

Effects of sodium chloride on sheep. 2. Voluntary feed intake and changes in certain rumen parameters of young Merino wethers grazing native pasture

H.O. de Waal,* Margarietha A. Baard and E.A.N. Engels

Agricultural Research Institute, Private Bag X01, Glen 9360, Republic of South Africa

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While grazing native pasture, seven groups of 4 young Merino wethers received the following supplements daily *via* rumen cannulae: 0, 5 (Control), 15 and 30 g salt (NaCl); and 5, 15 and 30 g NaCl + 20 g crude protein (CP) each. There was a non-significant ($P \leq 0,05$) tendency for digestible organic matter (DOM) intake to decrease with incremental levels of NaCl and to increase with CP supplementation (33,8; 34,5; 31,5; 31,3; 35,5; 35,8 and 31,3 g DOM / Wkg^{0,75} day⁻¹). Although only some of the differences were significant ($P \leq 0,05$), rumen pH tended to decrease with incremental levels of NaCl, as well as with CP supplementation (6,64; 6,58; 6,51; 6,59; 6,45; 6,51 and 6,25). CP supplementation had a significant ($P \leq 0,05$) elevating effect and incremental levels of NaCl a non-significant ($P \leq 0,05$) elevating effect on rumen NH₃ (4,72; 3,44; 3,51; 4,71; 7,74; 10,14 and 8,22 mg NH₃ / 100 ml rumen fluid). Volatile fatty acids (VFA) were, besides significant ($P \leq 0,05$) differences in acetic acid between a few treatments, apparently not affected to any real extent by either NaCl or CP supplementation and the overall pattern of VFA proportions remained similar for all groups with an approximate ratio of 76:15:9. The tendency for CP to reduce ruminal Na was not significant ($P \leq 0,05$), whereas the wethers receiving 0 g NaCl had a significantly ($P \leq 0,05$) lower rumen Na concentration (1,367; 2,385; 2,876; 2,632; 1,674; 2,458 and 2,293 g Na l⁻¹). The wethers receiving 0 g NaCl had a significantly ($P \leq 0,05$) elevated ruminal K concentration (2,821; 0,715; 1,031; 1,027; 0,747; 1,064 en 0,995 g K l⁻¹). Diurnal variations in rumen indices are also discussed. It is suggested that Na and K imbalances in the extra- and intra-cellular body fluid compartments, increased the maintenance energy expenditure of the wethers, thereby inducing the deleterious effects on production parameters.

Sewe groepe van 4 jong Merinohamels elk, het op veldweiding daaglik die volgende aanvullings *via* rumenkannules ontvang: 0, 5 (Kontrole), 15 en 30 g sout (NaCl); en 5, 15 en 30 g NaCl + 20 g ruproteïen (RP) elk. Daar was 'n nie-betekenisvolle ($P \leq 0,05$) neiging vir die inname van verteerbare organiese materiaal (VOM) om te daal met toenemende NaCl-peile en om te styg met RP-aanvulling (33,8; 34,5; 31,5; 31,3; 35,5; 35,8 en 31,3 g VOM / Wkg^{0,75} dag⁻¹). Die neiging vir rumen-pH om te daal met toenemende NaCl, sowel as met RP-aanvulling (6,64; 6,58; 6,51; 6,59; 6,45; 6,51 en 6,25), was slegs in enkele gevalle betekenisvol ($P \leq 0,05$). Rumen-NH₃ was betekenisvol ($P \leq 0,05$) hoër met RP aanvulling, maar het slegs hoër geneig met toenemende NaCl-peile (4,72; 3,44; 3,51; 4,71; 7,74; 10,14 en 8,22 mg NH₃/100 ml rumenvloeistof). Vlugtige vetsure (VVS) is, benewens betekenisvolle ($P \leq 0,05$) verskille in asynsuur tussen 'n paar behandelings, skynbaar weinig geaffekteer deur beide NaCl- en RP-aanvullings. Die algemene verhouding van VVS vir die verskillende behandelings is naasteby op 76:15:9 gehandhaaf. Aanvullende RP het 'n nie-betekenisvolle ($P \leq 0,05$) neiging getoon om rumen-Na-konsentrasie te verlaag, terwyl die hamels wat 0 g NaCl ontvang het, se rumen-Na-konsentrasie betekenisvol ($P \leq 0,05$) verlaag is (1,367; 2,385; 2,876; 2,632; 1,674; 2,458 en 2,293 g Na l⁻¹). Die hamels wat 0 g NaCl ontvang het, het 'n betekenisvolle ($P \leq 0,05$) hoër rumen-K-konsentrasie gehad (2,821; 0,715; 1,031; 1,027; 0,747; 1,064 en 0,995 g K l⁻¹). Daaglikse variasie in rumenparameters word ook bespreek. Wanbalanse tussen Na en K in die ekstra- en intraselulêre liggaamsvloeistowwe, het waarskynlik die onderhoudsenergie-uitgawe verhoog, met die gepaardgaande nadelige effek wat in produksie waargeneem is.

Keywords: Crude protein, grazing sheep, NaCl, rumen parameters, supplementation, voluntary feed intake.

* To whom correspondence should be addressed

Introduction

Salt (NaCl) is widely used to control the voluntary intake of supplementary feeding (licks) by grazing ruminants (Morris, 1980) and, as a secondary aim, to satisfy their specific nutrient requirement for NaCl (Agricultural Research Council, 1980). However, in developing the concepts of supplementary feeding strategies, the focus has invariably been centred on the other constituents, with little if any regard to NaCl. This is surprising, especially since there is no paucity of evidence on the adverse effects of high NaCl intake on ruminants (National Research Council, 1980). In this regard, De Waal, Baard & Engels (1989) have reported adverse effects of sustained high NaCl intake on growth rate and wool production of young Merino wethers grazing native pasture (veld). Furthermore, supplementary crude protein (CP) had alleviated these detrimental effects to

some extent. This was a confirmation of the suspicion broached earlier by De Waal, Engels, van der Merwe & Biel (1981) that high NaCl intake had been detrimental to grazing young sheep.

Despite numerous attempts towards some elucidation, the exact cause of the detrimental effect of NaCl on animals is still largely unknown. Therefore, in the present paper results are presented pertaining to the effects of NaCl and CP supplementation on voluntary feed intake and changes in certain rumen parameters of young Merino wethers grazing native pasture in the central Orange Free State.

Procedure

The experimental site, animals used, treatments applied and general experimental procedure have already been described (De Waal *et al.*, 1989). In brief, 28 young

Merino wethers cannulated at the rumen, were used as experimental animals. The experimental design (fully randomized) and the number of wethers per treatment, as well as the levels of NaCl and CP supplemented daily *via* rumen cannulae, are presented in Table 1.

Voluntary feed intake of the wethers was determined in May 1981. Total faeces excreted was collected over a 7-day period by means of faeces collection bags (De Waal *et al.*, 1981) and organic matter (OM) digestibility of the pasture was estimated as described by De Waal *et al.* (1989). Daily intake of OM was then estimated by means of the following equation :

$$\text{OM intake (g day}^{-1}\text{)} = \frac{100}{100 - \% \text{ OM digestibility}} \times \frac{\text{Daily excretion of OM (g)}}{1}$$

In May 1981, during the week preceding the collection of faeces, rumen fluid was sampled on 4 consecutive days from the wethers. In order to obtain an indication of the diurnal variation of certain rumen parameters, the following sampling schedule was devised :

- Day-1 sample at 08h00
- Day-2 sample at 12h00
- Day-3 sample at 16h00
- Day-4 sample at 20h00

It was assumed that this schedule would simulate the diurnal variation over a 24 h experimental 'day', without undue effect on the normal grazing pattern of the sheep (De Waal, 1986). During this period, the wethers received their daily supplements at 08h00. On Day 1 the sampling was done immediately before the supplements were administered *via* the rumen cannulae. Rumen fluid (*ca* 300 ml) was aspirated from the rumen *via* the cannulae by means of a stomach tube connected to a flexible plastic container (1-l capacity). The pH of the rumen fluid was then measured immediately with a portable digital pH meter, the fluid strained through 4 layers of cheesecloth and split into 2 subsamples. One subsample of 100 ml strained rumen fluid was acidified with 1 ml of concentrated H₂SO₄ in small plastic bottles with screw caps and stored at a temperature of -15°C.

Table 1 Experimental design with number of wethers per treatment

Treatment	Daily level of supplementation ^a	Number of wethers per treatment
1	0 g NaCl ^b	4
2 (Control)	5 g NaCl + 2,5 g P ^c	4
3	15 g NaCl + 2,5 g P	4
4	30 g NaCl + 2,5 g P	4
5	5 g NaCl + 2,5 g P + 20 g CP ^d	4
6	15 g NaCl + 2,5 g P + 20 g CP	4
7	30 g NaCl + 2,5 g P + 20 g CP	4

^a Administered daily *via* rumen cannulae directly into the rumen.

^b NaCl – sodium chloride.

^c P – phosphorus, derived from 15 g dicalcium phosphate.

^d CP – crude protein (provided by 33 g High Protein Concentrate 60 and 61% of the CP derived from urea).

Prior to analysis, these samples were thawed and then the rumen ammonia (NH₃) concentration was determined according to the method of distillation over MgO and expressed as mg NH₃ /100 ml rumen fluid (De Waal, 1986). The second subsample of 70 ml strained rumen fluid was mixed with 10 ml of a 2% HgCl₂ solution and stored in plastic bottles with screw caps below a temperature of 4°C. These samples were later split into 2 subsamples. One of these subsamples was spun down and a 15 ml aliquot was stored in McCartney bottles below a temperature of 4°C for analysis of volatile fatty acids (VFA) by means of gas chromatography. The remainder of the subsamples was used for analysis of sodium (Na) and potassium (K) by means of flame photometry.

Results

Results pertaining to voluntary feed intake by the wethers in the different treatments, are presented in Table 2.

Although the differences were not significant ($P \leq 0,05$) (Harvey, 1976), intake of digestible OM (DOMI) was apparently reduced by incremental levels of NaCl supplementation and increased by CP supplementation (Table 2). However, at this stage of the trial, different levels of NaCl and CP supplementation had already had a marked effect on the average body mass of the wethers (De Waal *et al.*, 1989). Therefore, if the daily DOMI is expressed per unit metabolic size (Wkg^{0.75}), some of the differences between treatments are apparently eliminated.

The rumen pH and NH₃, VFA, Na and K concentrations for the different treatments, at fixed intervals after administration of the daily supplements, are presented in Figures 1–5. The mean effects of NaCl and CP supplementation over a 24-h period on the same rumen indices, are shown in Table 3.

In this trial, 4, 8, 12 and 24 h had elapsed, respectively, during Days 2, 3, 4 and 1 between supplementation at 08h00 and sampling of the rumen fluid. Although the samples were taken on 4 different days, the mean interval between sampling times was still

Table 2 Effect of NaCl and crude protein (CP) supplementation on intake of digestible organic matter (DOMI) by young Merino wethers

Treatment	DOMI	
	g day ⁻¹	g / Wkg ^{0.75} day ⁻¹
1	443,1	33,77
2 (Control)	510,9	34,46
3	461,4	31,48
4	406,6	31,29
5	559,5	35,47
6	524,3	35,82
7	450,2	31,32
SEM	48,2	2,29

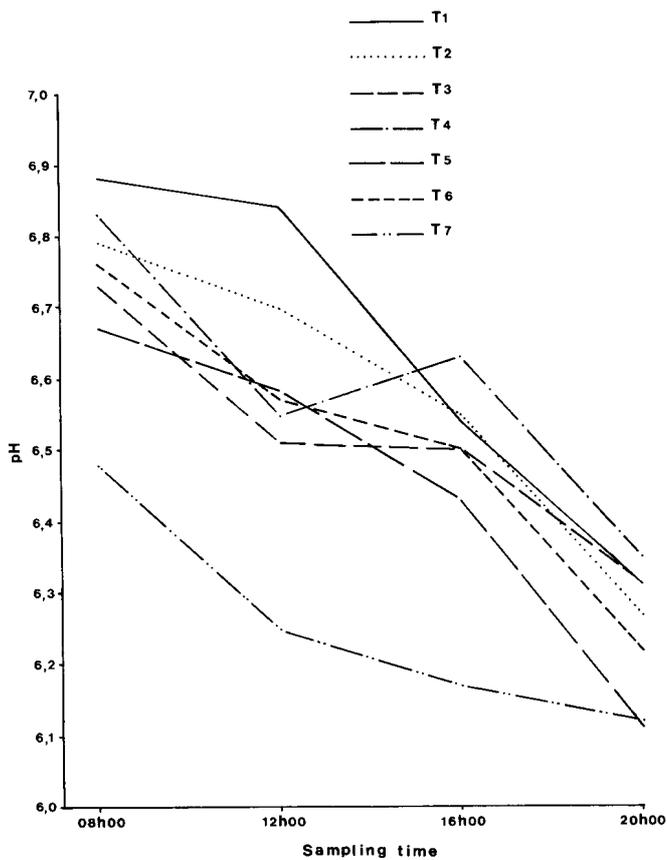


Figure 1 The average rumen pH of the wethers in the different treatments at fixed intervals after supplementation (08h00)

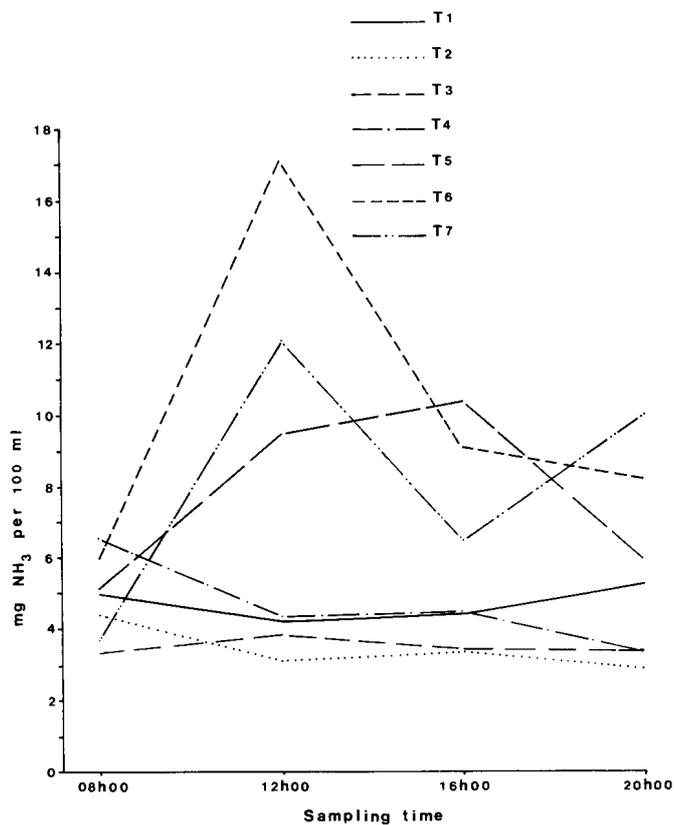


Figure 2 The average rumen NH₃ concentration of the wethers in the different treatments at fixed intervals after supplementation (08h00)

regarded as being 4 h. An interval of 4 h between samplings is obviously too long to detect transient shifts in the rumen parameters. Therefore, it should be noted that the peak or low values for the different rumen parameters, as depicted in the respective figures, does not necessarily reflect the absolute highest or lowest values for a particular parameter, but is merely a reflection of the values at the time of sampling.

In general, ruminal pH declined from 08h00 to 20h00 (Figure 1). The rumen pH of the wethers in Treatment 7 was, however, distinctly lower than those of the other groups and may be ascribed to the elevated ruminal VFA concentrations (Table 3). Furthermore, although there was a tendency for rumen pH to decrease with incremental levels of NaCl, as well as with CP supplementation, only some of these differences were significant ($P \leq 0,05$; Harvey, 1976; Table 3). It was calculated from the data that the average rumen pH of the wethers receiving 0, 5, 15 and 30 g NaCl day⁻¹, was respectively 6,64, 6,52, 6,51 and 6,42. In this regard, a decrease in rumen pH of grazing lactating ewes, due to incremental levels of supplementary NaCl, has also been noted by De Waal (1985, unpublished data). Furthermore, the average rumen pH of the wethers receiving no supplementary CP was 6,58, whilst those receiving supplementary CP had an average rumen pH of 6,40.

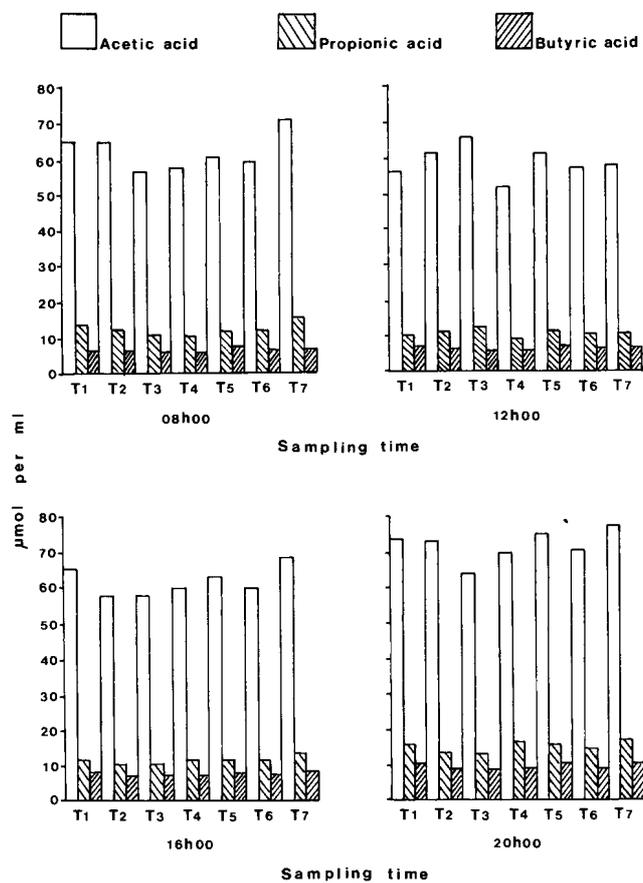


Figure 3 The average rumen VFA concentrations of the wethers in the different treatments at fixed intervals after supplementation (08h00)

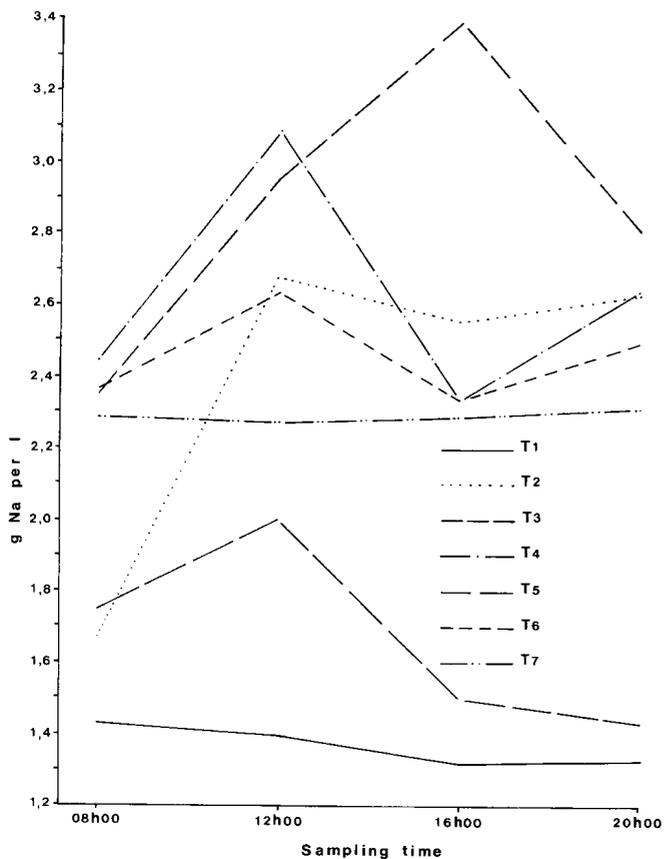


Figure 4 The average rumen Na concentration of the wethers in the different treatments at fixed intervals after supplementation (08h00)

According to the results in Table 3, CP supplementation had a significant ($P \leq 0,05$) effect on the prevailing rumen NH_3 concentration of the wethers. In general, rumen NH_3 concentration of the wethers in Treatments 5, 6 and 7 increased, following supplementation at 08h00 and was sustained at elevated levels till at least 20h00 (Figure 2). At 08h00 the rumen NH_3 of the wethers in these treatments had returned to levels between 3,7 and 6,0 mg $\text{NH}_3/100$ ml rumen fluid.

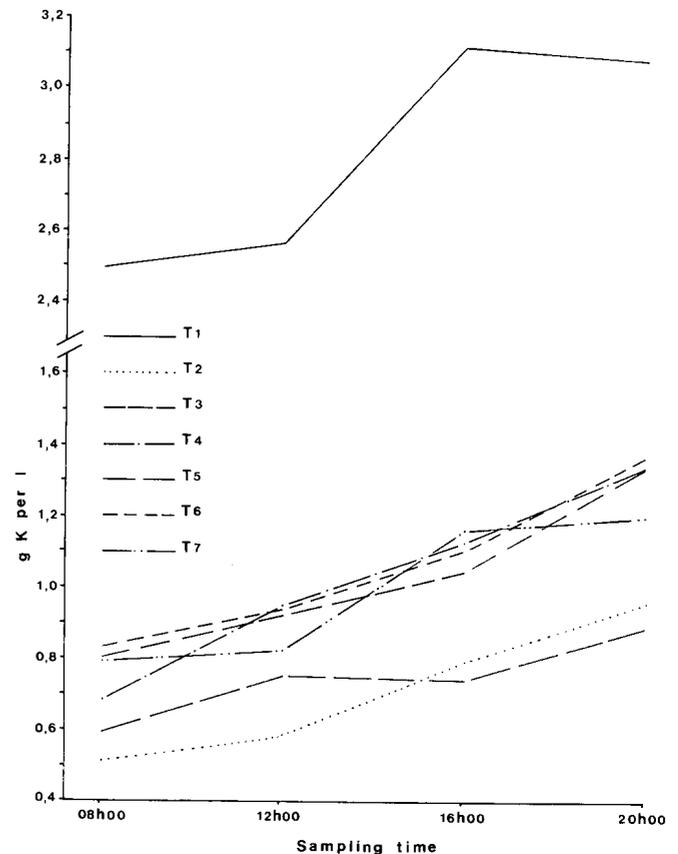


Figure 5 The average rumen K concentration of the wethers in the different treatments at fixed intervals after supplementation (08h00)

In contrast, the rumen NH_3 of the wethers receiving no supplementary CP (Treatments 1, 2, 3 and 4) varied between the narrow margins of 2,9 and 6,5 mg $\text{NH}_3/100$ ml rumen fluid. It was also calculated from the data that incremental levels of NaCl had an elevating, though non-significant ($P \leq 0,05$), effect on the average NH_3 concentration. The average rumen NH_3 for the 0, 5, 15 and 30 g NaCl levels was, respectively, 4,72, 5,59, 6,83 and 7,98 mg $\text{NH}_3/100$ ml rumen fluid.

Table 3 Effect of NaCl and crude protein (CP) supplementation on rumen indices in grazing young Merino wethers

Rumen index	Treatment							SEM
	1	2	3	4	5	6	7	
pH	6,64 ^a	6,58 ^a	6,51 ^a	6,59 ^a	6,45 ^{ab}	6,51 ^a	6,25 ^b	0,072
NH_3 (mg 100 ml ⁻¹)	4,72 ^a	3,44 ^a	3,51 ^a	4,71 ^a	7,74 ^b	10,14 ^b	8,22 ^b	0,975
Na (g l ⁻¹)	1,367 ^a	2,385 ^{bc}	2,876 ^{bc}	2,632 ^{bc}	1,674 ^{ab}	2,458 ^{bc}	2,293 ^{bc}	0,313
K (g l ⁻¹)	2,821 ^a	0,715 ^b	1,031 ^b	1,027 ^b	0,747 ^b	1,064 ^b	0,995 ^b	0,120
VFA (mmol l ⁻¹)								
Acetic acid	64,73 ^{ab}	64,15 ^{ab}	60,85 ^a	59,58 ^a	65,24 ^{ab}	61,75 ^a	68,63 ^b	1,911
Propionic acid	12,44	11,70	11,64	11,84	12,44	12,05	14,10	0,557
Butyric acid	8,04	7,30	7,09	7,06	8,36	7,40	8,25	0,392
Valeric acid	0,49	0,43	0,45	0,55	0,64	0,46	0,68	0,076

^{a,b,c} Treatments with the same superscript do not differ significantly ($P \leq 0,05$) (Harvey, 1976).

Rumen VFA concentrations were, apart from significant ($P \leq 0,05$) differences in acetic acid concentrations between a few treatments (Table 3), apparently not affected to any real extent by either NaCl or CP supplementation. However, a strong diurnal pattern was evident (Figure 3). The average total concentration of the rumen VFAs decreased from 08h00 (81 mmol l⁻¹) to 12h00 (77 mmol l⁻¹) and then increased substantially through 16h00 (82 mmol l⁻¹) towards the sampling time at 20h00 (97 mmol l⁻¹). However, within this general diurnal pattern of change in total rumen VFA concentration, the different VFAs (acetic, propionic and butyric acid) all evinced minor diurnal changes of their own (Figure 3).

Although the differences were not significant ($P \leq 0,05$), supplementary CP (Treatments 5, 6 and 7) tended to reduce rumen Na concentration (Table 3 and Figure 4). The wethers in Treatment 1 (0 g NaCl) also had a significantly ($P \leq 0,05$) lower rumen Na concentration. Although the rumen Na concentration of some treatment groups tended to increase after supplementation at 08h00, no clear pattern is discernible (Figure 4). In contrast, the rumen K concentration of the wethers in all treatment groups increased from 08h00 to 20h00 (Figure 5). Furthermore, a clear pattern with regard to rumen K concentration is evident between the different treatment groups. Firstly, the wethers in Treatment 1 (0 g NaCl) had the highest rumen K concentration, significantly ($P \leq 0,05$) different from the other treatments (Table 3). Secondly, the wethers in Treatments 3, 4, 6 and 7 can be classified as an intermediate group in terms of their prevailing rumen K concentrations. Lastly, the wethers in Treatments 2 and 5 (5 g NaCl and 5 g NaCl + 20 g CP) made up the third group with the lowest rumen K concentrations. However, the differences in ruminal K concentration between Treatments 2 to 7 were not significant ($P \leq 0,05$).

Discussion

The daily maintenance requirement of grazing sheep has been estimated at 33,5 g DOM/Wkg^{0,75} (Engels, 1972), which is in close agreement with the 34,5 g DOM/Wkg^{0,75} estimated by Young & Corbett (1968), as well as the estimates by various other reports (De Waal, 1986). This means that, despite the fact that the material selected by the sheep during May 1981 had a CP content of 8,3% and a DOM of 58,4% (De Waal *et al.*, 1989), the DOMI of some of the wethers (Table 2) was barely enough to satisfy their maintenance requirements. Similar observations have been made by Engels & Malan (1978) with regard to DOMI by Merino wethers; lactating SA Mutton Merino ewes (Engels & Malan, 1979) and young Merino and Dorper wethers (De Waal *et al.*, 1981). The results reported by De Waal *et al.* (1989) have shown that the body mass losses of the wethers in all treatments became more pronounced from the beginning of May 1981. Furthermore, when the DOMI was estimated in May, body mass had already been affected by the respective treatments (De Waal *et*

al., 1988). It should be noted that in studies of this nature, where treatments have a pronounced effect on body mass, it may not be advisable to express feed intake as a function of body size (Wkg^{0,75}) or even body mass (kg), since it tends to cancel or mask real differences between treatments. Nevertheless, it was calculated from the data in Table 2 that the average daily DOMI of the wethers receiving 0, 5, 15 and 30 g NaCl d⁻¹ was, respectively, 33,8, 35,0, 33,7 and 31,3 g DOM/Wkg^{0,75}. Although the differences in daily DOMI between treatments might seem small, the accumulative effect on body mass changes could account for some of the observed differences between treatments. However, the adverse effect of high NaCl intake on body mass changes cannot be attributed to differences in feed intake alone. This is in agreement with results published by Kromann & Meyer (1966), Kromann & Ray (1967) and Jackson, Kromann & Ray (1971).

In the present study, DOMI was estimated on the assumption that the DOM of the ingested plant material was not affected by either supplementary CP (De Waal *et al.*, 1981) or NaCl. It has been reported that high levels of NaCl in the rumen may reduce DOM (Wilson & Dudzinski, 1973; Moseley & Jones, 1974; Hemsley, Hogan & Weston, 1975; Godwin & Williams, 1986). In this regard, Godwin and Williams (1986) have suggested that, especially when roughages low in nitrogen (N) are ingested, NaCl intake should be kept below a level of 1,17 g NaCl kg body mass⁻¹ day⁻¹ to prevent a decline in DOM and any consequent reduction in protein availability to sheep. However, Moseley & Jones (1974) and Moseley (1980) have shown that a reduction in DOM was only evident at a level of 3% Na in the diet or 1,46 g NaCl kg body mass⁻¹ day⁻¹. Since the highest level of NaCl supplementation (30 g NaCl day⁻¹) in the present study corresponded to an intake of only 0,91 g NaCl kg body mass⁻¹ day⁻¹, the likelihood of any real effect by NaCl on DOM seems negligible.

The utilization of potential energy sources like cellulose and hemicellulose, depends on the activity of the micro-organisms in the rumen. Also, the micro-organisms play an important role with regard to both the amount and quality of amino acids available for absorption in the lower alimentary tract. Therefore, although the differences in DOMI between sheep might have been small (Table 2), the effect of supplementary CP and/or NaCl on the rate and extent of fermentation, as well as microbial protein synthesis in the rumen, could have had a pronounced effect on animal production.

The general decline in rumen pH from 08h00 to 20h00 (Figure 1), can be attributed to the grazing habits and pattern of feed intake by the sheep (De Waal, 1986). Diurnal variation in rumen pH is an indication of the accumulation of organic acids in the rumen (Leng, 1970), as well as the secretion of saliva into the rumen (Church, 1973). Furthermore, the diurnal variation in concentration of organic acids in the rumen, and thus ruminal pH, is primarily determined by the feeding schedule and not the time of day at which it was measured (Warner, 1965). In conventional studies of this kind, rumen fluid is usually sampled at fixed intervals

after feeding. In the present study, as well as in the study by De Waal, Engels and van der Merwe (1980), rumen fluid was sampled at fixed hours of the day, whereas the supplementary feeding was administered *via* rumen cannulae at 08h00 to the grazing sheep. Although the feed intake of grazing sheep may be regarded as a continuous process, there are certain times of the day when they are not grazing (Arnold & Dudzinski, 1978; De Waal, 1986). It has been observed that during the summer, sheep were already actively grazing at sunrise (05h30), while in winter grazing only started after sunrise (07h00) (De Waal *et al.*, 1980; De Waal, 1986). Similar observations were made in the present study. Since the rumen fluid was only sampled at 08h00, or later during the day, the sheep obviously had had the opportunity to graze until the rumen fluid was sampled. Therefore, the samples taken at 08h00 could be regarded as representative of a phase during or just after feeding (De Waal *et al.*, 1980). Ruminal metabolic activity usually reaches a peak within a few hours after feeding (Warner, 1965), with a concomitant decline in ruminal pH (Du Plessis & van der Merwe, 1970; Leng, 1970). The decline in ruminal pH from 08h00 to 20h00 (Figure 1), can therefore be ascribed to an increased ruminal metabolic activity.

Although some effect of supplementary CP and NaCl on the prevailing ruminal pH of the wethers was evident (Figure 1), these differences could hardly have had any significant effect on events in the rumen. On the other hand, the sharp decline in ruminal pH after 16h00, could have inhibited the cellulolytic bacteria (Terry, Tilley & Outen, 1969; Mann & Ørskov, 1975; Mackie, Gilchrist, Robberts & Schwartz, 1978), with a concomitant reduction in digestion of cellulose and hemicellulose (Terry *et al.*, 1969; Armstrong & Smithard, 1979; Henning, van der Linden, Mattheyse, Nauhaus, Schwartz & Gilchrist, 1980; Ørskov, 1982). The exceptionally low prevailing rumen pH of the wethers in Treatment 7 (Figure 1) can only be ascribed to a sustained elevated level of ruminal VFAs (Table 3). Apparently no cellulolytic activity exists below a rumen pH of 6,1 to 6,2 (Ørskov, 1982). Hence, the wethers in Treatment 7 should have died of 'starvation', yet their performance was very similar to those in Treatment 1 (De Waal *et al.*, 1989), but with a big difference in prevailing ruminal pH (Figure 1). Since ruminal pH was only measured over a 12-h period (08h00 to 20h00), it is not possible to tell whether it declined any further after 20h00. However, it seems justified to assume that by morning the ruminal pH had returned to the relatively high values observed at 08h00.

Since ruminal NH_3 is utilized by most rumen bacteria as a primary N source, microbial protein synthesis depends on the availability of NH_3 in the presence of suitable fermentable substrates in the rumen (De Waal, 1986). Therefore, if it is assumed that 2—5 mg $\text{NH}_3\text{-N}/100$ ml rumen fluid is the optimum concentration for microbial protein synthesis (Satter & Slyter, 1974; Hogan, 1975; Satter & Roffler, 1975), and allowing for the different modes in which ruminal NH_3 is

expressed (NH_3 vs $\text{NH}_3\text{-N}$), the rumen NH_3 of the wethers in Treatments 1, 2, 3 and 4 (Figure 2) could not have been limiting bacterial protein synthesis. The big difference in ruminal NH_3 concentration between the wethers in Treatments 2 and 5 (Figure 2), compared to the small difference in animal performance between these treatments (De Waal *et al.*, 1989), is a further indication that ruminal NH_3 could not have been a limiting factor in either ruminal activity or animal production. De Waal *et al.* (1980) suggested that, due to the more continuous process of feed intake by grazing ruminants (Arnold & Dudzinski, 1978), a small diurnal variation in ruminal NH_3 is to be expected. The results of the present study (Treatments 1, 2, 3 and 4), as well as those by De Waal (1986), are in general agreement with this suggestion. It is also evident that the strong diurnal variation with regard to ruminal pH (Figure 1), was lacking with regard to ruminal NH_3 (Figure 2).

The elevating effect of incremental NaCl levels on ruminal NH_3 , is in direct contrast to the results published by Hemsley *et al.* (1975) and Godwin & Williams (1986), but in agreement with those by De Waal *et al.* (1980). However, in the latter study, this interaction between ruminal NH_3 and differential levels of NaCl was not recognized as such. Godwin & Williams (1986) ascribed the decline in ruminal NH_3 to an increased rumen turnover rate, as the result of a pronounced increase in water intake. It seems justified to assume that water intake, as well as the frequency of water intake, by grazing sheep differs substantially from those of penned sheep. Therefore, many of the effects of NaCl on animal performance and changes in ruminal parameters, which are observed in penned sheep, may have no bearing on the situation under truly extensive grazing conditions. In this regard De Waal *et al.* (1989) have suggested that, in accordance with the hypothesis by Drori (1976), the water intake, both volume and frequency of intake, by the grazing wethers may have been insufficient to maintain normal water and electrolyte balance and unimpaired energy utilization.

Although there were some differences for individual VFAs (acetic, propionic and butyric acid) between groups and sampling times (Figure 3), the overall pattern of VFA proportions remained similar for all groups with an approximate ratio of 76:15:9. Similar observations have been made by Moseley (1980). The sharp increase in total VFA concentration from 16h00 to 20h00 (Figure 3), was reflected in the decline in ruminal pH during this period (Figure 1) and was probably the result of an increased ruminal metabolic activity, as well as concentrating and diluting effects in the rumen.

There is conflicting evidence in the literature on the effect of high levels of NaCl intake on VFA production in the rumen and mass gain and fat deposition in sheep (Kromann & Meyer, 1966; Kromann & Ray, 1967; Jackson *et al.*, 1971; Hemsley *et al.*, 1975). Furthermore, on high concentrate diets, changes in the molar proportions of VFAs, usually an increase in acetic acid and a decrease in propionic acid, are apparently more easily affected by high NaCl intake, than on predominantly roughage diets (Rogers, Marks, Davis &

Clark, 1979; Rogers & Davis, 1982; Croom, Harvey, Linnerud & Froetschel, 1982). High NaCl intake may also reduce the numbers of some micro-organisms in the rumen (Potter, Walker & Forrest, 1972; Wilson & Dudzinski, 1973; Hemsley *et al.*, 1975), suggesting some adaptation of the rumen microbial population to high Na over a long period (Potter *et al.*, 1972). Despite the conflicting evidence regarding high NaCl intake on ruminal VFA production, mass gain and fat deposition in sheep, Moseley (1980) conceded that the transient elevation of ruminal NaCl levels can induce a small effect on digestion rate and consequently intake. However, the discrepancies in the literature would suggest that the effect of high dietary NaCl on the proportions of ruminal VFA may not be of significance to any changes which might occur in energy gain and fat deposition (Moseley, 1980). Therefore, if the apparent lack of any real effect by either supplementary CP or NaCl on the prevailing ruminal VFA concentrations in the present study is considered, the conclusion by Moseley (1980) must be supported.

Although supplementary CP tended to reduce ruminal Na concentration, this effect became less evident with increasing NaCl levels (Figure 4). Furthermore, with the exception of the wethers in Treatment 5 and to a lesser extent those in Treatment 2, the prevailing ruminal Na concentrations were sustained at fairly high levels between 08h00 and 20h00 (Figure 4). The low ruminal Na of the wethers in Treatment 1 (Figure 4) was obviously compensated for by a massive increase in ruminal K concentration (Figure 5). According to McDougall (1948), Na and K constitute about 98% of the cations of saliva, and Bailey & Balch (1961) have shown that Na depletion reduced the Na concentration in saliva, with a commensurate increase in the K concentration. Since the wethers in Treatment 1 were apparently Na-deficient (De Waal *et al.*, 1989), the deficiency was obviously physiologically compensated for by K substitution in the saliva. Furthermore, since the K could only have originated from an endogenous source, namely the intracellular fluid of the body (Guyton, 1971), undue loss of K from the intracellular fluid compartment would certainly have had some effect on the normal functioning of the Na⁺/K⁺ transport mechanism across membranes. However, the loss of K from the intracellular fluid was apparently accompanied by a simultaneous loss of Na from the extracellular fluid, as reflected by the relatively high ruminal Na concentration of the wethers in Treatment 1 (Figure 4).

Na, as the principal cation of the circulating extracellular fluids of the body (Denton, 1969; National Research Council, 1980; Conrad, McDowell, Ellis & Loosli, 1986), is essential for a number of important physiological processes, notably those of maintaining osmotic pressure, body fluid balance and hydration of tissues. Drori (1976) has also shown depressed weight gain and fat deposition in rats given high levels of NaCl and concluded that this was due to a disturbance in the water-electrolyte balance induced by hypodipsia (subliminal thirst). NaCl induces thirst and it has been shown with rats (Richter & Mosier, 1954, cited by Drori,

1976), that free access to water is necessary to maintain a food intake compatible with survival and health. Nevertheless, there is no evidence to indicate that animals offered NaCl in their diet take a sufficient amount of water to maintain normal water and electrolyte balance and unimpaired energy utilization (Drori, 1976). Therefore, high levels of NaCl intake could also have created imbalances in the extra- as well as the intracellular body fluid compartments, with a commensurate loss of K from the intracellular fluid. The increase in rumen K of the wethers receiving 15 or 30 g NaCl day⁻¹ (Figure 5), was probably a reflection of this effect. In this regard, Baldwin, Smith, Taylor & Sharp (1980) have indicated that 20 to 30% of the basal energy expenditure of animals is accounted for by Na⁺/K⁺ transport across membranes. It is therefore possible that the supplementary NaCl might have interfered with the normal functioning of the Na⁺/K⁺ transport mechanism across membranes. Hence, the energy expenditure towards normal ion transport and thus the maintenance requirement of the animals, would have increased and less energy would have been available for production, with a concomitant reduction in body mass gain and wool production (De Waal *et al.*, 1989).

In conclusion, the deleterious effect of high NaCl intake (De Waal *et al.*, 1989) was probably precipitated by an insufficient water intake (Drori, 1976; Agricultural Research Council, 1980; Morris, 1980; National Research Council, 1980), which was further exacerbated by nutritional stress factors, peculiar only to truly extensive grazing conditions (De Waal, 1986). Therefore, the observed changes in rumen indices were probably only a reflection of events taking place on a cellular level. These aspects are further investigated.

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