

## Nutritional studies on East African herbivores

### 2.\* Losses of nitrogen in the faeces

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1. A series of nitrogen-balance trials was done using groups of four animals of various species of wild and domesticated ruminants using pelleted diets (Arman & Hopcraft, 1975).

2. Various herbivores were given grass or grass hays, legumes, herbs and shrubs. Food and faecal samples were analysed for N.

3. With the pelleted diets, the N content of the faecal dry matter (DM) was low for eland (*Taurotragus oryx* Pallas), high for sheep and cattle (*Bos taurus* and *Bos indicus*) and intermediate for the three small antelope species (hartebeest (*Alcelaphus buselaphus cokei* Günther), Thomson's gazelle (*Gazella thomsonii* Günther) and duiker (*Sylvicapra grimmia* L.)). With the natural fodders, similar relationships were found, together with variations associated with the type of diet.

4. Three forms of equation were used to express the relationship between faecal N and food N. One of the forms, the linear regression of g faecal N/kg DM intake v. g food N/kg DM intake, fitted the results less well than did the other two and was not used to estimate metabolic faecal N (MFN) losses.

5. MFN was calculated by extrapolation of linear regressions of g faecal N/kg faecal DM v. g N intake/kg faecal DM for the pelleted diets. The range of values was (g N/kg faecal DM): Friesians 7.6, eland 8.1, zebu cattle 11.0 and small antelope and sheep 11.5–12.6. There were significant differences ( $P < 0.001$ ) between species in slopes and intercepts.

6. MFN was calculated from linear regressions of g faecal N/kg faecal DM v. g food N/kg food DM for all diets. This method gave the best fit for the pelleted diets. Values for these diets were (g N/kg faecal DM): eland 8.3, cattle and sheep 9.3–11.0 and small antelope 11.6–12.3. Species differences were significant ( $P < 0.001$ ). With grasses, values ranged from 5.9 for non-ruminants (rabbit (domesticated), warthog (*Phacochoerus aethiopicus* Pallas) and hippopotamus (*Hippopotamus amphibius* L.)) plus eland and wildebeest (*Connochaetes taurinus* Burchell), to 8.4 for the other ruminants (sheep, goat, hartebeest, gazelle, duiker, buffalo (*Syncerus caffer* Sparrman)), kob (*Adenota kob thomasi* Sclater), reedbuck (*Redunca redunca* Pallas) and topi (*Damaliscus korrigum* Ogilby). For ruminants (sheep, hartebeest, duiker and kob), excluding eland, given legumes the value was 8.6, and for sheep and duiker given herbs the value was 14.7. With shrubs, faecal-N losses were variable and sometimes high.

7. With the pelleted diets, true digestibilities of crude protein ( $N \times 6.25$ ) varied from 0.84 to 0.91.

8. The results are discussed in relation to the digestive physiology and feeding habits of the various species, and there is an examination of the feasibility of using linear regressions of crude protein in the diet v. N in the faecal DM for evaluating the quality of the diets selected by free-ranging East African herbivores.

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Table 1. *Animals used in addition to the eland (Taurotragus oryx Pallas), hartebeest (Alcelaphus buselaphus cokei Günther) and duiker (Sylvicapra grimmia L.) described by Arman & Hopcraft (1975) in the supplementary experiments with natural foods*

Species	No.	Sex	Remarks
Goat	1	Castrated ♂	Immature
Rabbit (domesticated)	2	♂	Immature
Buffalo ( <i>Syncerus caffer</i> Sparrman)	2	♀	Immature, tame
Reedbuck ( <i>Redunca redunca</i> Pallas)	1	♂	Immature, tame
Uganda kob ( <i>Adenota kob thomasi</i> Sclater)	2	♀	One nearly adult, one young, tame
Topi ( <i>Damaliscus korrigum</i> Ogilby)	1	♂	Nearly adult, fairly tame
Wildebeest ( <i>Connochaetes taurinus</i> Burchell)	2	♂	One adult, one immature, fairly tame
Hippopotamus ( <i>Hippopotamus amphibius</i> L.)	1	♂	One immature, one nearly adult, fairly tame
Warthog ( <i>Phacochoerus aethiopicus</i> Pallas)	1	♀	Immature, fairly tame

In a previous paper (Arman & Hopcraft, 1975) we described a series of digestibility trials using wild and domesticated East African herbivores given pelleted diets, obtaining values for the digestibilities of dry matter, crude fibre and crude protein (nitrogen  $\times 6.25$ ). There were no significant over-all differences between cattle (*Bos taurus* and *Bos indicus*) and sheep (Corriedale and fat-tailed), but there were significant differences between sheep and some of the antelope. There were species differences in apparent digestibility of crude protein, suggesting that there may also be differences in metabolic faecal-N losses (MFN). Variations in stomach anatomy (Hofmann, 1968), which might affect rumen retention time and the relative proportions of the total fermentation taking place in the stomach and large intestine respectively, suggest the same possibility. In this paper, we report MFN losses for animals given the pelleted diets.

In the tropics, the protein contents of grasses are often very low, especially in the dry season. Low protein intakes could in turn limit intakes of energy and other nutrients. The quality of the natural diet, as selected by the animal, may be fairly well indicated by its crude protein content, and methods of assessing the protein content of the diet would be valuable. Wild herbivores eat a great variety of plant species and plant parts, and reliable estimates of their protein intakes cannot be made from herbage samples. Research on the nutrition of wild animals is, therefore, limited by inadequate techniques for field work, and approximations would be useful. We have made a preliminary examination of the feasibility of using the N content of the faeces of free-ranging East African herbivores to estimate the protein content of their diets. This technique is a well-recognized one for use with domesticated animals grazing simple swards (e.g. Bredon, Harker & Marshall, 1963), provided that the regressions used are derived from forages resembling those available to the grazing animal.

Analyses of food and faeces from a number of other experiments have been combined with trials (supplementary experiments) using natural, instead of pelleted,

Table 2. Nitrogen contents (g N/kg dry matter (DM)) of food and faeces of different species of East African herbivores given five pelleted diets containing different amounts of protein (high-low, E-A respectively) prepared from two batches of food (Arman & Hopcraft, 1975)

(Mean values for four animals of each species)

	Batch 1	Diets				
		E	D	C	B	A
Food DM	21.6	19.2	16.6	13.1	10.3	
Faecal DM						
Eland ( <i>Taurotragus oryx</i> Pallas)	14.5	13.6	12.2	11.8	11.0	
Hartebeest ( <i>Alcelaphus buselaphus cokei</i> Günther)	17.3	16.5	15.7	14.9	14.5	
Thomson's gazelle ( <i>Gazella thomsonii</i> Günther)	17.5	16.7	15.5	14.7	14.3	
Duiker ( <i>Sylvicapra grimmia</i> L.)	17.6	16.7	15.7	15.0	14.5	
Sheep*	18.7	17.4	15.3	14.9	14.2	
	Batch 2					
Food DM	21.9	18.6	13.9	11.5	10.4	
Faecal DM						
Sheep*	18.7	17.1	15.9	15.7	14.5	
Boran zebu ( <i>Bos indicus</i> )	19.2	17.5	17.2	15.4	14.0	
Friesians ( <i>Bos taurus</i> )	19.8	17.9	17.1	15.1	13.4	
Significance of difference between mean values for species: <i>P</i>						
Batch 1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
Batch 2	< 0.01	< 0.01	< 0.001	< 0.01	< 0.001	
Approximate SE of differences between mean values for species	0.28	0.21	0.15	0.11	0.17	

\* Two fat-tailed and two Corriedale sheep.

diets. The foods used included grasses, legumes, herbs and shrubs, and the differences in N excretion have been related to diet and animal species.

#### EXPERIMENTAL

The animals and experimental procedure used for the experiments with pelleted diets were those described by Arman & Hopcraft (1975). These experiments were carried out either at Athi River, near Nairobi, Kenya or at Makerere University, Kampala, Uganda. The additional animals used in the supplementary experiments, carried out at these two places and at the Nuffield Unit of Tropical Animal Ecology (now the Uganda Institute of Ecology), Ruwenzori National Park, Uganda, are described in Table 1.

#### Supplementary experiments

*Diets.* Food sources included: elephant grass (*Pennisetum purpureum*) and other grasses and grass hays, lucerne hay, *Desmodium uncinatum* (a forage legume), tops from sweet potato (*Ipomea batatas*), tops from carrot (*Daucus carota*), leaves of *Amaranthus* sp. (a herb) and leaves of *Acalypha wilkesiana*, *Hibiscus rosa-sinensis* and mulberry (*Morus nigra*) (shrubs). The number of animal-diet combinations studied was limited by the facilities available and by the dietary preferences of the various animal species.

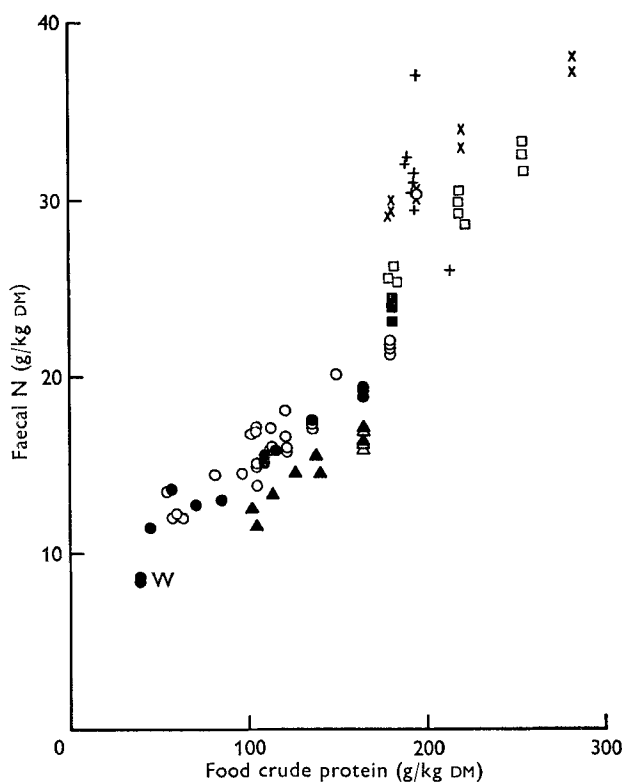


Fig. 1. The relationship between the nitrogen content of the faeces and the crude-protein ( $N \times 6.25$ ) content of natural fodders given to different species of East African herbivores.  $\circ$ , Sheep (Corriedale and fat-tailed) given grass;  $\bullet$ , small antelope (hartebeest (*Alcelaphus buselaphus cokei* Günther), reedbuck (*Redunca redunca* Pallas), kob (*Adenota kob thomasi* Sclater) and topi (*Damaliscus korrigum* Ogilby)) given grass;  $\bullet W$ , wildebeest (*Connochaetes taurinus* Burchell) given grass;  $\Delta$ , eland (*Taurotragus oryx* Pallas) given grass;  $\blacktriangle$ , non-ruminants (rabbits (domesticated), warthog (*Phacochoerus aethiopicus* Pallas) and hippopotamus (*Hippopotamus amphibius* L.) given grass;  $\square$ , sheep (both breeds) and small antelope (hartebeest, duiker and Uganda kob) given legumes;  $\blacksquare$ , eland given legumes;  $\times$ , sheep (both breeds) and duiker given herbs;  $+$ , sheep and small antelope (duiker and Uganda kob) given shrubs. DM, dry matter.

*Procedure.* The animals were fed *ad lib.* and were first offered the test food until they ate it freely. After a pre-feeding period of 8–12 d in individual pens, collections of faecal samples began. A freshly-voided sample was taken daily from each animal and analysed for N (fresh and dried faeces in some instances). The mean N content of the faeces over a 6 d period was calculated. In the collection period, the weights of food offered and rejected, and their N and dry matter (DM) contents, were recorded, and the N content of the food actually selected was calculated. The methods of analysis were the same as those used in the main experiments.

Table 3. *Linear regressions of g nitrogen/kg faecal dry matter (DM) (y) v. (1) N intake/kg faecal DM (x<sub>1</sub>) and (2) N intake/kg food DM (x<sub>2</sub>) for the two batches of five pelleted diets containing different amounts of protein given to different species of East African herbivores*

(Regression equation:  $y = bx + c$ , where  $b$  is the slope and the intercept  $c$  is the metabolic faecal N excretion expressed as g N/kg faecal DM)

Animals	$y$ v. $x_1$ *				$y$ v. $x_2$ †			
	$b$	SE	$c$	Residual SD	$b$	SE	$c$	Residual SD
Batch 1								
Eland ( <i>Taurotragus oryx</i> Pallas)	0.142	0.011	8.1	0.41	0.288	0.014	8.3	0.27
Hartebeest ( <i>Alcelaphus buselaphus cokei</i> Günther)	0.091	0.008	12.2	0.34	0.224	0.012	12.3	0.22
Thomson's gazelle ( <i>Gazella thomsonii</i> Günther)	0.124	0.009	11.5	0.38	0.267	0.013	11.6	0.25
Duiker ( <i>Sylvicapra grimmia</i> L.)	0.103	0.010	11.8	0.44	0.253	0.010	12.1	0.19
Batches 1 and 2‡								
Corriedale sheep	0.097	0.010	12.3	0.65	0.367	0.024	10.7	0.44
Fat-tailed sheep	0.088	0.013	12.6	0.87	0.341	0.027	11.0	0.53
Batch 2								
Boran zebu ( <i>Bos indicus</i> )	0.127	0.030	11.0	1.38	0.396	0.034	10.7	0.66
Friesians ( <i>Bos taurus</i> )	0.214	0.039	7.6	1.43	0.481	0.037	9.3	0.73

\* Regressions based on method b, see p. 270.

† Regressions based on method c, see p. 270.

‡ Significant differences between batches.

## RESULTS

### *N contents of the faeces*

The results for all experiments with pelleted diets are shown in Table 2. There are clear species differences in faecal-N contents, which were generally high for cattle (except at low protein intakes), very low for eland (*Taurotragus oryx* Pallas) and intermediate for the sheep and three species of small antelope.

For the supplementary experiments using natural fodders, the relationship between faecal-N content and the crude-protein contents of the fodders are shown in Fig. 1. The plotted points fell into fairly distinct groups according to types of diets, and there were also species differences within diet type. In particular, the non-ruminants (rabbit (domesticated), warthog (*Phacochoerus aethiopicus* Pallas) and hippopotamus (*Hippopotamus amphibius* L.)) given grass had lower faecal-N contents than most of the ruminants. The faecal-N contents for eland were again low, as with the pelleted diets. The two results for wildebeest (*Connochaetes taurinus* Burchell) were also low, but two values alone could not be regarded as conclusive. Faecal-N contents were higher for animals given legumes and herbs than for those given grasses, and faecal-N contents for animals feeding on shrubs were variable and sometimes high.

Table 4. *Linear regressions of g nitrogen/kg faecal dry matter (DM) (y) v. g N/kg food DM (x) for natural fodders given to different species of East African herbivores*

(Regression equation:  $y = bx + c$ , where  $b$  is the slope and the intercept  $c$  is the metabolic faecal N loss in g N/kg faecal DM)

Animals	Diet*	No. of results	$b$	$c$	Residual SD
Sheep†, goat, hartebeest ( <i>Alcelaphus buselaphus cokei</i> Günther), gazelle ( <i>Gazella thomsonii</i> Günther), duiker ( <i>Sylvicapra grimmia</i> L.), buffalo ( <i>Syncerus caffer</i> Sparrman), kob ( <i>Adenota kob thomasi</i> Sclater), reedbuck ( <i>Redunca redunca</i> Pallas) and topi ( <i>Dama-liscus korrigum</i> Ogilby)	Grass	40	0.433	8.4	0.92
Non-ruminants‡ plus eland ( <i>Taurotragus oryx</i> Pallas) and wildebeest ( <i>Connochaetes taurinus</i> Burchell)	Grass	13	0.400	5.9	0.59
Ruminants (sheep,† hartebeest, duiker and kob) excluding eland	Legumes	10	0.592	8.6	0.77
Sheep† and duiker	Herbs	9	0.510	14.7	0.58

\* For details, see p. 267.

† Corriedale and fat-tailed.

‡ Rabbit (domesticated), warthog (*Phacochoerus aethiopicus* Pallas) and hippopotamus (*Hippopotamus amphibius* L.).

#### *Relationships involving faecal N and metabolic faecal losses*

*Pelleted diets.* Using the results from the N-balance trials, three types of regressions were calculated: (a) regressions based on food DM, where  $y$  is g faecal N/kg food DM and  $x$  is g food N/kg food DM; these were curved (particularly in values for cattle) and gave, in most instances, the highest values for residual SD and were not suitable for extrapolation; (b) regressions based on faecal DM, where  $y$  is g faecal N/kg faecal DM and  $x$  is g food N/kg faecal DM; (c) regressions of g faecal N/kg faecal DM ( $y$ ) v. g food N/kg food DM ( $x$ ).

With regressions based on (b) and (c) the relationships appeared to be linear and equations were calculated as shown in Table 3. These are each based on twenty observations, one from each of four animals on each of five diets. The combination of results from individual animals was valid except for the sheep. For regressions based on (b), both the slopes and intercepts varied significantly from one sheep to another ( $P < 0.01$ ) but for regressions based on (c) the differences were less marked and were confined to the fat-tailed sheep. The slopes were higher and the intercepts lower for the sheep given diets from batch 1 than for those given diets from batch 2 and it may be assumed that differences between the batches of food were responsible for the individual animal differences.

For each species, the regression equations based on (c) gave lower residual SD values, indicating that they fitted the results better than those of regressions based on (b), and the intercepts of the former were therefore the more reliable estimates of MFN losses. The MFN estimates were lowest for the eland and the Friesians, inter-

mediate for the Borans and sheep and greatest for the small antelope. However, these values for MFN excretion do not necessarily give a reliable indication of the relative efficiencies of protein digestion at more normal levels of intake, as these also depend on the regression coefficients which reflect true N digestibility. With the high-protein diets, faecal-N concentrations were very low for eland and high for the domesticated animals (Table 2).

The species differences in MFN were tested by substituting the results into a series of equations all with the same intercept, and assessing the degree of fitness. The best values were found to be 11.0 for regressions based on (b) and 10.7 for those based on (c), but these common-intercept equations fitted the results less well ( $P < 0.001$ ) than did the equations in Table 3. A set of parallel lines also fitted the results less well, suggesting that there were significant differences between the species both in the intercepts and in the slopes.

*Natural fodders.* The results of supplementary experiments using natural foods were used to calculate MFN losses by regressions based on (c), but could not be used in those based on (b). The calculated regressions are shown in Table 4. Analysis of all the results for the grass diets showed significant species differences in the faecal N *v.* food N relationships. The species fell into two groups. Most of the ruminants (sheep, goat, buffalo (*Syncerus caffer* Sparrman), hartebeest (*Alcelaphus buselaphus cokei* Günther), reedbuck (*Redunca redunca* Pallas), Uganda kob (*Adenota kob thomasi* Sclater) and topi (*Damaliscus korrigum* Ogilby)) had relatively high faecal-N contents ( $P < 0.001$ ) as compared with those for the non-ruminants (rabbit, warthog and hippopotamus), the eland and wildebeest. There were no statistically significant differences in the relationship between the species, within either of these two groups. Similarly for the legume diets, the eland had significantly ( $P < 0.05$ ) lower faecal-N contents than did the other ruminant species (sheep, hartebeest, Uganda kob and duiker (*Sylvicapra grimmia* L.)). The results for the two species given herbs (sheep and duiker) could be combined into a single relationship.

In Fig. 1 faecal-N contents were higher for animals given legumes than for those given grasses and were higher still for animals given herbs and shrubs. The faecal-N contents for animals given the few shrubs used were very variable and no regression equation could be calculated. The equations for grasses, legumes and herbs are given in Table 4.

#### *True digestibility of crude protein in the pelleted diets*

The apparent digestibilities of crude protein were given in the preceding paper (Arman & Hopcraft, 1975). They fell in the order: eland, duiker and hartebeest > sheep (both breeds) and Thomson's gazelle (*Gazella thomsonii* Günther). The true digestibility of crude protein may be defined as the (food N – faecal N + MFN):food N ratio and may be calculated using the regression equations based on (c) (p. 270), which may be rearranged as follows: (faecal N – MFN) ÷ food N =  $b \times DM$  indigestibility, where  $b$  is the regression coefficient. The true digestibility of crude protein is therefore  $(1 - (b \times DM \text{ indigestibility}))$ . For the animals fed on batch 1 diets, values calculated using this formula were: sheep 0.83, eland 0.86, Thomson's gazelle 0.88

Table 5. *Linear regressions of g crude protein (nitrogen  $\times$  6.25)/kg food dry matter (DM) (y) v. g N/kg faecal DM (x) for natural fodders given to different species of East African herbivores*

(Regression equation:  $y = bx + c$ , where  $b$  is the slope)

Animals	Diet*	No. of results	$b$	$c$	Residual SD
Sheep†, goat, hartebeest ( <i>Alcelaphus buselaphus cokei</i> Günther), gazelle ( <i>Gazella thomsonii</i> Günther), duiker ( <i>Sylvicapra grimmia</i> L.), buffalo ( <i>Syncerus caffer</i> Sparrman), kob ( <i>Adenota kob thomasi</i> Sclater), reedbuck ( <i>Redunca redunca</i> Pallas) and topi ( <i>Dama-liscus korrigum</i> Ogilby)	Grass	40	12.8	-95	12.6
Non-ruminants‡ plus eland ( <i>Taurotragus oryx</i> Pallas) and wildebeest ( <i>Connochaetes taurinus</i> Burchell)	Grass	13	15.0	-84	9.0
Ruminants (Sheep†, hartebeest, duiker and kob) excluding eland	Legumes	10	9.9	-70	7.9
Sheep† and duiker	Herbs	9	12.0	-170	7.0

\* For details, see p. 267.

† Corriedale and fat-tailed.

‡ Rabbits (domesticated), warthog (*Phacochoerus aethiopicus* Pallas) and hippopotamus (*Hippopotamus amphibius* L.).

duiker 0.90, hartebeest 0.91. For the animals fed on batch 2 diets, the values were: Friesians 0.83, Boran zebus 0.87, sheep 0.90.

#### *Use of faecal-N regressions in field studies*

To predict the protein contents of the diets of free-ranging herbivores from faecal analyses, variations in N losses with the species of animal and the type of diet must be considered. Table 5 shows a series of regression equations, based on the results with natural fodders of the type which might be used for this purpose.

#### DISCUSSION

##### *Components of the faecal N*

Faecal N in ruminants can be divided into undigested dietary N, which varies with the type of animal and the nature of the dietary protein and associated constituents such as tannins, structural material, etc., and non-dietary faecal N. The latter comprises water-soluble N, bacterial N and endogenous N. The relative proportions of the fractions depends on the nature of the diet, its protein content and the amount of food eaten (Mason, 1969, 1971). MFN consists of bacterial and endogenous N, and is defined as the N excretion associated with a N-free diet of adequate energy content.

The concentration of faecal N is related to the amount of N lost and to the extent of dilution by undigested dry matter. Faecal N losses depend partly on the amount of bacterial N produced, the site of its production (rumen or colon) and the extent



of its subsequent digestion (this may vary with species of animal). Hungate, Phillips, McGregor, Hungate & Buechner (1959) have shown that the rate of rumen fermentation is greater in small species (not established with diets of constant composition): this might enhance the formation of bacterial N. Furthermore, small animals, with a large surface: volume ratio in the gut, might lose more endogenous N, therefore MFN may be higher in small species than in large ones.

#### MFN

MFN losses, reviewed by Blaxter (1964) and the Agricultural Research Council (1965), are one of the main factors affecting the dietary protein requirement of ruminants. Values for MFN can either be measured direct, using a N-free diet (less satisfactory in ruminants because bacterial growth in the rumen depends on a supply of N) or calculated by extrapolation of results obtained with a series of diets of differing protein contents. The two methods give values of about 5 g MFN/kg DM intake (DMI) for ruminants and for non-ruminants the loss is lower (about 1-2 g MFN/kg DMI), largely because less bacterial N is formed.

Majumdar (1960) obtained a MFN value of 4.1 g/kg DMI for goats and Moir & Swain (1972) obtained a value of 6.0 g N/kg food organic matter for cattle and sheep. Hironaka, Bailey & Kozub (1970) analysed the results from forty-five diets fed to cattle and sheep and found a closer relationship between N excretion and faecal DM than between N excretion and food DM. They suggest that using excretion rather than intake as a basis gives a value related to diets of differing digestibilities.

We have also examined the different methods for calculating MFN by extrapolation (Hironaka *et al.* 1970). The three types of regression are: (a) where  $y$  is faecal N/kg DMI and  $x$  is food N/kg DMI; in the work of Hironaka *et al.* (1970) as in our own this method gave the poorest fit and the regressions were curved and not suitable for extrapolation; (b) where  $y$  is faecal N/kg faecal DM and  $x$  is N intake/kg faecal DM; Hironaka *et al.* (1970) found this method to give the best fit, but in our work it was intermediate. They calculated an intercept of 8.9 g N/kg faecal DM when N intake was zero. With our pelleted diets A-E, there were significant ( $P < 0.001$ ) differences between animal species in both the intercepts (MFN) and slopes of these lines. MFN values ranged from 7.6 g N/kg faecal DM for Friesians to 8.1 for eland, 11.0 for Boran zebus and 11.5-12.6 for small antelope and sheep; (c) where  $y$  is faecal N/kg faecal DM and  $x$  is food N/kg DMI; this method gave the closest fit for our results but was intermediate for Hironaka *et al.* (1970), who obtained a value of 11.2 g N/kg faecal DM for cattle and sheep combined. Our results ranged from 8.3 for eland to 9.3-11.0 for cattle and sheep and 11.6-12.3 for small antelope given the pelleted diets. There were significant ( $P < 0.001$ ) differences between animal species for both slopes and intercepts. Using this method with the natural fodders, we obtained values ranging from 5.9 for the three non-ruminant species plus eland and wildebeest to 8.4 for small ruminants given grass diets. The MFN for small ruminants given legumes was 8.6 g N/kg faecal DM and with herbs was 14.7. Generally our results were similar to published results.

No experiments were done using cattle given natural fodders. As faecal regressions

vary with the diet and type of cattle it is important, for comparison, that published values should be those obtained under African conditions. McKay (1971), using Boran cattle in Kenya, derived the equation: crude protein (CP) in faeces (%) =  $0.56 \times \text{CP in food (\%)} + 3.78$ , giving an MFN value of 6.0 g N/kg faecal DM. Bredon *et al.* (1963), working with zebu cattle in Uganda, calculated the equation: CP in food DM (%) =  $1.677 \times \text{CP in faecal DM (\%)} - 6.93$ . Our results with pelleted and grass diets compared with these two relationships suggest that in cattle, faecal N at high protein intakes is higher than that in small ruminants.

The increased N contents of faecal DM associated with diets containing dicotyledonous plant species may result from: (1) their high digestibility; (2) very rapid fermentation in the rumen, forming much bacterial N, and (3) the presence in dicotyledons of varying amounts of protein precipitants such as tannins or leucoanthocyanins (Osbourn, Terry, Cammell & Outen, 1971) which may reduce protein digestibility or inhibit digestive enzymes (Milić, Stojanović & Vučurević, 1972). Different species of grass show only minor variations, but this is clearly not true of dicotyledons, especially shrubs, and there appears to be no hope of establishing universal relationships between faecal-N losses and protein intakes.

#### *Differences between animal species*

Among the ruminants there are considerable variations in feeding habits and in the anatomy of the stomach (Hofmann, 1968; Hofmann & Stewart, 1972). Species differences in the efficiency of digestion do occur (Arman & Hopcraft, 1975). Selective feeders digest protein efficiently but may, as for the eland, make relatively inefficient use of structural carbohydrate. For the eland, MFN losses may be low as a result of low bacterial-N production and dilution of faecal N by undigested fibre. This situation is similar to that in a non-ruminant herbivore in which MFN is very low. For roughage eaters, or grazers, the experimental diets may have been retained in the large rumen for longer, forming more bacterial N: the efficient use of fibre would result in a high faecal-N concentration. MFN associated with a given diet may, therefore, be greater in grazers than in selective feeders and perhaps greater in small animals than in large ones. Among the ruminants, these predictions are generally supported by our results. The lowest MFN values were associated with the eland, a large selective feeder, and the highest with the hartebeest, the smallest grazer studied. The two low faecal-N values for wildebeest are unexpected but need confirmation.

MFN values should be measured at a constant intake relative to body-weight or metabolic body-weight ( $\text{body-weight}^{0.75}$ ), but in our experiments the animals were fed to appetite and showed variations in intake. Food intakes will be dealt with in a later paper.

MFN values would provide a guide to the actual protein requirements at normal levels of protein intakes only if the slopes of the regression lines relating N losses to N intake were similar for all species. This condition was not met and there were species differences in the true digestibility of protein. It must be emphasized that this study of species variations is a preliminary one, and some of the relationships need more experimentation before they can be regarded as established.

*The use of faecal-N regressions to estimate the protein intakes  
of free-ranging herbivores*

It would be a useful method in range ecology and wildlife research if relationships between the N in the faeces and the crude protein in the diet could be established and used to estimate, even if only approximately, the quality of the diets actually selected by free-ranging herbivores, and the variations with area and season. Results from our preliminary study (Table 5) show that the possibilities of doing this are limited, especially in Africa, where there is such a wide variety of plant and animal species.

In the instance of animals which feed largely on grasses (e.g. cattle, buffalo, some antelope including hartebeest, wildebeest, topi and Uganda kob) and non-ruminants (e.g. the zebra (*Equus burchelli* Gray and *E. grevyi* Oustalet) and hippopotamus) it may be possible to make fairly good assessments of the quality of their diets, given adequate calibration. For the rest of the herbivores which eat a mixture of dicotyledons or dicotyledons plus grasses, only very rough estimates of dietary quality will be possible. Limited comparisons, e.g. for one species in different areas or seasons, may be possible, although even these may be rendered difficult by dietary variations. Values for faecal-N contents for various East African herbivores, in relation to species, area and season, will be discussed in a separate paper.

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