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THE EFFECTS OF SALT LOADING VIA TWO DIFFERENT ROUTES ON FEED INTAKE, BODY WATER TURNOVER RATE AND ELECTROLYTE EXCRETION IN SHEEP

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ABSTRACT

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The effect of dosing identical amounts of sodium chloride, via 2 different routes, on feed intake and water and electrolyte balance was investigated in sheep. Feed intake and plasma sodium concentrations were unaffected by salt loading, while water intake, fractional turnover of body water, plasma and urine potassium concentrations and urine sodium concentration changed significantly from control values ($P<0,05$). With a few exceptions, parameters were in general similar irrespective of the route whereby sodium chloride was administered.

INTRODUCTION

Although some data has been reported on the effect of an increased salt load on water and electrolyte balance of sheep (see below), these are often irreconcilable due to the wide range of methods used to investigate this issue. *Inter alia,* different breeds of sheep (MacFarlane, Howard & Siedert, 1967; Michell & Moss, 1987), and combinations of variables (Jones, Potter & Reid 1970; Wilson & Dudzinski, 1972), have been selected by individual researchers.

For example, in one trial drinking water containing 2 % NaCl severely depressed food intake to the point where death resulted in some animals (Peirce, 1957). In another, sheep dosed with NaCl at the rate of 2 g/kg body mass, but with free access to fresh drinking water showed few untoward symptoms (Hamilton & Webster, 1987). Furthermore, the type of sodium salt taken in is of importance, e.g. chloride or bicarbonate. Thus sodium as the bicarbonate salt is less well tolerated than the chloride salt when ingested via the drinking water (Peirce, 1968).

Generally, experiments investigating this domain may be divided into two categories:

(i) those in which the ratios of NaCl to water (i.e. concentration) taken in are fixed by experimental protocol. The amount of solution dosed or taken in is therefore the only variable (Peirce, 1957; Potter, 1961; Jones *et al.* 1970);

(ii) those in which the ratio of water to NaCl taken in may be controlled by the animal. A known mass of NaCl is taken in, either as part of the feed or by intraruminal infusion, and the sheep is allowed free access to fresh drinking water (Meyer & Weir, 1954; Wilson, 1966a; Godwin & Williams, 1986; MacFarlane *et al.*, 1967).

Often, when the effects of high NaCl intakes were investigated in sheep, large boluses of NaCl were administered directly into the rumen once or twice per day (Wilson & Dudzinski 1973). Such bolus additions of NaCl probably exceed normal physiological limits, as rumen osmolality would be affected. As a consequence ruminal digestive processes and the absorption of salt and water from the intestinal tract would also change (Stacy & Warner, 1966).

It is therefore obvious that the effect of an excess intake of NaCl on the water, and most probably also on the electrolyte balance of sheep will depend on both the form and the rate of NaCl intake and also on whether fresh water is available to assist in the excretion of this salt.

In this trial therefore, aspects of water and sodium metabolism were investigated under both of the above conditions (i and ii), but in order to make meaningful comparison of results, the mass of NaCl dosed in each situation was kept similar.

The experiment was thus aimed at simulating two possible situations in the field. In one, the animal is exposed to saline drinking water and has no control over the NaCl:water ratio taken in and in the other, herbage eaten contains a high salt content (e.g. saltbush), but fresh drinking water is freely available, i.e. the ratio of NaCl:water taken in may be controlled.

MATERIALS AND METHODS

Animals

Six S.A. Mutton Merino wethers, aged 1–2 years, with body mass ranging from 39–53 kg, were fed chopped lucerne hay *ad libitum* and had free access to water prior to the experiment. Feed sufficient for the trial was chopped, mixed and bagged. About 5 months before the trial, each animal had been surgically fitted with a standard, hard-rubber, rumen cannula (ID = 22 mm, OD = 30 mm). One week before the experiment, the sheep were confined to individual metabolic crates in a room where ambient temperature varied between 16 and 23 °C over the experimental period. Relative humidity over the same time ranged between 40 and 90 %.

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Experimental design and procedure

The experimental period (total = 30 d) was divided into 3 phases as follows:

Phase 1 Day 1–6 = Control phase; during which fresh water was available *ad libitum*.

Phase 2 Day 7–15 = Saline phase; during which drinking water was replaced by isotonic saline solution (0,9 % NaCl in water), which was availble *ad libitum*.

Interim Day 16–20 = Recovery phase. During which fresh drinking water replaced the saline solution and was freely available.

Phase 3 Day 21–30 = Intraruminal salt phase. The mean daily intake of NaCl by each animal during phase 2 was calculated. This same amount of salt, in the form of a 10 % solution, was added directly into the rumen each day of phase 3. The required amount of solution was allowed to drip into the rumen, via a cannula, over a 24 h period by suitable selection of the flow rate on a standard fluid administration set. Fresh water was available *ad libitum* throughout this phase.

Protocol

Tritiated water was injected (6 mℓ of 3,7 mBq/mℓ per sheep) intravenously after taking 2 mℓ of venous blood sample for background radio-activity determination on day 1.

Two further doses of tritiated water (10 mℓ of 3,7 mBq/mℓ per sheep) were similarly administered after establishing background activity on days 11 and 24 respectively. The second and third doses of tritiated water were injected only after the daily excretion of sodium in the urine had attained plateau values following salt loading.

Venous blood samples (8 mℓ) were withdrawn daily, between 09:00–10:00, into evacuated tubes containing Li-heparinate (Vac-U Test, Radem laboratory equipment, Sandton). The plasma was obtained by centrifuging down the cellular elements of the blood and was stored at 4 °C until further analysis.

The total urine output and drinking water intake (fresh or saline) was recorded daily. During phase 3, water introduced into the rumen by way of the 10 % NaCl solution each day, was added to water taken in orally (the sum being reflected in Table 3). A subsample (about 50 mℓ) of the total, mixed daily urine voided per sheep was retained for later analysis.

Feed intakes were recorded on a daily basis.

Sheep dosed with extra NaCl were regarded as having reached a steady state with respect to sodium and water balance, during phases 2 and 3, once the daily sodium excretion via the urine had reached a plateau (i.e. ratio of sodium excreted per day to sodium taken in per day was constant). Only following the latter event were readings considered to be representative of a particular phase and were recorded as such.

Analysis

Water was extracted from a portion of the daily plasma sample (about 2 mℓ) by vacuum sublimation. After mixing 0,2 mℓ of this water with 2 mℓ scintillation fluid ("Instagel"—Packard, Illinois, USA) in duplicate, the radioactivity was measured (cpm) in a Packard Scintillation Spectrometer Model 3385 (Packard, Illinois, USA).

The remainder of the plasma sample and the urine sample retained each day was used to determine the concentrations of sodium and potassium, by means of a selective ion electrode method (Instrument Laboratory System 501, Instrument Laboratory, Paderno Dugnano, Italy).

Urine osmolality was determined each day by means of the freezing point depression technique (Knauer electronic semi micro osmometer, Knauer, Berlin, Germany).

Calculations

Fractional turnover rate of body water (k).

Fractional turnover rate of body water was calculated from the equation (Holleman, White & Luick, 1982):

$$/n\,S_t = /n\,S_o - kt \quad \text{..... Equation 1.}$$

where $/n\,S_t$ = natural logarithm of the concentration of tritiated water at time t

$/n\,S_o$ = natural logarithm of the concentration of tritiated water at time zero

t = time (d), and

k = fractional turnover rate of body water (per d).

The values of k and $/nS_o$ were obtained from a least-squares regression analysis of the specific concentrations of tritiated water against time.

The biological half time ($T_{\frac{1}{2}}$) of isotope in the body was calculated from the k values as follows,

$$T_{\frac{1}{2}} = \frac{/n\,2}{k} = \frac{0{,}693}{k} \quad \text{.....Equation 2.}$$

on the assumption that the biological half time of tracer is equal to that of tracee i.e. body water. This assumption is only valid for a specific group of water molecules present in the total body water pool at a specific time (Holleman *et al.*, 1982).

Total sodium and potassium excreted daily (mMol/d) via the urine was calculated as the product of sodium or potassium concentrations in the urine and the daily volume of urine produced by each animal.

Statistical Analysis of Observations

The data were analysed using a one way analysis of variance within a block design. Data were blocked for individual sheep. Scheffe's test was used for comparing the means of different treatments. Data were considered to be significantly different when $P<0{,}05$.

RESULTS

Data reported in this trial represent near steady state conditions. In particular, animals were monitored to determine the attainment of equilibrium fol-

lowing salt loading, from which point, data was accumulated for analysis.

Effect of NaCl on feed intake

Salt intakes, such as occurred in this experiment, had no significant effect on feed intake (Table 1).

TABLE 1 Mean daily feed intakes (kg/d) for sheep (n=6) during phases 1, 2 and 3 of trial (standard deviation in brackets)

Sheep	Phase 1	Phase 2	Phase 3
Mean	2,12[a] (0,218)	2,03[a] (0,148)	2,02[a] (0,165)

[a] No statistically significant differences between mean values (P<0,05)

Intake of NaCl

Sodium chloride loading during phase 2 (via drinking water) and during phase 3 (direct intraruminal route) appear in Table 2. By experimental design the amounts of salt dosed per sheep during phase 3 were the same as those taken in voluntarily during phase 2.

TABLE 2 Mean daily NaCl loading* (g/d) during phases 2 and 3. Salt intake per kg body mass (g/kg/d) in brackets

Sheep A	72,9	(1,39)
Sheep B	73,4	(1,82)
Sheep C	77,2	(1,87)
Sheep D	85,9	(1,54)
Sheep E	90,7	(1,73)
Sheep F	97,3	(1,99)
Mean (n=6)	82,9	(1,72)

* Excludes NaCl in feed

Effect of NaCl on water intake and urine output, composition and osmolality

Daily water intake was significantly greater (P<0,05) during the salt loading periods than over the control phase. In addition, there was a statistical difference in water intake between phases 2 and 3; intake during the latter phase being lower than that in the former (Table 3).

The volume of urine produced per day was also significantly higher when salt intake was high. Urine volumes obtained over phases 2 and 3 however were similar (Table 4).

TABLE 3 Mean daily water intake (ℓ) per sheep for phases 1, 2 and 3 (Standard deviation in brackets)

Sheep	Phase 1	Phase 2	Phase 2*
A	6,68 (0,78)	8,10 (0,95)	7,81 (0,60)
B	5,91 (0,73)	8,15 (1,09)	7,45 (0,58)
C	5,91 (1,29)	8,58 (1,44)	8,71 (1,29)
D	7,58 (0,85)	9,54 (0,78)	9,04 (0,49)
E	7,12 (1,18)	10,08 (1,49)	9,20 (0,96)
F	7,50 (1,13)	10,81 (1,42)	10,09 (1,07)
Mean (n=6)	6,78 (0,66)[a]	9,21 (0,79)[b]	8,72 (0,88)[c]

[a, b and c] significantly different from each other (P<0,05)

* During phase 3 the values shown here represent the sum of volume of water used to dissolve intraruminal NaCl (10 % solution) and the drinking water taken in

TABLE 4 Daily urine outputs (ℓ) of individual sheep (A to F) for phases 1, 2 and 3 (Standard deviation in brackets)

Sheep	Phase 1	Phase 2	Phase 3
A	1,41 (0,29)	3,31 (0,47)	3,28 (1,51)
B	1,67 (0,49)	3,96 (0,75)	4,2 (0,61)
C	1,70 (0,73)	4,33 (0,82)	4,13 (0,38)
D	2,08 (0,35)	5,06 (0,48)	5,16 (0,41)
E	1,94 (0,49)	5,63 (0,66)	4,82 (0,73)
F	1,32 (0,39)	5,31 (0,96)	5,13 (1,49)
Mean	1,69 (0,23)[a]	4,6 (0,82)[b]	4,45 (0,65)[b]

[a] significantly different from [b] at P<0.05 level

Urine sodium concentrations rose abruptly from values that were nearly undetectable during the control phase, to 200–240 mMol/ℓ, within two days of exposure of the animals to saline drinking water. During the intraruminal salt phase, a further rise in urinary sodium concentrations occurred, the increase being statistically significant (Table 5).

Total sodium excretion per day via the urine followed a similar pattern with salt loading, but no significant difference (P<0,05) was obtained in this variable between phases 2 and 3 (Table 6).

TABLE 5 Mean concentrations of sodium and potassium in urine as well as urine osmolality of sheep (n = 6) during phases 1, 2 and 3 (Standard deviations in brackets)

	Sodium (mMol/ℓ)	Potassium (mMol/ℓ)	Osmolality (mOsm/kg)
Phase 1	4 (3)[a]	333 (49)[a]	1687 (118)[a]
Phase 2	211 (49)[b]	214 (20)[b]	1256 (71)[b]
Phase 3	244 (30)[c]	171 (17)[c]	1211 (179)[b]

[a, b and c] significantly different from each other (P<0,05)

TABLE 6 Total sodium and potassium excreted per day via the urine. Mean values (n=6) for all the sheep over each period of the trial (Standard deviations in brackets)

	Sodium (mMol/d)	Potassium (mMol/d)
Phase 1	6,7 (3,6)[a]	558 (82)[a]
Phase 2	968 (157)[b]	981 (172)[b]
Phase 3	1083 (205)[b]	756 (96)[c]

[a, b and c] significantly different from each other at P<0,05 level

Concentrations of potassium in the urine decreased during phase 2 and followed a further decline during phase 3. The differences between all three phases were statistically significant (P<0,05) (Table 5). Total potassium excretion per day increased with salt loading but was lower in phase 3 than in phase 2 (Table 6). The values obtained were all statistically different from each other (P<0,05).

Urine osmolality decreased significantly while the animals were on high salt intakes, but the mean values for phases 2 and 3 were similar (Table 5).

Effect of NaCl on plasma electrolyte concentrations

The values obtained for the concentrations of sodium and potassium in the plasma appear in Table 7.

TABLE 7 Mean concentrations of plasma sodium and potassium for sheep (n = 6) during phases 1, 2 and 3 (Standard deviations in brackets)

	Sodium (mMol/ℓ)	Potassium (mMol/ℓ)
Phase 1	141 (0,8)[a]	4,2 (0,1)[a]
Phase 2	141 (1,0)[a]	4,5 (0,1)[b]
Phase 3	141 (1,0)[a]	4,7 (0,1)[b]

[a] significantly different from [b] at P<0,05 level

Plasma sodium concentrations remained virtually constant at 140 mMol/ℓ throughout phases 1, 2 and 3 of the trial. Plasma potassium concentrations were significantly higher than control values (P<0,05) during NaCl loading. There was, however, no statistically significant difference in potassium levels between the saline drinking water and intraruminal salt phases (phases 2 and 3).

Fractional turnover rate (k) and half time values ($T_{\frac{1}{2}}$) of body water

Values for fractional turnover rate of body water and half times are given in Table 8. The fractional turnover rate of body water increased when the animals were offered saline drinking water or were given salt intraruminally. The differences in both *k* and $T_{\frac{1}{2}}$ values between phase 1 on the one hand and phases 2 and 3 on the other, were significant (P<0,05). No significant differences were obtained when the two salt loading phases were compared.

TABLE 8 Fractional turnover rates (*k*) and half times of body water ($T_{\frac{1}{2}}$) of sheep for phases 1, 2 and 3

Sheep	Phase 1		Phase 2		Phase 3	
	k (/d)	$T_{\frac{1}{2}}$ (d)	*k* (/d)	$T_{\frac{1}{2}}$ (d)	*k* (/d)	$T_{\frac{1}{2}}$ (d)
A	0,18	3,85	0,20	3,47	0,20	3,47
B	0,20	3,47	0,23	3,00	0,23	3,00
C	0,21	3,30	0,24	2,89	0,25	2,77
D	0,19	3,65	0,22	3,15	0,24	2,89
E	0,21	3,30	0,28	2,48	0,25	2,77
F	0,26	2,67	0,29	2,39	error	
Mean (n = 6)	0,21	3,33[a]	0,24	2,85[b]	0,23	2,96[b]
SD*	(0,028)	(0,43)	(0,035)	(0,40)	(0,021)	(0,26)

[a] significantly different from [b] at P<0,05 level

DISCUSSION

This experiment attempted to simulate two field situations, one in which sheep are exposed to saline drinking water (phase 2) and one in which they take in feed with a high salt content but have free access to fresh drinking water (phase 3). Over each 24 h period of the latter phase the daily dose of NaCl was introduced into the rumen by continuous infusion. The object of this method of salt administration was to minimize any rise in rumen osmolality and thereby more closely reproduce field conditions where herbage of a high salt content (e.g. saltbush) is grazed over the greater part of the day.

The bolus addition of the total dose of NaCl directly into the rumen (phase 3) would approximately have doubled rumen fluid osmolality (1,3–1,7 M NaCl per day per sheep; rumen volume approximately 15 ℓ).

Feed intake

Feed intake was unaffected by the amounts of NaCl dosed in this trial irrespective of the method of increasing NaCl intake. Where saline water was the sole source of drinking water (phase 2), the concentration of the NaCl (0,89 %) falls well below those values which were established to suppress feed intake, viz. 1,5–2,0 % (Peirce, 1957). During phase 3 where the animals had free access to fresh drinking water, the masses of NaCl dosed daily also fall below those amounts which reportedly have a negative effect on feed intake. Sheep with unlimited access to fresh water are able to tolerate high intakes of NaCl via the feed. Thus ewes fed a lucerne/barley ration with 13,1 % NaCl (equivalent to a daily dose of 260 g NaCl) showed little reduction in feed intake (Meyer & Weir, 1954).

Water intake

The higher water intake by the sheep while on high intakes of NaCl is probably due to:

(i) An increase in osmolality of the extracellular fluid (ECF) and subsequent stimulation of the thirst centre (Bie, 1980). Such a rise in osmolality of the ecf can be ascribed to the administration of a hypertonic solution to the system in phase 3. During phase 2, however, where isotonic saline was the method of salt loading, the osmolality of the ecf would presumably only be affected after some degree of insensible water loss had occurred.

(ii) Increased water loss via the kidneys. Water loss via the kidneys is positively related to the amount of sodium (and potassium) which is excreted via the urine (Wilson & Dudzinski, 1973). In order to compensate for the greater loss of water via the urine during phases 2 and 3 of this trial, greater intake of water was necessary.

The significantly greater water intake obtained on saline drinking water than on intraruminal NaCl (P<0,05), may be ascribed to the fact that salt (taste) receptors in the mouth ultimately have connections with structures in the hypothalamus which control the ingestion of salt and water (Denton, 1981). Where NaCl is dosed intraruminally such salt receptors are bypassed and, it is possible that although similar amounts of NaCl are dosed by the two routes, more water is taken in when dosage of salt is via the oral route.

The ratio of water to NaCl taken in was 111 mℓ water:g NaCl in phase 2 and 104 mℓ water:g salt in phase 3. Comparison of these ratios with those obtained in other experiments (Wilson, 1966b; Hamilton & Webster, 1987) is difficult because factors such as ambient temperature (MacFarlane & Howard, 1972), breed of sheep (MacFarlane *et al.*, 1967) and state of production (Michell & Moss, 1987) may all affect water intake and hence the ratio of water to NaCl consumed

Fractional turnover rates of body water

The tritiated water dilution method is of particular

use in studying water metabolism in animals where total water input or total water loss are difficult to measure. In this trial changes in the fractional turnover rate of body water were followed in order to quantify the effect on this variable of high NaCl intake.

Although daily water intake increased by about 40–45 % (i.e. 2–2½ ℓ/d) during the salt loading phases, the increase, as a proportion of total body water, was relatively small (total body water assumed to be 50 to 78 % of body mass) (Till & Downes, 1962). For this reason, although the differences in fractional body water turnover rates *(k)* between control and salt loading phases were not great, they were nevertheless statistically significant ($P<0,05$).

The fractional turnover rates in body water over phases 2 and 3 were similar. This can probably be ascribed to the fact that although water intakes were significantly different ($P<0,05$) between the two NaCl loading phases, they were not markedly different and the method of evaluating *k* may not have been sensitive enough to reflect these differences.

By comparison, it was shown that where a group of sheep received saline water (1,3 % NaCl) as their sole source of drinking water for a period of 8 months, turnover rates of body water as measured by the dilution of tritiated water yielded a $T_{\frac{1}{2}}$ value of 2,2 d compared to 4,8 d in control animals on fresh water (Jones, Potter & Reid, 1970).

Although these sheep were of comparable body mass to those used in the current trial, the water intakes of control animals were notably less than those of the sheep used during the control period of this trial (3,2 ℓ/d compared to 6,8 ℓ/d). The type of diet and environmental conditions may have accounted for the differences in water intake (and hence also in *k*).

Urinary parameters

The increase in urine volume during phases 2 and 3 is typical of that found in an osmotic-type diuresis (Potter, 1957).

The observation of a decrease in urine osmolality, together with an increase in total osmoles excreted per day during salt loading, agrees with previous work (Godwin & Williams, 1986). The decrease in urine osmolality shown when the animals were NaCl loaded is probably linked to a low priority to retain water and hence to low ADH concentrations in the plasma (Brook, Radford & Stacy, 1968). Plasma levels of the latter hormone were not assessed in this trial, but it is assumed that the ratio of water to salt in phase 2 and with fresh water being freely available in phase 3, a condition of water stress did not arise such that greater concentration of the urine would have been necessary. Wilson & Dudzinski (1973) found that where different volumes of various dilutions of a salt solution (0, 1,5 and 2 % NaCl) were administered intraruminally, urine osmolality was an inverse function of the volume of fluid dosed (i.e. highest osmolality at lowest volumes dosed), rather than of the degree of salinity of the water (urine osmolality was not affected by the addition of salt to the water).

After initiation of salt loading, either via the drinking water or the intraruminal route, daily loss of sodium via the urine reached a plateau after about 3–4 days suggesting that a state of equilibrium had been reached. In humans, a period of several days is required for sodium intake to equal sodium output following sodium loading, while in the rat a period of only some hours is required (Holtzman, Braley, Williams & Hollenberg, 1988).

Sodium concentrations in the urine rose sharply with salt loading from less than 10 mMol/ℓ to more than 200 mMol/ℓ. Concurrent with this observation, urinary potassium concentrations decreased. This inverse relationship between sodium and potassium concentrations is probably associated with the effect of aldosterone on the distal nephron tubule (Sansom & O'Neile, 1985).

Plasma aldosterone concentrations do fall when NaCl intake is increased in sheep (Meintjes, unpublished data) and this explains the relative decrease in potassium concentration in the urine together with the rise in that of sodium over phases 2 and 3. Furthermore, in spite of the similar daily sodium intakes during phases 2 and 3, urinary sodium and potasium concentrations were statistically different ($P<0,05$) between these two phases. (Sodium concentration higher in phase 3 and potassium concentration higher in phase 2). As hypertonic conditions in the rumen promote the uptake of sodium by the ruminal wall (Stacy & Warner, 1966), it is assumed that absorption of NaCl from the rumen was greater in phase 3 than in phase 2. It follows that aldosterone concentrations in the plasma were probably even lower in the former than in the latter phase, thus accounting for the observed differences in the urinary concentrations of sodium and potassium between the two salt loading phases.

In agreement with the trend in urinary potassium concentration, total potassium excreted per day in the urine was also significantly lower during phase 3 than phase 2 (similar urine volumes but lower potassium concentrations). Although total daily sodium excreted via the urine was higher during phase 3 than in phase 2, the difference was not statistically significant.

Plasma parameters

Plasma sodium concentrations remained remarkably stable and did not change between the 3 phases of the experiment. This finding serves to illustrate how efficiently the sodium concentration of the extracellular fluid is maintained even when sodium intake is significantly changed, an aspect of homeostasis which is largely a function of antidiuretic hormone (Mitchell, 1985). This observation agrees with data published by others (Godwin & Williams, 1986) and, taken together with the excretory patterns of sodium during recovery from salt loading, supports the hypothesis that the set point of sodium homeostasis revolves more around *total* body sodium than around plasma sodium concentration (Bonventre & Leaf, 1982).

The statistically significant rise in plasma potassium concurrent with high salt intakes is in keep-

ing with the decreased excretion of potassium over the salt loading phases.

CONCLUSION

S.A. Mutton Merino sheep, in the mass range of 40–50 kg, are able to tolerate NaCl dosed at 73–97 g/d for 5 days, either via the drinking water or dosed intraruminally, without apparent adverse effect.

Changes in most of the observed variables, with the exception of sodium concentration in the plasma, occurred with salt loading.

When the two methods of salt loading were compared, significant differences were obtained in the sodium and potassium concentrations in the urine and in the total amounts of potassium excreted via the urine each day. This pattern was presumably due to greater NaCl absorption from the gastrointestinal tract where salt was administered in concentrated form into the rumen and the significantly lower water intake which was concurrently measured.

Increased water intake during salt loading was reflected in a small yet statistically significant increase in the fractional turnover rate of body water (0,21/d compared to 0,24/d) as measured by the tritiated water dilution technique. Had there been a greater difference in drinking water intake between control and salt loading phases, a far larger difference in *k* would probably have been observed.

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