but still elevated in lactating goats. Plasma renin activity increased after rehydration.
5. Rapid blood volume loss of 21–28% increased plasma arginine vasopressin concentration to 16–35 pg/ml in non-lactating and to 70 or > 500 pg/ml in lactating goats.
6. It is concluded that black Bedouin goats are well adapted to endure severe dehydration and rapid rehydration, but that they (especially lactating animals) react strongly to rapid volume depletion.

INTRODUCTION

Animals inhabiting the desert are expected to be adapted to water shortage. The black Bedouin goat (Capra hircus) graze all day fully exposed to sun and dry air which causes large water losses. Yet these goats can endure 4 days without drinking water and still continue to eat and to produce milk. The Bedouin goats are apparently equipped with special characteristics such as high total body water and large plasma volume, which increase even further during lactation (Hix et al., 1972; Shkolnik et al., 1979; Maitz and Shkolnik, 1980; Shkolnik et al., 1980). After 4 days of dehydration the plasma volume is at a level which is considered normal for water replete goats of other breeds (Hix et al., 1959). Moreover, when given access to water, Bedouin goats replenish their water deficit within a few minutes. They can drink up to 40% of their dehydrated body wt without apparent ill effect; this is due largely to the ability of the rumen to prevent the water from entering the blood too rapidly (Choshniak and Shkolnik, 1977a; Choshniak and Shkolnik, 1977b; Shkolnik et al., 1979).

Two hormonal systems are of special importance in the regulation of water balance and maintenance of plasma volume, vasopressin and the renin-angiotensin-aldosterone system. Vasopressin release is regulated principally by the osmotic (Na-) concentration of the extracellular fluid (Verney, 1947; Robertson et al., 1976; Andersson et al., 1980), but its release may be modified by changes in plasma volume. Thus, the sensitivity of cerebral receptors to osmotic stimulation increases during moderate hypovolemia in humans (Robertson and Athar, 1976), dogs (Kozlowsky and Szczepańska-Sadowska, 1975) and rats (Dunn et al., 1973). This sensitization may be mediated by the renin-angiotensin system (Fitzsimons, 1972) and a striking interaction between cerebral Na-sensitive receptors and angiotensin II has been observed (Andersson, 1977). In addition, reflex modulation of the vasopressin secretion by an inhibitory tonus from distension receptors in the heart and pulmonary veins contributes to the homeostatic control of the extracellular fluid volume (Gauer et al., 1970). It seemed of interest to study the plasma vasopressin (plasma arginine vasopressin = pAVP) conc. and the plasma renin activity (PRA) during 4 days of water deprivation in Bedouin goats, which repeatedly have to endure such severe dehydrations. We also compared the level of PAVP during dehydration with that which is seen during rapid hemorrhagic volume depletion.

MATERIALS AND METHODS

Animals

Black Bedouin goats were purchased from Bedouins in the eastern Sinai along the Gulf of Elat and kept and bred in the research zoo of Tel Aviv University. All goats were penned together outdoors and exposed to solar radiation with no access to shade. (Noon temperature in the shade was 25 ± 2°C and RH 68 ± 5%). Three lactating (3 months post-partum) and three non-lactating goats were used. The body wt of the lactating goats was 25.2 ± 3.1 kg and of the non-lactating ones 24.3 ± 2.5 kg. The animals were routinely kept on low quality hay with resultant low milk yield. A fortnight before onset of the experiments, the diet was changed to alfalfa hay without added concentrates and this diet was maintained throughout...
the experimental period. The animals were fed in the morning and in the afternoon. Immediately before afternoon feeding, the animals were given water and allowed to drink to satisfaction. The water was then removed and the kids were allowed to suck. The kids also sucked at 08.00 a.m. The milk yield (17.35 g/kg/day) was calculated from the weight gains of the kids as measured before and after sucking by an electronic balance. At other times the kids were kept separated from their mothers but could be seen and heard by them.

Dehydration experiments

The animals were allowed to drink as usual in the afternoon on day 0 and were then given no water until the evening 4 days later. On the morning of the first day the animals were fed as usual and the kids allowed to suck. The animals were then weighed and a polyethylene catheter inserted into the jugular vein. Blood samples were taken in the morning and afternoon each day. In addition, blood samples for determination of plasma volume were taken morning and afternoon on day 1 and every afternoon on days 2, 3 and 4. After a control sample, Evans blue was injected intravenously and thereafter timed blood samples were taken. After 4 days of water deprivation the animals were given a bucket full of water at 18.00 p.m. and allowed to drink to satisfaction and water consumed was measured. A blood sample was taken within 2 min after drinking, followed by a second sample after 60-90 min and a final sample after 4-4.5 hr.

Haemorrhage experiments

In the morning just before the sun reached the animals, one of the goats was brought indoors, weighed and placed in a metabolic cage in which only the turn around movement was restricted. The temperature of the room varied from 20°C in the morning to 30°C in the afternoon. A polyethylene catheter was inserted into one of the jugular veins and plasma volume (pV) and hematocrit were measured and blood trapping between the red blood cells. At 10.00-11.00 a.m. a second polyethylene cannula was placed in the contralateral jugular vein and the animal was bled at a rate of 20-40 ml/min. The blood was collected in heparinized polyethylene bags. The animals were bled until forced breathing indicated that the arterial blood pressure had fallen, which previously had been shown to coincide with a conspicuous pAVP release (Larsson et al., 1978). The hemorrhage was then stopped. Blood samples for pAVP analyses were taken before and at regular intervals during and after bleeding. A second measurement of plasma volume was performed at about 2.5 hr post-bleeding in five of the animals. In the sixth animal the hematocrit had fallen as low as 13% and therefore, the blood was immediately returned intravenously. In the other five animals, the blood was returned about 4 hr after the end of bleeding. After the blood had been returned, water was offered.

Analyses

Blood for hematocrit, plasma osmolality (pOsm), Na (pNa), K (pK) and measurements of Evans blue colour, was drawn into heparinized plastic tubes. The hematocrits were obtained by centrifuging (in triplicates) microhematocrit tubes at 4000 rpm in a clinical centrifuge for 20 min. The pOsm was analysed by freezing-point depression (Adv. Instrument osmometer) and pNa and pK by internal standard flame photometry (IL 343) Blood for analysis of pAVP and PRA was taken into pre-chilled tubes containing Na+-EDTA as an anticoagulant. Samples were spun at +4°C and the plasma transferred to plastic tubes (the ones for pAVP analyses containing 0.1 ml acetic acid per 1 ml of plasma) which were kept at -17°C until analysed. Plasma AVP was analysed by radio-immunoassay technique (Husain et al., 1973). PRA was analysed by radio-immunoassay as described by Fyhrquist et al. (1976).

Plasma volume was determined as the dilution volume of Evans blue (T6H2E) in the manner described by Maltz and Shkolnik (1980).

The data are presented as mean ± SE of the mean.

RESULTS

Water deprivation

During 4 days of water deprivation the goats lost large volumes of water. Non-lactating goats lost 5.6 ± 2 kg or 23% of their initial body wt (Table 1). The lactating goats lost 7.9 ± 3.1 kg or 32% of their body wt, part of which was due to milk loss via the udder. The milk yield was 470 ± 100 ml/day and was maintained at this level during the first two days of dehydration, but decreased to about 35% of the initial yield on the fourth day of dehydration. On the morning of day 1 the lactating goats had plasma volumes similar to those of the non-lactating animals (Table 1). However, as dehydration proceeded the lactating goats retained more fluid in the plasma than the non-lactating animals. On the second day of dehydration the lactating goats had lost 177 ± 63 ml and the non-lactating animals as much as 315 ± 55 ml. At the end of the fourth day the plasma volume had dropped 406 ± 67 ml in lactating goats and 455 ± 16 ml in the non-lactating ones. Thus lactating animals maintained their plasma volume/body wt relationship in contrast to the non-lactating goats (Table 1).

The water loss was reflected in pOsm which was already evident in the evening of day 1 (Fig. 1). The pNa rose from 141 ± 1 to 162 ± 2 mM/l during the four days of water deprivation (lactating goats). In non-lactating animals the pNa increased from 146 ± 0 to 164 ± 1 mM/l. Plasma K concentrations showed no significant change in lactating goats (4.4 ± 2 before, and 4.3 ± 0.2 mM/l at the end of water deprivation), but fell slightly in the non-lactating animals (from 4.5 ± 0.2 to 4.0 ± 0.2 mM/l).

Although pOsm had increased markedly the first day of dehydration the increase of pAVP was delayed until the second day (Fig. 1). At the end of the water deprivation period, the plasma pAVP was 21.3 ± 3.6 pg/ml in lactating goats and 26.2 ± 4.5 pg/ml in non-lactating goats. The plasma pAVP was significantly lower in lactating than in non-lactating goats (Table 1). Plasma pAVP was determined by radio-immunoassay technique (Husain et al., 1973).

Table 1. Changes in body wt and plasma volume during 4 days of water deprivation in three lactating and three non-lactating goats.

<table>
<thead>
<tr>
<th></th>
<th>Loss in body wt (% of initial)</th>
<th>Loss in plasma volume (% of initial)</th>
<th>Plasma volume as % of body wt</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-lactating</td>
<td>Lactating</td>
<td>Non-lactating</td>
</tr>
<tr>
<td></td>
<td>kg</td>
<td>kg</td>
<td>kg</td>
</tr>
<tr>
<td>Initial</td>
<td>24.3 ± 2.5</td>
<td>25.2 ± 3.1</td>
<td>1370 ± 84</td>
</tr>
<tr>
<td>Day 2</td>
<td>14 ± 1.1</td>
<td>19 ± 1.1</td>
<td>23 ± 4</td>
</tr>
<tr>
<td>Day 3</td>
<td>20 ± 1.1</td>
<td>29 ± 3</td>
<td>32 ± 0</td>
</tr>
<tr>
<td>Day 4</td>
<td>23 ± 1.1</td>
<td>32 ± 1</td>
<td>34 ± 2</td>
</tr>
</tbody>
</table>
Water deprivation or hemorrhage in Bedouin goats

deprivation period the absolute increase in pAVP was similar in both groups.

On day 2, PRA started to increase (Fig. 1). The PRA continued to rise in all animals but was slightly higher in the non-lactating goats until the end of the dehydration period, when the mean values of PRA in the lactating goats exceeded those seen in the non-lactating ones. The rise in PRA was similar in the two groups of animals, if the percentage loss of plasma volume was considered, whereas the PRA rose more in relation to the loss of body wt in the non-lactating than in the lactating animals. Thus, at a loss of 23% of the initial body wt, the PRA exceeded 3 ng/ml/hr in the non-lactating goats, but was only 2.1 ng/ml/hr when the lactating goats had lost 26% of their body wt.

Rehydration

After 4 days of water deprivation the animals were allowed to drink water to satisfaction. Lactating animals immediately drank 7.2±0.7 l and non-lactating ones 6.8±0.1 l. In the blood samples taken within 2 min after completion of drinking, there was no change either in pOsm or pNa (Fig. 1). Plasma K concentration was 4.3±0.3 mM/l in lactating goats and 4.5±0.1 mM/l in non-lactating ones. The PRA remained elevated, but the pAVP concentration fell markedly (Fig. 1). The next blood samples were taken 60-80 min after drinking. The pOsm had still not decreased in non-lactating animals, but had done so in the lactating goats. Also a minor decrease in pNa was observed in both groups of animals (to 156±2 and 157±1 mM/l). The plasma K concentration was 4.0±0.1 and 4.0±0.1 mM/l respectively. At this time, the PRA reached the highest values noted during the experiment (Fig. 1). The pAVP concentration had fallen considerably in the non-lactating goats, but remained above 20 pg/ml in the lactating animals. In the final blood samples which were taken 4-4.5 hr after drinking, pOsm and pNa had fallen almost to pre-dehydration values in the non-lactating goats, but were still considerably elevated in the lactating goats. The pK concentration now reached its highest level in both groups of animals or 5.2±0.6 mM/l in lactating goats.

Hemorrhage

All animals were bled until forced breathing began to appear. This did not occur until more than 23% of the initial blood volume had been withdrawn from two of the non-lactating animals, and was still hardly noticeable in the third non-lactating goat at this volume loss. However, bleeding was stopped in that animal when 28% of the blood volume had been removed. No release of vasopressin was seen in one of the animals (bled 23%), a rise to 11 pg/ml occurred in one animal (bled 28%) and a rise to 35 pg/ml in the third (bled 25%) (Fig. 2). Fifteen minutes after cessation of bleeding, the pAVP was moderately increased in all three animals. It continued to increase in one of the animals 45 min after the end of bleeding, but declined thereafter in all animals. Except for an increased respiratory rate (50-100 breaths/min), the animals did not seem disturbed by bleeding. They ate or ruminated during the whole post-bleeding observation period. The measurement of plasma volume which was made 2.5-3 hr post-bleeding revealed that the animals had...
not compensated for their volume loss at this time (Table 2). The animals had had no access to water during the day. Yet none of the animals drank when they were offered water at the end of the experiment, although the plasma osmolality had risen by 13 ± 1 mOsm/kg during the day.

Hemorrhage in lactating goats caused a more serious reaction, although these animals also were relatively tolerant to bleeding. In the three lactating goats, the bleeding was stopped after 21, 22 and 27% of blood withdrawal because of respiration rates above 80/min. In the animal bled of 27% of its initial blood volume, pAVP had increased to above 500 pg/ml. At this time, the pAVP conc. in the other two animals was 60 and 125 pg/ml respectively (Fig. 2). In one of the animals the hematocrit fell to 13%, and the second plasma volume measurement was therefore not performed. Instead, the blood was returned, after which she drank 3.8 l of water (her plasma osmolality had increased by 18 mOsm/kg during the day). Plasma volume had not recompensated after 2.5 ± 3 hr in the two other lactating goats (Table 2). Although the animals had had no access to water since the previous afternoon, one of them did not drink at all (increase in plasma osmolality during the day: 7 mOsm/kg), whereas the third lactating goat drank 1.2 l (increase in plasma osmolality: 6 mOsm/kg). The animals delivered the normal amount of milk after these experiments.

**DISCUSSION**

In comparison to previous studies on Bedouin goats (see Introduction) the initial plasma volumes were comparatively low in both lactating and non-lactating goats used in this study. However, when these goats were deprived of water for 4 days, the lactating goats maintained their plasma volume/body wt relationship, in contrast to the non-lactating goats. The increase of pOsm, pNa and pAVP were similar in all animals. Therefore, it appears that lactating black Bedouin goats maintain their plasma volume by withdrawal of isotonic fluid from other body fluid compartments.

PRA or plasma renin concentration increase in response to dehydration in man (Maebashi and Yoshinag, 1967), rats (Gross et al., 1965; Rosenthal et al., 1969), sheep (Blair-West et al., 1972) and goats (Olsson et al., 1978; Olsson et al., 1982). In this study, the PRA did not increase in the lactating animals until 13% of the plasma volume had been lost. At this stage,

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**Table 2.** The blood loss and plasma and blood volumes before and 2-2.5 hr post-bleeding are presented. Goats Nos. I, II, III were non-lactating, goats IV, V, VI were lactating.

<table>
<thead>
<tr>
<th>Goat</th>
<th>Body wt</th>
<th>Plasma volume (ml)</th>
<th>Blood volume (ml)</th>
<th>Amount bled (% of blood volume)</th>
<th>Amount bled (% of body wt)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>24.1</td>
<td>1550</td>
<td>1558</td>
<td>2067</td>
<td>20</td>
</tr>
<tr>
<td>II</td>
<td>20.5</td>
<td>1069</td>
<td>910</td>
<td>1444</td>
<td>28</td>
</tr>
<tr>
<td>III</td>
<td>27.5</td>
<td>1512</td>
<td>1253</td>
<td>1900</td>
<td>25</td>
</tr>
<tr>
<td>IV</td>
<td>27.0</td>
<td>1861</td>
<td>1681</td>
<td>2386</td>
<td>21</td>
</tr>
<tr>
<td>V</td>
<td>19.5</td>
<td>1022</td>
<td>856</td>
<td>1470</td>
<td>27</td>
</tr>
</tbody>
</table>

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Fig. 2. Effects of bleeding on the plasma vasopressin concentration. Open bars = lactating goats. Shaded bars = non-lactating goats. Each goat is represented in the same position relative to the other animals at all times. C = pre-bleeding values (mean of three samples from each goat).
the non-lactating goats had lost 23% of their plasma volume which may explain why the PRA was higher in these animals (Table 1 and Fig. 1). The PRA of the lactating animals was slightly lower in all blood samples taken during dehydration, until the last blood sample taken before the animals got water. In goats, the normal increase in blood flow to the udder at the onset of lactation is achieved mainly by local vasodilation (Linzell, 1974). A delayed and reduced increase in PRA probably prevents a rapid rise of the potent vasoconstrictor angiotensin II, which would cause vasoconstriction in the udder. A reduction in milk production could thus be prevented. In support of this theory is the fact that the milk yield was almost unaffected during the first 48 hr in this as well as in previous studies (Maltz and Shkolnik, 1980) and during this time there was only a minor rise in PRA in the lactating animals.

In man, a close correlation between pAVP and pOsm has been demonstrated (Robertson et al., 1976), and a similar correlation has been shown to exist also between pNa and pAVP in goats (Olsson et al., 1978). In our experiments, the water loss was accompanied by marked increases in pOsm and in pNa concentration by the first evening in all animals, but thereafter, these variables increased only slowly. In contrast, the pAVP concentration did not start to increase until the second evening (Fig. 1), and marked increases in pAVP were not seen until during the third and fourth day of dehydration.

AVP at high levels is a potent vasoconstrictor agent particularly of the vessels to the gastrointestinal tract (Saamali, 1978). It may be suggested that the delayed, modest increase of the pAVP, especially in the lactating Bedouin goats, prevents a reduction of the blood supply to the gastrointestinal tract, enabling the animals to continue to eat and digest food. It is likely, that this is even more true in other Bedouin goats, since they normally keep a higher plasma volume than the goats used in this study. Furthermore, AVP in high doses (Konar and Thomas, 1970) but not in low doses (Peaker and Linzell, 1973) has been shown to reduce milk production. Thus the delayed increase of PRA and of AVP during water deprivation could be the reason why Bedouin goats can continue to produce almost normal amounts of milk despite periods of water shortage.

Following drinking that ended dehydration, all goats regained their initial body wt during one continuous drinking session, which is in agreement with previous dehydration experiments (Choshniak and Shkolnik, 1977b; Maltz and Shkolnik, 1980). During the first minutes following drinking, pOsm and pNa remained elevated, whereas pAVP concentration dropped markedly, especially in the non-lactating goats (Fig. 1). Similar effects have been reported in dogs (Thrasher et al., 1981), which made these authors conclude that oropharyngeal factors account for the rapid inhibition of the AVP release. In support of this conclusion, is the findings by Vincent et al. (1972) that the neurosecretory cells of the supraoptic nuclei are inhibited when monkeys consume water. In the non-lactating Bedouin goats, pAVP had returned to basal levels 4-4.5 hr post-drinking. However, pOsm was still elevated at this stage, which supports the observation that plasma volume is not yet back to normal (Choshniak and Shkolnik, 1977b). Also in lactating goats the pAVP concentration dropped immediately after drinking, but the values were around 20 pg/ml 90 min post-drinking, and 4-4.5 hr post-drinking they were still as high as around 12 pg/ml. The pAVP values corresponded to the slow decrease of the pOsm in the lactating goats. The delayed return to basal levels of plasma volume, pOsm and pAVP concentration upon rehydration is by all probability due to the modest absorption of water from the rumen to the plasma (Choshniak and Shkolnik, 1977b).

In agreement with previous findings in sheep (Blair-West et al., 1972; Blair-West et al., 1979) and goats (Olsson et al., 1978), PRA did not fall, but increased after rehydration. In the sheep experiments, it was suggested that the rise in renin concentration after rehydration was due primarily to a reduced pK. However, in this study the pK increased after rehydration. Urine flow is very low after rehydration in the Bedouin goats (Choshniak and Shkolnik, unpublished observations) and it has been suggested that an altered sodium transport at the macula densa may be the stimulus for renin release. Recent experiments in the lactating Swedish goat showed that after 48 hr dehydration the sight of the water bucket caused an immediate, pronounced increase in arterial blood pressure and heart rate, which persisted during the drinking session. The blood pressure remained elevated for about 1 hr post-drinking (Olsson K., unpublished observations). One of the stimuli for renin release (Ganong, 1981) is sympathetic stimulation, and it is possible that the rise in PRA immediately after drinking may have been due to such a stimulation. The combination of an increased sympathetic tone and the persistently reduced plasma volume may explain the slow return of PRA to basal values after rehydration.

Changes in plasma volume have been shown to shift the osmotic threshold for AVP release (Robertson and Athar, 1976). Yet the plasma pAVP concentrations seen during dehydration involving a plasma volume loss of 32-34%, with accompanying hyperosmolality are in the range of, or considerably lower, than those obtained after a blood loss of 21-28% (Figs. 1 and 2). These results therefore strengthen the hypothesis made by Arnauld et al. (1977) and Larsson et al. (1978) that it is not hypovolemia per se, which causes the huge pAVP release during hemorrhage but rather the fall in arterial blood pressure. Although, the arterial blood pressure was not measured in this study, forced breathing was seen in all animals at the cessation of hemorrhage, indicating that a fall in arterial blood pressure indeed had occurred. The forced breathing is also compatible with the idea that hypoxia may contribute to the large AVP release which is seen during hypotensive hemorrhage (Forsling and Ullman, 1976). An alternate explanation for the difference between the magnitude of AVP release after hemorrhage and after dehydration may be the existence of receptors sensitive to rate of volume change. Thus, during the rapid blood withdrawal, the loss of plasma volume could not be replaced immediately by fluid from other body compartments. Then, lactating goats responded with a rapid and pronounced increase of pAVP, whereas non-lactating goats, which apparently were better prepared to withstand a diminu-
shed plasma volume, only got a comparatively small increase of pAVP.

In all animals plasma osmolality rose considerably during the day they were bled. Yet only two of the lactating goats drank at the end of the experimental day. The reason why the other four animals did not drink may be: (1) the blood which was returned to the animals had been taken from them when the plasma osmolality still was low; (2) by the time the lost blood was returned the goats had reabsorbed some of the lost volume from other body fluid compartments (Table 2), causing plasma expansion (Larsson et al., 1978) after that the blood was retransfused.

REFERENCES


