# Feeding standards for ruminants: A progress report of research under controlled conditions in South Africa

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The last 20 years of research in South Africa on feeding standards is reviewed. A major contribution to quantitating energy requirements for growth has been the advent of growth-curve analysis which enable accurate pattern description of genotype and dietary responses. It has been established that indigenous cattle and sheep very often differ from their exotic counterparts in composition of gain and efficiency of feed utilization because of animal – feed interaction. Therefore, they would most probably also differ in most of the feed requirements for growth. A large proportion of the effort in protein metabolism research concentrated on NPN utilization, but progress, as abroad, has been hampered by unsatisfactory techniques to quantitatively distinguish between microbial protein and undegraded feed protein reaching the duodenum. Mineral metabolism research established toxic levels of and antagonisms between a number of minerals.

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Navorsing oor voedingstandaarde gedurende die laaste 20 jaar in Suid-Afrika word oorsigtelik bespreek. 'n Belangrike bydrae tot die poging om energiebehoeftes vir groei te kwantifiseer, was die tegniek van groeikurwe-analise, waardeur 'n akkurate patroon-beskrywing van genotipe-en voedingsreaksies verkry kan word. Dit is vasgestel dat inheemse beeste en skape dikwels van uitheemse tipes in samestelling van groei en doeltreffendheid van voerverbruik verskil as gevolg van dier – voerinteraksie. Gevolglik is dit waarskynlik dat hulle ook ten opsigte van die meeste voedingsbehoeftes vir groei kan verskil. 'n Groot deel van die navorsingspoging in proteïenmetabolisme is gewy aan NPN benutting, maar vordering is, net soos oorsee, beperk deur onbevredigende tegnieke om kwantitatief te onderskei tussen mikrobiese- en nie-gedegradeerde voerproteïen wat die duodenum bereik. In mineraalmetabolisme is baie aandag geskenk aan toksiese vlakke van en antagonismes tussen verskillende minerale.

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## Introduction

The original intent of the Organizing Committee to review all controlled (indoor) nutrition research in the Republic, and for me to then give my views on how to proceed was surely very ambitious. It is indeed a privilege to be part of such a gallant effort, for which I humbly thank the Organizing Committee. However, I would have been naïve if not downright presumptuous if, at any stage during the preparation of this manuscript I thought it possible to summarize all the pioneering work done earlier this century, or endeavoured to give my views on the intricacies of aspects of ruminant nutrition in which I am a complete layman. I would suggest that the amount of work which has accumulated warrants another congress or even a third one.

As a consequence, I decided to limit this contribution to the last *ca* 20 years and to data on aspects of ruminant nutrition which can be classified as 'feeding standards'. This may include metabolism in general, voluntary intake, requirements and the important question of resource utilization.

## 1 Feed evaluation and energy requirements for growth

### 1.1 Local requirement and study philosophy

South African contributions centered around two major fields of interest:

(i) Quantification of the growth response and the composition of growth under various feeding regimes for indigenous genotypes or genotypes introduced to Southern Africa.

(ii) Studying and predicting *ad libitum* intake to estimate the potential value for growth of typical feedstuffs when fed alone or in feed mixtures. Most forages under consideration are subtropical, bearing very little resemblance to the temperate species which underlie the bulk of European and American knowledge.

It is my contention that progress in the field of energy requirements for growth and energy metabolism in general, has been hampered by some static and even conceptually wrong ideas existing at most leading laboratories in the world. Some of these are:

(a) Intake cannot be scaled between species or breeds by standardizing the exponent of live mass to 0,75 (so-called metabolic mass, Meissner & Roux 1983b).

(b) A constant linear relationship between intake, energy retention and maintenance has been proposed. This however, could only be a reasonable approximation for some portion of the growth period, it cannot be true over the whole interval (Meissner & Roux, 1983b).

(c) Energy retention cannot be profitably separated by a multiple linear regression approach into maintenance and protein and fat components because of multicollinearity between the variables which results in unstable estimates (Roux, Hofmeyr & Jordaan, 1982).

To avoid these problem areas the approach adopted at the Animal & Dairy Science Research Institute at Irene is based on growth-curve analysis. A descriptive function is used to describe the growth response as time proceeds (Roux, 1976; Meissner, 1977; Meissner & Roux, 1979). A distinct advantage of this particular function is that growth data are transformed into a logarithmic form, which enables the study of a multiplicative growth process in convenient additive terms and consequently ordinary statistical tests, which are all based on the assumption of additive error structure, can be used. The model further enables accurate predictions of canalization of feed energy into protein or fat deposition and energy expended in non-productive functions without the need to make assumptions on the partial efficiencies concerned.

The metabolizability of a feedstuff contributes considerably to variation in *ad libitum* intake. Cell wall constituents and their *in vitro* rates of fermentation or potential digestibilities, especially in subtropical forages, also affect intake. These factors form the basis of intake-predicting models in many countries. The contention of Pienaar and his co-workers at Irene is that voluntary intake should also be studied through the behaviour of the feedstuff in the rumen; with the amount of digesta in the rumen and elsewhere, the rate of fermentation and the rate of outflow of digestible and indigestible matter from the rumen as major variables in the study model (Pienaar, Roux, Morgan & Grattarola, 1980). Substantial progress in intake prediction has been realized through a study of the digesta parameters. This should however, coincide with a parallel empirical study of the parameter pattern in the growth descriptive function which changes systematically between feeds and genotypes (also sexes), and which has the additional advantage that the intake response is monitored over time as the animal ages (Meissner & Roux, 1983b; Roux & Meissner, 1983), as discussed in section 1.5.

## 1.2 The composition of growth

As the amount of energy retained during growth is deterministic in quantification of the efficiency of growth and consequently the energy requirements for growth, it is important to investigate the proportions of protein and fat being deposited in the important cattle and sheep breeds in South Africa under various feeding conditions.

In cattle the available results suggest that differences between breeds in the composition of growth can largely be explained by differences in frame size which is in accordance with most overseas reports (Meissner & Roux, 1983b). At equal sizes, differences in the proportion of fat in the gain could exceed 50 %, while differences in the proportion of protein rarely exceed 20 % (Table 1). These differences tend to decline as growth proceeds, which suggests that the differences in energy requirements for growth also decline towards maturity. There are however, indications that the indigenous (indicus blood) types could have differential depositional responses at different sizes compared to taurus types (Table 1), which of course hampers effective quantification. However the relative differences in composition of gain between indicus and taurus types on concentrate and roughage diets, at least at *ad libitum* intake, are not unduly dissimilar which may simplify quantification (Table 2). It should be recognized that compositional

differences between breeds (Table 2) and, as can be gathered from overseas literature, also sexes, could be less on low dietary energy concentrations (roughages) than on high ones (concentrates).

Sex differences in the composition of gain have also been quantitated rather satisfactorily. It has been shown that castrates deposit more fat and less protein at equal sizes than do males, while females deposit more fat and less protein than castrates, although it is usually difficult to prove significant differences between castrates and females, especially in sheep (Meissner, de la Rey, Gerhard & van der Westhuizen, 1976). As with genotype, differences in mature size because of sexual dimorphism, may explain some of the differences in the composition of gain (Meissner & Roux, 1983b), although the contribution of hormones is probably more important. The energy content of the gain in castrates and females could be double that in males depending on intake, but the difference is not merely proportional because of sex − size interaction. This suggests that effective predictions of energy requirements for growth is dependant on knowledge of the total growth curve, a field of study on which appreciably more data are needed.

In sheep breeds differences in the composition of gain are even more substantial than in cattle breeds. The differences

**Table 1** Composition of gain in steers at *ad libitum* intake on concentrate diets as affected by genotype (Charolais = 100)

|  | Empty body mass (kg) | | | |
| Breed | 200 | 300 | 400 | 500 |
|---|---|---|---|---|
| Protein in empty body gain | | | | |
| Charolais | 100 (170)[a] | 100 (159) | 100 (151) | 100 (146) |
| Simmentaler | 94 | 94 | 95 | 96 |
| Bonsmara | 93 | 92 | 93 | 96 |
| Brahman | 88 | 88 | 90 | 93 |
| Afrikander | 88 | 89 | 88 | ? |
| Hereford | 82 | 83 | 85 | 87 |
| Fat in empty body gain | | | | |
| Charolais | 100 (237)[b] | 100 (298) | 100 (343) | 100 (368) |
| Simmentaler | 116 | 113 | 110 | 108 |
| Bonsmara | 121 | 118 | 112 | 107 |
| Brahman | 138 | 128 | 117 | 110 |
| Afrikander | 138 | 124 | 122 | ? |
| Hereford | 152 | 139 | 129 | 122 |

[a] g protein/kg empty body gain. [b] g fat/kg empty body fat. Results were adapted from Naudé (unpublished) and Meissner & Roux, (1983b).

**Table 2** Fat in empty body gain of bulls of three breeds on a concentrate and roughage diet at *ad libitum* intake (Hereford = 100)

|  | Concentrate | | Roughage | |
|  | Empty body mass (kg) | | Empty body mass (kg) | |
| Breed | 200 – 300 | 300 – 400 | 200 – 300 | 300 – 400 |
|---|---|---|---|---|
| Hereford | 100 (178)[a] | 100 (190) | 100 (139) | 100 (144) |
| Afrikander | 94 | 96 | 94 | 95 |
| Simmentaler | 83 | 87 | 86 | 89 |

[a] g fat/kg empty body gain. Results were adapted from Meissner, van Staden & Pretorius (1982).

are obviously also size-related, but more dominating factors are; production purpose (woolled *vs* non-woolled breeds); early and late maturing mutton producers (British types *vs* types originating from Western Europe); and climatic extremes (fat-tailed types of dry, hot areas in Southern Africa *vs* non-fat-tailed types from temperate regions). Most of the genotypic variation in composition of growth can be explained by these classifications (Hofmeyr, 1972; Meissner *et al*, 1976; Meissner & Roux, 1983b).

Modification of the composition of growth in the ruminant through nutritional means has long been a controversial subject both here and abroad. More recent results indicate that both level of intake and dietary energy concentration at a standardized intake could have profound effects on the composition of gain (Meissner *et al.*, 1976; Meissner, 1977; Meisner, Hofmeyr & Roux, 1977; Meissner & Roux, 1983b). It is more difficult however, to show large differences in body composition at specific sizes, obviously because the cumulative effect of energy retained during an experimental period could still only constitute a small proportion of total energy already in the animal body.

Results from Irene show that a change in the composition of growth is largely a function of the rate of gain, although dietary energy concentration will have an additional effect if rate of gain is standardized (Table 3 a,b,c). The general pattern with regard to feeding level effects on the other hand, is not well established. Some results suggest very little change be-tween feeding levels corresponding to about 70 to 95 % of calculated *ad libitum* intake, (Meissner, 1983) as shown in Table 3 a,b,c, while others apparently disagree (Meissner *et al,* 1977; Meissner & Roux, 1983b). Nevertheless, because the effects on composition of growth are evidently small, feeding level within these limits is apparently not of particular concern in determining feed efficiency.

Future effort, in conclusion, should be directed at interactions in the composition of growth, especially those between animal and diet or feeding level. Although the effects of interaction are considerably reduced by scaling relative to frame size, as in the functions proposed by Roux & Meissner (1983), there are strong indications that indigenous Southern African cattle and sheep tend to fall out of 'line' to the depositional responses of exotic types.

## 1.3 The efficiency of growth

Compositional changes affect efficiency and consequently one would expect that the same variables which influence the composition of gain could have a parallel effect on the efficiency with which this gain is realized. The available evidence as shown in Table 3, a,b,c apparently confirms this.

In cattle it has been shown that size and efficiency in terms of live mass produced per unit of feed intake, is highly significantly correlated; in fact more than 80 % of the apparent genotypic variation is explained by size (Meissner & Roux, 1983a) in *B. taurus* types. There are however, as in the case

**Table 3a** Composition of empty body gain as affected by dietary energy concentration in sheep (Meissner & Roux, 1983b)

|  | % Concentrate in diet | | | | | |
|---|---|---|---|---|---|---|
|  | 0 | 20 | 40 | 60 | 80 | 100 |
| ME intake (MJ/day) | 14,2 | 14,5 | 14,8 | 14,8 | 14,7 | 14,7 |
|  | (100) | (102) | (104) | (104) | (104) | (104) |
| Empty body gain (g/day) | 148 | 197 | 237 | 247 | 247 | 243 |
|  | (100) | (133) | (160) | (167) | (167) | (164) |
| Protein in gain (g/kg) | 163 | 152 | 148 | 142 | 138 | 139 |
|  | (100) | (93) | (91) | (87) | (85) | (86) |
| Fat in gain (g/kg) | 252 | 294 | 333 | 368 | 385 | 387 |
|  | (100) | (117) | (132) | (146) | (153) | (153) |
| Efficiency (g gain/MJ ME) | 10,4 | 13,6 | 16,0 | 16,7 | 16,8 | 16,5 |
|  | (100) | (131) | (154) | (161) | (162) | (159) |

**Table 3b** Composition of empty body gain as affected by dietary energy concentration and feeding level in cattle (Meissner, 1983)

|  | % Concentrate in diet | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
|  | 20 | | | 50 | | | 80 | | |
|  | [a]H | M | L | H | M | L | H | M | L |
| ME intake (MJ/day) | 65 | 59 | 52 | 64 | 58 | 52 | 65 | 57 | 50 |
| Feeding level (% of *ad lib.*) | 94 | 86 | 75 | 93 | 84 | 75 | 94 | 83 | 72 |
| Empty body gain (g/day) | 530 | 490 | 450 | 698 | 650 | 588 | 780 | 690 | 600 |
|  | (100) | (92) | (85) | (132) | (123) | (111) | (147) | (130) | (113) |
| Protein in gain (g/kg) | 211 | 216 | 216 | 194 | 191 | 199 | 197 | 198 | 192 |
|  | (100) | (102) | (102) | (92) | (91) | (94) | (93) | (94) | (91) |
| Fat in gain (g/kg) | 165 | 156 | 157 | 207 | 207 | 196 | 208 | 214 | 228 |
|  | (100) | (95) | (95) | (125) | (125) | (119) | (126) | (130) | (138) |
| Efficiency (g gain/MJ ME) | 8,15 | 8,31 | 8,65 | 10,9 | 11,2 | 11,3 | 12,0 | 12,1 | 12,0 |
|  | (100) | (102) | (106) | (134) | (137) | (139) | (147) | (148) | (147) |

[a] H : High; M : Medium; L : Low.

**Table 3c** Composition of empty body gain as affected by feeding level in sheep (Meissner, Hofmyer & Roux, 1977)

| | Feeding level | |
| --- | --- | --- |
| | 95 % *ad libitum* | 76 % *ad libitum* |
| ME intake (MJ/day) | 11,0 | 8,80 |
| Protein in gain (g/kg) | 150 | 153 |
| | (100) | (102) |
| Fat in gain (g/kg) | 301 | 253 |
| | (100) | (84) |
| Efficiency (g gain/MJ ME) | 13,7 | 13,5 |
| | (100) | (99) |

of the composition of gain, reasons to believe that indigenous types *(B. indicus* blood) could deviate from a generalized relationship in an erratic way, which hampers confident quantification.

In sheep, as with the composition of growth, the efficiency of utilization of dietary energy for gain (also of dietary nitrogen for that matter) is dominated by production function and climatic adaptation. Efficiency expressed in any terms, is a function of energy canalization, whether to lean meat production (Mutton Merino), to lean meat plus wool production (Döhne Merino), to wool production (Merino) or to storing fat for survival as in the indigenous fat-tailed Pedi or Karakul breeds (Jacobsz, Cronjé, Blom & Swart, 1970; Jacobsz, Cronjé, Blom & Skea, 1971; Hofmeyr, 1972; Meissner, 1977; du Plessis & de Wet, 1981).

The effects of energy intake on the efficiency of growth can be summarized as follows: Efficiency is improved by an increase in the level of concentrate if mixed diets are used as would be expected (Cloete & Rossouw, 1970; Meissner & Roux, 1983 a,b). This is a function of improvement both in the level of intake (less physical limitation) and in metabolizability, *i.e.* dietary energy concentration. However, unlike the contentions of many research workers here and abroad, the results from Irene suggest that efficiency for growth, expressed both in DM and energy units, would level off at about 60 % concentrates in the diet, *i.e.* a metabolizability value of *ca* 0,6 (see equation 7 in section 1.4). The extent of this 'levelling-off' response, one would imagine, could depend on the physical form of the concentrate and the site(s) of digestion.

If the effects of dietary energy concentration *per se* and feeding level *per se* are evaluated, the indications are that: Efficiency is increased with increasing proportions of concentrates in the diet, but with an ever declining slope, especially above the 60 % concentrate level (Table 3 a,b,c). The efficiency response at a particular dietary energy concentration on the other hand, appears to be largely independent of the level of intake between *ad libitum* and about 70 % of *ad libitum,* although there are exceptions. Thus, the efficiency response pattern, as influenced by these two variables, is in close association with the pattern shown by the composition of gain, as expected (Table 3 a,b,c).

The above-mentioned results on the effects of dietary energy concentration and feeding level agree with the principles incorporated in the most recent estimations of the energy requirements for growth by the ARC (1980). Some of the more recent publications on this subject are very intriguing (see list in Meissner & Roux, 1983a). It is shown that the feed conversion ratio could be even better between 70 to 90 % of *ad libitum* than at *ad libitum* intake for quite divergent dietary regimes. A change in body composition (Meissner, Hofmeyr & Roux, 1977) and a lowering in maintenance expenditure (Nel, Grunow, Hugo, Pienaar & Voss, 1964; Coetzee, Nel & Joubert, 1969) apparently share the explanation for this favourable response. Below 60 to 70 % of *ad libitum* intake the feed conversion ratio may rise sharply as shown in Table 4 compiled from a selection of South African results.

**Table 4** Feed conversion ratios at different energy levels

| Animal | Relative feed intake | Relative feed conversion ratio | Source |
| --- | --- | --- | --- |
| Pedi, Merino and | 95 | 100 | Hofmeyr |
| Mutton Merino wethers | 75 | 94 | (1972) |
| | 55 | 109 | |
| | 35 | 156 | |
| Afrikander, Drakens- | 95 | 100 | Van Rooyen |
| berger, Hereford and | 85 | 96 | (1975) |
| Simmentaler steers | 75 | 102 | |
| | 65 | 131 | |
| | 55 | 178 | |
| Mutton Merino cross | 95 | 100 | Meissner, |
| wethers | 76 | 102 | Hofmeyr & |
| | | | Roux (1977) |
| Simmentaler steers | 94 | 100 | Meissner |
| | 84 | 99 | (1983) |
| | 74 | 98 | |
| Mutton Merino cross | 95 | 100 | Meissner & |
| wethers | 89 | 100 | Roux (1983b) |
| | 87 | 101 | |
| | 82 | 101 | |
| | 75 | 101 | |
| | 66 | 112 | |
| | 60 | 116 | |

The question of animal-feed interaction, as is the case with the composition of gain, is also of particular concern in efforts to effectively quantitate the efficiency of feed energy utilization for gain in different breeds or sexes, and dietary treatments. In beef cattle, if indigenous types are excluded, interaction on concentrate and roughage diets can largely be accounted for if comparisons are made relative to the same proportion of mature size (Meissner & Roux, 1982), see Table 5. This is also true for apparent differential responses at different feeding levels on the same dietary energy concentration (Meissner & Roux, 1983a), although there are indications that some interaction between indigenous and exotic cattle may remain (van Rooyen, 1975). The latter may be ascribable to differences in non-productive energy expenditure (van der Merwe & van Rooyen, 1979; Meissner & Roux, 1983a), possibly maintenance.

In sheep, differences in production function largely explain the interaction with feeding level which may be observed (Jacobsz *et al,* 1971; Hofmeyr, 1972; du Plessis & de Wet, 1981). Hofmeyr (1972) showed that the Merino breed requires less feed per kilogram live mass at low feeding levels and more at high feeding levels than the fat-tailed Pedi, while the fast growing Mutton Merino requires least at all levels (Table 5). As the feeding level increases, progressively more

energy is canalized into the development of skin area and wool in the Merino, while energy allocation to carcass growth progressively declines. The Pedi breed has very little skin cover and consequently all energy is canalized to body growth, especially to filling fat stores when the level of intake is adequate. In the Mutton Merino breed some energy is allocated to wool growth but most to promoting lean growth in the carcass.

**Table 5** Animal-feed interaction in cattle and sheep

| Animal | Dietary energy conc. or feeding level | | | | | Source and units |
|---|---|---|---|---|---|---|
| **Beef cattle** | Feeding level: *ad lib.* Dietary energy conc. | | | | | Adapted from Meissner & Roux (1982) |
| | [a]q = 0,6 | | q = 0,6 | | | |
| Hereford | 110 | | 100 | | | Mass produced/unit of |
| Simmentaler | 110 | | 110 | | | ME intake (Hereford = 100) |
| Afrikander | 84 | | 88 | | | |
| **Beef cattle** | Dietary energy conc. q = 0,6 Feeding level (% of *ad lib.* | | | | | Adapted from Van Rooyen (1975) kg DM/kg empty body gain |
| | 95 | 85 | 75 | 65 | 55 | |
| Afrikander | 7,7 | 7,8 | 8,1 | 10,1 | 13,5 | |
| Drakensberger | 7,6 | 7,4 | 8,0 | 10,5 | 14,2 | |
| Hereford | 7,7 | 7,3 | 7,7 | 10,1 | 13,8 | |
| Simmentaler[b] | 8,5 | 7,8 | 8,4 | 10,7 | 14,6 | |
| **Sheep** | Dietary energy conc. q = 0,6 Feeding level (% of *ad lib.*) | | | | | Adapted from Hofmeyr (1972) kg food/kg live mass gain |
| | 95 | 75 | 55 | 35 | | |
| Pedi | 5,5 | 5,1 | 5,9 | 9,2 | | |
| Merino | 5,6 | 5,2 | 6,2 | 8,8 | | |
| Mutton Merino | 4,6 | 4,5 | 5,2 | 6,6 | | |

[a] q: Metabolizable energy as a proportion of gross energy.
[b] The figures of the Simmentaler are higher than those of the other breeds because they were heavier and apparently also older.

The need to accumulate knowledge on the efficiency response under different growth conditions is imperative for the calculation of energy requirements. Research workers in this field should probably, as is the case with the composition of growth, pay more attention to the question of animal-feed interaction and how to cope with it, than to anything else. It appears from available evidence that this problem could be of more importance in Southern Africa, or even Africa as a whole, because of our vast collection of indigenous cattle and sheep, and presumably also goats. In these studies, as proposed by Elliot (1966), it is conceivable that experimental procedures make provision for studying at least a major part of the growth curve for effective evaluation or quantification. It is not possible to draw reliable conclusions from short-term comparative slaughter or calorimetric studies. Such studies form the bulk of experiments done abroad which endeavoured to quantitate the energy requirements for growth.

### 1.4 Towards quantitating energy requirements for growth

The components of the growth descriptive function mentioned earlier should be outlined for effective clarification (See Roux, 1976; 1981, and Meissner, 1977 for more details). Growth is described with time and in terms of intake *vs* gain in mass or the components of body composition as time progresses. Two sets of functions are defined which in effect interrelate:

Consider $x_i(t)$, where $x_i(t)$ can be ln (cumulative feed intake), ln (live mass), ln (body protein), ln (body fat) or even ln (cumulative energy expenditure in maintenance). The growth of $x_i$ at times t and $t-1$ is described by

$$x_i(t) = \alpha_i (1 - \rho) + \rho \, x_i (t - 1) + \Sigma_i (t) \qquad (1)$$

a form recognizable as a regression equation with $x_i(t)$ as the dependent variable and $x_i (t - 1)$ as the independent variable; $\rho$ is the so-called autoregression coefficient; $\alpha_i (1 - \rho)$ is the intercept and $\Sigma_i(t)$ is an error term. By repeated substitution for $x_i(t)$ in terms of $x_i (t - 1)$ for all values of t it follows from (1) that

$$x_i(t) = \alpha_i - (\alpha_i - x_i (o)) \rho^t \qquad (2)$$

plus an error term on the right hand side.

The determining parameters in (2) are evidently $\alpha_i$, and $\rho$, [$x_i$ (o) is static] and by studying the pattern description of these parameters over time, or their relationship with genotype, dietary energy concentration, or feeding level, one is able to make accurate judgements as to the differences which may be encountered for the purposes of estimating energy requirements.

The second set of functions are allometric equations in linearized (logarithmic) form, which describe the relationship between cumulative feed intake and body mass or the components of body composition:

$$x_2, \text{ or } x_3, \text{ or } x_4 = a_i + b_i x_1, \text{ plus an error term} \qquad (3)$$

where $x_2, x_3, x_4$ = ln (body mass), ln (body protein), ln (body fat) *etc.*, $x_1$ = ln (cumulative feed intake), $a_i$ = intercept, $b_i$ = slope, which describes the proportional amount of $x_2, x_3$,

**Table 6a** ME requirements (MJ/day) of steers[a] as calculated by the allometric-autoregressive model compared at 1,0 kg gain per day for different frame sizes to the estimates of NRC (1970) and ARC (1980) (q = 0,6)

| | Allometric-autoregressive model Exp $\alpha_m$ | | | NRC (1970) Frame size apparently small | ARC (1980) Frame size | | |
|---|---|---|---|---|---|---|---|
| Live mass (kg) | 600 | 800 | 1000 | | Small | Medium | Large |
| 200 | 55 | 53 | 52 | 60 | 56 | 51 | 47 |
| 300 | 76 | 72 | 70 | 82 | 73 | 67 | 61 |
| 400 | 95 | 89 | 85 | 101 | 88 | 80 | 74 |
| 500 | 114 | 105 | 100 | 124 | 102 | 94 | 86 |
| 600 | – | 120 | 113 | – | 115 | 106 | 97 |

[a] Adapted from Roux & Meissner (1983).

$x_4$ produced per unit of $x_1$.

Since a is geometrically bound to b, it follows that only a study of the pattern description of b is necessary to get similar information to that of $\alpha_i$ and $\rho$ above.

The interrelationship between (2) and (3) follows from knowledge that:

$$b = \frac{[(\alpha_2 - x_2(o)]}{[\alpha_1 - x_1(o)]} \quad \text{and}$$

$$a = \frac{\alpha_2 - \alpha_1 [\alpha_2 - x_2(o)]}{[\alpha_1 - x_1(o)]}$$

The parameter pattern study revealed very interesting concepts and encouraging relationships. In beef cattle for example, $\alpha_m$, defined as the asymptotic value of Ln (live mass) or 'mature' size, proved to be of particular importance in influencing growth, feed intake and efficiency (Meissner & Roux, 1983 a; Roux & Meissner, 1983). The parameter $\alpha_m$ accounted for some 98 % of the variation in feed intake parameters ($\alpha_f, \rho$) and 88 % of the variation in the efficiency parameter (b), provided that *B. indicus* cattle were omitted. As previously mentioned, these types do not closely associate with *B. taurus* types and their responses apparently have to be quantitated one by one in exhaustive trials.

The relevant equations relating $\alpha_m$ to the intake and efficiency parameters for beef cattle are:

$$\alpha_f = 1,5032 \; \alpha_m - 1,3183 \tag{4}$$
$$\gamma = \alpha_m / (293,85 \; \alpha_m - 1715,1) \tag{5}$$
$$b = 0,0579 \; \alpha_m + 0,1873 \tag{6}$$

where $\alpha_f$ = 1n (cumulative DM intake) at t $\infty$ and $\gamma = - \ln\rho . \rho$ and b were defined in (1) and (3), respectively.

The relationship of b to dietary energy concentration at *ad libitum* intake was exceptionally similar between experiments with steers on pelleted concentrate - lucerne/Eragrostis mixtures (Meissner, 1983) heifers on unpelleted concentrate - coarse Eragrostis mixtures and wethers on pelleted concentrate - lucerne mixtures (Roux & Meissner, 1983). The relationships are second order polynomials with very little difference in the regression coefficients, showing that the major influence, irrespective of animal species, is exerted by the roughage, here denoted by the intercepts:

$$b_{steers} = 0,4232 + 0,4404 \; p - 0,3278 \; p^2$$
$$b_{heifers} = 0,3095 + 0,4229 \; p - 0,3208 \; p^2 \tag{7}$$
$$b_{wethers} = 0,4621 + 0,4428 \; p - 0,1874 \; p^2$$

where p is the proportion of concentrates in the diet.

Equation (7) shows that b and consequently efficiency, is not maximal at 100 % concentrate level, but at a point somewhat below 100 %, in fact between 60 and 80 % concentrates, as mentioned earlier. The parameter b actually declines again towards 100 % concentrate level, but one would imagine that the degree of processing of the concentrate could vary this response.

The relationship of $\alpha_f$ and $\gamma$ with the proportion of concentrates is strictly linear:

$$\alpha_f = 9,1388 - 0,4422 \; p \tag{8}$$
$$\gamma = 0,0149 + 0,0259 \; p \tag{9}$$

where $\alpha_f$ and $\gamma$ are as in (4) and (5) respectively.

The best description of parameter b with feeding level, where feeding level was studied between *ad libitum* and 55 % of *ad libitum* intake (Roux & Meissner, 1983), was also a second order polynomial:

$$b = 0,3004 + 0,8035 \; v - 0,5167 \; v^2 \tag{10}$$

where $v$ is the proportion of *ad libitum* intake which suggests that b and thus efficiency, is not maximal at a 100 % *ad libitum* intake, but rather somewhere between 75 and 85 %. This concept was discussed earlier on (see Table 4).

Parameter $\alpha_f$ is constant for all levels of intake below *ad libitum* and this value differs from the *ad libitum* figure by approximately 8% in the arithmetic (ordinary) scale:

$$\exp \alpha_f \text{ (limited)} = 0,9189 \; \alpha_f \; \textit{(ad lib.)} \tag{11}$$

Parameter $\gamma$ increases linearly with feeding level until just below *ad libitum* intake. The *ad libitum* value is somewhat lower than expected which shows a levelling-off response.

Parameter $\alpha_m$ ('mature' size) is constant for all levels of intake between 55 and 100 % of *ad libitum*, but drops off sharply at levels below 55 %. According to theory (Roux, pers. comm.) the maintenance level of intake should be between 40 and 50 % of *ad libitum*, which explains the sharp decline in $\alpha_m$; the expected mature size would never be reached if intake is only sufficient for maintenance.

By combining the equations of different sizes of beef cattle with the equations describing dietary energy concentration and feeding level, and by taking differentials to calculate rates of intake and gain, it is possible to estimate energy requirements for growth. Such estimates are compared to estimates by the NRC (1970) and the ARC (1980) in Table 6 a,b for a ME concentration of 11 MJ/kg (q = 0,6).

The estimates at specific rates of gain and similar frame sizes agree with those of the NRC (1970) and the ARC (1980) as shown in the Table 6a. At different rates of gain the present estimates are lower on the lower rates of gain and higher on the higher rates of gain (Table 6b). This agrees with what was previously shown in sheep (Meissner, 1977). The explanation could be that, at high levels of intake (therefore gain), high rates of fat deposition are realized. This is instrumental in poor efficiency and consequently higher energy requirements than anticipated by the ARC (1980) who relied on rather short-term studies for their calculations. At lower levels of intake, maintenance requirements apparently decrease in the long term as has been shown on a number of occasions in direct and indirect studies both abroad and in South Africa (Nel *et al*, 1964; Coetzee *et al*, 1969; Hofmeyr, van Rensburg, Kroon & Olivier, 1976; Jacobs & de Wet, 1977). Therefore, requirements are lower at low rates of gain than anticipated by the ARC (1980). The method used to calculate maintenance requirements in many leading laboratories, as discussed in section 1.1, or the short-term nature of experiments, could be responsible for the higher estimates of the ARC (1980).

In conclusion, the methods proposed could form the basis of extensive estimates of energy requirements for growth under various feeding conditions and for different types of livestock, but more data are required especially under extreme conditions and for quantification of our rather peculiar indigenous livestock. A comprehensive review and guide on this subject is given by Meissner & Roux (1983b).

## 1.5 Prediction of voluntary feed intake

It has been proposed that the mass of organic material in the

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rumen and elsewhere equals intake multiplied by the mean retention time of organic material in the rumen or total digestive tract. In quantitative terms, rate of outflow of undigested matter, which is the reciprocal of the retention time of that matter, and the amount of OM present in the rumen under steady-state conditions, have the most profound effect on voluntary intake (Pienaar *et al,* 1980). In a simplified approach therefore, intake can be predicted if sufficient knowledge of the amounts of digesta and the retention times of various feedstuffs or feed mixtures has accumulated. One should however recognize that the amount of digesta is not merely a function of the particular feedstuff, but that it is also under physiological control. However, it would appear that retention time can roughly be regarded to be at least independent of the animal's age or size (Meissner & Roux, 1983b).

Because of physiological control and differences in mature

**Table 6b** ME requirements (MJ/day) of steers as calculated by the allometric-autoregressive model at different rates of gain for medium frame sizes compared to the estimates ARC (1980) (q = 0,6)

| | Allometric-autoregressive model[a] | | | ARC (1980) | | |
| | Rates of gain (kg/day)[b] | | | Rates of gain (kg/day) | | |
| Live mass (kg) | 0,5 | 0,75 | 1,0 | 0,5 | 0,75 | 1,0 |
|---|---|---|---|---|---|---|
| 200 | 28 | 39 | 53 | 36 | 43 | 51 |
| 300 | 37 | 51 | 72 | 48 | 56 | 67 |
| 400 | 46 | 62 | 89 | 58 | 68 | 80 |
| 500 | 53 | 71 | 105 | 67 | 79 | 94 |
| 600 | 61 | 81 | 120 | 76 | 89 | 106 |

[a] Adapted from Roux & Meissner (1983).

[b] Exp $\alpha_m$ : 800 kg.

size *etc.,* efforts to predict from digesta content and retention time should be modified by the growth descriptive function to account for these differences as well as those developing when the animal ages.

The retention time of the digesta is associated with the quality of a roughage, a particular roughage therefore has a profound influence on the retention time of the concentrates in a feed mixture (Campher, 1982; Campher, Roux & Meissner, 1983) as shown in Table 7. The intercept value in the prediction equations in Table 7 gives the retention time at a 100 % concentrate level. Theoretically it should be the same for all feed mixtures, but the fact that they differed significantly probably indicates the influence of the particular roughage. Another interesting feature in Table 7 is the stability of the slope. The slopes did not differ significantly in nine experiments with experimental animals including intact and rumen cannulated steers, heifers and, in one instance, even wethers. This suggests that there was no interaction between roughage type and inclusion level within the boundaries of these experiments.

A further point of interest from a summary of some six experiments here and abroad (See Meissner & Roux, 1983b), is that the retention time of roughages in cattle at *ad libitum* intake is about seven to eight hours longer than in sheep, if the total digestive tract is considered. The reasons for the difference are unresolved but the relative fill of the rumen is apparently not of prime importance. This may however, partially account for the well known observation that cattle apparently digest

roughages better at comparable levels of intake than do sheep.

From an analysis of data here and those given on pages 39

**Table 7** Retention times of feed mixtures[a] in the rumen of cattle: prediction equations and the values at 100 % roughage and 100 % concentrate respectively

Form of equations: Y = a + bx. Where Y = retention time in days and x = level of roughage inclusion (proportion)

| Roughage in feed mixture | Prediction equation | | Retention time (hours) | |
| | slope | intercept | 100 % roughage | 100 % concentrate |
|---|---|---|---|---|
| Hulls and husks | 0,97 ± 0,10 | 0,60 | 37,7 | 14,4 |
| *E. curvula* hay 25 + 51 mm screen | " | 0,50 | 35,3 | 12,0 |
| 13 mm screen | " | 0,41 | 33,1 | 9,8 |
| 6 mm screen | " | 0,31 | 30,7 | 7,4 |
| Bagasse | " | 0,42 | 33,4 | 10,1 |
| Wheat straw | " | 0,22 – 0,38 | 28,6 – 32,4 | 5,3 – 9,1 |

[a] Summary of nine experiments, adapted from Campher *et al.,* 1983.

and 40 of the ARC (1980) publication as set out by Meissner & Roux (1983b), the probable amounts of digesta in the digestive tract under various feeding conditions have been calculated (Table 8 a,b,c). In general, the amounts are reduced when roughages are processed or concentrates are added. The amounts are also lower when wet roughages, such as pasture or silage are fed than when dry roughages are fed.

From the principles on retention time discussed previously, the probable retention times of the feeds in Table 8 a,b,c have been calculated and voluntary intakes predicted as shown in Table 9 a,b. On two occasions the values were modified for two mature sizes according to the growth descriptive function. The estimates are evidently of acceptable accuracy.

The present approach appears a satisfactory means of quantitating voluntary intake. A basis for future studies has been given but a lot more data are required to get reliable estimates. The rumen, because of the dynamics of flow and digestion, obviously has to play a central role in refinement efforts.

## Protein metabolism and resource utilization

Research in South Africa has concentrated more on description (in terms of amino acids and their variation) and utilization of protein sources than on establishing what the ruminant needs under various physiological conditions. Probably rightly so, because in the short space of time of only fifteen years we changed from a situation where van der Merwe (1967) could confidently declare, 'South Africa has a bountiful production of good quality fish meal, in fact a production far in excess of our requirements', to a situation where we have to import a considerable amount and a general protein deficit which could have far reaching implications at the turn of the century (Griesel, 1979; Cloete, 1981; 1982).

Because of this alarming fact, every endeavour will have to be made to exploit NPN to the maximum. A vast amount of work has been done on the use of urea, biuret, *etc.* as supplements since the pioneering days of Groenewald & van der

**Table 8a** DM content (kg) in the digestive tract of cattle on different feeds

| Feedstuff | Live mass (kg) | | | | |
|---|---|---|---|---|---|
| | 200 | 300 | 400 | 500 | 600 |
| Dry roughages | 5,4 | 7,3 | 9,1 | 10,6 | 12,0 |
| Processed roughages | 4,9 | 6,6 | 8,2 | 9,4 | 10,6 |
| Pastures | 3,6 | 4,7 | 5,6 | 6,4 | 7,0 |
| Roughages + concentrates | 5,4 | 6,9 | 8,2 | 9,3 | 9,9 |
| Concentrates | 3,2 | 4,0 | 4,3 | 4,7 | 4,8 |

**Table 8b** DM content (kg) in the digestive tract of sheep on different feeds

| Feedstuff | Live mass (kg) | | | | |
|---|---|---|---|---|---|
| | 20 | 30 | 40 | 50 | 60 |
| Dry roughages | 0,62 | 0,86 | 1,08 | 1,32 | 1,44 |
| Processed roughages | 0,49 | 0,63 | 0,76 | 0,84 | 0,92 |
| Pastures | 0,40 | 0,54 | 0,65 | 0,75 | 0,84 |
| Roughages + concentrates | 0,53 | 0,68 | 0,78 | 0,87 | 0,92 |
| Concentrates | 0,36 | 0,44 | 0,47 | 0,48 | 0,47 |

**Table 8c** Retention time (days) of different feeds in the digestive tract of cattle and sheep

| Feedstuff | Cattle | Sheep |
|---|---|---|
| Dry roughages | 1,45 | 1,16 |
| Processed roughages | 0,79 | 0,64 |
| Pastures | 0,92 | 0,77 |
| Roughages + concentrates | 0,83 | 0,68 |
| Concentrates | 0,50 | 0,45 |

**Table 9a** Predicted voluntary feed intake (kg/day) in cattle from the ratio of contents in the digestive tract to retention time

| Feedstuff | Live mass (kg) | | | | |
|---|---|---|---|---|---|
| | 200 | 300 | 400 | 500 | 600 |
| Dry roughages | 3,7 | 5,1 | 6,3 | 7,3 | 8,3 |
| Processed roughages | 6,2 | 8,4 | 10,3 | 11,8 | 13,4 |
| Pastures | 3,9 | 5,1 | 6,1 | 7,0 | 7,6 |
| Roughages + concentrates: | 6,6 | 8,3 | 9,8 | 11,2 | 12,0 |
| exp $\alpha_m$ = 800[a] | 6,3 | 8,6 | 9,4 | 9,2 | 7,8 |
| exp $\alpha_m$ = 1000 | 6,1 | 8,5 | 10,7 | 11,9 | 12,1 |
| Concentrates | 6,5 | 7,9 | 8,6 | 9,4 | 9,6 |
| exp $\alpha_m$ = 800 | 6,1 | 8,2 | 9,3 | 9,0 | 7,2 |
| exp $\alpha_m$ = 1000 | 5,4 | 8,2 | 10,3 | 11,6 | 11,8 |

[a] Modified according to growth description function.

**Table 9b** Predicted voluntary feed intake (kg/day) in sheep from the ratio of contents in the digestive tract to retention time

| Feedstuff | Live mass (kg) | | | | |
|---|---|---|---|---|---|
| | 20 | 30 | 40 | 50 | 60 |
| Dry roughages | 0,54 | 0,75 | 0,93 | 1,14 | 1,24 |
| Processed roughages | 0,77 | 0,98 | 1,18 | 1,31 | 1,44 |
| Pastures | 0,55 | 0,74 | 0,89 | 1,03 | 1,15 |
| Roughages + concentrates | 0,78 | 1,00 | 1,15 | 1,28 | 1,35 |
| Concentrates | 0,80 | 0,97 | 1,03 | 1,07 | 1,03 |

Merwe (1941) and Altona's group in the fifties (van der Merwe, 1967), and a considerable amount of know-how exists with regard to the acceptability and response of poultry manure not only in licks but also in feedlot diets (Kargaard & van Niekerk, 1977), growth diets (van der Westhuizen & Hugo, 1972b; van der Merwe, Pretorius & du Toit, 1975) and winter supplementing systems (van der Westhuizen & Hugo, 1972a). Nevertheless, we do not know how far we can stretch our natural protein resources by utilizing NPN to its utmost potential. In the dairy cow for example, the potential of NPN to support reasonable milk yields is rather poor, but there are indications that by strategic supplementation of relatively small amounts of by-pass protein, NPN could indeed make a very substantial contribution during the lactation cycle. Some experiments to this effect are now in progress at Irene (Neitz, pers. comm.).
in progress at Irene (Neitz, pers. comm.)

The problem which we are facing as far as NPN is concerned is a basic one, not just here but worldwide. It is mainly microbially related, although the physiology of N-recycling is also rather inadequate (Ørskov, 1982). We need to know the specific N requirements of microbial species and strains but, to enable maximum growth yields we also need to know their specific needs for peptides and branched-chain fatty acids as well (Kistner, 1982; van Gylswyk, 1982), some of which are merely required as C-structures which can serve as building blocks in the sequence of forming microbial protein. The latter suggests that supplementation with some easily fermentable carbohydrate such as molasses could increase the efficiency with which NPN-N is utilized (van Gylswyk, 1982), a concept which has been incorporated in practical feeding, but unfortunately with variable success. This, by implication, again stresses our limited knowledge and shows that the efforts of the microbiologists at the ADSRI and the CSIR need all the encouragement that they can get.

Documentation of amino acid composition and variation has attracted much attention. The studies of Wessels (1970; 1976) and Dennison & Gouws (1980) amongst others, are noteworthy. Efforts to protect the amino acids from degradation in the rumen by formaldehyde, maleic anhydride (de Wet, Schoeman & Burger, 1969; Schoeman, de Wet & Burger, 1972; de Wet, 1975; Wessels & Marshall, 1975) or heat treatment *etc.,* have shown some progress. The Stellenbosch group, for example, through consistent experimentation since the sixties have shown substantial increases in wool production if the S-containing amino acids are protected. It appears that in most cases methionine and lysine are the first and second limiting amino acids, certainly in woolled sheep, but apparently also in other ruminants or production functions (de Wet, 1982). Nevertheless, our knowledge of the major limiting essential amino acids is inadequate, mainly because of the limitations of techniques aimed at measuring amino acids absorbed from the small intestine in conjunction with techniques to estimate the amino acid requirements of tissues (Cloete, 1982). This is a field of study which needs urgent attention.

Knowledge of the amount of microbial protein (NAN) reaching the duodenum and the amount of feed protein which escapes rumen fermentation, is basic to any protein evaluation system or protein feeding standard. Both essentials are poorly quantitated because of shortcomings in measurement techniques. The determination of microbial protein flow from the rumen presents two problems in practice (Meyer, 1982):

(i) Collection of representative samples of digesta leaving the rumen over 24 hours where the types of cannulas in use

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present difficulties.

(ii) Marking of the microbial fraction of the protein where all markers currently used have limitations.

Two major factors hamper successful distinction between rumen degradable and undegradable (by-pass) protein:

(i) Unsatisfactory *in vitro* and *in vivo* methods to measure either solubility or degradation. Cronjé (1982) uses the artificial fibre bag technique at Irene with some success but the method needs standardization in pore size and sample treatment.

(ii) Degradation in the rumen differs according to the components of the diet and the rate of outflow of digesta.

In conclusion, I would refer the reader to the proceedings of a workshop held at the National Chemical Research Laboratory during 1982 through the initiative of Dr Schwartz and the ADSRI. Sensing the urgent need for basic research on nitrogen metabolism in the ruminant, this workshop evaluated what is known and where we have to go. Suffice it for me to say that the laboratories represented there should take notice of the urgency of the protein dilemma for the livestock industry. Perhaps also, the idea of Cloete (1982) that the Department of Agriculture should consider a permanent Protein Administration to assess the supply-demand situation and to direct and coordinate protein research is the answer.

## 3. Mineral metabolism and interaction

Certain regions in South Africa are notorious for lack of certain essential minerals. The amount of documentation on phosphorous deficiencies, is noteworthy especially in the Armoedsvlakte area — work initiated through the contributions of Theiler and colleagues as early as 1912 (Boyazoglu, 1973; van der Merwe, 1974; Engels, 1981) — as well as on copper, cobalt and in some cases, molybdenum deficiencies in the south-eastern coastal regions (van der Merwe & Perold, 1967). As a consequence much attention has been paid to the supplementing of the grazing animal to correct possible deficiences. Also, recently the Glen group managed to differentiate between physiological states in terms of requirements and ability to select a diet of sufficient mineral status from natural pasture (de Waal, pers. comm.).

While the general approach in South Africa has been to correct for nutritional deficiencies in the grazing animal, one would have expected at least some 'back-up' studies in the laboratory to quantitate mineral requirements under different simulated conditions, possibly in terms of a function of feeding level. On scanning the literature one is amazed to find such limited data. The attitude appears to be rather to supplement in excess of requirements since the costs involved are not extravagant (Boyazoglu, 1973). While this attitude in practical nutrition is not without merit, it does not help much in understanding mineral metabolism and why imbalances so frequently occur.

In the latter field a systematic effort has been launched since the sixties by Boyazoglu (Boyazoglu, Jordan & Meade, 1967), Boyazoglu, Barrett & du Toit, 1972; Nel (Nel & Moir, 1968; 1974; Nel, 1976) and van Ryssen (van Ryssen, Channon & Stielau, 1977; van Ryssen & Stielau, 1980; van Ryssen & Jagoe, 1981) and their colleagues. Some of the interactions are quite intriguing and quantitative knowledge thereof is undoubtedly very important not only for establishing requirements, but also for limiting the effects of, or preventing toxicity. For example, the presence of sulphur, can limit the build up of copper in the liver (Boyazoglu *et al.*, 1972; van Ryssen & Jagoe, 1981) while it may also limit the retention of manganese, magnesium and zinc. On the other hand, excessive calcium in the presence

of phosphorus may precipitate hypomagnesaemia (Nel, 1976) and one is inclined to think that the addition of high levels of CaCO₃ to prevent acidosis in high energy diets could be counterproductive in the long run because of mineral imbalances. This field should receive even more attention in future studies.

In conclusion, I appeal for a more purposeful approach towards developing reliable mineral feeding standards for Southern Africa. In the ruminant it should be borne in mind that rumen microbes have specific requirements, so does the host animal. It is therefore obviously essential that such an effort should be an integrated effort between microbiologists and nutritionists.

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