Diurnal Fluctuations in Plasma Ions and Water Intake of Dairy Cows as Affected by Lactation in Warm Weather[1]

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ABSTRACT

The presumption that water, Na, K, and Cl homeostasis is affected by the initiation of lactation, especially in hot weather, was examined. The study was conducted using five Israeli Holstein cows at 1 to 2 wk before parturition (period 1) and at 2 wk (initiation of lactation) and 7 wk (established lactation) postpartum (periods 2 and 3, respectively). In period 1, most water intake was related to feed (in the absence of overt Na or osmotic stimuli). In contrast, during lactation, drinking was probably a combined response to feed-related and hypertonicity stimuli. Diurnal fluctuations in plasma ions, frequency of drinking, and volume ingested at each drinking increased postpartum. In period 2, plasma ion concentrations still were regulated around mean values, which was not the case in period 3, during which large diurnal variation in mean values occurred. The lowest values and highest variabilities were recorded in period 3 at midday. With the transition from the dry period to lactation, plasma concentrations of Na and Cl were reduced and became more labile, but the relationships between them remained sta-ble. Plasma K seemed to vary independently of the two other ions. The reduced homeostatic efficiency of plasma ions during early and established lactation in hot weather may have consisted of an accumulation of their deficiencies, enhanced excretion of K in sweat, and sequestration of Na and Cl in the rumen. (Key words: drinking frequency, diurnal fluctuations, ions, hematocrit)

Abbreviation key: DEI = digestible energy intake, RCW = respiratory-cutaneous water, WTO = water turnover.

INTRODUCTION

The regulation of extracelluar fluid volume and its ionic composition is essential to mammals (1). In domestic animals, body fluid homeostasis is maintained under most circumstances when access to water is not limited (19). In the dairy cow, selection for high milk production has so increased water output that daily water turnover (WTO) probably is among the highest recorded for mammals. Under moderate environmental conditions, the daily WTO rate may range from 25% of total body water in cows producing 33 kg/d of milk to 35% of total body water in cows producing 50 kg/d of milk (17, 18, 35).

Water metabolism consists of water intake; water shifts among gut and vascular, intercellular, and intracellular compartments; and water excretion. In ruminants, the exchange between gut and systemic fluids is particularly large because of the great water intake, diffusion of water between the systemic fluid and the gut, and saliva production. During lactation, >250 L/d may be secreted as saliva (3), its

Na content being approximately five times greater than that present in plasma (29). Milk production enhances ion turnover; Na, K, and Cl constitute approximately 40% of milk osmolality (1, 20). In early and established lactation, cows secrete more Na and Cl in milk than is excreted in urine (25). The intake of water and ions is episodic, in contrast to the continuous nature of water and ion output through milk, urine, feces, respiration, and cutaneous evaporation, and may create transient discrepancies between ion input and output. These discrepancies may vary from surplus to deficiency, even though a zero balance might be maintained over the day. Such discrepancies may be exacerbated in cattle, in which much of the water and feed intake takes place during light hours, which may pose a short-term homeostatic problem. However, most mammals having free access to water manage to regulate their plasma osmolality within a narrow range (7, 10, 13, 21). In addition to the well-characterized water intake in response to challenges to fluid homeostasis, an additional drinking mechanism, defined as feed-related drinking, was described for many mammals (2, 7, 13, 21, 22, 26, 33); this drinking mechanism can be efficient enough to prevent significant shift in osmoconcentration in blood plasma. However, for dairy cows, large increments in the continuous loss of water and ions associated with lactation and heat stress may impose constraints upon maintenance of homeostasis.

In this study, we examined diurnal changes in plasma ion concentrations and water intake during the precalving dry state, soon after initiation of lactation, and during established lactation of cows exposed to mild heat stress. The part of the study related to ions and water balances has been reported previously (25).

MATERIALS AND METHODS

Experimental Procedure

The full experimental procedures used in this study have been described (25); the elements pertinent to this study are presented here. The experiment was carried out between mid-July and mid-September with five Israeli-Holstein cows approaching their second parturition. Unregulated natural fluctuations in am-

bient indoor temperatures at 1230 h were 28 to 30°C, and relative humidity was 65 to 70%. Six weeks before expected parturition, cows were transferred, with no change in diet, to individual indoor stalls in which feed and water intake were monitored individually. Before parturition, cows were fed for ad libitum intake wheat silage (42.3% DM) containing 8.00, .71, 4.08, and 1.37% CP, Na, K, and Cl, respectively, on a DM basis. During lactation, the cows were fed a 65% DM complete ration prepared daily. The concentrate:forage ratio of the ration was 66:34, and the ration contained 16.3, .32, 1.83, and .61% CP, Na, K, and Cl, respectively, on a DM basis. Half of the daily ration was given at 0800 h and the remainder at 1330 h. The cows were milked at 0500, 1300, and 2000 h, and milk yield was recorded. Water was available from individual drinking cups connected to electronic meters (Arad Dalia Ltd., Israel; accurate to ±1.0 L). Water output was scanned and stored hourly by a computer. Water intake data included the frequency of drinking events and the amount of water ingested at each drinking event.

Plasma Na and K were analyzed by flame photometry (Corning 480; Medical and Scientific, Corning Ltd., Halsted, Essex, England) and Cl by titration (Chloride Titrator CMT 10; Radiometer, Copenhagen, Denmark). Heparinized capillary tubes were used to determine hematocrit of blood samples.

One week before expected parturition (period 1), cows were fitted with jugular catheters (maintained patent with Li-heparin), and blood samples were withdrawn hourly for 24 h. This procedure was repeated at wk 2 postpartum (period 2) to represent the start of lactation and at wk 7 (period 3) postpartum to represent established lactation. Data reported pertain to these periods.

Data Analysis

The hourly changes in functions (water intake, electrolyte concentrations in plasma) represented deviations from tentative, regulated concentrations, the zero offset of the homeostatic mechanisms. The determination of these deviations must take into account that the regulated levels may shift and that the extent of the shift may differ among animals. Such shifts may occur as a response to changes in

the environment or to passage from pregnancy to lactation. To estimate the hourly changes in function independently of the aforementioned factors, the within-cow residuals were calculated for each period separately by the GLM procedure (23) with cow as the independent term in the model. The three sets of residual data were analyzed jointly by a GLM procedure with period, stage of day, and their interaction as independent terms in the model. Statistical significance of the differences were estimated by the contrast routine. The effect of period (dry, early lactation, and established lactation) on the within-cow variance (differences between different hours within a day) was estimated by a GLM analysis of the aforementioned residual variance; period was the independent term in the model. Statistical significance was assessed by the contrast routine. Linear and multiple linear relationships (stepwise procedure), and partial correlations were estimated by regression procedures. The analyses were carried out using SAS (23).

RESULTS

Mean Data for Periods

Full details were reported previously (25) for mean values for water and feed intake, ion plasma, and ion balances in the dry period, at initiation of lactation, and during established lactation. Generally, BW declined from period 1 (683 ± 21 kg) to period 2 (565 ± 25 kg) and decreased further to period 3 (549 ± 32 kg). Water intake increased ($P < .05$) from 50 L/d prepartum to 104 L/d in period 2 and 109 L/d in period 3. The change in feed intake was similar to that of water intake. Milk yield was similar in the two periods (34.1 ± 1.2 and 31.4 ± 2.6 kg/d, respectively). Mean hematocrit decreased from 32.1 ± 1.1 in period 1 to 26.3 ± .8 and 25.5 ± .4 in periods 2 and 3, respectively. The trend was similar for plasma Na and Cl concentrations, which also were lower during lactation. Mean Na concentrations during the dry period and periods 2 and 3 were 143 ± 4, 139 ± 6, and 131 ± 6 meq/L, respectively; for Cl, they were 106 ± 2, 103 ± 5, and 100 ± 4 meq/L, respectively. Mean concentration of plasma K remained relatively stable at approximately 3.9 meq/L (25).

Patterns of Drinking

In period 1, most water intake occurred during two intervals: at 0900 to 1400 h, representing 50% of total daily intake, and 1700 to 2200 h (Figure 1). Very little drinking took place from 2300 to 0800 h. Lactation was associated with an increase in drinking activity and its extension over most of day and night hours. Mean daily intake did not change much from periods 2 to 3; however, in period 3, the diurnal variation in hourly water ingestion was markedly greater than that in period 2. In period 3, hourly water intake fluctuated from 1.5 to 16 L/h, in contrast to the relatively stable intake of close to 5 L/h in period 2. This difference in water consumption pattern prevailed in spite of very similar patterns of drinking frequency in periods 2 and 3. This difference should suggest a larger variability in
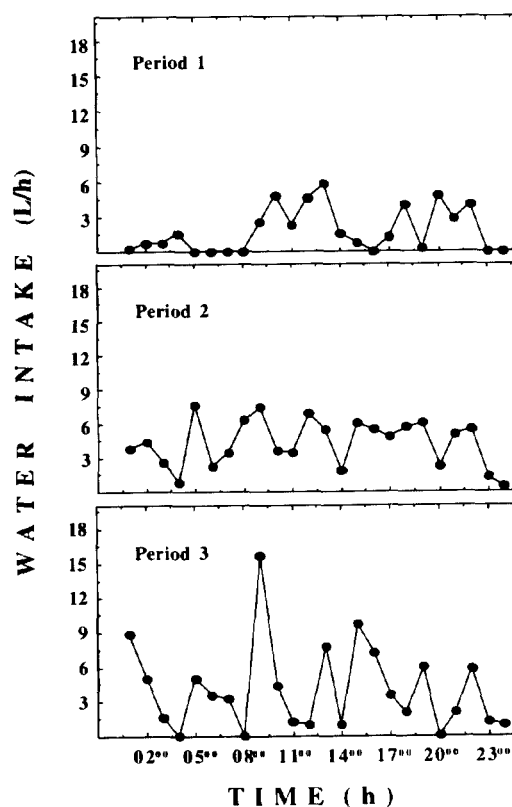

Figure 1. Hourly water intake throughout the day for five cows before parturition (period 1) and 2 wk (period 2) and 7 wk (period 3) after parturition.

TABLE 1. Estimates of diurnal variation in the dry period (period 1), early lactation (period 2), and established lactation (period 3) of Israeli-Holstein cows.

Parameter	Period		
	1	2	3
Na			
X̄	3.55[c]	6.74[b]	11.22[a]
CV	4.1[c]	7.7[b]	12.5[a]
Cl			
X̄	2.43[c]	5.09[b]	8.23[a]
CV	3.6[c]	7.9[b]	11.6[a]
K			
X̄	.165[b]	.301[a]	.355[a]
CV	6.4[b]	11.9[a]	14.0[a]
Hematocrit			
X̄	.675	.725	.751
CV	4.2	4.6	3.9
Water, X̄	2.28[b]	4.29[a]	4.60[a]
Na:K, X̄	1.43[b]	1.94[a]	2.20[a]

[a,b,c]Means and CV with different superscripts differ ($P < .01$).

amount of water ingested per drinking event in period 3.

Period Effects on Variability

The residuals for the variance within cow and within period were converted to absolute values to estimate the diurnal variability in parameters. Differences between periods were assessed as well as coefficients of variation (Table 1).

Hematocrit was the only parameter for which the extent of the diurnal variation was not significantly modified by the transition from the dry state to early lactation and further to established lactation. For all other parameters measured, the diurnal variation was less in period 1 than in later periods. The variance increased from early to established lactation for Na and Cl only. Significantly, the change in variance of Na was reflected only partly in the variance of the Na:K ratio. The change in diurnal variation from periods 2 to 3, relative to the variation in period 1, was similar for Na and Cl. Changes in diurnal variation as expressed in coefficient of variation units were similar to those in absolute units.

Diurnal Patterns

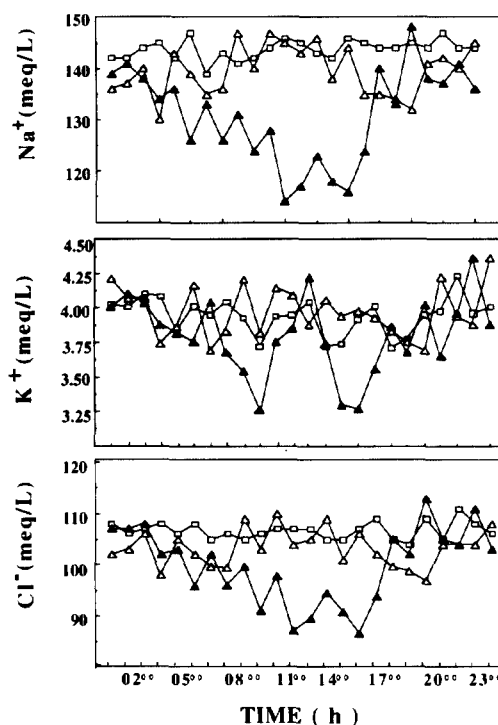In period 3, but not in periods 1 or 2, the cycle in mean concentrations of plasma ions

Figure 2. Diurnal pattern in plasma Na, K and Cl concentrations in five cows before parturition (□) and 2 wk (△) and 7 wk (▲) after parturition.

clearly was diurnal and declined during the day (0700 to 2000 h) to recover during the evening and night (Figure 2). No such pattern was observed for hematocrit (Figure 3). The three ions differed in that pattern: for Na and Cl, concentrations were reduced during most of the day, but K underwent a transient increase from midday to late afternoon.

The diurnal effect was examined by classifying the residuals within cow and within day to day or night hours during the three periods. The model used time (day or night) as an independent term in the analysis, which was carried out for each period separately. No differences between day and night hours were significant for plasma Na, K, Cl, Na:K ratio, or water intake residuals for all three periods (data not shown), indicating no significant diurnal variability in these parameters.
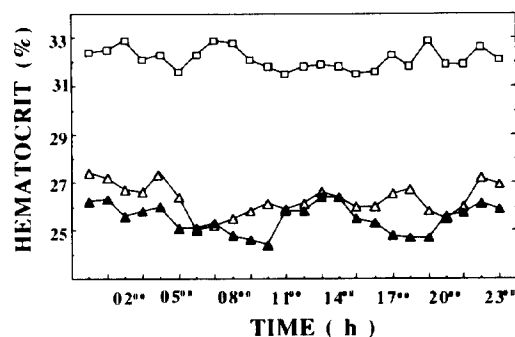
Figure 3. Diurnal pattern in hematocrit in five cows before parturition (□) and 2 wk (△) and 7 wk (▲) after parturition.

Individual Patterns

The individual cows varied markedly in the extent to which the diurnal variation in Na, K, and Cl changed between periods (Figure 4). For cows 1 and 2, changes in state between periods had little effect on the diurnal variation in these parameters. However, for cows 3, 4, and 5, lactation increased the relative variation in parameters. However, the occurrence of the change in diurnal variation differed among cows. For cow 3, the greatest change occurred with the onset of lactation, and, for cows 2 and 3, only slight change was observed between stages of lactation. For cow 4, the greatest change in diurnal variation occurred between periods 2 and 3. The larger diurnal variation recorded in period 3 might therefore be attributed to the large change in response that occurred in two of the five cows.

Relationships Between Ions

The relationship between concurrent variations in plasma Na, K, and Cl was examined by correlation analysis of the pooled residual variances. The correlation between Na and K was .69, between Na and Cl was .94, and between K and Cl was .77 ($P < .01$). These correlations indicated that, in the three periods, the diurnal changes in Na, K, and Cl were highly correlated with each other, which indicates concurrence of variations. Results were very similar when the correlations were calculated for the raw data for plasma concentration. The latter suggests that the pattern of within-

cow relationships is similar to that between cows. Such concurrence might, however, be apparent only. Therefore, the interrelations were also examined by partial correlation analysis of the residuals (Table 2), which indicated that a significant partial correlation prevailed only between Na and Cl: partial correlations were very small between other parameter combinations. The correlation tended to increase with period. However, regression coefficients that estimated the quantitative relationship between these parameters in the three periods did not change markedly (Table 2), which indicates that deviations of Na plasma concentrations from the mean were only slightly correlated, if at all, with concomitant changes in K deviations from the mean.
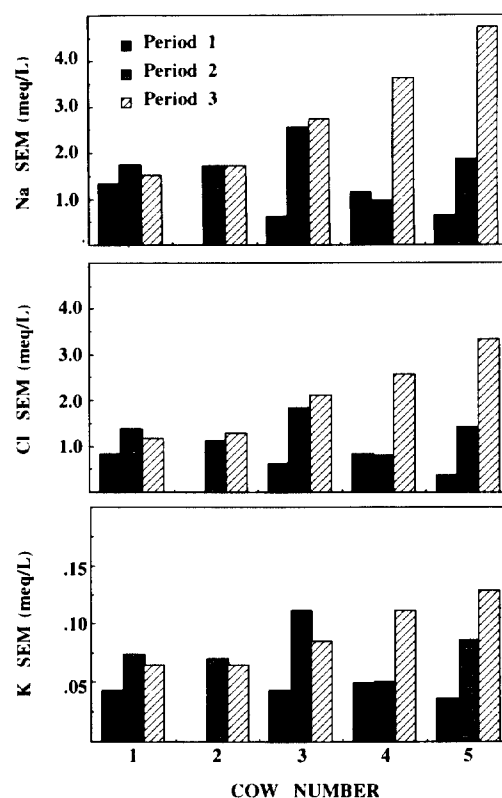

Figure 4. Individual variability (SEM) in plasma Na, K and Cl in five cows before parturition (period 1) and 2 wk (period 2) and 7 wk (period 3) after parturition.

TABLE 2. Partial correlation and regression coefficients between residual data of concentrations of Na, K, and Cl.

	Period			
	1	2	3	All
Correlation coefficient				
Na × K	.03	.04	.02	.02
Na × Cl	.52*	.77*	.87*	.81*
K × Cl	.02	.02	.01	.03
Regression coefficient				
Na × Cl	1.0	1.2	1.3	1.3
SE	± .1	± .1	± .1	± .1
Na × K				
	2.7	2.3	1.7	1.7
SE	± 1.6	± 1.1	± 1.1	± .7

*P < .01.

Changes in plasma K occurred and were of similar relative magnitude as those in plasma Na, as indicated by similar coefficient of variation. However, changes in concentrations of Na and K plasma did not seem to occur concomitantly. However, partial correlation was significant between Na and Cl (Table 2; Figure 5). An apparent trend was found toward an increase in correlation with transition from the pregnant, nonlactating state to early lactation and, subsequently, to established lactation (Figure 5). The relationships between plasma ions in the individual cows across periods were almost identical to those obtained by pooling data for all cows (Table 3).

DISCUSSION

Types of Drinking

Many species drink a large portion (~ 75%) of their daily water intake before, during, and shortly after meals (13). In this experiment, only total daily feed consumption was recorded, but, in the pregnant, nonlactating state, the cows consumed most of their morning feed within 3 to 4 h. Water intake paralleled feed intake, which was not true for the ration fed at 1330 h: water intake started rising after 1700 h and remained high until 2200 h. It is possible, though, that feed intake was delayed, occurring some time after its presentation, in the afternoon hours. This pattern is common in practice, when feed is offered at the hottest time of the day, when cows seldom eat. We tentatively suggest that most drinking by these cows was associated

with feed intake. However, unlike humans, rats, and pigs, all of which exhibit a periprandial drinking pattern (7, 10, 21), most drinking followed feeding of the dry, late pregnant cows. Nonlactating, nonpregnant goats resembled our dry cows in drinking pattern (26). The results of the study indicated little diurnal change in concentrations of Na and Cl plasma in the late pregnant, nonlactating state. These two ions, rather than K concentration, play a major role in plasma tonicity. The results presented here, as well as data for humans and pigs (10, 21), are consistent in suggesting that substantial changes in osmoconcentration and plasma volume do not develop before the occurrence of several successive bouts of drinking. Thus, drinking may occur in these mammals in the absence of the classic hypertonic stimuli.
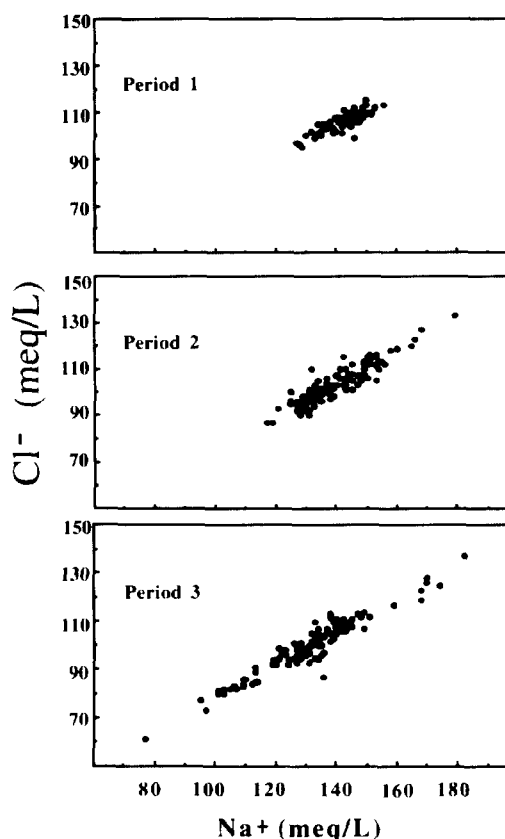

Figure 5. Interrelationship between plasma Na and Cl concentrations in five cows before parturition (period 1) and 2 wk (period 2) and 7 wk (period 3) after parturition.

TABLE 3. Partial correlation and regression coefficients between residual data of Na, K, and Cl in the individual animals.

	Animal				
	1	2	3	4	5
Correlation coefficient					
Na × K	.05	.01	.04	.01	.01
Na × Cl	.52*	.50*	.85*	.89*	.91*
K × Cl	.02	.16	.01	.11	.01
Regression coefficient					
Na × Cl	1.4	1.2	1.4	1.4	1.3
SE	± .1	± .1	± .1	± .1	± .1

*$P < .01$.

The transition into lactation almost doubled feed intake, which probably extended the periods in which the cows were engaged in eating. Drinking events also spread over almost all hours of the day and night. Changes of approximately 5 meq/L in Na and of 10 meq/L for combined Na plus Cl plasma concentration are thought to act as stimuli for drinking in humans, rats, pigs, and ponies (2, 13, 21, 33). In early and established lactation, fluctuations in plasma concentrations of Na and Cl were larger than the aforementioned threshold values. Drinking during lactation thus probably was the result of a response to combinations of feed-related stimuli and hypertonicity stimuli. The frequent drinking bouts may be reflected in the numerous fluctuations in concentrations of plasma ion that typically were observed in the lactating state, but not in the dry state (Figure 2).

During established lactation, approximately 20% of water intake occurred between 0800 to 1600 h, when plasma Na and Cl were the lowest, and thus took place in the absence of a hypertonic stimulus. This result may indicate a predominance of feed-related drinking during these hours, which possibly overrides the quenching effect of hypotonicity.

Diurnal Fluctuations

In very early lactation, fluctuations in plasma Na, K, and Cl concentrations around mean values were considerably higher than prepartum, particularly during daytime. In established lactation, during daytime hours, a marked drop occurred in plasma Na, K, and Cl concentration, which suggests an impaired ability to maintain homeostasis. Only at night did concentrations of these electrolytes return to normal. We previously reported (25) that the cows in this experiment were in negative Na, K, and Cl balance. The failure to sustain normal ion concentrations in period 3 may be due to this negative balance as well as to effects related to the cows being subject to such a negative balance over an extended time. Indeed, evidence for depletion of Na in rumen fluid may exist in the reduction of the fecal Na:K ratio (25). Approximately 50% of the Na secreted with the saliva is reabsorbed from the rumen (5); however, total tract Na absorption is well above 90% (28, 29). The absorption of Na from the rumen is active and depends upon the concentration of VFA in rumen fluid (8, 32). Indeed, feed deprivation induces hyponatraemic hypovolemia in ruminants (4). Heat stress may induce a direct effect on the production of VFA in the rumen and an indirect effect by reducing feed intake (12, 28, 34), thus impairing the absorption of Na during the day. Transiently impaired Na absorption may be another factor contributing to the transient midday decline in plasma Na concentration.

The reduction in Cl concentration during the day was so large that it reached levels definable as hypochloridonemic (6). Concentrations of Cl in sweat and saliva are relatively high (11, 30). Absorption of Cl from the rumen is related closely to Na absorption (5). Thus, a midday reduction in Cl also may have been related partially to transient Cl sequestration in the rumen and partially to its excretion with sweat.

Despite the failure of the cows to maintain plasma Na and Cl concentration during the

day, the relationship between these two ions was remarkably stable. Sodium and Cl are the major contributors to the anion-cation balance of extracelluar fluid. A large deviation in one of these ions, unaccompanied by a parallel change in the counter ion, will be associated with a profound change in the acid-base balance and pH of extracellular fluid. Although both Na and Cl fluctuated widely, the constant ratio between Na and Cl prevented large shifts in the acid-base balance and in plasma pH, but the maintenance of this constant ratio had no overt physiological explanation.

In established lactation, plasma K gradually declined during the day, rose temporarily at midday, and was followed by an increase during the evening and night hours. Reduction in K concentration during the day could have been a result of its increased secretion in sweat. The cows in our experiment were subjected to heat load (25), and K is the major cation in ruminant sweat (11). The transient rise in plasma K between 1100 and 1500 h started approximately 2.5 h prior to the midday meal and, therefore, could not be associated with it, especially because no similar rise occurred at the time of the morning meal. This result could reflect an exaggerated response to the fall in plasma K, its subsequent decline indicating a possible transient depletion of the extracelluar compartment. However, no evidence was found to support this contention.

The onset and establishment of lactation did not alter the ability of the cow to maintain apparent plasma volume within a narrow range; hematocrit values were relatively stable. A 6 to 7% decrease in blood volume is considered to be the threshold for drinking behavior for some mammals (2, 22). Unless the threshold in cows is much lower, changes in blood volume would have been unlikely to have induced drinking in the present experiment.

Increased intake volume of drinking bouts was expected to reduce the tonicity of rumen fluid (27). Reduction in the tonicity of rumen fluid would facilitate net absorption of water from the rumen to blood (27). Expansion of the portal blood system induces recycling of water to the rumen through acceleration of saliva secretion (27). These responses may explain the capacity of the cows to prevent large shifts in blood volume despite irregularity in drinking and despite the large amount of water consumed in each drinking bout.

A Model to Explain Individual Patterns in Ion Fluctuations

The small number of cows and the large individual variability among cows in diurnal variation of Na, K, and Cl restricts the ability to draw general conclusions, unless the individual variability can be explained by a general model.

In the following equation, the independent variables accounted for 77% of the variation of the sum of Na, K, and Cl concentrations in plasma of all the cows in the three experimental periods (P < .001; n = 18).

$$\text{Variance} = 4.5 \ (2.6) + \text{WTO} \times .11 \ (.02) + \text{DF} \times - .999 \ (.26)$$
[1]

The dependent variables are the related WTO rates (kilograms per day) and drinking frequency, DF (times per day). The standard errors of the related variables are given in parentheses.

The validity of a statistical model is strengthened if it has a physiological basis. Rate of WTO or free water intake are mostly functions of DMI and milk yield (9). A separate equation, however, is needed to describe the free water intake or WTO rate (excluding metabolic water) of dry and lactating cows (9). Silanikove (26) has shown in goats (supported by available data on other species of ruminants and mammals) that the linear relationship between feed intake and WTO (or free water intake) is, in fact, a derivation of a more basic relationship between digestible energy intake (DEI) and WTO rate. Furthermore, the slope of the relationship between DEI and WTO rate in lactating cows essentially is similar to that of nonlactating cows if the amount of water secreted in milk is subtracted from the WTO rate. Indeed, a significant linear relationship (P < .002) was found between milk free water balance of all the cows in the three experimental periods and the related DEI [by analysis of data in (24, 25)]. The study of Holter and Urban (9), which was carried out under controlled thermoneutral conditions, allowed estimation of the basal respiratory-cutaneous water (RCW) loss in dairy cows. Assuming that metabolic water production was approximately 6 L/d in the dry cows and 14 L/d in lactating

cows (25), the basal RCW loss appeared to be approximately 20 L/d in dry cows and 40 L/d in lactating cows; RCW during prepartum, early lactation, and established lactation was 23, 25, and 35 L/d, respectively, higher than the respective values in the study by Holter and Urban (9). These higher RCW losses were consistent with the conclusion that the cows were under heat load and, therefore, the water lost for cooling increased. Consequently, 97% of the variability of milk free water balance (MFWB) (kilograms per day) can be explained in Equation [2] by DEI (megacalories per day) and RCW (kilograms per day) loss as dependent variables ($P < .0001$; for the intercept $P < .03$; for DEI, $P < .002$; and for RCW loss, $P < .0001$; n = 18; the values in brackets are the standard error of the respective variables).

$$MFWB = 11.7\ (4.9) + DEI \times .56\ (.14)$$
$$+ RCW\ loss \times .97\ (.07) \qquad [2]$$

Rate of WTO seems to be a good criterion to reflect the strain on the regulatory system because of the following relations: 1) DMI, hence, the ion inflow into the system; 2) milk production (through its relationship to DEI), hence, with one of the major avenues which determine ion outflow from the system; 3) RCW loss, hence, a major factor that increases ion outflow under heat load.

The positive effect of drinking frequency on the ability to regulate plasma ions within a narrow range also has a logical basis: it attenuates the typical postfeeding increase in rumen osmolality and the potential effect of such response on transepithelial movement of water from the blood to the rumen along the osmotic gradient (28). In addition, Silanikove (27) found that drinking stimulated Na absorption from the rumen in rehydrating cows.

Peak feed intake and milk yield, and their patterns, varied considerably among individual cows under similar husbandry conditions (14, 15, 16, 31). Because the rate of changes in feed intake and milk yield, and, hence, in WTO rate, affects the concentrations of ions within and between periods, the large individual variation can now be explained by individual differences in adaptation of cows to the stage of lactation. Overall, results of the present experiment stress the importance of analyzing

the nutritional and physiological response of dairy cows in this critical period by a dynamic approach.

CONCLUSIONS

In our previous report (25), we suggested that negative electrolyte balance in early lactation might impair the thermoregulation capacity of cows. The present report provides evidence suggesting that heat stress during early and established lactation may be associated with impairment in the capacity of the cows to regulate plasma Na, K, and Cl concentrations within a narrow range. Impairment of concentrations of plasma ions is an additional factor that may be involved in the seasonal depression of milk yield during summer.

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