Reviews on the mineral provision in ruminants (IV): SODIUM METABOLISM AND REQUIREMENTS IN RUMINANTS

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PREFACE

In the Netherlands the ´Handleiding Mineralenonderzoek bij rundvee in de praktijk´[1] is a well-known publication that has been used already for decades as a guide to trace and treat mineral disorders in cattle. The fifth edition of this guidebook was published in 1996. The content of this publication was largely identical to that of the fourth edition (1990). Therefore the (independent) committee that is responsible for the contents of the guidebook (the 'Commissie Onderzoek Minerale Voeding'[2], COMV) decided in 2000 that a thorough revision was desired.
The committee was of the opinion that, if possible, the available scientific literature should be summarized and evaluated once again. Furthermore, attention should be paid to the mineral provision of categories of cattle other than dairy cattle, as well as to that of sheep and goats. Finally, the basic principles for the calculation of the mineral requirements should be described in a transparent way.

The intended revision was made possible as the Dutch 'Ministerie van Landbouw, Natuur en Voedselkwaliteit' (LNV), the 'Productschap Diervoeder' and the 'Productschap Zuivel'[3] were willing to subsidize this extensive and ambitious project.
The COMV decided to execute the project as follows.

- External experts, invited by the COMV, should summarize and evaluate the relevant literature in a so-called 'basal document' (with two exceptions to be written in English).
- Subsequently, these documents should be critically evaluated by the COMV.
- These basal documents should then be used to write and arrange the several chapters of the revised 'Handleiding'.

The revised 'Handleiding' is available (in the Dutch language) since October 2005, under the title 'Handleiding mineralenvoorziening rundvee, schapen en geiten.'[4] This book is published by the 'Centraal Veevoederbureau' (CVB; Central Bureau for Livestock Feeding) in Lelystad, as was also the case for the previous edition.

The COMV was of the opinion that the valuable basal documents, that became available during the course of this project, should be published too. By doing so everyone has the possibility to trace the basis for the text of the revised 'Handleiding'. The CVB was gladly willing to issue these documents as CVB Documentation reports. In connection with this the authors and the members of the COMV have disclaimed all rights and have assigned them to the Productschap Diervoeder, of which the CVB is one of the services.
For an overview of the CVB Documentation Reports that will appear in this context, you are referred to an Annex in the back of this report.

Utrecht/Lelystad, September 2005.

Professor dr. ir. A.C. Beynen	Dr. M.C. Blok
Chair of the COMV	Secretary of the COMV and Head of the CVB

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[1] Guidebook on mineral research for cattle in practice.
[2] Committee for research on mineral nutrition
[3] The Ministry for Agriculture, Nature and Food quality, the Product Board Animal Feed and the Dutch Dairy Board, respectively.
[4] Guidebook mineral provision cattle, sheep and goats.

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CONTENT

LIST OF ABBREVIATIONS

Abbreviation	Unit	Description
ADH		Anti-diuretic hormone
ARC		Agricultural Research Council (UK)
BW	kg	Body weight
$BW^{0,75}$	$kg^{0,75}$	Metabolic body weight
CVB		Centraal Veevoederbureau (NL) (Central Bureau Livestock Feeding)
DLG		Deutsche Landwirtschaft Gesellschaft (G)
DM	kg	Dry matter
DMI	kg/day	Dry matter intake
ECF		Extracellular fluid
GFR		Glomerular filtration rate
Ha		Hectare
INRA		Institute National de la Recherche Agronomique (F)
L		Litre
Mg		Milligram
MJ		Megajoules (= 10^6 Joules)
Mmol		Millimoles
MM		Millimolair
NEl	MJ	Net Energy lactation (G)
PD	mV	Potential difference
NRC		National Research Council (USA)
SD		Standard deviation
Vol	L	Volume
Wt	kg	Weight

1. PHYSIOLOGICAL FUNCTIONS OF SODIUM [50]

Sodium (Na) is the principal cation in extracellular fluid (ECF). Therefore, it is the major determinant of the osmotic pressure of ECF and is of great importance in maintaining water balance in animals. The typical intra- and extracellular distribution of Na (and potassium, K) is regulated by Na/K-pumps, which are vital for the generation (and maintenance) of membrane potentials. Furthermore, Na also plays an important role in the regulation of acid-base balance in body fluids, although this is secondary to its role in maintaining osmotic pressure of ECF. Apart from the physiological functions of Na mentioned above, Na is also required for the absorption of glucose and galactose, most of the peptides and amino acids and bile acids from the gastro-intestinal tract (50, 68).

2 DISTRIBUTION OF SODIUM BETWEEN TISSUES

The Na content of the body of adult cattle (BW = 500 kg) and sheep (BW = 45 kg) has been estimated to be about 1.3 and 1.2 g/kg BW, respectively (3). Roughly, 45% of the body store of Na is found in the ECF, while only 10% is found within cells; the remainder of the Na present in the animals body is found in bone (47, 51). Typical Na concentrations in ECF are 142-146 mM and 142-145 mM in plasma and interstitial fluid, respectively, while intracellular concentrations are rather low; i.e. 12-14 mM (51, 92). Nearly one-half of the Na in bone is adsorbed on the surfaces of hydroxyapatite crystals deep in long bones and therefore non-exchangeable with Na ions in fluid compartments (51).

3 SODIUM METABOLISM

3.1 Absorption

From studies with cannulated cows and steers (Table 1), it appeared that the amount of Na passing either the abomasum or proximal duodenum exceeds that of dietary intake by a factor ranging from 1.6 to 10.4, with a mean value of 3.8. However, studies with cannulated sheep (Table 1) suggest that the amount of Na passing either the abomasum or proximal duodenum was 4.5-16.4 (mean of 7.1) times greater then the amount of Na ingested. Thus, net secretion of Na occurs before the abomasum /proximal duodenum in cows, steers and sheep. This net secretion is caused by a considerable flow of Na containing saliva into the rumen. The mean Na concentrations of bovine saliva from animals with an adequate provision of Na, observed by Bailey and Balch (5), Kemp and Geurink (57), Rogers and Van't Klooster (91) and Schonewille et al. (100) ranges from 138-161 mmol/L while Cook (20) reported a value of 166 mmol/L for ovine saliva. It was calculated by Rogers and Van't Klooster (91) that salivary Na was responsible for 95% of the total Na entrance into the rumen. Furthermore, these authors (91) also showed that from the total amount of Na which entered the rumen, 10 % was absorbed in the rumen, 42 % was absorbed in the omasum and 48 % passed the proximal duodenum. Thus, although there is a net secretion of Na before the proximal duodenum, large amounts of Na are absorbed before the proximal duodenum, especially in the omasum. Extensive absorption of Na between the rumen and abomasum was also observed in ruminating bull calves by Erdrise et al. (33); 54% of the amount of sodium that left the rumen was absorbed in the omasum.
Although there is a net secretion of Na in the duodenum (91), originating from bile and pancreas, the overall net absorption of Na in the intestine was 94% of the amount, which passed either the abomasum or proximal duodenum of cows, steers and sheep (Table 1). Furthermore, it is clear that next to the small intestine, the large intestine also play an important role in post-duodenal Na absorption (Table 1). These calculations are corroborated by Van Weerden (122), who demonstrated a sharp decrease in the Na concentration of chyme collected after the small intestine.
Finally, it can be calculated that net Na absorption, expressed as a percentage of the amount passing either abomasum or proximal duodenum, is higher in sheep then in cows and steers, the values being 97 % and 90% respectively. Because endogenous Na losses, i.e. inevitable Na losses associated with mucosal cells and gastro-intestinal juices, are quantitatively negligible between the large intestine and faeces, the latter values are probably more or less similar to the true absorption coefficients of Na. However, as far as we know, there are no experimental data available that corroborate the speculation that Na absorption is more efficient in sheep than in cows.

3.1.1 Mechanisms of Na absorption

On the basis of in-vitro experiments, it has been shown that Na is actively absorbed in the rumen (103, 113) and this process is powered by a Na/K-ATPase localized in the basolateral membrane of rumen epithelial cells. The process of ruminal Na uptake is electroneutral and is mediated by a Na/H exchanger located in the apical membrane of rumen epithelial cells (67). Furthermore, Martens et al (67) and Diernaes et al. (28) observed a constant coupling between ruminal Na and Cl transport, and on the basis of in-vitro experiments with isolated bovine rumen epithelium (103), it was suggested that there is a Cl/HCO_3 exchanger working in parallel with the Na/H exchanger.

Table 1: Flow of sodium along the gastro intestinal tract of cows, steers and sheep

Reference	Species	Body weight (kg)	n	Na-intake (g/day)	Na-intake + saliva- Na (g)	Rumen (g)	Abomasum (g)	Proximal duodenum (g)	Terminal ileum (g)	Faeces (g)
(91)	cow	441	2	26.7	580.5	524.5		278.2	106.7	4.0
(87)	Cow	615	5	57.2				260.9		30.0
			5	58.2				246.3		25.7
			5	65.7				261.1		30.0
			5	59.7				318.3		28.1
			5	64.1				289.0		25.2
(42)	steers	261	6	12.2			40.6		30.0	3.7
			6	11.6			32.4		32.4	2.7
			6	10.9			22.9		23.5	1.9
(62)	Cow	648	8	107.3				172.2		16.0
			8	98.3				187.6		26.3
			8	118.6				278.0		32.9
			8	91.1				226.4		23.4
(86)	Sheep	42	6	1.04		22.7	17.1		18.1	0.33
			6	1.01		14.1	9.6		15.1	0.12
(82)	Sheep	adult	2	2.47				16.4	20.4	0.85
			2	3.14				20.0	18.0	0.95
			2	3.14				17.6	13.4	0.71

Table 1: (continued)

Reference	Species	Body weight (kg)	n	Na-intake (g/day)	Na-intake + saliva- Na (g)	Rumen (g)	Abomasum (g)	Proximal duodenum (g)	Terminal ileum (g)	Faeces (g)
(43)	sheep	36	6	1.48			10.0		6.2	0.27
			6	1.51			7.5		5.9	0.18
			6	1.53			7.4		6.1	0.18
			6	1.50			8.7		6.3	0.21
			6	1.51			7.9		5.8	0.20
(41)	sheep	41	Not given	1.37				13.6	12.7	0.03
				2.20				16.0	12.2	0.20
				1.10				5.3	2.9	0.27
				1.76				18.1	11.5	0.56
				1.54				7.9	5.2	0.14
				2.46				11.1	8.5	0.25

Sodium uptake by omasal epithelial cells is, at least partly, pD dependent as was shown by Schultheiss and Martens (101). Currently, it is not known whether or not a carrier mediated transport mechanism is involved in the apical uptake of Na by omasal epithelial cells. Furthermore, it is not clear which anion is absorbed in parallel with Na, but it is unlikely that Cl accompanies transepithelial Na transport since Cl is secreted into the omasal contents (33) although (34, 109) it may be suggested that Na absorption is linked to the absorption of the volatile fatty acids because there is also a net absorption of volatile fatty acids in the omasum (34, 49). Such a linkage between the absorption of Na and volatile fatty acids was demonstrated in rumen epithelium of cows (28, 103), sheep (38) and in the colon of sheep (93) and goats (4).
As was mentioned above, Na is required for the absorption of glucose; i.e. co-transport. Indeed, Na-glucose co-transporters are demonstrated in ruminating sheep (7), bull calves (72) and lactating cows (81) and it was shown in lactating cows that they are widely distributed along the gastro-intestinal tract (81). The activity of Na-glucose co-transporters declines rapidly after weaning, when milk fed calves change to a roughage-rich ration (97, 98, 105). This drop in activity of Na-glucose co-transporters is caused by the limited amounts of sugars that reach the intestine of ruminating animals compared to monogastric animals (106,128), indicating that the activity of Na-glucose co-transporters is directly related to the amount of glucose available (36, 105, 123). Indeed, when sugars are introduced directly into the intestine, the levels of Na-glucose co-transporters increase rapidly again (106). Apart from glucose, Na is also required for the uptake of some amino acids. Sodium dependent co-transport is demonstrated for alanin (21), methionin (45), proline (106) and lysine (127), but it is also reported that the absorption of lysine occurs independent from Na (45). Next to Na co-transport with glucose and/or amino acids several other co-transport mechanisms have been identified; i.e Na/Cl, Na/H in parallel with Cl/HCO_3 and Na/K/2Cl (68). Apart from the Na linked co-transporters mentioned above, it is suggested that Na uptake also occurs passively through Na channels located in the apical membrane of intestinal epithelial cells (68). Thus, it is clear that Na can be absorbed by many pathways along the intestinal mucosa, but, as far as we know, no quantitative data are available about the relative importance of the individual transport mechanisms.

3.1.2 Na absorption in relation to Na source

Data from balance trials with bovine and ovine species are presented in Table 2 and 3 respectively. The overall apparent Na absorption, expressed as a % of intake, was found to be 83.9% (SD ± 9.4, n = 35) in bovine and 80.8% (SD ± 11.9, n = 34) in ovine species. For the calculation of the latter value the aberrant first observation from the study of Van Houtert et al. (53) was excluded, i.e. 17.9% (Table 3). The values, both the mean and standard deviation, of apparent Na absorption calculated on the basis of Tables 2 and 3, correspond very well with those presented by Kemp (56); i.e. 81% (SD 10.5, n = 47). Thus, when a coefficient of variation of about 12 % on apparent Na absorption is taken into account, it is difficult to see that there are systematic differences in apparent Na absorption between the different rations/feeds (Table 2 and 3). On the basis of the data of Godwin et al. (39) the fractional absorption of Na from supplemented NaCl can be calculated; i.e. (Δ apparent Na absorption / Δ Na intake) x 100%, and a mean value of 91.4% was found. This relative high value is, at least partly, explained by the method of calculation because the faecal endogenous Na losses, if any, are fully assigned to the faecal excretion of the basal ration. This value of 91.4% is similar to the value calculated on the basis of balance data from Bell and Sly (9) (same method of calculation), i.e. 90%. In this study also $NaHCO_3$ was used as a source of supplemental Na and the fractional absorption of Na was calculated to be 85%. However, on the basis of this study (9), it cannot be concluded that the availability of Na from bicarbonate is lower then that of chloride because the Na intake from the basal ration was not kept constant among the treatments.

Table 2: Na balances in bovine species from various rations

Reference	Species	BW[1]/ Milk (kg) / (kg/day)	n	Ration			Na-intake[2] (g/day)	Na-content ration[3] (g/kg DM)	Apparent digestibility (% of in-take)
				Type of Roughage	Type of Concen-trates	Proportion of roughage (% of total DM[4])			
(87)	cow	615[5] / 20.0							440
			5	40% alfalfa hay(lage), 20% corn silage	grain-based	40%	57.2	3.29	55.1[6] (grab)
(62)	cow	648[5]/ 27.7							
			8	alfalfa silage	grain-based	50%	107.3	5.47	85.1[6] (grab)
			8	barley silage	grain-based	50%	98.3	5.28	73.2 (grab)
			8	oat silage	grain-based	50%	118.6	7.10	72.3 (grab)
			8	triticale silage	grain-based	50%	91.1	5.30	74.3 (grab)
(107)	cow	654 / dry	6	wheat hay		100%	45.4	5.96	80.9[7] (tot)
		550 / 39.4	6	9.2% vetch hay, 25.6% corn silage	grain-based	35%	47.1	2.45	77.6 (tot)
		550 / 41.5	6	9.2% vetch hay, 25.6% corn silage	grain-based	35%	66.7	2.67	74.8 (tot)
(104)	cow	683 / dry	5	wheat silage[8]		100%	25.3	3.16	80.3 (tot)
		565 / 34.1	5	wheat silage	grain-based + cottonseed	33%	28.1	1.98	83.2 (tot)
		549 / 31.4	5	wheat silage	grain-based + cottonseed	33%	29.1	1.91	82.1 (tot)
(25)	cow	514 / 23.2	18	50% corn silage, 10 % haylage	soybean-based	60%	75.1	4.50	89.1 (tot)
		518 / 23.4	18	alfalfa (hay)lage	soybean/ear corn-based	55%	66.4	3.98	87.8 (tot)

Table 2: (continued)

Reference	Species	BW/ Milk (kg) / (kg/day)	n	Ration			Na-intake (g/day)	Na-content ration (g/kg DM)	Apparent digestibility (% of in-take)
				Type of roughage	Type of Concen-trates	Proportion of roughage (% of total DM)			
(24)	Cow	496 / 19.5	18	alfalfa (hay)lage	grain/soybean-based	51%	62.7	3.87	93.3% (tot)
		477 / 18.3	18	alfalfa hay(lage)	grain/soybean-based	51%	64.7	4.26	94.9% (tot)
		523 / 18.9	18	alfalfa hay(lage)	grain/soybean-based	49%	65.4	3.85	95.7% (tot)
		514 / 18.2	18	alfalfa hay(lage)	grain/soybean-based	49%	63.2	4.05	95.9% (tot)
		603 / 15.3	18	alfalfa hay(lage)	grain/soybean-based	56%	77.0	4.33	94.8% (tot)
		596 / 14.9	18	alfalfa hay(lage)	grain/soybean-based	56%	77.2	4.60	95.6%(tot)
(23)	Cow	723 / dry	11	30% timothy hay, 70% alfalfa hay		100%	16.6	1.63	83.1%(tot)
		720 / dry	10	30% timothy hay, 70% alfalfa hay		100%	15.8	1.56	75.9%(tot)
(42)	Steer	261							
			6	orchard grass hay	concentrate	40%	15.1	4.31	74.2% (tot)
			6	orchard grass hay	concentrate	40%	14.4	4.11	82.6%(tot)
			6	orchard grass hay	concentrate	40%	14.5	4.14	87.6%(tot)
(91)	Cow	440 / 11	2	various rations			26.7	2.63	85.0%(tot)

Table 2: (continued)

Reference	Species	BW/ Milk (kg) / (kg/day)	n	Ration			Na-intake (g/day)	Na-content ration (g/kg DM)	Apparent digestibility (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM)			
(99)	cow	671 / dry							
			6	artificially dried grass	concentrate	86%	31.1	4.82	93.2%(tot)
			6	artificially dried grass	concentrate	85%	31.2	4.84	94.9%(tot)
			6	artificially dried grass	concentrate	83%	32.2	4.79	95.0%(tot)
(56)	cow	NG / 15.8	5	fresh grass		100%	6.8	0.53	80.9%(tot
		NG / 17.6	10	fresh grass		100%	10.5	0.85	85.7%(tot)
		NG / 17.0	6	fresh grass		100%	21.7	1.81	83.4%(tot)
		NG / 8.6	2	fresh grass		100%	43.0	4.75	90.7% (tot)
		NG / 13.4	6	fresh grass		100%	83.7	7.73	90.2%(tot)
		NG / dry	4	hay	oatmeal	NG	17.5	2.80	77.7%)tot)
		NG / 11.8		hay/corn	Beet pulp / concentrate	NG	18.1	1.34	69.1%(tot)

[1] BW = Body Weight
[2] Na intake from ration and non-orally supplemented Na, if any.
[3] Na concentration of ration alone. Thus, without the Na supplemented non-orally
[4] DM = Dry Matter
[5] Pooled data, data of separate experimental treatments were not given
[6] Calculated on the basis of an indigestible marker (faecal grab samples)
[7] Calculated on the basis of total faeces collection
[8] The wheat silage contained 7.1 g Na/kg dry matter, although not mentioned it was probably treated with NaOH.
[9] NG = Not Given

Table 3: Na balances in ovine species from various rations

Reference	Species	BW[1] (kg)	n	Ration			Na-intake[2] (g/day)	Na-content ration[3] (g/kg DM)	Apparent digestibility (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[4])			
(86)	wethers	42	6	orchard grass hay		100%	1.04	1.40	70.2[5](tot)
		42	6	orchard grass hay	100 g $KHCO_3$ in rumen	100%	1.01	1.40	89.1%(tot)
(41)	sheep	41[6]							
			NG[7]	ryegrass		100%	1.37	2.50	97.8(tot)
			NG	ryegrass		100%	2.20	2.50	90.9%
			NG	short rotation ryegrass		100%	1.1	2.00	75.5%
			NG	short rotation ryegrass		100%	1.76	2.00	68.2%
			NG	clover		100%	1.54	2.80	90.9%
			NG	clover		100%	2.46	2.80	89.8%
(53)	wethers	33.2	8						
				Urea treated chopped oaten hay	Oaten hay/ Lucerne pellet	84%	2.80	2.88	17.9%
				Urea treated chopped oaten hay	Oaten hay/ Lucerne pellet	86%	2.60	2.41	78.1%
(82)	sheep	adult							
			2	hay		100%	2.47	3.32	65.6[8](grab)
			2	hay	barley + $NaCO_3$ (0.89 g Na)	68%	3.14	3.05	69.7
			2	hay	barley + $NaCO_3$ (1.84 g Na)	34%	3.14	1.72	77.4

Table 3: (continued)

Refer-ence	Species	BW[1] (kg)	n	Ration			Na-intake[2] (g/day)	Na-content ration[3] (g/kg DM)	Apparent di-gestibility (% of intake)
				Type of Rough-age	Type of Concen-trates	Proportion of roughage (% of total DM[4])			
(39)	ewes	39.8							
			4	Lucerne	oat chaff	12%	2.90	4.03	88
			4	Lucerne	oat chaff	12%	3.30	4.02	88
			8	Lucerne	oat chaff	12%	2.90	4.03	85
			8	Lucerne	oat chaff + 11.5 g Na infused[9]	12%	14.4	4.03	90
			8	Lucerne	oat chaff + 17.3 g Na infused	12%	20.2	4.03	91
			8	Lucerne	oat chaff + 23.0 g Na infused	12%	25.9	4.03	89
			8	Lucerne	oat chaff + 28.8 g Na infused	12%	31.7	4.03	89
			8	Lucerne	oat chaff + 34.5 g Na infused	12%	37.4	4.03	94
			8	Lucerne	oat chaff + 46.0 g Na infused	12%	48.9	4.03	91
(114)	sheep	55							
			8	Chopped hay	concentrate	30%	2.02	2.36	58.4
			8	Chopped hay	concentrate + KCl in diet	30%	2.01	2.35	64.7
			8	Chopped hay	concentrate + wa-ter	30%	2.02	2.36	58.4
			8	Chopped hay	concentrate + KCl infused	30%	2.02	2.36	60.9
			5	Chopped hay	concentrate	30%	3.78	4.38	63.2
			5	Chopped hay	concentrate + KAc	30%	3.77	4.37	84.4

Table 3: (continued)

Reference	Species	BW[1] (kg)	n	Ration: Type of Roughage	Ration: Type of Concentrates	Ration: Proportion of roughage (% of total DM[4])	Na-intake[2] (g/day)	Na-content ration[3] (g/kg DM)	Apparent digestibility (% of intake)
(85)	wethers	40							
			6	ground orchard grass	corn-based +1.2 g Na infused[10]	9.3%	3.44	3.11	68.6
			6	ground orchard grass	corn-based + 10.6 g Na infused	9.3%	12.84	3.11	91.6
			6	ground orchard grass	corn-based + 19 g K infused[11]	9.3%	2.24	3.11	80.8
(43)	wethers	36							
			6		Corn-based, 0.6% K[12]	0%	1.43	2.00	86
			6		Corn-based, 1.2% K	0%	1.45	2.03	89
			6		Corn-based, 4.8% K	0%	1.46	2.04	93.2

[1] BW = Body Weight
[2] Na intake from ration and non-orally supplemented Na, if any.
[3] Na concentration of ration alone, thus, without the Na supplemented non-orally
[4] DM = Dry Matter
[5] Calculated on the basis of total faeces collection
[6] Pooled data, data of separate experimental treatments were not given
[7] NG = Not Given
[8] Calculated on the basis of an indigestible marker (faecal grab samples)
[9] Na infused intraruminally in the form of NaCl
[10] Na infused intravenously in the form of NaCl
[11] K infused intravenously in the form of KCl
[12] KCl incorporated in the ration

3.2 Excretion[51]

The regulation of Na balance is closely related to that of water balance. As mentioned previously, Na is the main cation of the ECF and together with its associated anions it accounts for more than 90% of the osmotic pressure of the ECF. The Na concentration of the ECF is the primary subject of regulation. An increase of the Na concentration of the ECF results in an increase of the waterconsumption and triggers the release of anti-diuretic hormone (ADH), which increases the re-absorption of water from the tubular fluid of the nephron. These two actions will counteract the initial increase of the Na concentration of the ECF. However, at this stage the total amount of Na and volume of the ECF are raised. This rise of ECF volume includes a rise of blood pressure, which enhances glomerular filtration rate (GFR). The excess of Na and water are excreted by the kidneys, thereby restoring ECF volume to its normal level. Furthermore, at increased rates of filtered Na, tubular re-absorption of Na is less efficient causing increased rates of Na excretion by the kidney.
A deficit of Na in the ECF hampers the release of ADH, which causes a rapid excretion of excess water so as to increase the Na concentration of the ECF. When blood pressure becomes depressed, GFR is lowered and less Na is flitered out from the blood. Furthermore, secondary to the stimulation of the renin-angiotensin system (restore blood pressure), the release of aldosterone is stimulated, which enhances the tubular re-absorption of Na. Aldosterone is only important during Na deficiency. The combination of these mechanisms can cause a drop in urinary Na excretion so that virtually no Na is excreted by the kidneys during prolonged Na deficiency. Furthermore, it should be stressed that apart from the kidneys, especially the large intestine (122) play a very important role in reducing the faecal Na losses to almost zero, during Na deficiency (88, 89).

4. SODIUM REQUIREMENTS

Theoretically, the minimum net requirement of Na for maintenance is the amount Na required to compensate the inevitable Na losses by the animal; i.e. the inevitable faecal, urinary and dermal (hair, sweat) losses. Strictly speaking, the concept of an inevitably faecal loss of Na may not be applicable because under various conditions there might be substantial interchange between the Na in the gut and that in the body
(3). Furthermore, the inevitable faecal loss of Na may be dependent on the level of potassium (K) intake; it appears that a drop in the Na concentration of faecal water is accompanied by a raise of the K concentration of faecal water so as to keep the sum of Na and K more or less constant (31, 122). This reasoning is corroborated by the observations in sheep that an increase of the K intake results in a decrease of the faecal Na excretion (43, 86, 114). However, because there are no sufficient experimental data available to establish the quantitative relationship between the obligatory faecal Na losses and K intake, this interaction with K is neglected.
Apart from maintenance, the minimum daily net requirement of Na is also determined by the amount of Na retained by either the gravid uteri and/or growth of the animal, or the amount of Na that is associated with milk production. Consequently, the minimum gross Na requirement is calculated by dividing the total net Na requirement by the coefficient of true Na absorption. In the following sections, the estimates of the previously mentioned factors used by different councils and in the literature for dairy cows, beef cattle, sheep and goats are listed and commented when appropriate. Because the Dutch Central Bureau for Livestock Feeding (CVB) (16) only provides guidelines based on balance trials to calculate the Na requirement of dairy cows, tentative factorial estimates for dairy cows and other ruminant species are proposed.

4.1 Dairy cows

4.1.1 Maintenance

The current Dutch estimate for the gross Na requirement for maintenance of an adult cow with a body weight of 600 kg, is 7 g/day (16). This value is not based on estimates of inevitable Na losses (Table 4) but is taken from the outcome of balance trials with lactating dairy cows fed fresh grass (56). In this study, the mean Na balance was 2.5 g/day at Na intakes higher than 7 g/day and it was reasoned that the retained amount of 2.5 g Na/day was part of the endogenous losses (hair, sweat, dripped saliva), thereby neglecting the fact that retention on the basis of balance trials may be overestimated (32). Then, the amount of “available Na” (56) (available Na = Na intake – Na faeces – Na milk) was calculated by subtracting the value of 2.5 g Na/day from the observed retentions. Thereafter, the amount of available Na was regressed against Na intake, and it appeared that at Na intakes > 3 g/day, available Na was quantitatively excreted with urine. These observations and considerations resulted in an estimated Na requirement for maintenance of 5.5 g/day. It is clear that this value, apart from the incorporation of the observed retentions, most likely overestimates the Na requirement for maintenance because urinary losses were higher then the inevitable urinary Na losses. Indeed, it was shown by Kemp (56) that at Na intakes lower than 8 g/day by lactating cows excreting 5 g of Na with milk, the urinary Na excretion dropped to approximately 0.5 g/day which was associated with a calculated Na balance of –0.8 g/day. Furthermore, Kemp and Geurink (57) observed that urinary Na excretions dropped to values < ± 0.5 g/day during Na deficiency. Thus, an amount of 0.5 g Na/day may be considered as the inevitable urinary loss of Na by the cows used the studies of Kemp (56) and Kemp and Geurink (57).

Table 4: Summary of estimates of endogenous Na losses expressed in mg/kg BW, unless otherwise noted

	Endogenous/inevitable losses			
	Der-mal/Sweat	Faecal	Urine	Total
Dairy cows				
CVB (16)	not given	not given	not given	not given
ARC (3)	0.6[1]	5.8	negligible	6.4
DLG (31)	not given	not given	not given	0.35 g/kg faecal water[2]
NRC (79)				
non-lactating	1[3]	15 (faeces + urine)		16
lactating	1[3]	38 (faeces + urine)		39
INRA (44)	not given	5	10	15
Beef cattle				
CVB (16)	not given	not given	not given	not given
ARC (3)	1.0[4]	5.8	negligible	6.8
DLG (30)	not given	not given	not given	0.55 g/kg DM intake
NRC (78)	not given	not given	not given	not given
INRA (44)	not given	5	10	15
Sheep				
CVB (16)	not given	not given	not given	not given
ARC (3)	negligible	5.8	20	25.8
NRC (77)	not given	not given	not given	not given
INRA (44)	not given	5	10	15
Goats				
CVB (16)	not given	not given	not given	not given
ARC (3)	not given	not given	not given	not given
NRC (76)	not given	not given	not given	not given
INRA (44)	not given	not given	not given	not given
Kessler(60)	not given	not given	not given	15

[1] Temperate conditions (no further specifications).
[2] Calculated on the assumption that faecal water contains 15 mmol Na/L.
[3] At temperatures between 25-30 °C.
[4] No specifications provided.

The German estimate for the maintenance requirement of Na is entirely based on the faecal excretion of Na (Table 4). A value of 0.35 g Na/kg faecal water was adapted by the DLG as an estimate for the inevitable faecal Na losses (Table 4). Assuming a digestibility of the dry matter of 65% (a value corresponding to a NEl of 5.2 MJ/kg DM (= equivalent to 750 VEM) and a dry matter content of faeces of 15%, each kg of dry matter ingested yields 2 kg of faecal water. In order to maintain energy balance, a cow with a body weight of 600 kg requires

6.6 kg dry matter of feed with an energy content of 5.2 MJ NEl (roughage), resulting in a faecal loss of 4.6 g of Na/day; i.e 7.7 mg/kg BW. This value is about 30% higher than the corresponding value estimated by the ARC (Table 4) but the value of 7.7 mg/kg BW probably contains a safety margin because the Na concentration in faecal water can drop to a value as low as 0.12 g/kg faecal water (31) at low Na intakes (actual Na intake not given), resulting in a minimum faecal Na loss of 1.6 g Na/day; i.e. 2.6 mg Na/kg BW. Indeed, Boencke et al. (13) and Renkema et al. (89) reported that the Na concentration in faecal water can drop to value as low as 0.07 g Na/kg. Thus, following the German assumptions for estimating the endogenous faecal Na losses, values may range between 2.6 and 7.7 mg/kg BW. Dermal (including sweat) and urinary Na losses are not estimated by the DLG (31).
The ARC estimates for the endogenous faecal losses are 5.8 mg/kg BW (Table 4). This value was derived from the pooled regression (7 studies) of faecal output of Na on intake of Na; i.e. Faecal Na (g/day) = 0.086 x Na intake (g/day) + 2.88 (r = 0.35, p <0.001). Thus, on the basis of this regression the faecal Na loss at zero Na intake appears to be 2.88 g/day. Then, the intercept was divided by the assumed BW of the animals (500 kg), resulting in a value of 5.8 mg/kg BW (3). A similar approach to the data presented in Table 2, using only balance data from studies with dairy cows which provide quantitative information with respect to Na intake and faecal Na excretion, resulted in the following regression formula: Faecal Na (mg/kg BW/day) = 0.047 x Na intake (mg/kg BW/day) + 4.43 (r = 0.48, p = 0.014). Thus, the estimated faecal Na loss at zero Na intake, appears to be 4.4 mg Na/kg BW. The French (44) estimates for the endogenous faecal losses are more or less taken from the ARC (3). A reason for the difference between their value and that of the ARC, i.e. 5 vs. 5.8 mg/kg BW, is not given. Furthermore, a value of 10 mg endogenous urinary Na loss /kg of BW is incorporated in the French recommendation for estimating the net maintenance requirement of Na, but this value is not further explained. It may be suggested that an inevitable urinary Na loss of 10 mg/kg BW is somewhat high. As was mentioned earlier, Kemp (56) observed an urinary Na excretion of 0.5 g/day which was accompanied with a small negative Na balance. Assuming that the cows used in this study had a BW of 500 kg (actual BW was not reported), it can be calculated that urinary Na loss was 1 mg/kg BW. Such a low inevitably urinary Na loss agrees with the ARC (3). Nevertheless, the total net requirement for maintenance set by INRA was estimated to be 15 mg/kg BW (44). This value has been adapted by the NRC for non-lactating cows (Table 4). On the basis of observational studies (94, 95) maximum lactational responses were reported after feeding rations with Na concentrations of 0.7 - 0.8 % (DM-basis). Therefore, the NRC empirically set the net maintenance requirement of Na, without dermal/sweat losses, at 38 mg/kg BW (Table 4). Thus, it seems that Na intakes far in excess of minimum requirement, enhance milk production. However, it is difficult to explain these effects of high dietary Na concentrations on either DM intake or on milk yield, and it was suggested by the NRC (79) that more research is needed for proper estimates of endogenous Na losses under various conditions.
On the basis of faecal Na excretion regressed against Na intake, two independent estimates of the endogenous faecal Na loss are given; 5.8 mg/kg BW by the ARC (3) and 4.4 mg/kg BW (Table 2). Thus, it is suggested to take the mean of these two values so as to estimate the endogenous faecal Na losses in cows; i.e. 5.1 mg/kg BW. This estimate of endogenous faecal Na loss, falls within the range indicated by the DLG (31). Clearly, the current proposal with respect to the endogenous faecal Na losses is higher than the minimum faecal Na loss estimated on the basis of minimum Na loss with faecal water. However, it seems that there are not enough data available in literature to establish a reliable quantitative relationship between dry matter intake, Na- and K intake and the amount of Na excreted in faeces.
Furthermore, it seems that there is a very low inevitably urinary Na loss in the order of 1 mg/kg BW (56). Because there are no other data available for estimating inevitable dermal Na losses (sweat, skin), we suggest to use the estimate provided by the ARC (3). Thus, the suggested total net Na requirement for maintenance in dairy cows is : 5.1 (faecal loss) + 1 (urinary loss) + 0.6 (dermal/sweat) = 6.7 mg/kg BW.

4.1.2 Pregnancy

The net requirement for pregnancy set by the ARC (Table 5) was calculated on the basis of following formula:

Na content of foetus and adnexa (g) =

$$0.025 \text{ x Birth weight x } 10^{5.203 - 6.153*(EXP(-0.00253*D))}$$

D = days from conception in the range of 141 to 281 (= parturition)

Assuming a birth weight of 44 kg, Na retention in foetus and adnexa was calculated to be 1.5 and 2.4 g/day during the first and second month of the dry period respectively. The net requirement for pregnancy set by the NRC (Table 5) is derived from slaughter experiments of House and Bell (52). They reported a Na accretion rate of 1.4 g/day between 190 and 270 days after conception. The same value is obtained on the basis of the formula provided by the ARC (3). Thus, this formula may be used to predict Na accretion rate of the gravid uteri. The net requirements for pregnancy set by the DLG (31) are lower than those estimated by the ARC (3) which may be explained by the fact that the German estimates for Na accretion rate in foetus and adnexa are based on beef cattle delivering calves with a lower birth weight (31). The net Na requirement for pregnancy provided by INRA (44) is somewhat lower than that estimated on the basis of the formula provided by the ARC for the last 12 weeks of pregnancy; i.e. 1.6 g/day. This discrepancy cannot easily be explained since the value provided by INRA (44) is not explained.
Sodium accretion rate during pregnancy seems to be properly predicted by the formula provided by the ARC (3). Thus, it is suggested to adapt the formula of the ARC to calculate the net Na requirement of the gravid uterus during pregnancy.

4.1.3 Growth

The value adapted as the Na requirement for growth, in the range from 150 to 600 kg BW, by the NRC (79) was taken from INRA (44) and both councils do not provide any further information. The Na requirement for growth was arbitrarily set on 1.5 g/kg growth by the ARC (3) and this value is based on body content of Na of castrated beef Shorthorn and Hereford males or German black pied steers. However, it must be noted that the estimated Na required for growth on the basis of the studies with beef cattle were either 1.6 or 1.1 g/kg growth (100 - 500 kg BW). The latter value correspond with the estimated Na requirement for growth provided by the DLG (31), who based their estimate also on whole body Na contents of young steers (no further information). Thus, the Na requirement for growth appears to range from 1.1 to 1.6 g/kg of growth. Because the mean of these two values correspond well with the estimates set by the NRC (79) and INRA (44), it is suggested to adapt a value of 1.4 g/kg growth as the estimate for the net Na requirement for growth for replacement heifers ranging from 100 to 600 kg of BW.

Table 5: Summary of estimates of net Na requirements for foetal retention, growth and milk

	gravid uterus (g/d)	growth (g/kg gain)	milk (g/L)
Dairy cows			
CVB (16)	not given	not given	0.4
ARC (3)	1.5[1] (8-4 weeks ante partum)	1.5 (75-500 kg BW)	0.58[2]
	2.4[1] (4-0 weeks ante partum)		0.64[3]
DLG (31)	0.6 (6-4 weeks ante partum)	1.2	0.5
	0.8 (3-0 weeks ante partum)		
NRC (79)	1.4 (190-270 days of gestation)	1.4 (150-600 kg BW)	0.63
INRA (44)	1.3 (12 weeks ante partum)	1.4 (150-600 kg BW)	0.45
Beef Cattle			
CVB (16)	not given	not given	not given
ARC (3)	not given	not given	not given
DLG (30)	not given	1.2 (<900 g growth/d)[4] 1.1 (1200 g growth/d)[4]	not given
NRC (78)	not given	not given	not given
INRA (44)	not given	not given	not given
Sheep[5]			
CVB (16)	not given	not given	not given
ARC (3)	0.26 (9-5 weeks ante partum)[6]	1.1 (4-45 kg BW)	0.4
	0.13 (4-0 weeks ante partum)[6]		
NRC (77)	not given	not given	0.4
INRA (44)	0.3 (6 weeks ante partum)	0.9 (10-50 kg)	not given
Goats			
CVB (16)	not given	not given	not given
ARC (3)	not given	not given	not given
NRC (76)	not given	not given	not given
INRA (44)	0.3 (6 weeks ante partum)	not given	not given
Kessler (60)	[7]	1.6 (< 32 kg) 0.4 (> 32 kg)	0.4 (Saanen/Alpine breeds) 0.6 (African/Asian breeds)

[1] Calf with birth weight of 44 kg.
[2] British Friesian cows
[3] Holstein Friesian cows
[4] Fleckvieh steers with a BW in the range from 200 to 650 kg.
[5] Na accretion due to wool production range from 3 to 12 mg/day at growing rates from 2.7-11.0 g/day (3).
[6] Total birth weight of 8 kg
[7] Accretion of Na during pregnancy is not given, but the Na content of goat foetus is estimated to be 1.7 g Na/kg foetus at term.

4.1.4 Milk production

The estimated Na concentration in milk varies from 0.4 to 0.63 g/L (Table 5). Adrian (1) provided a similar range of the Na concentration in milk. The estimate provided by the CVB (16) seems to be taken from the study of Kemp (56) who observed a Na content of milk ranging from 0.31 to 0.49 g Na/L, with a mean value of 0.38 g Na /L. The origin of the French (44) and German (31) estimates for the Na content of milk is not further specified. The ARC (3) values for the Na content of milk of each breed are each derived from one study. The NRC (79) adapted the ARC (3) value listed for the Holstein-Friesian breed. Furthermore, from studies by Delaquis and Block (25), Shalit et al. (104) and Silanikove et al. (107) mean Na contents of milk were 0.29, 0.42 and 0.45 g/kg respectively. The mean of all values referring to the Na content of milk, reported in this section is 0.46 g Na/kg, and it is suggested to adapt this value for calculating the net Na requirement due to milk production.

4.2 Beef cattle

4.2.1 Maintenance

The net maintenance requirements set by the ARC (3) for beef cattle are similar to those of dairy cattle with the exception that a somewhat higher value (reason unknown) was used to estimate the dermal Na losses (Table 4). The French estimates (44) for the net maintenance requirements of Na for beef cattle are equal to those for dairy cattle. As already mentioned above, the estimate for the inevitably urinary Na loss may be too high (see previous section). The German (30) estimate for the inevitable Na losses is expressed as a function of feed intake; i.e. 0.55 g/kg DM. This value is calculated under the assumption that the inevitable Na loss equals 11 mg/kg BW and that the animals have a DM intake of 2% of BW.
Essentially, both the ARC (3) and INRA (44) do not distinguish between dairy cows and beef cattle in their approach for estimating the Na requirement for maintenance. Therefore, we consider it opportune to apply also a value of 5.1 mg/kg BW for estimating the obligatory faecal Na losses for beef cattle and a value of 1 mg/kg BW as an estimate for the inevitably urinary Na loss. Because no other data are available to estimate dermal and or sweat losses, we suggest to use the value adapted by the ARC (3). Thus, the suggested total net Na requirement for maintenance in beef cattle is : 5.1 (faecal loss) + 1 (urinary loss) + 1 (dermal/sweat) = 7.1 mg/kg BW.

4.2.2 Growth

Specific factorial estimates concerning the net Na requirement for growth in steers (Table 5) are only provided by the DLG (30). However, the Na requirements for growth provided by the ARC are also based on observations in beef cattle (see section about dairy cows). Therefore, we suggest to adapt the same value for growth in beef cattle; i.e. 1.4 g Na/kg growth. The NRC (78) only gives a recommended dietary Na concentration in rations for beef cattle; i.e. 0.6 - 0.8 g Na/kg DM. Factorial estimates with respect to pregnancy and milk (suckling cows) are not given by any of the listed councils.

4.3 Sheep

4.3.1 Maintenance

The estimates for the faecal endogenous Na losses set by the ARC (3) and INRA (44) are more or less similar, values are 5.8 and 5 mg/kg BW respectively (Table 4). The difference between these values is unclear because INRA refers to the ARC for the French estimate. The estimate for the faecal endogenous Na losses of sheep provided by the ARC is not based on sheep data, but is derived from the previous mentioned regression calculated for cows (section 4.1.1.) because there were no suitable data available at that time (3). However, regression of faecal Na excretion (g/day) on Na intake (g/day), on the basis of the data

provided by Godwin et al. (39), resulted in the following equation: Faecal Na (g/day) = 0.083 x Na intake (g/day) + 0.22 (r = 0.94, p<0.001). Mean BW of the sheep used in this study was 40 kg, which results in a faecal Na loss of 5.5 mg Na/kg BW at a zero Na intake. This value corresponds reasonably with the above-mentioned value provided by the ARC (3). The inevitable urinary Na losses are estimated at 20 mg/kg BW by the ARC (Table 4). According to Todd (116) the obligatory losses estimated by the ARC are probably too high. Therefore, the French estimate for the inevitable urinary losses were arbitrarily set at 10 mg/kg BW (Table 4). Indeed, Underwood and Suttle (119) also mentioned that the maintenance requirements of Na are overestimated by the ARC; the maximum value for inevitably urinary Na loss listed by Underwood and Suttle (119) was 1 mg/kg BW. Furthermore, Vincent et al. (124) observed very low urinary Na losses ranging from 16 to 23 mg/day in Blackface sheep during pregnancy while dietary intake of Na ranged from 0.07 to 0.16 g/day. Body weight of the sheep was not mentioned in this study (124), but assuming a BW of 40 kg, inevitable urinary Na loss would range from 0.4 to 0.6 mg/kg BW.
With respect to the estimation of the endogenous faecal Na losses we suggest to use the value of 5.5 mg/kg BW because this value was actually derived from data obtained from sheep (39) instead of cows (3). It was shown by Vincent et al. (124) that sheep also can reduce their obligatory urinary Na losses to almost zero when a low Na diet is fed. Therefore, we suggest to adapt a value of 1 mg/kg BW, as an estimate of the inevitably urinary Na losses. Sodium losses due to sweat production are ignored because sweating is not an important way of thermoregulation in sheep (2). Thus, the suggested total net Na requirement for maintenance of sheep is : 5.5 (faecal loss) + 1 (urinary loss) = 6.5 mg/kg BW.

4.3.2 Pregnancy

The net requirement for pregnancy set by the ARC (Table 5) was calculated on the basis of following formula:

Na content of foetus and adnexa (g) = 0.25 x Birth weight x $10^{1.13 - 4.142*(EXP(-0.02987*D))}$

D = days from conception in the range of 63 to 147 (= parturition)

Assuming a total birth weight of 8 kg, Na retention in foetus and adnexa was calculated to be 0.26 and 0.13 g/day during 9 to 5 weeks and 4-0 weeks before parturition respectively. The net Na requirement for pregnancy provided by INRA (44) is about twice the value than that estimated on the basis of the formula provided by the ARC for the last 6 weeks of pregnancy; i.e. 0.3 g/day. This discrepancy cannot easily be understood since the value provided by INRA (44) is not explained nor an indication of total birth weight is given. We arbitrarily suggest to adapt the formula provided by the ARC (3) to estimate the Na requirement of the gravid uteri during gestation.

4.3.3 Growth and milk production

With respect to the net requirement of Na for growth and milk production, there are no considerable differences between the ARC and INRA (Table 5). Therefore, we suggest to adapt the following values for the net requirement of Na for milk production and growth; a value of 0.4 g Na/kg of milk and a value of 1.1 g/kg growth for sheep with BW ranging from 4 to 45 kg. The NRC (77) gives no factorial estimates with respect to the net Na requirement of sheep but recommend a dietary Na concentration of 0.9-1.8 g/kg DM for sheep.

4.4 Goats

4.4.1 Maintenance

An estimate about inevitable Na loss in goats is not known (60), but was taken from sheep (INRA,(44)); i.e. 15 mg/kg BW (60). As far as we know, there is no experimental proof that Na depleted goats can reduce the obligatory urinary Na loss to negligible amounts but it seems likely that a value of 15 mg/kg BW overestimates the inevitable Na losses, because goats resemble cattle in terms of their (digestive) physiology. Therefore, we suggest that the approach to calculate the net maintenance requirements of Na in goats can be similar to that of cattle. Thus, we suggest that the total net Na requirement for maintenance in goats can be estimated as follows : 5.1 (faecal loss) + 1 (urinary loss) + 0.6 (dermal/sweat) = 6.7 mg/kg BW.

4.4.2 Growth and milk production

A specific factorial estimate for goats with respect to the requirement for growth has been only provided by Kessler (60), but the origin of this, relative high value is not clear. Therefore, it was arbitrarily decided to adapt a value similar to that of cattle; i.e. 1.4 g of Na / kg growth. Furthermore, Kessler (60) uses a value of 1.7 g Na/kg foetus as the net requirement for pregnancy. However, it appears that this value represents the Na content of newborn goat kids (60), which is obviously not the same as the Na accretion rate (g/d) during pregnancy. According to INRA(44), Na accretion rate during pregnancy in goats is similar to that of sheep (Table 5). Therefore, we suggest to use the formula for sheep set by the ARC (section 4.3.2.) to calculate the net Na requirement for pregnancy. For Saanen/Alpine breeds, the Na content of milk was estimated by Kessler (60) to be 0.4 g/L, but Jenness (55) reported a range of 0.4 to 0.53 g Na/L for Saanen, Toggenburg and Alpine goats, with a mean value of 0.46 g Na/L. Thus, we suggest to adapt this latter value to calculate the Na requirement for milk production in dairy goats. For Anglo-Nubian goats, Jenness (55) reported a value of 0.56 g Na/L, which is similar to the estimate of Kessler (60) for African breeds. Therefore, we suggest a value of 0.6 g Na/L to calculate the Na requirement for milk production in goats of African breeds.

The NRC (76) does not provide factorial estimates with respect to the net Na requirements of goats (Angora, dairy- and meat goats) but they recommend to supplement the ration with 0.5% Na when Na is not supplied free of choice.

4.5 Coefficient of absorption

As far as we know, data on the basis of the radio-isotope of Na to asses the efficiency of true absorption of Na are not available. The ARC (3) arbitrarily adapted a value of 91% for the true absorption of Na which is similar to the value taken by INRA (44) and the DLG publication (31) concerning dairy cows (Table 6). Although the nature of the coefficient of Na absorption is not specified, the value for efficiency of absorption set by the NRC (79) is of the same magnitude. In contrast to dairy cows, the DLG adapted a value of 80% as coefficient of true Na absorption in beef cattle (30), but a reason for this difference with dairy cows is not provided. Similarly, Kessler (60) does not explain why a value of 80% as coefficient of true Na absorption was adapted in goats. The absorption coefficient used by the CVB (16) seems to be the coefficient of apparent Na absorption since it was based on the study of Kemp (56). Furthermore, the value adapted by the CVB (16) appears to contain a safety margin because the mean apparent Na absorption coefficient reported by Kemp (56) was 85%. Finally, differences between species (cattle vs. sheep) in the ability to absorb Na are not reported by the CVB, NRC and INRA. Only the ARC mentions specifically that they adapted the same coefficient of Na absorption for both cattle and sheep.

On the basis of the data presented in Table 1, it appeared that net Na absorption expressed as the amount passing either abomasum or proximal duodenum x 100%, had a calculated value of 90 %. Because the endogenous Na losses associated with mucosal cells and gastro-intestinal juices, are quantitatively negligible in the large intestines, this value is probably more or less similar to the coefficient of true absorption. Therefore, it is suggested to adapt a value of 90% as the true absorption coefficient in cattle. Furthermore, data presented in Table 1 suggest that sheep absorb Na more efficiently than cows; Na absorption expressed as the amount passing abomasum / proximal duodenum x 100%, had a calculated value of 97 %. However, we are somewhat reluctant to adapt this value as the true absorption coefficient of Na in sheep, because other recommendations do not distinguish between cattle and sheep with respect to the true absorption coefficient of Na (Table 6). Furthermore, we arbitrarily suggest to adapt also the value of 90% as the true absorption coefficient of Na for goats.

Table 6: Summary of estimates for the coefficient of Na absorption (% of intake)

	true absorption	**nature of absorption not specified**
CVB (16)		80
ARC (3)	91	
DLG (31)	95	
DLG (30)	80	
NRC (79)		90
INRA (44)	90	
Kessler (60)	80	

4.6 Na allowances

It was already mentioned (sections 4.1.4 and 4.4.2) that the reported Na contents in milk varies considerably. Therefore, it was considered opportune to incorporate a safety margin of 1.3 in order to calculate the Na allowance for lactating animals so as to ensure Na supply in lactating cows, sheep and goats with a high Na concentration in milk.

5. SODIUM DEFICIENCY

The first sign of Na deficiency in milking cows is polyuria/polydipsia (125) and a pica or craving for salt manifested by avid licking of wood or soil and the urine or sweat of other animals (119). However, salt hunger is non-specific and some animals eat salt when they are not deficient (26, 120). Nevertheless, it was shown that Na-deprived calves had a specific appetite for Na versus K and the anion seemed to be unimportant except in the case of carbonate (8). Furthermore, Na deprived cows and sheep exhibited a specific preference for Na (salt hunger or appetite), which is induced by high levels of circulating aldesteron (27) and a subsequent increase of angiotensin II (11, 12). An extreme appetite for salt can occur within 2-3 weeks of deprivation. Then, feed intake begins to decline and the animal develops a rough coat, loses weight and reduces milk yield (57, 119). The relative large time lag between an inadequate supply of Na and manifestation of clinical signs can be explained by the amount of Na present in the rumen liquid which acts as a reserve during an insufficient supply of dietary Na (57). Kemp and Geurink (57) suggested that the amount of Na that can be safely withdrawn from the rumen contents of dairy cows may be considerable higher than 200 g. Furthermore, the skeleton may also acts as a Na reserve, but nearly half of the Na in bone is non-exchangeable with fluid compartments (51). Therefore, Na present in bone plays only a modest role in maintaining extracellulair Na concentration (69)

6. SODIUM INTOXICATION

Na (salt) intoxication most frequently occurs in poultry and pigs and is more related to water deprivation than directly to salt poisoning (54). Indeed, water deprivation caused death of 4 lambs, out of 100, after avid consumption of a mineral supplement containing 4% NaCl (96). A similar case in sheep has been reported by Schulz et al. (102). Furthermore, Rademacher and Lorenz (84) reported a case of salt intoxication in calves after feeding of highly concentrated milk replacers without having free access to water. However, after ingestion of a diet containing 17.7 g Na/kg dry matter (15 g Na from supplemented NaCl), Hampshire x Suffolk wether lambs (40 kg) tolerated a restriction of water intake of 15% relative to voluntary water intake (117).
It has been reported by the CVB (16) that cows can consume at least 500 g NaCl/day. The maximum tolerable level set by the NRC is 4% NaCl (DM-basis, equivalent to 16 g Na/kg dry matter) for lactating cattle and 9% (DM-basis, equivalent to 35 g Na/kg dry matter) for other classes of cattle and sheep (77-79). The values reported are only acceptable under the assumption that enough fresh drinking water is provided (16, 77-79).
In a study with dairy cows an increase of the dietary Na content from 3 to 8 g/kg dry matter, was associated with positive lactational responses without any health problems (17). Another study from the same group (83) did not report any health problems after the feeding of a ration containing 12 g Na/kg dry matter. In beef cattle, with body weight ranging from 230-380 kg, supplemental NaCl resulted in increased Na intakes ranging from 49 to 611 g/day (22). The associated dietary Na contents were 1.5 and 18.5 g/kg dry matter and there are no health problems reported in this study while animal performance was somewhat increased (22). The latter observation was not corroborated by Harvey et al. (48). Leontowicz et al. (63) studied the effect of supplemental NaCl on selected digestive characteristics in Merino wether lambs (24 kg). It appeared that a dietary Na content of 17 vs. 1.2 g/kg dry matter only reduced apparent potassium absorption (63) while digestibility's of dry- and organic matter were not affected. Furthermore, there are no indications that lambs suffered from diarrhoea (63, 64). In contrast, disturbances in feed intake and diarrhoea in lambs are reported by Hamilton and Webster (46) after oral supplementation with NaCl (2 g/kg BW), which is equivalent to 13 - 25 g Na /kg DM. In this study, the supplemented vs. control lambs had a 10% lower body weight after 5 - 6 months. Overall, it may be concluded that dietary Na contents up to at least 10 g Na /kg DM are well tolerated by ruminants when they have free access to fresh water.

7. SODIUM STATUS

The amount of Na absorbed in excess of requirement is excreted in urine. During Na deficiency, there is aldosterone induced (90) decrease of the urinary excretion of Na and a decrease of the salivary Na concentration which is accompanied by a simultaneous increase of the salivary K concentration (27, 57, 59). Thus, urinary Na excretion is reduced to almost zero during Na deficiency. However, estimates of the animal's Na status based only on urine samples are inaccurate due to the diurnal variation of the Na concentration in urine, even when Na supply is sufficient (37, 57, 121). Consequently, only the absolute 24 h excretion of urinary Na excretion can be used to asses Na status, which requires quantitative collection of urine. Thus, under practical conditions the Na status of the animal is difficult to asses on the basis of urine and the assessment of Na status on the basis of salivary Na concentration is preferred (59). It was reported by Kemp and Geuring (57) that Na concentrations in saliva ranged from 130 to 152 mmol/L while cows excreted large amounts of Na with urine (> 22 g Na/day), indicating that Na intake was in excess of requirement. Schonewille et al. (100) reported salivary Na concentrations in pregnant heifers (490-590 kg) > 130 mmol/L when Na intake was at least 38 g/day. Furthermore, Rogers and Van't Klooster (91) reported Na concentrations in saliva ranging from 148 to 156 mmol/L in dairy cows (440 kg) at a Na intake of >25 g/day. Likewise, Grace (40) reported salivary Na concentrations ranging from 136 to 150 mmol/L in non-lactating dairy cows receiving 31.2 g Na/day and it appeared that the salivary Na concentration was not sensitive to dietary K intake, at least in the range of 109 to 380 g K/day. Chiy and Philips (19) observed salivary Na concentrations in steers ranging from 162 to 174 mmol/L at Na intakes 26 to 70 g/day respectively. Finally, Bailey and Balch (5) found in dry short horn cows, salivary Na concentrations ranging from 153 to 166 mmol/L after the feeding of hay in combination with free access to salt. Thus, it seems that the Na concentrations of saliva are at least 130 mmol/L when the dietary supply of Na is sufficient. The highest salivary K concentration reported in these studies was 13 mmol/L (5, 19, 40, 57, 91, 100). These values are the equal to the values set by Kemp and Geurink as tentative criteria for a sufficient supply of dietary Na (58).

In experimentally Na depleted animals (exteriorisation of one parotid duct) or dietary induced Na deficiency, salivary Na concentrations ranged from 116 to 24 mmol/L while salivary K concentrations ranged from 26 to 107 mmol/L respectively, in calves (10, 90, 110), sheep (71), goats (6, 71), Hereford cows (75), steers (74) and dairy cows (57, 125). The observed Na and K concentrations in saliva from steers fed a Na deficient ration for 28 days (0.4 g Na/day) were 53 and 83 mmol/L, respectively (74). Likewise, salivary Na and K changed from 133 to 100 mmol/L (range 78 - 113, n = 4) and 9 to 35 mmol/L (range 26 - 56, n = 4) respectively, in lactating dairy cows with an initial milk production of 25 kg/day, fed grass with a Na content of 0.5 g/kg dry matter. After another 3 weeks the mean Na concentration in saliva was 85 mmol/L and this value was associated with a mean salivary K concentration of 45 mmol/L (57).

Overall, the highest salivary Na concentration and lowest salivary K concentrations observed under Na deficiency were; 116 mmol Na/L and 8.4 mmol K/L (different studies). Morris et al. (73) indicated that salivary Na and K concentrations of ≤ 120 mmol/L and ≥ 15 are associated with increased levels of aldosterone, i.e. Na deficiency. At least with respect to Na, the criterion for Na deficiency on the basis of the salivary Na concentration set by Morris et al. (73) is corroborated by the values presented in this section and falls within the range of tentative criteria for an insufficient supply of dietary Na suggested by Kemp and Geurink ((58), i.e. 87-130 mmol/L. It was observed by Bailey and Balch (5) that at salivary Na concentrations ≥ 120 mmol/L, the total content of Na and K was 166 mmol/L. However, it can be estimated that the total concentration of Na and K decreases to a value within the range of 140-150 mmol/L when salivary Na concentrations are lower than 120 mmol/L (5). Thus, at a salivary Na concentration of 120 mmol/L, an accompanying salivary K content of at least 20 mmol/L is expected. Indeed, a salivary K content ≥ 20 mmol/L is only observed during Na deficiency (this section). This criterion falls within the range of salivary K concentrations indicative for an inadequate supply of dietary Na as set by Kemp and Geurink (58). Therefore, we propose to set salivary Na concentrations ≥ 120 mmol/L in combination with a salivary K content of ≤ 20 mmol/L as the lower and upper values for the Na and K content of saliva indicative for a sufficient supply of dietary Na. On the basis of these values, it follows that a Na : K ratio of 6 in saliva, dietary Na supply should be sufficient and plasma aldosterone levels should not be significantly elevated. Indeed, it was reported by McSweeney et al. that plasma aldosterone levels increased substantially at Na : K ratio's of 4 and lower, at least in goats and sheep. When salivary Na and K concentrations do not conclusively indicate Na deficiency, we suggest to asses Na status again after three weeks, because a sustained inadequate dietary supply of Na further decreases the salivary Na content, accompanied with an increased salivary K concentration (58, 74). However, in practice, clinical signs of Na deficiency (125) may be an important trigger to asses Na status but clinical signs of Na deficiency only occurs when salivary Na concentration have been dropped to at least 100 mmol/L (58). Thus, under practical conditions, interpretation of the observed salivary Na and K concentrations with respect to the Na status of the animal may be beyond doubt.

8. PREVENTION OF SODIUM DEFICIENCY

8.1 Short term

Common salt is a cheap source of supplemental Na (66, 80) but the use of Na-bicarbonate ($NaHCO_3$) and Na-sesquicarbonate ($Na_2CO_3.NaHCO_3$) may be beneficial when dietary buffers are required to enhance buffer capacity of the rumen contents and or enhance milk(fat) production (14, 15, 35, 115, 118). When 0.75 to 1.25 % Na-bicarbonate is added to the ration of lactating cows (14, 35), the Na content increases by 2.0 and 3.4 g/kg dry matter respectively, leading to a Na content of the ration which is in excess of the minimum requirement, even when intrinsic Na is neglected.
In practice, addition of Na to a Na deficient ration in the form of common salt (NaCl) can be achieved by the provision of saline water, loose salt, salt blocks or NaCl present in (multi)mineral mixtures either incorporated into concentrates or fed alone. Dixon and Milligan (29) offered steers (2 yr, 309 - 343 kg BW) 5.5 kg/day mature grass hay and either fresh or salt water (1% NaCl, wt/vol). Water intake was significantly higher when saline water was provided. Likewise, Na intake and urine excretion (L/day) increased, but apparent ill effects were not observed. Furthermore, Van Leeuwen (121) cited work of Frens (1946) showing that water containing 1% NaCl (wt/vol) was well tolerated by cattle, but water containing 1.5% NaCl (wt/vol) was associated with a reduced feed intake and milk production and an increased incidence of diarrhoea and nervous signs. Thus, on the basis of the above observations (121) a NaCl concentration of 1% (wt/vol) of drinking water may be considered safe. This implicates that at NaCl concentrations > 1% (wt/vol) of saline water, fresh drinking water must be available so as to prevent the negative consequences of excess Na intake. Sheep seems to be more tolerant to saline water then cattle. Singh and Taneja (108) showed that Marwari sheep tolerated drinking water containing up to 1.5% NaCl (wt/vol) under desert conditions. This observation was substantiated by Wilson and Dudzinski (126) in Merino sheep fed indoors either oaten chaff or lucerne chaff based diets. Indeed, Van Leeuwen (121) cited work of Pierce (1957) who reported that saline water containing 1.5 % NaCl (wt/vol) was tolerated by most of the animals (number of animals unknown). Finally, Loosli (65) calculated that saline water containing about 0.5% NaCl would meet Na requirements of cattle and sheep. Thus, saline water with higher NaCl concentration than 0.5% would appear to be unnecessary so as to prevent Na deficiency.
Sodium can also be provided *ad libitum*, either as a loose salt or in the form of a salt block. The supply of *ad libitum* salt in the form of either loose salt or salt blocks, easily results in luxury consumption especially when it is provided as a loose salt (111, 112, 120). Furthermore, caution is warranted when loose salt is provided *ad libitum* to Na deficient (“salt hunger”) animals because of excess salt intake may cause Na intoxication when no, or a limited amount of fresh drinking water is available (65, 96). Thus, it is recommended to supplement appropriate, fixed amounts of Na either in the form of common salt or a mineral mixture, if necessary.

8.2 Long term

Sodium deficiency due to low intrinsic Na content of roughages can be prevented by fertilization of soils with appropriate amounts of Na. The lowest Na contents of fresh grass are observed in April/May and the values increase in the course of the growing season (61), www.blgg.nl). However, the application of appropriate amounts of Na-fertilizer effectively increases the Na content of grass. It has been shown by Chiy et al (18), that the Na content of fresh grass (*Lolium perenne L.*) increased in a dose-dependent fashion from 2.7 to 5.2 g/kg DM, when the soils were fertilized with up to 100 kg NaCl/ha, one month prior to grazing. In this experiment all plots received an accumulated amount of 300 kg N/ha prior to sampling of the grass. McKenzie and Jacobs (70) found Na contents of grass ranging from 2.0 to 2.7 g/kg DM after the administration of similar accumulated amounts of N fertilizer. Furthermore, they observed that lower rates of N fertilization < 45 kg N/ha/sward were associated with somewhat lower Na contents of spring grass (values were shown only in graphs). Thus, under less intensive production circumstances lower Na contents of grass may be anticipated. Finally, under the assumption that all manure produced on a farm is used to fertilize its associated soils, it must be noted that supplementation of Na in excess to Na requirement, indirectly contributes to the prevention of Na deficiency on the long term.

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