

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

WATER AND ELECTROLYTE TRANSFERS IN RUMINANTS

A thesis presented in partial fulfilment of the requirements  
for the Degree of Doctor of Philosophy at Massey University.

Heather Vivian Simpson

1969

### ACKNOWLEDGEMENTS

I would like to thank my supervisors Professor D.A. Titchen, Professor M.C. Lancaster and Dr C.S.W. Reid, D.S.I.R. for their advice and encouragement during this work, and in particular Dr Reid for the many hours spent in discussion. I would also like to thank Professor Titchen and Dr Reid for the surgical preparation of the animals.

The enthusiastic technical assistance and help with the care of animals of Misses J. Harper and B. Lewis is gratefully acknowledged. I wish to thank the staff of D.S.I.R. and Massey University for assistance in many ways: in particular Dr R.M. Greenway for helpful criticism and discussion; Miss N.Gordon for performing statistical analyses on the computer; the librarians and Miss M. Soulsby for photographing the figures; also Mrs J. Lockett for typing this thesis.

## TABLE OF CONTENTS

	<u>Page</u>
LIST OF ABBREVIATIONS	
LIST OF TABLES	
LIST OF FIGURES	
PREFACE	i
CHAPTER 1 WATER AND ELECTROLYTE METABOLISM IN RUMINANTS	1
I. Water and electrolyte transport across the gut wall	1
II. Exchange of water and electrolytes between ECF and ICF	11
III. Renal excretion of water and electrolytes	17
IV. Regulation of water and electrolyte metabolism	36
V. Conclusions	49
CHAPTER 2 CHANGES IN URINE AND BLOOD COMPOSITION UNDER A RESTRICTED FEEDING REGIME	51
Materials and Methods	54
Results	64
Discussion	87
CHAPTER 3 CHANGES IN URINE AND BLOOD COMPOSITION DURING AD LIBITUM FEEDING	108
Materials and Methods	109
Results	110
Discussion	113
CHAPTER 4 INFUSION INTO THE RUMEN OF WATER AND ELECTROLYTE SOLUTIONS	116
Materials and Methods	118
Results	121
Discussion	135
CHAPTER 5 INFUSION OF NaCl INTO THE DUODENUM OF SHEEP	153
Materials and Methods	153
Results	155
Discussion	160
CHAPTER 6 INTRAVENOUS INFUSION OF KCl AND NaCl	164
Materials and Methods	167
Results	169
Discussion	175
CHAPTER 7 GENERAL DISCUSSION	183
SUMMARY	200
APPENDIX	202
REFERENCES	204



### LIST OF ABBREVIATIONS

ACTH	adrenocorticotrophic hormone
ADH	antidiuretic hormone
B.P.	blood pressure
CSF	cerebrospinal fluid
DOCA	deoxycorticosterone acetate
ECF	extracellular fluid
Fig	figure
GFR	glomerular filtration rate
gm	gram
Hb	haemoglobin
ICF	intracellular fluid
i/v	intravenous
kg	kilogram
l	litre
m-equiv	milliequivalent
min	minute
ml	millilitre
mosm	milliosmole
M	molar
O.P.	osmotic pressure
PAH	para-amino hippuric acid
PCV	packed cell volume
P.D.	potential difference
RBF	renal blood flow
S.G.	specific gravity
[ ]	concentration of

# LIST OF TABLES

## Facing page

<u>Table 1.</u>	Feed intake under different experimental conditions for 3 sheep.	64
<u>Table 2.</u>	Feed and water intake of sheep feeding for 3 hours daily.	64
<u>Table 3.</u>	Frequency of observation of the 3 water intake patterns during feeding.	65
<u>Table 4.</u>	Association of feed and water intake patterns.	65
<u>Table 5.</u>	Extent of prefeeding diuresis in 8 sheep.	65
<u>Table 6.</u>	Urine volumes for latter 2½ hours of feeding.	65
<u>Table 7.</u>	Urine volume in 3½ hours after feeding.	67
<u>Table 8.</u>	Maximum post-feeding Na <sup>+</sup> excretion under different experimental conditions.	71
<u>Table 9.</u>	Change of Na <sup>+</sup> , K <sup>+</sup> , [H <sup>+</sup> ] excretion during feeding under different experimental conditions.	73
<u>Table 10.</u>	Significant multiple regression equations between ΔNa <sup>+</sup> , ΔK <sup>+</sup> , Δ[H <sup>+</sup> ] for 7 groups.	73
<u>Table 11.</u>	Effect of feeding on Cl <sup>-</sup> excretion under the different experimental conditions.	74
<u>Table 12.</u>	Relative plasma volume under different experimental conditions during a 3 hour feed.	81
<u>Table 13.</u>	Relative plasma volume 3½ hours after the end of a 3 hour feed (4.15 p.m.) under different experimental conditions.	81
<u>Table 14.</u>	Average minimum relative plasma volume during feeding, and average feed intake in the first 30 minutes in 3 sheep.	81
<u>Table 15.</u>	Plasma volume from Evan's Blue dilution before feeding and 7 hours after feeding.	81
<u>Table 16.</u>	Plasma osmolality during feeding under the different experimental conditions.	82
<u>Table 17.</u>	Comparison of the plasma [Cl <sup>-</sup> ] increase during feeding with the different experimental conditions and with two methods of plasma preparation.	84

<u>Table 18.</u>	Average percentage of time spent feeding, ruminating and resting on 6 days under <u>ad libitum</u> feeding conditions.	111
<u>Table 19.</u>	Intraruminal infusions: volume, concentration, sheep used and dates.	119
<u>Table 20.</u>	Excretion of water following intraruminal infusion, expressed as % of the load for the 3 litre infusions, and as ml of the 300 ml water load retained after correction for the basal rate for the hypertonic infusions.	122
<u>Table 21.</u>	Intraruminal NaCl infusion: $\text{Na}^+$ excretion related to other parameters.	125
<u>Table 22.</u>	$\text{K}^+$ excretion following intraruminal NaCl infusion, expressed as % change from the preinfusion rate; the extra m-equiv of $\text{K}^+$ excreted relative to a basal excretion of 16% decline; and the same calculation based on a 20% decline.	127
<u>Table 23.</u>	Intraruminal infusions: % change in $\text{HCO}_3^-$ excretion from the preinfusion rate.	128
<u>Table 24.</u>	Plasma volume and total solute content relative to the 9.15 a.m. value after intraruminal infusion of NaCl solutions.	132
<u>Table 25.</u>	Intraduodenal NaCl infusion: rates of infusion and total dose.	154
<u>Table 26.</u>	Intraduodenal 1.5M NaCl infusion: $\text{Na}^+$ excretion related to other parameters.	158
<u>Table 27.</u>	Sheep used for intravenous infusions given at 1 ml/min for 120 minutes.	168
<u>Table 28.</u>	Excretion of $\text{Na}^+$ , $\text{Cl}^-$ and water after intravenous infusion of 0.15M NaCl.	169

# LIST OF FIGURES

	<u>Facing page</u>
<u>Fig 1.</u> Arrangement of the nephron and its blood supply.	18
<u>Fig 2.</u> Effect of no drinking water during a 3 hour feed on the half-hourly feed intake in 4 sheep.	64
<u>Fig 3.</u> Lack of effect of acetazolamide on the half-hourly feed intake; no drinking water.	64
<u>Fig 4.</u> Feed intake patterns during a 3 hour feed.	64
<u>Fig 5.</u> Water intake patterns during a 3 hour feed.	65
<u>Fig 6.</u> Urine volume relative to a once-daily 2 or 3 hour feed at different times of the day; water <u>ad libitum</u> .	65
<u>Fig 7.</u> Urine volume relative to a once-daily 2 hour feed; water <u>ad libitum</u> .	66
<u>Fig 8.</u> Urine volume relative to a once-daily 2 hour feed; water <u>ad libitum</u> .	66
<u>Fig 9.</u> Urine volume relative to a once-daily 2 hour feed; water <u>ad libitum</u> .	66
<u>Fig 10.</u> Urine volume relative to a once-daily 3 hour feed; no water all day, acetazolamide.	66
<u>Fig 11.</u> Urine volume relative to a once-daily 2 hour feed; water <u>ad libitum</u> , acetazolamide.	66
<u>Fig 12.</u> Urine pH and $\text{HCO}_3^-$ excretion relative to a 2 or 3 hour once-daily feed; water <u>ad libitum</u> .	67
<u>Fig 13.</u> Urine pH and $\text{HCO}_3^-$ excretion relative to a once-daily 3 hour feed; no water all day.	67
<u>Fig 14.</u> Urine pH and $\text{HCO}_3^-$ excretion relative to a once-daily 2 hour feed; water <u>ad libitum</u> , acetazolamide.	68
<u>Fig 15.</u> General diagram showing regression lines of electrolyte excretion at a selected time (feeding or prefeeding) on that in the first prefeeding period (8.30 - 9.30 a.m.).	68
<u>Fig 16.</u> Effect of the prefeeding diuresis, feeding and acetazolamide on $\text{HCO}_3^-$ excretion.	68
<u>Fig 17.</u> Distribution diagram of the minimum urine pH before feeding, and during feeding under the different experimental conditions.	69

<u>Fig 18.</u>	Urine pH relative to a once-daily 3 hour feed; water <u>ad libitum</u> , feeding at varying times.	69
<u>Fig 19.</u>	$\text{Na}^+$ excretion relative to a <del>once-daily</del> 2 or 3 hour feed; 5 gm NaCl on feed, a - water <u>ad libitum</u> , b - no water all day.	70
<u>Fig 20.</u>	$\text{Na}^+$ excretion relative to a <del>once-daily</del> 2 hour feed; salt lick, water <u>ad libitum</u> .	70
<u>Fig 21.</u>	$\text{Na}^+$ excretion relative to a <del>once-daily</del> 2 hour feed; 5 gm NaCl on feed, water <u>ad libitum</u> , acetazolamide.	70
<u>Fig 22.</u>	$\text{Na}^+$ excretion relative to a <del>once-daily</del> 2 or 3 hour feed; 5 gm NaCl on feed, acetazolamide, a - water <u>ad libitum</u> , b - no water all day.	70
<u>Fig 23.</u>	Effect of the prefeeding diuresis, feeding and acetazolamide on $\text{Na}^+$ excretion.	70
<u>Fig 24.</u>	$\text{K}^+$ excretion relative to a <del>once-daily</del> 2 hour feed; water <u>ad libitum</u> .	71
<u>Fig 25.</u>	$\text{K}^+$ excretion relative to a <del>once-daily</del> 2 hour feed; water <u>ad libitum</u> , acetazolamide.	71
<u>Fig 26.</u>	$\text{K}^+$ excretion relative to a <del>once-daily</del> 2 or 3 hour feed; acetazolamide, a - water <u>ad libitum</u> , b - no water all day.	71
<u>Fig 27.</u>	Effect of the prefeeding diuresis, feeding and acetazolamide on $\text{K}^+$ excretion.	72
<u>Fig 28.</u>	Significant correlations between $\Delta\text{K}^+$ , $\Delta\text{Na}^+$ and $\Delta\text{free } [\text{H}^+]$ during feeding under 7 experimental conditions and for all groups combined.	73
<u>Fig 29.</u>	$\text{Cl}^-$ excretion relative to a <del>once-daily</del> 2 hour feed; water <u>ad libitum</u> .	74
<u>Fig 30.</u>	$\text{Cl}^-$ excretion relative to a <del>once-daily</del> 2 hour feed; water <u>ad libitum</u> .	74
<u>Fig 31.</u>	$\text{Cl}^-$ excretion relative to a <del>once-daily</del> 3 hour feed; no water all day.	74
<u>Fig 32.</u>	$\text{Cl}^-$ excretion relative to a <del>once-daily</del> 2 hour feed; water <u>ad libitum</u> , acetazolamide.	74
<u>Fig 33.</u>	Effect of prefeeding diuresis, feeding and acetazolamide on $\text{Cl}^-$ excretion.	74

<u>Fig 34.</u>	Effect of prefeeding diuresis, feeding and acetazolamide on $\text{Cl}^-$ excretion.	74
<u>Fig 35.</u>	Urea excretion relative to a once-daily 2 hour feed; water <u>ad libitum</u> .	75
<u>Fig 36.</u>	Urea excretion relative to a once-daily 2 hour feed; water <u>ad libitum</u> , acetazolamide.	75
<u>Fig 37.</u>	Total solute and $\text{K}^+$ excretion relative to a once-daily 3 hour feed; water <u>ad libitum</u> .	76
<u>Fig 38.</u>	Total solute, $\text{K}^+$ and $\text{Cl}^-$ excretion relative to a once-daily 3 hour feed; no water all day.	76
<u>Fig 39.</u>	Total solute and $\text{K}^+$ excretion relative to a once-daily 3 hour feed; no water all day, acetazolamide.	76
<u>Fig 40.</u>	Total solute and $\text{Cl}^-$ excretion relative to a once-daily 3 hour feed; no water all day, acetazolamide.	76
<u>Fig 41.</u>	Urinary total and individual solute excretion each half hour relative to a once-daily 3 hour feed; water <u>ad libitum</u> .	77
<u>Fig 42.</u>	Urine osmolality and specific gravity relative to a once-daily 3 hour feed; water <u>ad libitum</u> .	77
<u>Fig 43.</u>	Comparison of changes in urine osmolality in a sheep relative to a once-daily 3 hour feed under 3 different experimental conditions: a - water <u>ad libitum</u> ; b - no water all day; c - no water all day, acetazolamide.	77
<u>Fig 44.</u>	Graph of solute-free water reabsorption ( $T_{\text{H}_2\text{O}}^c$ ) against osmolar clearance ( $C_{\text{osm}}$ ) for all urine samples with a midpoint blood sample, irrespective of the experimental conditions or the relationship to feeding.	78
<u>Fig 45.</u>	Blood pH (jugular) relative to a once-daily 2 hour feed; water <u>ad libitum</u> .	79
<u>Fig 46.</u>	Blood pH (a - jugular, b - carotid) relative to a once-daily 3 hour feed; a - no water all day, b - no water during feed, water <u>ad libitum</u> after feed.	79
<u>Fig 47.</u>	Blood pH (a - carotid, b - jugular) relative to a once-daily 2 or 3 hour feed; acetazolamide, a - water <u>ad libitum</u> , b - no water during feed, water <u>ad libitum</u> after feed.	79
<u>Fig 48.</u>	Blood total $\text{CO}_2$ content (jugular) relative to a once-daily 2 or 3 hour feed; a - water <u>ad libitum</u> , b, c - no water all day.	79

- Fig 49. Blood total CO<sub>2</sub> content (a - jugular, b - carotid) relative to a once-daily 2 hour feed; water ad libitum, acetazolamide. 79
- Fig 50. Graph of the plasma volume calculated from the change in [plasma protein] at the time of the minimum relative plasma volume against the minimum relative plasma volume. 80
- Fig 51. [Plasma protein], PCV, [Hb] and relative plasma volume relative to a once-daily 3 hour feed; water ad libitum. 80
- Fig 52. [Plasma protein] and relative plasma volume relative to a once-daily 3 hour feed; no water all day. 80
- Fig 53. [Plasma protein] and relative plasma volume relative to a once-daily 3 hour feed; no water all day, acetazolamide. 80
- Fig 54. [Plasma protein] and relative plasma volume relative to a once-daily 3 hour feed; no water all day, acetazolamide. 80
- Fig 55. [Hb] relative to a once-daily 3 hour feed; water ad libitum. 80
- Fig 56. Graph of relative plasma volume at 1 p.m. against the minimum relative plasma volume during feeding. 80
- Fig 57. Plasma osmolality relative to a once-daily 3 hour feed; water ad libitum. 82
- Fig 58. Plasma osmolality relative to a once-daily 3 hour feed; water ad libitum. 82
- Fig 59. Plasma osmolality relative to a once-daily 3 hour feed; no water all day. 82
- Fig 60. Plasma osmolality relative to a once-daily 3 hour feed; no water all day, acetazolamide. 82
- Fig 61. Graph of the change in plasma osmolality from 9.15 to 10.15 a.m. (45 minutes before to 15 minutes after the start of feeding) against the relative plasma volume at 10.15 a.m. 82
- Fig 62. Plasma [Na<sup>+</sup>] relative to a once-daily 3 hour feed; water ad libitum (plasma separated under paraffin). 83
- Fig 63. Plasma [Na<sup>+</sup>] relative to a once-daily 3 hour feed; no water all day (plasma separated under paraffin). 83

- Fig 64.** Plasma  $[Na^+]$  relative to a once-daily 3 hour feed; no water all day, acetazolamide (plasma separated under paraffin). 83
- Fig 65.** Plasma  $[Cl^-]$  relative to a once-daily 3 hour feed; water ad libitum (plasma separated under paraffin). 84
- Fig 66.** Plasma  $[Cl^-]$  relative to a once-daily 3 hour feed; no water all day (plasma separated under paraffin). 84
- Fig 67.** Plasma  $[Cl^-]$  relative to a once-daily 3 hour feed; no water all day, acetazolamide (plasma separated under paraffin). 84
- Fig 68.** Distribution diagram of prefeeding  $[K^+]$  with two methods of plasma separation, in open tubes and under paraffin. 85
- Fig 69.** Plasma  $[K^+]$  relative to a once-daily 3 hour feed; water ad libitum (plasma separated under paraffin). 85
- Fig 70.** Plasma  $[K^+]$  relative to a once-daily 3 hour feed; no water all day (a - plasma separated under paraffin, b - open tubes). 85
- Fig 71.** Plasma  $[K^+]$  relative to a once-daily 3 hour feed; no water all day, acetazolamide (plasma separated under paraffin). 85
- Fig 72.** Plasma  $[K^+]$  relative to a once-daily 2 hour feed; water ad libitum, acetazolamide (carotid blood, plasma separated in open tubes). 85
- Fig 73.** Erythrocyte volume relative to a once-daily 3 hour feed; a - water ad libitum, b - no water all day. 86
- Fig 74.** Erythrocyte volume relative to a once-daily 3 hour feed; no water all day. 86
- Fig 75.** Erythrocyte volume relative to a once-daily 3 hour feed; no water all day, acetazolamide. 86
- Fig 76.** Erythrocyte  $[K^+]$ ,  $[Na^+]$ ,  $K^+$  and  $Na^+$  content relative to a once-daily 3 hour feed; water ad libitum. 87
- Fig 77.** Erythrocyte  $[K^+]$ ,  $[Na^+]$ ,  $K^+$  and  $Na^+$  content relative to a once-daily 3 hour feed; no water all day. 87
- Fig 78.** Erythrocyte  $[K^+]$ ,  $[Na^+]$ ,  $K^+$  and  $Na^+$  content relative to a once-daily 3 hour feed; no water all day, acetazolamide. 87



- Fig 79.** Erythrocyte  $[K^+]$ ,  $[Na^+]$ ,  $K^+$  and  $Na^+$  content relative to a once-daily 3 hour feed; no water all day, acetazolamide. 87
- Fig 80.** Kymograph tracing of jaw movements showing the characteristic patterns of feeding and rumination. 110
- Fig 81.** Feeding and ruminating activity in 3 sheep with ad libitum access to feed and water. 110
- Fig 82.** Urine volume, total solute, pH,  $Na^+$ ,  $K^+$ ,  $Cl^-$  and  $HCO_3^-$  excretion in a sheep with ad libitum access to feed and water. 111
- Fig 83.** Urine volume, total solute, pH,  $Na^+$ ,  $K^+$ ,  $Cl^-$  and  $HCO_3^-$  excretion in a sheep with ad libitum access to feed and water. 111
- Fig 84.** Urine volume, total solute, pH,  $Na^+$ ,  $K^+$ ,  $Cl^-$  and  $HCO_3^-$  excretion in a sheep with ad libitum access to feed and water. 111
- Fig 85.** Relative plasma volume,  $[plasma\ protein]$ , O.P.,  $[Na^+]$ ,  $[K^+]$  and  $[Cl^-]$  and blood total  $CO_2$  content in a sheep with ad libitum access to feed and water. 112
- Fig 86.** Relative plasma volume,  $[plasma\ protein]$ , plasma O.P.,  $[Na^+]$ ,  $[K^+]$  and  $[Cl^-]$  and blood total  $CO_2$  content in a sheep with ad libitum access to feed and water. 112
- Fig 87.** Relative plasma volume,  $[plasma\ protein]$ , plasma O.P.,  $[Na^+]$ ,  $[K^+]$  and  $[Cl^-]$  and blood total  $CO_2$  content in a sheep with ad libitum access to feed and water. 112
- Fig 88.** Erythrocyte volume,  $[Na^+]$ ,  $[K^+]$ ,  $Na^+$  content and  $K^+$  content in a sheep with ad libitum access to feed and water. 113
- Fig 89.** Erythrocyte volume,  $[Na^+]$ ,  $[K^+]$ ,  $Na^+$  content and  $K^+$  content in a sheep with ad libitum access to feed and water. 113
- Fig 90.** Erythrocyte volume,  $[Na^+]$ ,  $[K^+]$ ,  $Na^+$  content and  $K^+$  content in a sheep with ad libitum access to feed and water. 113
- Fig 91.** Urine volume following intraruminal infusions: a - control; b,c - 3 l water; d - KCl (3 l, 0.15M); e,f,g - NaCl (3 l, 0.15M); h - KCl (0.3 l, 1.5M); i - NaCl (0.3 l, 1.5M). 122
- Fig 92.** Urine  $Na^+$  excretion following intraruminal infusions: a,b,c - control; d,e - 3 l water. 124

<u>Fig 93.</u>	Urine $[Na^+]$ following intraruminal infusion of 3 l of water.	124
<u>Fig 94.</u>	Urine $Na^+$ excretion following intraruminal infusions: a - NaCl (3 l, 0.15M); b - NaCl (0.3 l, 1.5M); c, d - KCl (3 l, 0.15M); e, f - KCl (0.3 l, 1.5M).	125
<u>Fig 95.</u>	Urine $K^+$ excretion following intraruminal infusions: a, b - control; c - 3 l water; d, e - KCl (3 l, 0.15M); f, g - KCl (0.3 l, 1.5M); h - NaCl (3 l, 0.15M); i - NaCl (0.3 l, 1.5M).	126
<u>Fig 96.</u>	Urine $Cl^-$ excretion following intraruminal infusions: a, b - control; c, d - 3 l water; e - KCl (3 l, 0.15M); f - KCl (0.3 l, 1.5M); g - NaCl (3 l, 0.15M); h - NaCl (0.3 l, 1.5M).	127
<u>Fig 97.</u>	Urine $HCO_3^-$ excretion following intraruminal infusions: a - control; b - 3 l water; c - NaCl (3 l, 0.15M); d - NaCl (0.3 l, 1.5M); e - KCl (3 l, 0.15M); f - KCl (0.3 l, 1.5M).	128
<u>Fig 98.</u>	Urine urea excretion following intraruminal infusions: a - control; b - KCl (3 l, 0.15M); c - 3 l water; d - NaCl (3 l, 0.15M).	129
<u>Fig 99.</u>	Urine pH following intraruminal infusions: a - control; b - 3 l water; c - KCl (3 l, 0.15M); d - NaCl (3 l, 0.15M); e - KCl (0.3 l, 1.5M); f - NaCl (0.3 l, 1.5M).	129
<u>Fig 100.</u>	Relative plasma volume following intraruminal infusions: a, b - control; c, d - 3 l water; e - NaCl (3 l, 0.15M); f - NaCl (0.3 l, 1.5M); g - KCl (3 l, 0.15M); h - KCl (0.3 l, 1.5M).	130
<u>Fig 101.</u>	Plasma osmolality following intraruminal infusions: a, b - control; c-f 3 l water; g - NaCl (3 l, 0.15M); h - NaCl (0.3 l, 1.5M); i - KCl (3 l, 0.15M); j - KCl (0.3 l, 1.5M).	131
<u>Fig 102.</u>	Plasma total solutes following intraruminal infusions: a - control; b - 3 l water; c - NaCl (3 l, 0.15M); d - NaCl (0.3 l, 1.5M); e - KCl (3 l, 0.15M); f - KCl (0.3 l, 1.5M).	131
<u>Fig 103.</u>	Plasma $[Na^+]$ following intraruminal infusions: a - control; b - 3 l water; c - NaCl (0.3 l, 1.5M); d - KCl (3 l, 0.15M).	133
<u>Fig 104.</u>	Plasma $[Cl^-]$ following intraruminal infusions: a - control; b - 3 l water; c - NaCl (0.3 l, 1.5M); d - KCl (0.3 l, 1.5M).	133

- Fig 105.** Plasma  $K^+$  content following intraruminal infusions:  
a - control; b - 3 l water; c - KCl (3 l, 0.15M);  
d - KCl (0.3 l, 1.5M); e - NaCl (0.3 l, 1.5M);  
f - NaCl (3 l, 0.15M). 133
- Fig 106.** Plasma  $[K^+]$  following intraruminal infusions: a, b -  
control; c - 3 l water; d - KCl (3 l, 0.15M); e-g -  
KCl (0.3 l, 1.5M); h - NaCl (0.3 l, 1.5M); i - NaCl  
(3 l, 0.15M). 134
- Fig 107.** Urine  $Na^+$  excretion, relative plasma volume and total  
solute content following intraduodenal 0.15M NaCl  
infusion. 156
- Fig 108.** Relative plasma volume and  $[$ plasma protein $]$  following  
intraduodenal 0.15M NaCl infusion. 156
- Fig 109.** Urine volume following intraduodenal 0.15M NaCl  
infusion. 156
- Fig 110.** Urine  $Cl^-$  excretion following intraduodenal 0.15M  
NaCl infusion. 156
- Fig 111.** Urine  $HCO_3^-$  excretion following intraduodenal 0.15M  
NaCl infusion. 156
- Fig 112.** Plasma  $[K^+]$  and  $K^+$  content following intraduodenal  
0.15M NaCl infusion. 157
- Fig 113.** Urine  $K^+$  excretion following intraduodenal 0.15M NaCl  
infusion. 157
- Fig 114.** Urine  $Na^+$  excretion following intraduodenal 1.5M NaCl  
infusion: a - 450 m-equiv  $Na^+$ , b - 300 m-equiv  $Na^+$ ,  
c - 225 m-equiv  $Na^+$ . 158
- Fig 115.** Plasma total solute content following intraduodenal  
1.5M NaCl infusion: 225 m-equiv  $Na^+$ , 300 m-equiv  $Na^+$ ,  
450 m-equiv  $Na^+$ . 158
- Fig 116.** Relative plasma volume following intraduodenal 1.5M  
NaCl infusion: a - 450 m-equiv  $Na^+$ , b - 300 m-equiv  $Na^+$ ,  
c - 225 m-equiv  $Na^+$ . 158
- Fig 117.** Urine volume following intraduodenal 1.5M NaCl infusion. 158
- Fig 118.** Plasma O.P. following intraduodenal 1.5M NaCl infusion. 158
- Fig 119.** Plasma  $[Na^+]$  following intraduodenal 1.5M NaCl  
infusion. 158
- Fig 120.** Urine  $Cl^-$  excretion following intraduodenal 1.5M NaCl  
infusion. 159

<u>Fig 121.</u>	Urine $\text{HCO}_3^-$ excretion following intraduodenal 1.5M NaCl infusion.	159
<u>Fig 122.</u>	Plasma $[\text{K}^+]$ and $\text{K}^+$ content following intraduodenal 1.5M NaCl infusion.	159
<u>Fig 123.</u>	Urine $\text{K}^+$ excretion following intraduodenal 1.5M NaCl infusion.	160
<u>Fig 124.</u>	Urine $\text{Na}^+$ excretion following intravenous 0.15M NaCl infusion.	169
<u>Fig 125.</u>	Urine volume following intravenous 0.15M NaCl infusion.	169
<u>Fig 126.</u>	Urine $\text{Cl}^-$ excretion following intravenous 0.15M NaCl infusion.	169
<u>Fig 127.</u>	Urine $\text{K}^+$ excretion following intravenous 0.15M or 0.09M NaCl infusion.	169
<u>Fig 128.</u>	Urine $\text{HCO}_3^-$ excretion and urine pH following intravenous 0.15M NaCl infusion.	170
<u>Fig 129.</u>	$[\text{Plasma protein}]$ , relative plasma volume, plasma O.P. and total solute content following intravenous 0.15M or 0.09M NaCl infusion.	170
<u>Fig 130.</u>	Plasma $[\text{Na}^+]$ and $[\text{Cl}^-]$ following intravenous 0.09M NaCl infusion.	170
<u>Fig 131.</u>	Plasma $\text{K}^+$ content following intravenous 0.15M or 0.09M NaCl infusion.	170
<u>Fig 132.</u>	Urine $\text{Na}^+$ excretion following intravenous 1.5M NaCl infusion.	170
<u>Fig 133.</u>	Urine volume and total solute excretion following intravenous 1.5M NaCl infusion.	171
<u>Fig 134.</u>	$[\text{Plasma protein}]$ and relative plasma volume following intravenous 1.5M NaCl infusion.	171
<u>Fig 135.</u>	Plasma total solute content following intravenous 1.5M or 0.9M NaCl infusion.	171
<u>Fig 136.</u>	Plasma O.P. following intravenous 1.5M NaCl infusion.	171
<u>Fig 137.</u>	Plasma $[\text{Na}^+]$ and $[\text{Cl}^-]$ following intravenous 0.9M or 1.5M NaCl infusion.	171
<u>Fig 138.</u>	Urine $\text{Cl}^-$ excretion following intravenous 1.5M NaCl infusion.	172

Facing page

<u>Fig 139.</u>	Urine pH following intravenous 1.5M NaCl infusion.	172
<u>Fig 140.</u>	Urine $K^+$ excretion following intravenous 1.5M NaCl infusion.	172
<u>Fig 141.</u>	Plasma $[K^+]$ and $K^+$ content following intravenous 1.5M or 0.9M NaCl infusion.	172
<u>Fig 142.</u>	Urine $K^+$ excretion following intravenous 1.0M KCl infusion.	173
<u>Fig 143.</u>	Plasma $[K^+]$ following intravenous 1.0M KCl infusion.	173
<u>Fig 144.</u>	Plasma $K^+$ content following intravenous 1.0M KCl infusion.	173
<u>Fig 145.</u>	Urine $Na^+$ excretion following intravenous 1.0M KCl infusion.	173
<u>Fig 146.</u>	Urine volume following intravenous 1.0M KCl infusion.	173
<u>Fig 147.</u>	Urine total solute excretion following intravenous 1.0M KCl infusion.	174
<u>Fig 148.</u>	Relative plasma volume and $[plasma\ protein]$ following intravenous 1.0M KCl infusion.	174
<u>Fig 149.</u>	Plasma total solute content following intravenous 1.0M KCl infusion.	174
<u>Fig 150.</u>	Plasma C.P. following intravenous 1.0M KCl infusion.	174
<u>Fig 151.</u>	Plasma $[Na^+]$ and $[Cl^-]$ following intravenous 1.0M KCl infusion.	174
<u>Fig 152.</u>	Urine $Cl^-$ excretion following intravenous 1.0M KCl infusion.	174
<u>Fig 153.</u>	Urine $HCO_3^-$ excretion following intravenous 1.0M KCl infusion.	175
<u>Fig 154.</u>	Urine pH following intravenous 1.0M KCl infusion.	175

## PREFACE

At the present time, the economy of New Zealand is largely dependent upon the health and well-being of the ruminant animal. The national loss due to primary water and electrolyte disturbances, and to those secondary to other diseases, is of considerable importance. Deficiencies in our knowledge of water and electrolyte metabolism in the ruminant have become apparent, even of the principal cations sodium and potassium.

The specialized form of nutrition in the ruminant has entailed some changes in the water and electrolyte economy. In adapting to a diet of plant material rich in cellulose, they have developed a large forestomach, the reticulo-rumen, where a symbiotic population of bacteria and protozoa is maintained and exploited. Microbial fermentation breaks down plant cellulose, and converts carbohydrate to volatile fatty acids, principally acetic, propionic and butyric acids, which are rapidly absorbed by the host for use as an energy source. Microbial protein and certain vitamins are also made available further down the gastro-intestinal tract.

The development of the reticulo-rumen has resulted in an increase in the content and daily turnover of gut water and electrolytes. A major source of this content of the reticulo-rumen liquor, which provides a well-buffered medium for the microbes, is the copious salivary flow. The rumen of the sheep may contain 500-800 m-equiv of  $\text{Na}^+$ , approximately half that in the extracellular fluid. The daily digestive cycle of salivary secretion and later reabsorption may involve double this amount of  $\text{Na}^+$ .

The maintenance of water and electrolyte balance in the face of this

digestive cycle, coupled with the low  $\text{Na}^+$ -high  $\text{K}^+$  content of the diet, suggests that the ruminant has efficient homeostatic mechanisms in operation. Whether or not these are identical with those seen in other species, or have features unique to the ruminant, is not clear. While the enlarged digestive cycle would appear to impose an extra load on the regulatory mechanisms, the presence of the reticulo-rumen might confer advantages during times of stress, when rumen fluid can be called upon as a reserve of water and electrolyte. During dehydration, the ECF can draw upon gut fluids (Macfarlane, Morris and Howard, 1963; Hecker, Budtz-Olsen and Ostwald, 1964); and the rumen forms a  $\text{Na}^+$  store which can be drawn upon during reduced dietary intake (Denton, 1957; Kay and Hobson, 1963). The ability to repair a water deficit of up to 10% body weight (more in camels) within minutes would be an advantage in the natural environment.

Investigation in ruminants of the overall regulation of water and electrolyte metabolism has not been extensive. Most of our knowledge has been derived from studies of man, rodents and the dog. In the ruminant, more commonly, the longer term adjustments to dietary deficiency or supplementation, or to altered environmental conditions have been followed; less often, short-term water and electrolyte redistributions and mechanisms of elimination and conservation in varying physiological situations have been studied.

Some properties of the ruminant digestive tract, particularly regions of net addition and absorption, and the characteristics of rumen epithelial transport have been identified. However, in many cases the particular experimental situations employed make generalization uncertain. Thus, net transport is commonly estimated using a simple solution in an isolated, emptied and washed rumen or rumen pouch, a procedure providing an

abnormal environment for the rumen mucosa, and which can alter its transport properties (Masson and Phillipson, 1951; Armstrong, Blaxter and Graham, 1957; Ash and Dobson, 1963). Studies in the intact organ under physiological conditions present practical difficulties because of the continuous inflow of saliva and outflow to the omasum, and the lack of uniformity of composition of the contents in different regions of the reticulo-rumen. Accurate estimation of the rumen volume at any particular time is not an easy task. Direct measurement by total removal has a limited application, and marker dilution is only accurate during periods of relative constancy. In addition, to calculate a change in total electrolyte content an average ruminal concentration is required, although a uniform electrolyte concentration in the rumen is not usually a physiological reality.

The present thesis is concerned with short-term transfers, especially water and electrolyte movements between the contents of the reticulo-rumen and body fluid compartments. The rumen water and electrolyte status was altered rapidly in two ways: by once-daily feeding whereby there was net gain in the rumen at the expense of body fluids; and by infusion of known amounts of electrolyte. Net gain or absorption from the rumen has been followed by observing changes in urinary excretion and in blood composition. The rumen itself has not been sampled; it was considered that the advantages of direct rumen observations would be outweighed by the experimental errors and by the disturbance to the animal caused by the sampling. In the undisturbed sheep, relative plasma volume estimations can be inferred from the PCV and  $[Hb]$ .

Urine and blood changes associated with a single daily feed (Chapter 2) have confirmed and extended the observations of Stacy and Brock (1964), and are in agreement with later observations from that group. An attempt was



made to gain further information about the homeostatic mechanisms involved by the use of the diuretic, acetazolamide, and by restriction of drinking water. The relevance of these to variations seen in ad libitum fed animals was examined (Chapter 3).

Prior to the present experiments only isolated water and electrolyte infusions had been performed in ruminants (Sellers and Roepke, 1951; Lysov, 1960; Anderson and Pickering, 1962a) although more reports have appeared while the work was in progress (Potter, 1966, 1968; Keynes and Harrison, 1967; Devhurst, Harrison and Keynes, 1968). A series of intraruminal infusions of water, NaCl and KCl has been carried out (Chapter 4), integrated with the intraduodenal infusion of NaCl (Chapter 5) and the intravenous administration of sodium and potassium salts (Chapter 6). It would appear that, with the exception of sodium, net water and electrolyte movements across the rumen mucosa in physiological situations may be small in magnitude. Should this be so, then sensory receptors in the forestomach may be involved only in regulating the functions of the digestive tract itself, and not in the overall regulation of water and electrolyte metabolism. Thus, the homeostatic mechanisms in the ruminant may more closely approach those in the monogastric than would be likely if the rumen permitted freer exchange with the internal body fluids.