Effect of water restriction on feeding and metabolism in dairy cows

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Steiger Burgos, Martine, Markus Senn, Franz Sutter, Michael Kreuzer, and Wolfgang Langhans. Effect of water restriction on feeding and metabolism in dairy cows. Am J Physiol Regulatory Integrative Comp Physiol 280: R418–R427, 2001.—We investigated how lactating cows are able to cope with a sustained water restriction. In experiment 1, body weight and meal patterns were recorded with ad libitum access to water (baseline) and during 8 days of 25 and 50% restriction of drinking water relative to ad libitum intake. In experiment 2, indirect calorimetry was combined with nitrogen and energy balance and plasma hormone and metabolite measurements to assess the effects of 50% water restriction on digestion and metabolism. In experiment 1, food intake and body weight declined during the first 3 days of water restriction depending on the restriction level and stabilized thereafter at a lower level. The daily food intake reduction with 50% water restriction was entirely due to a reduction of meal size. The size of the first meal on every day was markedly (>50%) reduced with 25 and 50% water restriction. In experiment 2, urea concentrations in milk and blood as well as plasma sodium and hematocrit were increased by 50% water restriction. Energy balance was not affected by 50% water restriction, but nitrogen balance became negative, because, relative to intake, nitrogen excretion via urine and milk was higher. The lower energy intake during 50% water restriction was compensated by a lower milk production, a higher digestibility of organic matter and energy, and, apparently, a more efficient energy use. Through these changes and a preserved water balance, the cows reached a new equilibrium at a lower water turnover level, which enabled them to cope with a sustained drinking water restriction of 50%.

energy balance; nitrogen balance; water balance; dehydration; meal patterns; body heat production; adaptation

RESTRICTION OF WATER INTAKE has often been shown to reduce food intake in humans (18) and various animal species (e.g., Ref. 1), including ruminants (e.g., Refs. 7, 19, 26). Ruminants differ from monogastric animals because much more saliva is secreted during eating (3) and because they have a large fluid reserve in the rumen, which can buffer osmotic changes in the rumen derived from digesta. In previous studies from our laboratory, pygmy goats (24) and lactating cows (34) progressively reduced food intake during water deprivation and did not compensate for the dehydration-induced weight loss by increasing food intake during the subsequent rehydration period. These results contrast findings in rats, which are known to compensate for dehydration-induced body weight loss by markedly increasing food intake during the subsequent rehydration (1). This different response suggests that ruminants are better able to cope with dehydration than rats, i.e., a similar degree of dehydration presumably provokes a smaller energy deficit in ruminants than in rats. Two mechanisms may contribute to the limitation of the dehydration-induced energy deficit in ruminants: 1) the digestibility of forage-based diets may be higher during dehydration (4, 10, 35) and 2) resting metabolic rate may decrease with dehydration (9). Such adaptive mechanisms have mainly been shown in nonlactating, mostly small and desert-adapted ruminants (4, 9, 10, 35). Whether similar mechanisms or other compensatory changes in digestion and metabolism are activated by dehydration in lactating dairy cows, which are more susceptible to water shortages than desert goats, is unknown. The present study addressed this question by trying to identify and quantify such mechanisms in addition to the food intake suppression during graded levels of water restriction in lactating dairy cows.

In one experiment we characterized the feeding behavior of lactating cows in response to different levels of water restriction to see whether the cows are able to reach and maintain a new equilibrium under these conditions. In a second experiment we determined water, energy, and nitrogen balances as well as plasma metabolite and hormone concentrations when cows had ad libitum access to water and when they were subjected to the higher water restriction level of the first experiment.

METHODS

all pregnant (137 ± 8 days of pregnancy, 644 ± 13 kg body wt) were used. The cows were housed in a tying stable with ad libitum access to water. After food and water intake as well as milk yield for 5 days (baseline) were recorded, the cows were divided into two groups (matched for baseline food intake, milk yield, and water intake) that were subjected to 25% (n = 9) and 50% (n = 8) water restriction relative to individual ad libitum drinking water intake (mean baseline) for 8 days. These treatments are subsequently referred to as 25 and 50% water restriction, respectively. Note, however, that the total water intake (drinking water plus water in food) restriction level was somewhat less (see RESULTS) because food intake was not reduced by 25 and 50%. The restriction period was followed by a 4-day rehydration period with ad libitum access to drinking water. During the restriction period, the cows had access to drinking water every day from 0600, at the same time when food was first presented in the morning, until the allotted amount of drinking water was consumed. The cows were weighed once during baseline and every day during the restriction and rehydration periods.

In experiment 1, six lactating Brown Swiss cows [191 ± 23 kg body wt] had ad libitum access to drinking water for 5 days (baseline) and were then subjected to 50% drinking water restriction relative to individual baseline intake for 9 days (restriction period). During the restriction period, animals had access to drinking water from 0900, at the same time when food was first presented in the morning, until the allotted amount of water was consumed. The 5 baseline days and the 5 last days of the restriction period (days 5–9 of restriction) were used for data collection, assuming steady-state according to the results of experiment 1. During these days, feces, urine, and milk were collected. For respiratory measurements on days 3 and 4 of the baseline and on days 7 and 8 of the restriction period, two cows each were randomly placed into two respiration chambers. During all other days, they were housed in a tying stable with partly slatted floor designed for balance trials. On the last day of the baseline and restriction periods, the cows were weighed (at 0800) and a blood sample was taken (at 1500).

Feeding and meal patterns. During both experiments, the cows had ad libitum access to a mixed diet of grass silage (57%), corn silage (33%), and hay (10%). Diet composition was as follows: 51.9% dry matter (DM), 6.1 MJ/kg DM net energy for lactation, 78.1 g/kg DM digestible protein in the intestine, 124 g/kg DM crude protein, and 257 g/kg DM crude fiber. In experiment 1, the diet was provided three times a day (at 0600, 1030, and 1530). In experiment 2, the diet was provided at 0900 and 1530. The animals were adapted to the diet for at least 2 wk before the experiments. Food intake and meal patterns were continuously recorded online by a computerized feeding system similar to the one described previously by Senn et al. (34). Meals were defined as weight changes ≥50 g after electronic identification of a cow at the feeding trough, lasting ≥1 min (minimum meal duration), and separated by ≥8 min (minimum intermeal interval) from other weight changes, as described previously (34). Meals defined and recorded this way accounted for 99.9% of total daily food intake.

Drinking and water restriction. The drinking troughs were controlled by computer-assisted water meters and water valves (Bürkert, Fluid control systems, Ingelfingen, Switzerland). This system allowed for continuous recording (±1%) and automatic restriction of individual 24-h drinking water intake when a preset maximum volume of water was consumed, i.e., the water valve for a particular cow’s drinking trough was automatically closed until the next morning when this cow had consumed the amount allotted for the day.

Milk recording. Milk yield was recorded automatically throughout both experiments (METATRON, Westfalia Separator, Oelde, Germany).

Respiratory measurements. During experiment 2, oxygen consumption and the output of carbon dioxide and methane were measured by open circuit calorimetry (38) in the respiration chambers for 2 × 24 h in each data-collection period (baseline and restriction). The two chambers were air conditioned to match the climate in the tying stable [21.8 ± 0.1°C (mean ± SE) temperature and 59.8 ± 0.4% relative humidity]. Air flow was maintained at 28.6 ± 0.6 m³/h and recorded with inline electronic flowmeters (SWINGWHIRL DV 630, Flowtec, Reinach, Switzerland). Gaseous composition of the air flowing into and out of the chambers (internal volume: 20 m³ each) was measured using infrared analyzers (Binos, Leybold-Heareus, Zurich, Switzerland) for carbon dioxide and methane, and a paramagnetic analyzer (OXYMAT 3, Siemens, Dietikon, Switzerland) for oxygen. The whole system was manually calibrated each day before the onset of the respiratory measurements. Heat production of each animal was estimated according to the following equation (12): heat production (kJ) = 16.179 × O₂ (l) + 5.022 × CO₂ (l) − 2.168 × CH₄ (l) − 5.989 × N in urine (g).

Collection and processing of samples in experiment 2. During the 5-day baseline period and during the 5 data collection days of the restriction period in experiment 2, samples were taken either daily (feces, urine, milk) or every second day (food). The food samples were dried (60°C, 48 h) and milled to pass a 1-mm sieve for analysis. The dry food samples were stored in airtight polyethylene containers at −20°C until the end of the collection periods, when they were mixed to an aliquot for each period and cow. One part of each aliquot was dried and milled for the analysis of total ash, crude fiber, gross energy, carbon, and nitrogen content as described below. The daily samples of feces were stored at 4°C until the end of the respective collection periods, when they were mixed to an aliquot for each period and cow. One part of each aliquot was dried and milled for the analysis of total ash, crude fiber, gross energy, the other part was frozen and stored at −20°C until later analysis of carbon and nitrogen content.

Twenty-four hour urine was collected in two containers via a flexible urinal fixed on VELCRO tape that was glued onto the body with special adhesive (Cyanolit, 3M, Rueschlikon, Switzerland). The urine in one container was mixed with 60 ml sulfuric acid (5 M) to avoid N losses for further analysis of nitrogen. The urine in the second container was used for carbon analysis. The daily samples of acidified urine were stored at 4°C, whereas the nonacidified samples were frozen until the end of the collection periods. At the end of each collection period, the daily samples were pooled, frozen, and stored at −20°C until analysis of carbon and nitrogen.

For milk composition analysis, two samples per milking were taken automatically in the stable and manually in the respiration chambers. One of these samples was conserved with sodium acid (Bromopol, Bsm2, D&F Control, San Ramon, CA) and stored at 4°C for the weekly analysis of fat, protein, and lactose by the Swiss Brown Cattle Breeders’ Federation (Zug, Switzerland). The other sample was frozen and stored at −20°C until the end of the collection period and then also pooled. One part of this pooled sample was then frozen in liquid nitrogen and lyophilized for the analysis of dry matter and gross energy. The other part was used for the carbon and nitrogen analysis.

At 1500 on the last day of the baseline and restriction periods, ~35 ml blood was taken from the jugular vein. The blood was collected into EDTA (for hormone analysis), heparin, and NaF tubes (for analysis of metabolites, osmolality, and electrolytes). One milliliter of the EDTA-blood was
mixed with 500 kallikrein inactivating units (APROTININ, Böhringer Mannheim, Rotkreuz, Switzerland) for later analysis of glucagon. All blood samples were immediately centrifuged (1,600g, 4°C, 15 min), and the plasma was then frozen at −20°C until analysis.

Laboratory analyses. The Weende method was used to analyze total ash and crude fiber in food and feces (32). Carbon and nitrogen in food, feces, urine, and milk were analyzed using an automatic C/N analyzer (Leco-analyzer, Type FP2000, Leco Instruments, St. Joseph, MI); the samples were oxygenized at 950°C, and the carbon was then measured by an infrared cell; nitrogen was measured by a detector for heat conductivity with helium. The gross energy content of food, feces, and milk was measured with an adiabatic bomb calorimeter (IKA-calorimeter system C 700 T, IKA-Analysetechnik, Heitersheim, Germany). The gross energy content of urine was calculated by the following equation (20): gross energy in urine (kJ) = 33.1 × C in urine (g) + 9.2 × N in urine (g). Fat, protein, and lactose in milk were measured by an infrared-photometerspectrometer (MILKOSCAN 4000, Foss Electric, Hillerød, Denmark). Plasma glucose, lactate, free fatty acids (FFA), β-hydroxybutyrate (BHB), triglycerides, glycerol, urea, and protein were measured according to standard enzymatic procedures (16) using an automatic analyzer (Cobas-Mira, Roche Diagnostics, Basel, Switzerland). A freezing point osmometer (MULTI-OSEMETTE, Precision Systems, Natick, MA) was used to measure plasma osmolality. Plasma sodium, potassium, and chloride were determined by flame photometry (FLM3, Radiometer Copenhagen, Instrumenten-Gesellschaft, Zurich, Switzerland). Commercially available radioimmunoassay kits were used for the determination of plasma cortisol and glucagon (Diagnostic Products, Los Angeles, CA) and insulin (Pharmacia, Uppsala, Sweden). EDTA-blood was used to measure the hematocrit (Hettich Hematocrit centrifuge, 5 min).

Calculation of energy and nutrient balances. Intake was opposed to excretion for calculation of water, nitrogen, carbon, and energy balance. Metabolizable energy is defined as gross energy intake minus fecal, methane, and urinary energy. Retained energy comprises energy in milk and body energy balance. Body fat balance was calculated from carbon and nitrogen balances (12).

Statistics. In experiment 1, a repeated-measures ANOVA was performed to test for the effects of day and group and for day × group interactions. The data were analyzed in two steps: first baseline and restriction periods were compared, then baseline and rehydration. When the day effect was significant, pairwise comparisons of selected days were made with the paired t-test. In experiment 2, mean values were calculated for further analysis when more than one value was obtained for a given parameter during the data collection periods (e.g., daily milk production). Due to the small number of animals (n = 6), the data were often not normally distributed. Therefore, the nonparametric Wilcoxon test was used for the comparison of baseline and restriction period values of the same animals. All analyses were done with SYSTAT 7.0 (SYSTAT, Evanston, IL). Data are presented as means ± SE. P values <0.05 were considered significant.

RESULTS

Experiment 1. Baseline drinking water intake in experiment 1 was 59.8 ± 1.9 (5-day individual means ± SE) and 59.7 ± 3.3 l/day for the cows subsequently subjected to 25 and 50% drinking water restriction, respectively. Note, however, that total water intake (drinking water plus water in food) was reduced only ~22 and 44% with 25 and 50% water restriction, because food intake was reduced less than 25 and 50%, respectively. During the 8 days of water restriction, body weight decreased in cows with 50% restriction, but not in cows with 25% restriction (interaction group × day: P < 0.05, Fig. 1). Body weight stabilized around 99% (25% restriction) and 95% (50% restriction) of baseline values after 4 days of water restriction. On rehydration, the body weight of both restriction groups immediately increased above the baseline level and was higher (P < 0.05) than during baseline on all rehydration days. Daily food intake decreased in relation to the water restriction level (interaction group × day: P < 0.05, Fig. 2) during the first 3–4 days of water restriction and fluctuated around an 11 and 21% (with 25 and 50% water restriction, respectively) lower level for the remainder of the restriction period. Food intake immediately returned to the baseline level on rehydration. Meal pattern analysis revealed a particularly strong effect of water restriction (25 and 25% restriction) on the size of the first meal after the presentation of fresh food in the morning (Fig. 3). The first meal during water restriction started at about the same time as during baseline, but, from the third restriction day onward, it was >50% smaller (effect of day: P < 0.05) and shorter (effect of day: P < 0.05, data not shown) than baseline meals. Note that the size of the first meal was not affected on the first water restriction day because at that time the cows had not yet experienced any water restriction. On the first restriction day they ran out of water (reached their allotted amount) at 1200 (50% restriction) and 1700 (25% restriction), respectively. From the third day of 50% water restriction onward, the cows consumed all the allotted drinking water within the first 60 min of access. With 25% water restriction, they consumed about

![Fig. 1. Body weight changes (relative to the initial weight) of lactating dairy cows during 25 and 50% drinking water restriction (relative to baseline intake) and rehydration (experiment 1). Data are means ± SE of 9 (25% restriction) and 8 (50% restriction) cows. See RESULTS for further details.](http://ajpregu.physiology.org/Downloadedfrom)
65% of the allotted amount within the first 60 min. A more detailed analysis of feeding and drinking patterns during the first 60 min of access to drinking water showed that the cows irregularly alternated between drinking and feeding. On rehydration, the size of the first meal rapidly reached the baseline level again. The mean size of the second and of all following meals decreased by about one-third with 50% water restriction (effect of day: $P < 0.05$) and scarcely so with 25% water restriction. Meal frequency increased with 25 and 50% water restriction to reach a maximum on the third day of restriction (day 8, significantly higher than all baseline days, Fig. 4). On the first day of the rehydration period after 50% water restriction, meal frequency decreased (day 13 vs. day 14: $P < 0.05$) to approximately the baseline level. After 25% water restriction, meal frequency stayed as high as at the end of restriction. Milk yield was lower with 25 and 50% water restriction (effect of day: $P < 0.05$) than during baseline, decreasing with a delay of 1 day (Fig. 5). Milk yield also recovered with a 1-day delay during the subsequent rehydration period.

Experiment 2. With 50% drinking water restriction (37.7 ± 1.8 vs. 75.4 ± 4.5 l, $P < 0.05$), food intake during the 5 last days of the restriction period was ~20% lower than during the water ad libitum (baseline) period (25.7 ± 1.2 vs. 32 ± 1.2 kg/day, $P < 0.05$). The total water-to-food ratio [(intake of drinking water + water in food)/food DM (kg/kg)] decreased from 5.6 ± 0.2 (mean ± SE) in the baseline period to 4.3 ± 0.1 ($P < 0.05$) in the water restriction period. Body weight, measured on the last day of each period, decreased from 601 ± 23 kg (mean ± SE) to 535 ± 18 kg ($P < 0.05$). Compared with baseline, ~50% fewer feces ($P < 0.05$) were produced in the water restriction conditions.
Table 1. Composition of feces, urine, and milk of 6 lactating dairy cows with ad libitum access to water (Baseline) and with 50% water restriction (Restriction) in experiment 2

<table>
<thead>
<tr>
<th></th>
<th>Feces</th>
<th></th>
<th>Urine</th>
<th></th>
<th>Milk</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Baseline</td>
<td>Restriction</td>
<td>Baseline</td>
<td>Restriction</td>
<td>Baseline</td>
</tr>
<tr>
<td>WW, kg/day</td>
<td>41.5 ± 3.1</td>
<td>20.6 ± 1.2*</td>
<td>20.2 ± 1.0</td>
<td>11.5 ± 0.4*</td>
<td>18.7 ± 0.6</td>
</tr>
<tr>
<td>DM, g/kg</td>
<td>126.4 ± 5.4</td>
<td>170.0 ± 3.5*</td>
<td>35.5 ± 1.6</td>
<td>48.5 ± 3.1*</td>
<td>131.5 ± 2.1</td>
</tr>
<tr>
<td>GE, MJ/kg DM</td>
<td>19.0 ± 0.2</td>
<td>19.0 ± 0.03*</td>
<td>0.5 ± 0.01</td>
<td>0.7 ± 0.02*</td>
<td>24.8 ± 0.3</td>
</tr>
<tr>
<td>N, g/kg WW</td>
<td>3.6 ± 0.2</td>
<td>4.9 ± 0.1*</td>
<td>3.0 ± 0.1</td>
<td>4.9 ± 0.4*</td>
<td>5.1 ± 0.2</td>
</tr>
<tr>
<td>C, g/kg WW</td>
<td>60.4 ± 2.2</td>
<td>79.6 ± 1.0*</td>
<td>13.6 ± 0.3</td>
<td>19.9 ± 0.7*</td>
<td>73.6 ± 1.5</td>
</tr>
<tr>
<td>Fat, g/kg</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>46.2 ± 1.7</td>
</tr>
<tr>
<td>Protein, g/kg</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>33.7 ± 1.0</td>
</tr>
<tr>
<td>Lactose, g/kg</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>48.3 ± 0.8</td>
</tr>
<tr>
<td>Urea, mg/dl</td>
<td>ND</td>
<td>ND</td>
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<td>21.6 ± 1.8</td>
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</table>

Values are means ± SE of 6 cows throughout the 5-day baseline and water restriction collection periods. DM, dry matter; GE, gross energy; ND, not determined; WW, wet weight. *Significantly (P < 0.05) different from baseline (Wilcoxon test). Urine DM was estimated with the following formula (19): DM (%) = (urine density - 1) × 2.6 × 100.

period, but their DM content was markedly (P < 0.05) higher (Table 1). Similarly, the total volume of urine produced decreased (P < 0.05) during the water restriction period by 43%, but the urine was more concentrated (P < 0.05, Table 1). Milk production decreased (P < 0.05) during the water restriction period by ~27% from 18.7 to 13.6 kg/day, but milk composition did not change significantly, except for lactose and urea content, which were higher during the water restriction than during the baseline period (Table 1).

The total water-to-milk ratio [(intake of drinking water and water in food)/milk (kg/kg)] decreased from 4.9 ± 0.2 (baseline) to 3.8 ± 0.1 (restriction period) (P < 0.05). Water balance did not change between baseline and restriction periods (Table 2). The decreases (P < 0.05) in water excretion via urine, feces, and milk paralleled the reduced intake so that the water excretion-intake ratio remained <1, because water loss via body surface and lung was not considered in the balance calculation. Organic matter digestibility was higher during the restriction than during the baseline period (0.74 ± 0.01 vs. 0.70 ± 0.01, P < 0.05). Digestibility of the crude fiber tended to be higher in the restriction than in the baseline period (0.70 ± 0.01 vs. 0.66 ± 0.02, P > 0.05).

The nitrogen balance became negative during the water restriction period (P < 0.05, Fig. 6). Expressed as percent of nitrogen intake, the proportion of nitrogen excreted with milk and especially with urine was higher (P < 0.05) during the restriction than during the baseline period (Fig. 6). Therefore, nitrogen utilization was less efficient during water restriction than during the baseline period (0.53 vs. 0.65), and the cows had 44.6% less nitrogen available for production (retained N) than during the baseline period (P < 0.05, Fig. 7).

The energy balance did not change significantly with 50% water restriction (Fig. 8), because the decrease in absolute energy excretions with water restriction largely paralleled the decrease in energy intake. Furthermore, a reduction (P < 0.05) in the proportion of ingested energy lost through feces compensated for the increase (P < 0.05) in the proportion of energy excreted in urine during the same period (Fig. 8). Plotting the various stages of energy utilization during the baseline and restriction periods (Fig. 9) reveals that the difference (P < 0.05) between both periods at the level of gross energy intake became gradually smaller and disappeared at the level of retained energy. The coefficients of energy utilization tended to be higher during the restriction than during the baseline period, but this difference reached significance (P < 0.05) only for di-
gestibility (0.71 vs. 0.67). On the basis of the reduced 
\( P < 0.05 \) gaseous exchange during the restriction 
period, absolute heat production decreased \( P < 0.05 \) 
by 21.7% (Table 3), but again, the proportion of heat 
production relative to intake did not \( P < 0.05 \) (Fig. 8). Heat 
production can be divided into heat related to milk 
production \[ \text{calculated with } kl = 0.6 \] (30) and heat 
related to maintenance needs. Under the assumption 
of an unchanged efficiency of utilization of metaboliz-
able energy \( (kl) \), heat production for maintenance was 
reduced \( P < 0.05 \) by 17.8% during the restriction 
period (Table 3). In line with the trend observed in 
energy balance, the cows mobilized less \( P < 0.05 \) 
fat during water restriction than during baseline 
(Table 3).

The plasma concentrations of urea and sodium as 
well as the hematocrit were higher \( P < 0.05 \) during 
the water restriction than during the baseline period 
(Table 4). Plasma concentrations of lactate, BHB, and 
chloride, as well as plasma osmolality, tended to be 
higher during the water restriction period; plasma 
glucose, FFA, and glycerol tended to be lower (Table 4),
but all these differences did not reach significance. 
Plasma concentrations of insulin, cortisol, glucagon, 
triglycerides, protein, and potassium, did not change 
during water restriction (Table 4). The plasma concen-
trations of some metabolic hormones and metabolites 
showed great individual variations due to one animal 
that was in estrus during the baseline period.

**DISCUSSION**

This study shows that even lactating dairy cows are 
able to cope with a sustained 50% restriction of drink-
ing water intake (~44% of total water intake) and 
identifies some of the mechanisms involved. In demon-
strating that water restriction primarily reduces meal 
size, the results of the first experiment confirm and 
extend previous studies of our group in which rumi-
nants were completely deprived of drinking water for 
shorter periods of time (25, 34). The new finding is that 
this reduction in meal size was also present with sus-
tained water restriction and that it was particularly 
pronounced for the first meal on every day. This is 
surprising because the cows consumed substantial 
amounts of water around the time of this first meal. It 
is unlikely that meal size was somehow limited by the 
competing drinking behavior or by rumen space, be-
cause on the first day of rehydration after 25% water 
restriction, the size of the first meal was much bigger 
than during water restriction (see Fig. 3), although the 
cows ingested 38 l of water during the first hour of 
access, i.e., exactly the amount that was consumed in 
the same time with 50% restriction. Despite the sub-
stantial reduction in its size, the first meal was still the 
biggest meal of the day during water restriction. As 
rumen hypertonicity has been proposed to be a major 
control of meal size in ruminants (12), it is possible 
that the intake of a substantial amount of water before 
and together with the first meal allowed the cows to eat 
more in this meal before a level of rumen fluid or 
perhaps systemic osmolality was reached that limited 
meal size. In particular, with 50% water restriction,
cows with unlimited access to water and during water restriction (39) are consistent with the idea that an abnormal prandial increase in rumen fluid osmolality contributes to the meal size reduction during water restriction. Other possible factors include systemic hypertonicity (39) and cardiovascular and vascular volume effects of feeding related to the copious production of saliva in ruminants (3, 13, 37), which could not be detected with the design of the present study. Despite the marked reduction of the first meal’s size, it should be noted that the food intake suppression that occurred with 50% drinking water restriction was mainly due to the consistent reduction of the size of subsequent meals, because this effect, similar to the feeding depressive effect, was not observed with 25% water restriction.

Most of the parameters measured in the first experiment, in particular body weight, reached a new and remarkably constant level after 3–4 days of water restriction. Moreover, when water was offered ad libitum again, there was no sign of a compensatory increase in food intake. Thus the cows appeared to reach a new equilibrium after 3–4 days of water restriction. Other possible factors include systemic hypertonicity (39) and cardiovascular and vascular volume effects of feeding related to the copious production of saliva in ruminants (3, 13, 37), which could not be detected with the design of the present study. Despite the marked reduction of the first meal’s size, it should be noted that the food intake suppression that occurred with 50% drinking water restriction was mainly due to the consistent reduction of the size of subsequent meals, because this effect, similar to the feeding depressive effect, was not observed with 25% water restriction.

Most of the parameters measured in the first experiment, in particular body weight, reached a new and remarkably constant level after 3–4 days of water restriction. Moreover, when water was offered ad libitum again, there was no sign of a compensatory increase in food intake. Thus the cows appeared to reach a new equilibrium after 3–4 days of water restriction. The second experiment was based on the assumption that the cows were in stable energy balance during the balance measurement periods and that representative mean values could be calculated over the last 5 days.
sorption from the rumen (21), which usually drives fluid absorption, presumably contributed to the observed hypernatremia. Increased sodium retention in the kidney also helps to conserve water. It reflects the activation of compensatory endocrine mechanisms (renin-angiotensin system, aldosterone, vasopressin) by the reduction in plasma volume and the increase in plasma osmolality (5, 8, 23). With an increase in plasma sodium, renal sodium excretion eventually increases again (29, 31) and stabilizes plasma sodium at a higher level. Plasma sodium is also recycled and concentrated in the saliva (36).

Water restriction caused an increase in the apparent digestibility of organic matter and energy, which helped to maintain energy balance. It is unlikely that the better digestibility during water restriction was an artifact of the short collection period of only 5 days, because others reported similar results with longer adaptation and collecting periods (4, 35). One reason for the better digestibility is probably a longer mean retention time of the digesta in the gastrointestinal tract, in addition to a decrease in the size of particulate matter in the rumen (14). So, the marked osmotic changes that presumably occurred every morning when the cows quickly consumed the allotted amount of water did not seem to inhibit the fermentation capacity of the rumen microorganisms (6, 11). In another similar experiment from our laboratory (39) in which drinking water intake was restricted by 65% of ad libitum intake, rumen fluid osmolality in fact never reached 400 mosmol/kgH₂O, i.e., a level above which cellulose degradation appears to be inhibited (6).

The apparent digestibility of nitrogen was not improved, and, in fact, the nitrogen balance became negative when water was restricted. It is not clear why the apparent digestibility of nitrogen did not change. Brosh et al. (10) found the dehydration-induced increase in nitrogen digestibility to be inversely related to the quality of the diet. But the quality of our ration was not high enough for such an explanation. Perhaps enhancing effects of water restriction on nitrogen digestibility at the site of the rumen were compensated by the incomplete digestion of the rumen microbial protein synthesized from the additional ruminally fermented organic matter. It is of course also possible that changes in endogenous nitrogen excretion masked changes in true nitrogen digestibility. Further studies are necessary to clarify this question. The negative nitrogen balance was due to the relative increase in nitrogen excretions (in % of intake) in form of urinary urea and, partly, milk urea as a result of the elevated plasma concentration of urea. Tissue protein breakdown and the subsequent increase in amino acid metabolism was the most likely source of the increase in plasma urea concentration. Recycling urea in the kidneys helps to reduce urinary volume and, hence, to conserve water (28). The increased plasma urea content was unlikely to be a consequence of the reduced nitrogen needs for milk production because water restriction increases plasma urea also in nonlactating animals (e.g., Ref. 33).

During the water restriction period, the cows still had ~81% of the baseline metabolizable energy available. This energy was used for maintenance and milk production (neglecting the needs for early pregnancy). When water is limited, milk production declines according to the water and nutrient shortage (15), thus decreasing the energy needs for milk production to a certain extent. Interestingly, the results suggest that the energy needs for maintenance also declined. A similar observation was reported by Brosh et al. (9) in nonlactating, infrequently watered, desert-adapted goats. These authors based their conclusion on the reduced O₂ consumption under these conditions and on the fact that the goats did not lose body mass during dehydration except for body water. In the dairy cows of our study, the absolute heat production for maintenance was reduced by water restriction. According to the nitrogen and fat balance calculations, the cows may have lost ~60 g protein and 80 g fat per day during water restriction. This appears to be at odds with the numerically positive energy balance and the unchanged body weight, but all these changes were very small and are probably within the error range of the methods employed. Therefore, the present data do not allow us to judge whether the cows lost some solid substances during water restriction or not. In experiment 1, the cows completely regained their body weight during the first day of rehydration, suggesting that they had mainly lost water during the water restriction period. Silanikove and Tadmor (37) showed that body water loss accounted for ~89% of the total weight loss of nonlactating beef cows during 3 days of water deprivation. If a similar relationship held for the lactating dairy cows in the present study, they would have lost ~59 kg of water and 7 kg solid substances. This would have negligible effects on net energy for maintenance when using the following equation (2): net energy maintenance = (0.53 × body wt/1.08)0.67 + 0.0091 × body wt. The energy requirements for maintenance include the energy needed for gut metabolism (eating, food processing and absorption), which was found to decrease with the decrease of food intake in non-desert-adapted animals (40). This could contribute to the decrease in energy requirements for maintenance in the cows of the present study. All in all, it remains unsolved whether and to which degree reduced maintenance requirements and/or an increased efficiency of use of metabolizable energy for milk production was responsible for the slight increase in overall use of metabolizable energy during water restriction (0.34 vs. 0.32).

The results of the blood metabolite measurements fit the roughly stable energy balance. The lack of a change in plasma fat and carbohydrate metabolites indicates that there was no fat mobilization and, hence, no energy deficit during water restriction. The lack of changes in the plasma levels of metabolically active hormones is also consistent with this interpretation. In addition, the constancy of the plasma cortisol concentration across the baseline and water restriction periods suggests that the cows were not continuously
stressed by the water restriction. This is also interesting from an animal welfare point of view. In line with our findings, others (33) recently reported that also in South African indigenous goats several blood parameters changed during only the first few days of a 50% water restriction period and returned to baseline levels thereafter. Thus, in principle, it could be possible to extend the water restriction period for a longer period of time without additional effects, as did Little et al. (27) during 3 wk, but with a lower level of water restriction (40%).

To our knowledge, this is the first report in which calorimetry measurements in respiration chambers were used to critically examine the changes in metabolism as well as energy and fat balance during water restriction. The results reveal that dairy cows are able to cope with a sustained restriction of total water intake to almost 50%, i.e., the decrease in milk yield and food intake, with the concomitant decrease in heat production (metabolism) and improved water retention combined to save sufficient water to reach a new equilibrium at a lower water turnover level. The body weight and food intake data show that the cows reached a new balance after 3–4 days of water restriction. The food intake suppression was primarily due to a reduction in meal size, which fits the idea that an abnormal prandial increase in rumen fluid osmolality contributes to the food intake suppression during water restriction (39). The lower energy intake was compensated by a lower milk production, a higher digestibility, and, apparently, a more efficient metabolic energy utilization. Further studies should also critically examine nitrogen metabolism during water scarcity because a loss of nitrogen, which might occur based on our nitrogen balance calculations, could become limiting for long-term adaptation to water scarcity.

**Perspectives**

In many areas of the world, ruminants have to cope with temporary water shortages; even in industrialized countries, water availability may at times be insufficient. For example, in young animals shortly after weaning, when it takes days before the level of water intake reaches that of milk. Water intake may also be limited during early lactation in high-yielding dairy cows, when fluid balance is pushed to its limits. Moreover, pathological situations such as diarrhea, rumen acidosis, and other diseases can cause systemic dehydration. The present results demonstrate the amazing ability of ruminants to cope with water shortages. Initially, much of that ability is related to the water reservoir function of the rumen (36); with continuing water shortage, however, other mechanisms, including the food intake suppression, come into play. Eating less during water restriction helps to maintain osmotic balance, because smaller meals reduce the impact of an osmotic load (food) not balanced by adequate drinking water intake. If ruminants failed to decrease food intake during dehydration, it might even compromise the osmotic buffer function of the rumen, because it might increase rumen fluid osmolality so much as to prevent the use of rumen water to alleviate the systemic hypertonicity of dehydration. Thus the suppression of food intake during water scarcity represents a compromise between the needs to ingest nutrients and to maintain osmotic balance of body fluids and reflects a homeostatic mechanism that minimizes the negative consequences of dehydration.

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