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Rumen volume, saliva flow rate, and systemic fluid homeostasis in dehydrated cattle

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SILANIKOVE, NISSIM, AND AMNON TADMOR. Rumen volume, saliva flow rate, and systemic fluid homeostasis in dehydrated cattle. Am. J. Physiol. 256 (Regulatory Integrative Comp. Physiol. 25): R809-R815, 1989.—This work was carried out to test the hypothesis that the high level of salivary secretion containing much Na⁺ and the volume of fluid sequestered in the foregut of ruminants play an important part in water and Na⁺ homeostasis. Saliva flow and composition and water and Na⁺ balance in the rumen have been measured in hydrated and dehydrated cows with esophageal fistulas. Reduction of voluntary feed intake in beef cattle during water deprivation was related to the stage of dehydration. Salivary secretion rate was linearly related to voluntary feed intake (r = 0.96) and inversely and linearly related to plasma osmolality (r = 0.88). The reduction in the volume of water stored in the rumen contributed to the major portion (55%) of the total water loss. Utilization of gut water attenuated the rise in blood plasma osmolality, and this may be connected with an animal's ability to continue eating despite dehydration.

CATTLE HAVE a higher metabolic rate than most other domestic ruminants and have a poorly developed water-retention mechanism in the kidney and gut (17). Consequently, cattle reached a degree of dehydration similar to that of camels in one-half to one-third of the time (24). The rate of water use by cattle in a hot Mediterranean climate was about twice that of Merino sheep on a metabolic weight basis (27). Nevertheless, cattle, like other ruminants, easily survive a loss of 18% of their body weight by dehydration, a level considerably higher than could be tolerated by most monogastric animals (23).

Relative to other nonruminant mammals, the volume of digestive secretions in ruminants is large (2). This is mainly due to the high level of continuous alkaline salivary secretion, which serves to buffer the acid products of microbial fermentation in the rumen and provides a medium that facilitates the mixing and regurgitation of ingested material. The daily volume of salivary secretion in cattle may amount to as much as 100-190 l/day (2, 26, 28). The amount of Na⁺ secreted with the saliva may represent >15 times the daily amount of Na⁺ consumed with feed and >5 times the amount in all the blood plasma.

It is well known that low Na⁺/K⁺ ratio in saliva sensitively reflects Na⁺ deficiency and that a ruminant can quickly become Na⁺ depleted by diverting its saliva (14). It is also established that the rumen serves as a giant water reservoir that is utilized when water is not available (23). Yet the regulation of extracellular fluid volume and composition is considered to be mainly under the control of kidney function in ruminants (12) as well as in other mammals (1, 6). This work was carried out to test the hypothesis that the high level of digestive secretion and the volume of fluid sequestered in the gut of ruminants are important to the Na⁺ balance and circulatory homeostasis.

The response to water deprivation exemplifies the integrated consequences of physiological stress. Salivary flow rate and composition and the balance of water and Na⁺ in the rumen were measured at various levels of dehydration in beef cattle to evaluate their contribution to homeostasis.

METHODS

Site and animals. The experiments were carried out at the Karie Desch Beef Cattle Experimental Station, 10 km north of the Sea of Galilee and close to the Jordan River. Animals were kept outside, individually, in yards fully exposed to solar radiation throughout the day. Maximum daily temperatures ranged from 33 to 38°C, and relative humidity was not in excess of 45%.

Four beef cows (Simmental cross with local breeds, Bos taurus), neither lactating nor pregnant and weighing 420 ± 40 kg, were used. Three to six months before initiation of the experiments, the esophagus was exteriorized to the skin and a fistula was formed. This procedure was carried out in two stages. In the first stage the animals were anesthetized. The esophagus at a position ventral midline to the neck and about midway between the jaw and the brisket was freed from surrounding tissue and then adhered to the skin by oval circle of sutures. One week later, after establishment of the adherence of the esophagus to the skin, a fistula ~10 cm long was formed under local anesthesia. Usually the fistula was covered by a plug resembling that described as type A in the Van Dyne and Torrel review (see Fig. 3 of Ref. 33).

This procedure did not affect normal feeding and drinking and allowed complete diversion of the saliva when the plug of the fistula was opened.

Experimental procedures. Baled medium-quality wheat hay (dry matter 90.1%, crude protein 12.1%, and sodium 100 meq/kg, on a dry basis) was fed before and through-
out the experiment. Feed was provided once a day (0700 h) in amounts 15% more than the intake of the previous day. Water consumption was recorded daily.

Water was offered in large drums (90 liters) for 20 min in four different trials, each lasting 10 consecutive days: 1) twice a day, at 0800 and 1600 h (control period); 2) once a day at 1600 h; 3) once every 2 days at 1600 h; and 4) once every 3 days at 1600 h.

The following measurements were made during each period.

The cows were weighed daily (±0.5 kg) before watering, using electronic weigh scales (Carcom, Israel).

Total body water (TBW) was estimated by tritiated water dilution and plasma volume by the Evans’ blue dye (T-1824) method (25, 28). Each day at 0800 h during each experimental period, ~800 μCi of tritiated water and 500 mg of T-1824 in volumes of 10 ml were administered to each cow over 20 s via jugular catheter, followed by flushing with heparinized saline. Before dosing, blood samples were collected through the catheters into heparinized tubes. Blood was sampled at intervals of 10 min during the 1st h and then every hour for a duration of 6 h. The concentration (optical density) of T-1824 was determined shortly after collection. Plasma volume was calculated by dividing the dose with concentration at time 0. The concentration of T-1824 at time 0 was calculated by regression analysis of In T-1824 concentrations sampled during the 1st h after dosing (r2 ranged 0.94–0.97). TBW was calculated by dividing the dose with tritiated water activity after even distribution of the injected dose between systemic fluid (represented by plasma samples) and reticulorumen (RR or just rumen) fluid. Ruminal fluid sampling is described below.

Rumen volume and flow to the omasum were measured at noon (12–15 h) when the cows normally did not eat. The fistula was unplugged, and the saliva was collected in a graduated cylinder. Dependent on the amount of saliva produced, four measurements of 5 min each or three measurements of 10 min each were made. From each collection ~8 ml were taken for analysis. The remainder was introduced to the RR through the fistula.

After the above, a dose of 250 mg Cr-EDTA in 40 ml of water was introduced through the fistula, and then four samples of fluid were collected at intervals of 20 min by vacuum from a tube inserted through the fistula to the RR. Between samples, the fistula was plugged to maintain normal inflow of saliva to the RR. Two hours later the procedure was repeated. Rumen volume at each dosage was calculated by extrapolation of the In Cr-EDTA concentration to time 0 (32). Water flow to the omasum was calculated from the changes in the amount of water and from the concentration of a solute in the fluid entering the omasum (Eq. 17 of Ref. 16)

\[
\text{NOF} = \frac{V_{t1} \times C_{t1} - V_{t0} \times C_{t0}}{\text{CM}}
\]

where NOF is the outflow of fluid from the RR, Vt0 and Vt1 are RR volume at the beginning and at the end of measurement, Ct0 and Ct1 are the respective marker concentrations, and CM is the logarithmic average of marker concentration (Eq. 17 of Ref. 16)

\[
\text{CM} = \frac{C_{t0} - C_{t1}}{\ln (C_{t0}/C_{t1})}
\]

The error inherent in the method depends primarily on the volume change, but the duration of the measurement and the reduction of the marker concentration are also of importance (Eq. 20 of Ref. 16)

\[
\text{RE} = \frac{C_{t1}}{C_{t0} - \Delta V}
\]

where RE is the relative error and ΔV is the change in rumen volume during the experiment.

Another source of potential error may be overestimation of rumen volume in case of marker absorption. After introduction of Cr-EDTA to sheep and cattle (32) and thereby its exposure to both rumen and other absorptive regions of the gut, only 1–4% of the dose was recovered in the urine in 24 h. It therefore seems that marker absorption has no appreciable effect on the interpretation of these results in which measuring interval for a specific dose was only 2 h.

The rates of absorption of water and Na+ were calculated from the rate of entry (saliva flow) and exit (NOF) and from changes in the amount of water and from the Na+ concentrations in the latter. It was assumed that the concentration of a solute in the fluid entering the omasum was the same as that in the general RR fluids (32).

Analysis. Osmolality was determined in an osmometer (Vescoe model 5100C), Na+ by flame photometer, Cl− by automatic titrator, and phosphorus as recommended by the American Association of Analytical Chemists (12th ed., 1975, Washington DC). Concentration of HCO3− in saliva was determined by acidifying a sample to pH 4.5 (30) in a sealed serum bottle. The concentration of CO2 was measured by gas-liquid chromatography using Propak 80/100 mesh column (Unerts Associates) under the following conditions: carrier helium 20 ml/min; detector EC (electron capture); temperatures: injector 150°C, column 50°C, detector 200°C. Chromium concentration in RR fluid was determined by atomic absorption spectroscopy (Instrumentation Laboratory Video 22). Total plasma protein and plasma albumin were measured spectrophotometrically (24). Tritium activity in plasma samples was determined in liquid scintillation counter as described (28).

RESULTS

Feed intake during dehydration. Mean voluntary dry feed intake in cows with access to water twice a day was 17.5 g·kg−1·day−1. Restriction of water availability to once every 24, 48, and 72 h caused an average reduction...
of 39, 60, and 80% in the voluntary consumption of feed intake (Table 1).

**Saliva flow and composition during dehydration.** Dehydration caused a gradual increase in salivary osmolality and solute concentration (Table 2) and a parallel reduction in flow rate (Figs. 1 and 2). The main cause of increased saliva osmolality was Na\(^+\). This increased by 11.6% after a dehydration of 18% (Table 2), which also increased HPO\(_4\) by 48% (P < 0.01), HCO\(_3\) by 6%, (NS), and pH by 1.5% (P < 0.05); small increases in K\(^+\) and Cl\(^-\) concentrations were not significant. The osmolality of saliva, which in normally hydrated cows is hypotonic to plasma osmotic pressure, became almost isotonic after dehydration.

Saliva was swallowed at a rate of once per 51 ± 2, 55 ± 2, 58 ± 3, and 59 ± 2 s by cows A, B, C, and D, respectively. These individual swallowing rates were independent of the experimental conditions and the total volume of saliva swallowed each time was dependent on the saliva production rate.

Salivary flow rate was linearly and negatively correlated to the increase in plasma osmolality (Fig. 1, r = 0.88, P < 0.01). Reductions in feed intake and salivary secretion rate were linearly and significantly correlated (Fig. 2, r = 0.96, P < 0.01).

**Rate of dehydration and distribution of water loss between compartments.** Body weight decrease of the cows during water deprivation averaged 23 kg/day (Table 4), ~6% of body mass. TBW loss accounted for ~89% of the total weight loss (Table 4). The sum of total body mass and water content in dehydrated state and water imbibed when cows were given free access to water was similar to the total body mass and water content in hydrated cows (Table 3). This indicates that cows replenish their entire water deficit. Trislated water activity was the same in blood plasma and RR fluid after 4.5 ± 0.5 h in hydrated cows and after 6.0 ± 0.4 and 8.0 ± 0.5 h in cows dehydrated for 24 and 72 h. When the shortness of the experimental period is taken into account, a considerable part of apparent loss in body solids should reflect a reduction of dry matter content in the gut.

After 3 days of water deprivation, reduction in water stored in RR contributed ~55% of the total water loss (Table 4). The amount of water left in the RR was 49% of the initial volume (Table 6). Plasma volume in hydrated cows was 22 liters (5.2% of body mass). Reduction in plasma volume (5.7 liters) was ~26% of the initial volume (Fig. 3). This was higher than the percentage of reduction of total body water (Fig. 3). Total plasma protein concentration and albumin concentration increased by 19 and 9%, respectively. Na\(^+\) concentration in plasma increased by 12%, which was considerably smaller than the reduction in plasma volume. Increase in concentration of plasma K\(^+\) and Cl\(^-\) was only 1-2% (Fig. 3).

**Water and Na\(^+\) balance in the rumen.** The relative error in calculating NOF of water and Na\(^+\) (Eq. 3) was ~11% in hydrated and ~8% in dehydrated animals. This would cause overestimation of the net absorption values (Table 5). However, the magnitude of changes in NOF of water and Na\(^+\) imposed by the experimental conditions (dehydration) are considerably larger than the experimental error (635% for water and 542% for Na\(^+\)). Therefore the conclusion drawn below for the effect of dehydration on NOF and net absorption of water and Na\(^+\) are not hampered by the experimental error.

In normally hydrated cows saliva secretion and outflow rate from the RR at rest are equivalent to ~1.7 l/h and 3.3% of RR volume per hour, respectively (Table 5), whereas the net absorption of water from the RR amounted to 0.3 l/h (0.6% of RR volume per hour). The net absorption of Na\(^+\) was 82 meq/l, and its concentration in the absorbent was 273 meq/l. During dehydration, inflow of saliva to the RR remained about equal to the outflow to the omasum (0.25 l/h; 1.2% of RR volume/h). However, net absorption of water apparently completely ceased after dehydration of 18%. A similar pattern was observed with regard to the net absorption of Na\(^+\). The outcome of the increase in Na\(^+\) concentration of saliva and reduction of its net absorption in the RR resulted in apparent Na\(^+\) accumulation in RR fluid at a rate of 5 meq/h (Table 5).

The net changes in the content of RR water and Na\(^+\) pools as a result of exposure of the cows to dehydration (72 h) are summarized in Table 6. Na\(^+\) concentration in the RR increased by 17%, which is larger than the increase in plasma Na\(^+\). However, plasma and RR Na\(^+\) concentration at the end of dehydration were essentially similar (154 and 152 meq/l, respectively). The reduction

---

**TABLE 1. Effect of water deprivation on voluntary consumption of medium-quality hay by beef cows**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control*</th>
<th>24 h</th>
<th>48 h</th>
<th>72 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed intake, g dry matter/kg body wt(^{-1}), day(^{-1})</td>
<td>17.5 ± 0.3</td>
<td>10.6 ± 0.2</td>
<td>7.0 ± 0.2</td>
<td>3.5 ± 0.1</td>
</tr>
<tr>
<td>Values are means ± SD. * Water available twice a day.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**TABLE 2. Saliva osmolality pH and solute concentration in beef cows fed medium-quality hay and dehydrated to ~6, 12, and 18% of their initial mass**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Osmolality, (\mu)osmol/kg</th>
<th>Na(^+), meq/l</th>
<th>K(^+), meq/l</th>
<th>HCO(_3), meq/l</th>
<th>HPO(_4), meq/l</th>
<th>Cl(^-), meq/l</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control*</td>
<td>281 ± 4</td>
<td>163 ± 4</td>
<td>4.9 ± 1</td>
<td>66 ± 5</td>
<td>21 ± 3</td>
<td>26 ± 4</td>
<td>9.1 ± 0.08</td>
</tr>
<tr>
<td>6%</td>
<td>302 ± 5</td>
<td>166 ± 5</td>
<td>5.0 ± 1</td>
<td>67 ± 4</td>
<td>26 ± 4</td>
<td>25 ± 3</td>
<td>9.20 ± 0.06</td>
</tr>
<tr>
<td>12%</td>
<td>312 ± 5†</td>
<td>172 ± 5†</td>
<td>5.2 ± 2</td>
<td>68 ± 5</td>
<td>28 ± 4</td>
<td>27 ± 3</td>
<td>9.25 ± 0.07†</td>
</tr>
<tr>
<td>18%</td>
<td>320 ± 5‡</td>
<td>182 ± 5‡</td>
<td>6.0 ± 2</td>
<td>70 ± 5</td>
<td>28 ± 4</td>
<td>28 ± 4</td>
<td>9.29 ± 0.07‡</td>
</tr>
</tbody>
</table>

Values are means ± SD. † Significantly different from the respective values in hydrated (control) cows, according to paired t test comparison.
RESPONSE TO DEHYDRATION IN CATTLE

FIG. 1. Relation between plasma osmolality and salivary flow rate.

FIG. 2. Relation between decrease in feed intake during advance of dehydration and decrease of salivary flow rate.

TABLE 3. Water ingested and recovery of body mass and body fluids after three levels of dehydration by beef cows

<table>
<thead>
<tr>
<th>Length of Water Deprivation, days</th>
<th>n</th>
<th>Dehydrated Body Mass, kg</th>
<th>Water Ingestion, kg</th>
<th>% of Body mass</th>
<th>% of Body water</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>40</td>
<td>413±15</td>
<td>24±4</td>
<td>104±5</td>
<td>105±6</td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td>358±10</td>
<td>45±7</td>
<td>96±8</td>
<td>98±5</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>350±8</td>
<td>63±6</td>
<td>98±6</td>
<td>100±6</td>
</tr>
</tbody>
</table>

Values are means ± SD. n, no. of measurements per treatment (divided by 4 will give no. of measurement per cow in each treatment).

TABLE 4. Relative contribution of body compartments to weight loss at end of 72 h of water deprivation in beef cows fed medium-quality hay

<table>
<thead>
<tr>
<th>Body Unit</th>
<th>Body Solids Loss</th>
<th>Systemic Fluid Loss</th>
<th>Ruminal Water Loss</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight, kg</td>
<td>70±5</td>
<td>7.5±0.6</td>
<td>29±3</td>
</tr>
<tr>
<td>% of total loss</td>
<td>100</td>
<td>11±1</td>
<td>40±3</td>
</tr>
<tr>
<td>% of water loss</td>
<td>45±3</td>
<td>55±5</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SD. * Sum of intracellular and extracellular water loss (calculated as the difference between total body water losses and ruminal water losses).

DISCUSSION

The results here confirm those of Siebert and MacFarlane (24), who demonstrated that cattle lack the capability of the camel and other desert mammals to increase plasma colloidal osmolality resulting in reduction of the rate of water losses from the plasma relative to losses from other compartments.

The Na⁺ concentration of parotid saliva from sheep increased with increasing flow rate (13). However, parotid saliva Na⁺ was negatively correlated with salivary flow rate in Na⁺ replete sheep and goats (3-5, 22). In Na⁺-deficient sheep, mineralocorticoids act on the duct system of the parotid glands causing increased reabsorption of Na⁺ in exchange for K⁺ (9). Under such conditions, concentration of Na⁺ in the saliva is positively correlated with saliva flow (14). Since the Na⁺/K⁺ ratio in saliva actually increased during dehydration in the present experiment, mineralocorticoid-dependent reabsorption of Na⁺ was probably minimal. In agreement with this suggestion, Blair-West et al. (8) observed a fall in aldosterone in response to prolonged water deprivation in sheep and Thrasher et al. (31) failed to detect any change in aldosterone during 24 h of dehydration in dogs. The present results support the conclusion of Beal (4, 5) that saliva Na⁺ concentration in Na⁺-replete ruminants is inversely correlated to salivary flow rate. Changes in saliva flow and composition similar to those reported in the present work were found in camels dehydrated to 25% of body weight (15). Of particular interest is the observation of Olsson (22) that infusions of hypertonic NaCl into the cerebrospinal fluid of the goat caused a marked reduction in parotid salivary flow and increase of Na⁺ concentration.

Rumen volume in the present work (67 liters, 17% of body weight) exceeded typical values measured in cattle fed similar diets (13% of body weight). This may relate to the fact that the cows were exposed to the full impact of heat and solar radiation and with the observation that water content in the RR in cows tended to increase with acceleration of water turnover (27). In black Bedouin goats, which are highly adapted to desert life, RR volume increased from 20 to 35% of body weight (26) on exposure of the goats to shadeless conditions.

Connected with the large proportion of water in the...
RESPONSE TO DEHYDRATION IN CATTLE

TABLE 5. Water and Na⁺ balance in rumen at rest in hydrated beef cows and in cows dehydrated to ~18% of initial body mass

<table>
<thead>
<tr>
<th></th>
<th>Hydration</th>
<th>Dehydration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Water, l/h</td>
<td>Na⁺, meq/h</td>
</tr>
<tr>
<td>Saliva Inflow to Rumen</td>
<td>1.75±0.14</td>
<td>1.65±0.1</td>
</tr>
<tr>
<td>Outflow to Omasum</td>
<td>285±29</td>
<td>214±19</td>
</tr>
<tr>
<td>Relative Error,*</td>
<td>-11</td>
<td>82±7</td>
</tr>
<tr>
<td>Net Absorption</td>
<td>0.30±0.5</td>
<td>0.01±0.01</td>
</tr>
<tr>
<td>Maximal Deviation in Net Absorption*</td>
<td>58</td>
<td>58</td>
</tr>
<tr>
<td>Net Accumulation</td>
<td>-0.20±0.02</td>
<td>-0.02±0.01</td>
</tr>
</tbody>
</table>

Values are means ± SD. While measurements at rest were made, animals did not eat, drink, or ruminate. * Calculated according to Eq. 3 in METHODS. † Correction for the effect of experimental error in the determination of outflow to the omasum.

![DEHYDRATION (Days)](image)

**FIG. 3.** Changes in total body water (TBW), plasma volume (PV) in the content of plasma protein (P_pr), plasma albumin (P_alb), plasma Na⁺ (P_nata), plasma K⁺ (P_k+), and plasma Cl⁻ (P_cl-).

**TABLE 6.** Changes in content of rumen volume, Na⁺ concentration and Na⁺ pool in rumen as a result of dehydration to ~18% of initial body mass

<table>
<thead>
<tr>
<th></th>
<th>Rumen Volume, liters</th>
<th>Na⁺ Concentration, meq/l</th>
<th>Rumen Na⁺ Pool, meq</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydration</td>
<td>67±6</td>
<td>130±6</td>
<td>8,710±550</td>
</tr>
<tr>
<td>Dehydration</td>
<td>33±4</td>
<td>132±7</td>
<td>5,016±350</td>
</tr>
<tr>
<td>Net change (%)</td>
<td>-34±3</td>
<td>+22±3</td>
<td>-3,694±250</td>
</tr>
<tr>
<td>Net change, %</td>
<td>50.7±3</td>
<td>16.9±4</td>
<td>42.4±2</td>
</tr>
</tbody>
</table>

foregut, the net transfer of water and Na⁺ between extracellular fluid and foregut water is also considerable. The daily amount of saliva secretion in cows is twice the daily water turnover rate and equivalent to total exchange of foregut water with extracellular fluid (28). Na⁺ exchange through this circulation (enterohepatic circulation) represents ~15 times the amount of Na⁺ consumed with feed and total exchange of extracellular content (26, 28). The increase in the time needed for equilibrium of tritiated water with the advance of dehydration reflects at least partially a reduction in the net exchange between gut and systemic fluid. This change probably reflects change in blood flow to the gut and reduction in gut mobility.

When experiencing dehydration, cattle draw mainly on water stored in the RR to supply demand (Table 4). By similar calculation from the results of Chosniak et al. (12), it seems that 50% of the water lost in the desert black Bedouin goats was contributed by the RR pool. Rumen volume on these goats after 4 days of dehydration was 60% lower than the value recorded 7 h postdrinking. It seems that the role of the RR as a water reservoir, although more pronounced in desert species and breeds, is a general characteristic of ruminants. Thus regulation of water mobilization from this store must be an essential factor in the maintenance of osmotic homeostasis.

Na⁺ absorption from the gut is very high [98.5% (28); >90% (29)]. The amount of Na⁺ absorbed from the rumen after 3 days of dehydration amounted to ~3,800 meq (Table 6). Thus the amount of Na⁺ absorbed from the gut store was greater than that consumed with feed (600 meq) by ~630%. Utilization of gut water during dehydration results in a considerable increase of Na⁺ load. Urinary Na⁺ excretion during dehydration increased in beef cattle, sheep, camels, rabbits, and dogs despite water retention (19, 20, 24, 31). However, the continuation of enteric (saliva) flow is also important. Without saliva secretion the extracellular pool of Na⁺ would increase on a daily basis by >1,100 meq. This calculation is based on saliva flow (at least 6 liters at the 3rd day of dehydration, Table 4) and the Na⁺ concentration in saliva at that time (180 meq/l). Such accumulation would increase plasma osmolality by ~20 mosmol/kg and would enforce increased natriuresis with elevated diuresis, which would hasten the rate of dehydration. Because of the enormous increase in salivary flow that accompanied ingestion of feed and rumination (2), the above estimation on the effect of salivation on attenuation of plasma osmolality is probably considerably underestimated.

On the basis of the large reduction in plasma volume after 3 days of dehydration, it seems that the cows...
reached their physiological limit to dehydrate. There are no reports in the literature of European breeds of cattle that were dehydrated to a larger extent without ill effects. Their RR still contained a considerable amount of water (33 liters), which may potentially supply a cow’s entire water needs for 1 day. The availability of this pool, however, was limited because it became isotonic with body fluid and because their kidneys apparently lacked the ability to “desalt” this water. Accordingly, the ability of the kidney to produce a small volume of urine, with a negative ratio for free water clearance to osmotic clearance, seems to be the limiting factor affecting feed intake during dehydration.

As implicated by the above model, the ability to produce small amounts of highly concentrated urine with solutes, in addition to its contribution in reducing dehydration rate, allows the animals to exploit its large reserves in the RR more efficiently by allowing them to secrete more saliva. This caused mobilization of water from the RR and consequently its absorption, which reduced the dehydration rate of the systemic system. Sheep, goats, and camels, which have better water retention capacity than cattle, withstood higher dehydration rates (20–40%) (23). Animals inhabiting the desert and regularly exposed to dehydration and rehydration cycles may be expected to be adapted to water shortage. Reduction in feed intake, in response to water deprivation, was found to be smaller in desert ruminant breeds compared with nondesert breeds (25). The desert black Bedouin goats exhibited a delay and reduction in the increase of plasma renin activity and antidiuretic hormone observed during the first 48 h of dehydration (18). The importance of the above responses in maintaining feed intake and milk yield with almost no effect has been noted.

In the present study it has been shown that, despite the currently accepted concept that the kidney is the main regulator of the volume and composition of extracellular fluid (1, 6), at least in ruminants this may not be entirely so. Volume and Na\(^+\) homeostasis may not be fully understood without taking into consideration the large store of water in the gut and the enterohepatic circulation that connects the latter with the general circulation.

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