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PREDICTING VOLUNTARY INTAKE ON MEDIUM QUALITY ROUGHAGES

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(Sleutelwoorde: *Voorspelling, vrywillig inname, ruvoere, model)*

OPSOMMING: INNAMEVOORSPELLING MET MEDIUMGEHALTE RUVOER

'n Eerste-orde model vir innamevoorspelling is gebruik met skape wat ruvoere van uiteenlopende gehalte gevoer is. Belangrike veranderlikes, wat in hierdie studie geidentifiseer is, is die rumenkapasiteit van die diere, die eerste-orde vervalkonstante vir fermentasie van die dieet, die oplosbaarheid van die dieet en die nie-oplosbare fermenteerbare fraksie van die dieet.

Die eerste-orde vervalkonstantes wat die uitvloei van fermenteerbare- en nie-fermenteerbare organiesemateriaal (O.M.) beskryf was dieselfde ongeag die tipe dieet wat gevoer is. Beramings van hierdie veranderlikes is verkry van gekannuleerde skape en die innames van intakte skape wat dieselfde diete gevoer is, is voorspel. Resultate dui daarop dat 'n relatief onsydige voorspelling van die vrywillige voerinname van die onafhanklike groep skape verkry is deur hierdie metode te gebruik. Voorspelde gemiddelde inname was 665,9 g/dag terwyl werklike gemiddelde inname 666,5 g/dag was. Die standaardfout van die voorspelde gemiddeld was 4,90 g/dag.

SUMMARY:

A first order model for predicting voluntary intake was applied to sheep fed roughages differing in quality. Important variables identified in this study were the rumen capacity of the animals, the first order rate constant for fermentation of the diet, the solubility of the diets and the insoluble fermentable fraction of the diet.

The first order rate constants for the outflow of fermentable and unfermentable organic matter from the rumen were found to be the same irrespective of the diet. Using estimates of these variables obtained from caanulated sheep, the intakes of intact sheep fed the same diets were predicted. Results indicated that a relatively unbiased estimate of voluntary feed intake on diets, including a legume and grass of widely different qualities, were obtained with another group of sheep using this method. Predicted mean intake was 665,9 g/day whilst actual mean intake amounted to 666,5 g/day. The standard error of the predicted means was 4,90 g/day.

Crampton, Donefer & Lloyd (1960) concluded that digestibility determinations must be combined with an estimate of intake to give a reasonable indication of the productive value of a feed. Gill, Conrad & Hibbs (1969) found a good relationship between the rate constant for fermentation and voluntary intake in dairy cows fed silages cut at different growth stages. However on determining the rate constant for fermentation of two mutants of maize with different lignin contents, Lechtenberg, Colenbrander, Bauman & Rhykerd (1974) found that significant differences in voluntary intake could be detected between the two mutants, even though no significant difference existed in the rate constant for the *in vitro* fermentation of the cell wall constituents.

The processes of outflow through the whole digestive tract was described by Blaxter, Graham & Wainmann (1956) and Brand & Thacker (1958). They expressed outflow as a first order process which is comparable to the approach used by Waldo, Smith & Cox (1972) and Mertens (1977), except that the work of Waldo *et al.* (1972), was aimed only at the rumen, a single compartment, as the basis of the first order model description of fibre kinetics. By dividing voluntary feed intake into the fraction that is fermented in the rumen and the fraction which flows from the rumen, the basic model provides a logical way in which the problem of intake prediction may be approached. Therefore, we based our predictions of intake on this first order model and the assumption that the rate at which the animal fills its rumen by voluntary feed intake will be equal to the rate at which the rumen is emptied.

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Waldo *et al.* (1972), applied their model to a chemically homogenous substrate like cellulose. In this study it was applied to chemically heterogenous organic matter. The only attempt made to divide organic matter into more homogenous fractions was done by dividing it into an immediately soluble and an insoluble fraction. The rate of digestion of all insoluble components is approximated by one first order rate constant for each diet.

This constant would probably be different for different morphological tissues within a plant. The use of chemically homogenous substrates (e.g. cellulose) in an attempt to describe the rate of digestion in terms of more homogenous substances was avoided as it was suspected that the close physical proximity of different chemical components in plant tissue would result in different digestion rates for a single chemical compound in different tissues. Should furhter experimentation prove that the rate of digestion cannot be approximated by a single constant, appropriate adjustments for increased precision would be possible.

The aim of this experiment was to identify the factors that influence voluntary intake in sheep when roughages of widely different qualities are fed. The diets fed were selected to cause large variation in voluntary feed intake.

In a second experiment also reported here, the aim was to determine if the parameters calculated for the cannulated sheep used in the first experiment, could be applied to predict the intake of a different group of intact sheep on the same diets.

Procedure

Cannulated sheep

Seventeen South African mutton Merino wethers, approximately one year of age with a mean live mass of about 28 kg, were successfully fitted with rubber cannulae in the rumen, abomasum and ileum, using techniques described by Morgan (1979). Data from 6 of these sheep were deleted, due to unacceptable measurements, showing an inconsistency between flow as estimated by marker techniques and flow as determined by faeces excretion. The allocation of the eleven other sheep, whose results were used consequently, to 5 diet groups are shown in Table 1.

All diets were ground through a 25 mm sieve and thoroughly mixed. Diets were analyzed for mineral content and deficiences (N.R.C., 1971) were supplemented daily via the rumen cannuale. Twenty five grams of casein were infused daily *per rumen* and 80 grams *per abomasum*. Casein was infused *per rumen* to supply ammonia and amino acids to rumen micro-organisms. Fifty milligrams of ammonia nitrogen per litre of rumen liquor was considered sufficient for maximum microbial activity (Roffler, Schwabb & Satter, 1976). Casein was infused *per abomasum* to prevent any deficiency in protein restricting voluntary intake (Weston, 1973). Diets were supplied *ad lib* + 10% and sheep were fed twice daily at twelve hour intervals.

Table 1

The mean live masses with standard errors and numbers of animals within each treatment

Diet	Young Cenchrus	Lucerne	Mature Cenchrus	Maize cob leaves	Wheat straw
		(mean values with their standard errors)			
Cannulated sheep					
Number of sheep	2	2	2	3	2
Mean live mass (kg)	39,3 ± 3,9	38,5 ± 3,0	32,5 ± 3,9	36,3 ± 2,5	31,2 ± 3,9
Intact sheep					
Number of sheep		7			8
Mean live mass (kg)		29,8 ± 1,05			29,3 ± 0,98

Animals were allowed one month to adapt to the diets before the following measurements were made:

a) daily organic matter intake was determined continuously;
b) rumen dry and organic matter content were measured on rumen contents after emptying the rumen 4 times at +3, +6, +9 and +12 hours after feeding. Emptying was done only once a day with an interval of at least 2 days. This was done to accommodate diurnal variation in rumen contents without seriously disturbing the sheep;
c) total flow of digesta past the terminal ileum was measures using chromium EDTA and ruthenium phanantrholine complex as soluble and particulate markers respectively as described by Faichney (1975) and Morgan (1975).
d) a total collection of faeces was made for 4 days to determine apparent digestibility of organic matter;
e) retention time of water in the rumen was measured using Cr EDTA as described by Warner (1966) and 4 determinations were made on each sheep;
f) the rate at which organic matter disappeared from the rumen and small intestine was obtained by subtracting flow past the ileum from organic matter intake;
g) outflow of fermentable organic matter was calculated from digestibility values obtained from in vitro fermentation of the diets (Telley & Terry, 1963), but with a 75 h incubation time in the microbial phase. The calculated flow of unfermentable organic matter in the faeces was subtracted from the flow of organic matter past the ileum, to obtain the outflow of fermentable organic matter.

Intact sheep

As an independent control group 15 intact South African Mutton Merino wethers with a mean live mass of 29,5 ± 2,77 kg were divided into 2 groups (Table 1). The lucerne and wheat straw diets were offered at *ad lib* + 10% and sheep were fed at eight hour intervals. Minerals as required, N.R.C., 1971) together with 25 g of casein and 80 g of fishmeal were fed twice daily. Organic matter intake was determined. The quantity of dry- and organic matter in the rumen was determined after the animals were slaughtered.

Results and Discussion

The sub-division of organic matter intake

The model proposed by Waldo *et al.* (1972), divides dietary organic matter into a fermentable and unfermentable fraction. The unfermentable fraction of the feed can escape from the rumen only by outflow, while the fermentable fraction can escape by means of both outflow and absorption through the rumen wall. Thus estimates of the following have to be obtained:

1. the outflow of unfermentable O.M. from the rumen,
2. the outflow of unfermented fermentable O.M. from the rumen,
3. The organic matter fermented in the rumen.

The fact that during the processes of fermentation in the rumen some organic matter is also synthesized or solubilized, complicates the problem of estimating the outflow of fermentable and unfermentable dietary

Table 2

Organic matter intake, organic matter fermented and organic matter outflow from the rumen. (Mean values with their standard errors)

Measurement	Young Cenchrus	Lucerne	Mature Cenchrus	Maize cob leaves	Wheat straw
Organic matter intake (g/day)	998 ± 69 a	1 049 ± 69 a	621 ± 69 a	934 ± 56 ab	596 ± 69 b
Organic matter "fermented" in the rumen (g/day)	600 ± 30 a	537 ± 30 ac	303 ± 30 bc	561 ± 24 ac	253 ± 30 b
Organic matter outflow from the rumen (g/day)	398 ± 51 ab	513 ± 51 b	318 ± 51 a	373 ± 41 a	344 ± 51 a

Figures with different subscripts differ significantly $P \leq 0,05$ according to one-way analysis of variance and Tukey's T-test.

organic matter. It was postulated that, when flow is measured at the terminal ileum, most of the micro-organisms synthesized or volatile fatty acids produced during fermentation would be removed. It is known that very little fermentable structural components are removed by digestion in the small intestines. Therefore, with the type of diets used here the best estimate of the outflow of feed O.M. would probably be obtained at the ileum. The same is true for the estimation of O.M. fermented in the rumen, as the estimate obtained included the O.M. which disappeared in both the rumen and small intestine. Because it is hypothesized that the O.M. removed in the small intestine originated mainly from the fermented fraction it should be included in the estimation of O.M. fermented.

It would have been interesting to be able to compare O.M. flow past the ileum with O.M. flow past the abomasum as an indication of the magnitude of the difference. However, the flow estimates obtained with abomasal digesta proved to be very inaccurate, probably due to technical problems and was consequently not used.

Table 2 presents data on how total organic matter was divided into fermented feed. O.M. and outflow of feed O.M.

As can be seen from Table 2, differences observed in voluntary feed intake are mainly determined by the rate of fermentation and to a much lesser extent by the rate of outflow from the rumen. These rates, i.e. the outflow of feed O.M. (minus the fermentable fraction) and the fermentation of feed organic matter in the rumen per day as well as the masses of unfermentable and fermemtable organic matter in the rumen were used to calculate the rate constants for outflow and fermentation of organic matter in the rumen.

Calculation of first order rate constants

Waldo *et al.* (1972) proposed a first order model for the processes of outflow from the rumen and the fermentation of cellulose. This model implies the following expression for the outflow and fermentation of organic matter:

rate of fermentation or flow = − constant x amount of substrate

$$\text{or } \frac{dZ}{dt} = -\gamma Z. \qquad (I)$$

Here $\frac{dZ}{dt}$ is the rate at which organic matter is fermented in, or flows from the rumen, with dimensions gram per day. The amount of substrate in gram is termed Z. The rate constant γ has dimension day $^{-1}$.

Equation (I) corresponds to a regression equation through the origin, so that the rate constants for fermentation can be calculated by the use of multiple regression techniques with the fermentation rate $\frac{dZ}{dt}_1$ as y and the x's being equal to the amount of fermentable organic matter in the rumen Z_1, or equal to zero if a y-value for a non-corresponding treatment is entered. The design matrix is presented in Table 3 under appendix. The advantage of using a multiple regression in this way instead of a simple regression, results from the pooling of degrees of freedom allowing more sensitive tests.

Since it can be expected that the rate constant for outflow γ_2 is in some was related to the rate constant for fermentation γ_1, a so-called allometric equation for outflow of unfermentable organic matter is postulated,

$$\gamma_2 = a\gamma_1{}^b$$

and fitted by nonlinear regression with,

$$\frac{dZ}{dt}_2 = a\gamma_1{}^b Z_2 + e$$

as model, Z_2 being the mass of unfermentable organic matter in the rumen and a and b being constants. This model is compared to the first order model for predicting intake (Table 4).

In order to calculate the rate constant for fermentation, fermentable organic matter was divided into a soluble and insoluble fraction (Table 9, appendix). The soluble fraction was immediately (c 30 minutes) soluble in McDougall's saliva and was not included in the calculation of the first order rate constant for fermentation. The insoluble fraction had to be dissolved by microbial and enzymatic action. This rate was expressed in terms of a first order rate constant for fermentation γ_1.

The in vivo measurements of the rate constants for fermentation (γ_1), outflow of unfermentable organic matter (γ_2) and outflow of fermentable organic matter (γ_0) are presented in Table 4

The slopes of the lines that relate $\frac{dZ}{dZ}$ to Z were tested for homogeneity by the F-Test A significant F-value (Table 4) together with the consideration of the uniqueness of the chemical composition of the diets, resulted in the decision to calculate a γ_1 for each diet. In the situation where the F-values were non-significant, a common estimate was calculated for γ. In all situations tests resulted in non-significant intercepts, so that the lines were forced through the origin with a corresponding increase in accuracy indicated by the relatively small magnitudes of some of the standard deviations of the parameters.

Table 4

Rate constants for fermentation (γ_1) outflow of unfermentable O.M. (γ_2) and outflow of fermentable O.M. (γ_0) as measured in vivo

Rate constant for:	Rate constant day^{-1}	Standard error	Syx	F-value	95% confidence Interval	
Fermentation of O.M. (γ_1) (Individual estimates)			77,2	5,82*		
Young Cenchrus	1,224***	0,139			0,914	1,534
Lucerne hay	2,029***	0,300			1,361	2,697
Mature Cenchrus	0,769**	0,176			0,377	1,161
Maize cob leaves	1,030***	0,090			0,829	1,231
Wheat straw	0,576**	0,159			0,222	0,930
Outflow of unfermentable O.M. Common estimate (γ_2)	0,4915***	0,036	69,61	3,63 NS	0,411	0,572
Outflow of unfermentable O.M. (allometric model)			46,8			
a	0 4619***	0,027			0,402	0,522
b	0,4141**	0,115			0,104	0,511
Outflow of fermentable O.M. (Common estimate) γ_0	0,2939***	0,0281	34,86	1,99 NS	0,231	0,357

* $p \leq 0{,}05$, ** $p \leq 0{,}01$, *** $p \leq 0{,}001$

It would appear from the results that, within the limits of experimental error, common rate constants for the outflow of fermentable and unfermentable organic matter from the rumen may be calculated, irrespective of the diet consumed. This conclusion cannot be extrapolated beyond the limits set by the type of diet used in this experiment, since a faster outflow would be expected with finely ground or NaOH treated roughages. The results for unfermentable organic matter are graphically presented in Fig. 1.

From Fig. 1 the relationship does not appear close, but the fact that it could be forced through the origin, increased the accuracy, as indicated by a highly significant t-value ($t = 13{,}6$, $p < 0{,}001$) for the regression coefficient).

Waldo *et al.* (1972) suggested that the outflow of fermentable cellulose can be calculated by using a common rate constant γ_2 for the outflow of both fermentable and unfermentable cellulose. When this approach is applied to organic matter, the situation is complicated by the fact that fermentable organic matter in the rumen consists of a soluble and an insoluble fractions. However, the experimental procedure did non allow accurate estimates of separate rate constants.

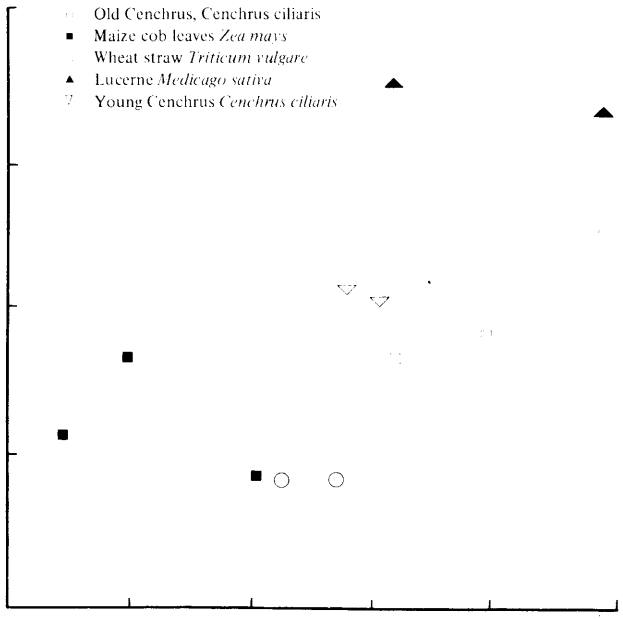

Fig. 1 Relationship between the mass of unfermentable Organic matter in the rumen and the outflow of unfermentable organic matter

Predicting voluntary feed intake and its validity

Voluntary feed intake was predicted for intact and cannulated sheep using equation (II), the derivation of which is given in the appendix. The symbols used are also explained in the appendix.

$$\frac{dZ}{dt} = \left[\frac{\gamma_2 (\gamma_1 + \gamma_0) Z}{(\gamma_1 + \gamma_0) k_2 + \gamma_2 k_1}\right] \frac{100}{100 - \%\,\text{Solubility}} \qquad \text{(II)}$$

In cannulated sheep their own rate constants were used to predict intake. For intact sheep the rate constants from cannulated sheep were used to predict intake, but rumen fill was directly obtained from the intact sheep by slaughtering the animals.

To predict the fraction of fermentable organic matter in the rumen $\frac{Z_1}{Z}$ the following equation is used:

$$\frac{Z_1}{Z} = \frac{\frac{k_1}{k_2}\,\gamma_2}{\gamma_0 + \gamma_1 + \gamma_2 \frac{k_1}{k_2}}$$

For the allometric model the same equation (II) is used but a $\gamma_1 b$ is substituted for γ_2. The results of the predictions are presented in tables 6 and 7.

In the regression equation between predicted and determined organic matter intake, the non-significant deviations from a slope of one and intercept of zero, (Table 6), indicate that both models give an unbiased, but inaccurate estimate of intake with cannulated sheep. With intact sheep a higher degree of accuracy is obtained in both models, but the allometric model is biased, as can be deduced from the significant intercept obtained. Where the intercept does not differ significantly from 0 and the slope does not differ significantly from 1, the variance of a predicted mean is calculated by means of the following formula:

$$\sigma = \sqrt{\frac{\Sigma y^2 - 2 \Sigma xy + \Sigma x^2}{n^2}}$$

The reason for the relative inaccuracy of the calculated intakes with cannulated sheep can be deduced from Table 7. The prediction of intake is over- or under-estimated in the same way that the fermentable fraction of the rumen contents is over- or underestimated. It was not clear whether this over or underestimation could be explained by the fact that different estimates of γ_2, which are assumed to be constants, vary according to diet. Hence intake and the fermentable fraction were also estimated using a separate estimate of γ_2 for each diet. However, only negligible increase in accuracy was obtained. It is concluded that the variation between the estimated and determined intake is due to experimental error and no motivation exists for the use of different values for γ_2 in this experiment.

The allometric model is not recommended because it proved to be biased when tested with intact sheep (the independent control group) where more degrees of freedom were available.

Comparison with previously recommended methods

Some methods previously used to determine the quality of a diet were *in vivo* or *in vitro* digestibility estimates, rate constants for fermentation Gill *et al.* (1969) and solubility of the diet. When a linear regression is fitted between voluntary intake y and these measurements, the following correlation coefficients are obtained: Digestibility r = 0,516 NS, rate constant for fermentation r = 0,711 ($P < 0,05$) and solubility r = 0,13 (NS). When the regression obtained for cannulated sheep was used to predict intakes of intact sheep the results presented in Table 10 were obtained.

The difference between predicted and actual intake (Table 10) indicates that the previously recommended methods are biased. This may be explained by the fact that important factors such as the ruminal capacity of sheep and other factors are not included in the estimate and the accuracy obtained with a single fit will not be repeated under changed circumstances.

Conclusion

A model was developed and its validity tested with dry roughages of widely differing quality. It was derived mathematically for steady-state conditions in the rumen and its use will be valid only when these conditions are met or approximated.

Table 10

A comparison of digestibility and the rate constant for fermentation for predicting voluntary feed intake of intact sheep
(± Standard errors)

Independent variable of linear	Diet	Predicted intake g/day	Actual mean intake g/day
Digestibility	Lucerne	750	954 ± 54
	wheat straw	698	414 ± 24
Rate constant for fermentation	lucerne	1 139	954 ± 54
	wheat straw	676	414 ± 24

The fact that the rate constants for outflow (γ_2, γ_0) could be estimated by constants irrespective of diet has obvious advantages for prediction purposes. However, it may not be valid to extrapolate beyond the limits set by the kind of diets used in this experiment, since it may be expected that common rate constants for outflow will not always be valid, as for example in the case of grinding and pelleting of diets.

The model was primarily developed to indicate the factors which should be measured in order to predict intake on widely different diets. In the approach used here, these factors were:

a) the solubility of the diet, which corresponds to a very fast digesting fraction,
b) the rate constant for outflow of fermentable organic matter (γ_0) which describes the disappearance of fermentable organic matter from the rumen in terms of outflow;
c) the rate constant for fermentation (γ_1) which describes disappearance of fermentable organic matter from the rumen in terms of fermentation,
d) the rate constant for outflow of unfermentable organic matter (γ_2) which describes the disappearance of unfermentable organic matter from the rumen in terms of outflow.
e) the insoluble fermentable fraction of the diet (k_1), which describes the total digestibility of the insoluble fraction of the diet,
f) the mass of organic matter in the rumen (Z), which describes the "ruminal capacity" of the animal.

The model we propose expresses intake as a function of all these factors combined into one equation which is related to the basic first order model. Therefore under the circumstances of our experiment it can be stated that intake can be predicted accurately when expressed as a function of the parameters above and applied to the first order model. If some of the parameters are not measured there may be a concomitant decrease in accuracy due to the use of inapplicable estimates of parameters.

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Appendix

The logic of the underlying model:

It was hypothesized that the digestive processes in the rumen can all be approximated by a first order homogenous differential equation (Waldo *et al.*, 1972).

$$\frac{dZ}{dt} = \gamma Z$$

This type of equation is applied to the insoluble fractions of the diet and for fermentation the following notation is used,

$$\frac{dZ_1}{dt} = \gamma_1 Z_1, \qquad (1)$$

Where Z_1 is the mass of fermentable organic matter and γ_1 is the rate constant for fermentation.

For the outflow of fermentable organic matter, write

$$\frac{dZ_1}{dt} = \gamma_0 Z_1 \qquad (2)$$

where γ_0 is the rate constant for outflow of insoluble fermentable organic matter.

For the outflow of unfermentable organic matter designate

$$\frac{dZ_2}{dt} = \gamma_2 Z_2 \qquad (3)$$

Where Z_2 is the mass of unfermentable organic matter in the rumen and γ_2 the rate constant for the outflow of unfermentable organic matter. For outflow and fermentation

$$\frac{dZ_1}{dt} = \gamma_1 Z_1 + \gamma_0 Z_1 \qquad (4)$$

At steady state in the rumen the mass of fermentable organic matter remain constant. Let the intake of digestible organic matter be $k_1 dZ$, and indigestible organic matter be $k_2 dZ$

Hence $$\frac{dZ_1}{dt} = -\gamma_1 Z_1 - \gamma_0 Z_1 + k_1 dZ = 0$$

and $$\frac{dZ_2}{dt} = -\gamma_2 Z_2 + k_2 dZ = 0 \qquad (5)$$

from which we obtain

$$\frac{k_1}{k_2} = \frac{(\gamma_1 + \gamma_0)\, Z_1}{\gamma_2\, Z2} \qquad (6)$$

Let $Z = Z_2 + Z_1$

hence $Z_2 = Z - Z_1$ so that (7)

$$\frac{k_1}{k_2} = \frac{Z_1\,(\gamma_1 + \gamma_0)}{(Z - Z_1)\,\gamma_2}$$

Hence $(\gamma_1 + \gamma_0)\, Z_1$

$$= \frac{k_1}{k_2}\,\gamma_2\,(Z - Z_1)$$

$$(\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2)\, Z_1$$

$$= \frac{k_1}{k_2}\,\gamma_2\, Z$$

and

$$Z_1 = \frac{(\frac{k_1}{k_2}\,\gamma_2)\, Z}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2} \qquad (8)$$

To calculate the rate of organic matter fermentation and rate of outflow equation 4 and 8 are used to derive:

$$\frac{dZ_1}{dt} = \gamma_1 \left[\frac{\frac{k_1}{k_2}\,\gamma_2\, Z}{\gamma_1 \pm \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right] + \gamma_0 \left[\frac{\frac{k_1}{k_2}\,\gamma_2 Z}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right]$$

$$\frac{dZ_1}{dt} = \frac{(\gamma_1 + \gamma_0)\,\frac{k_1}{k_2}\,\gamma_2\, Z}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2} \qquad (9)$$

and from equations 3, 7 and 8

$$\frac{dZ_2}{dt} = \gamma_2 \left[Z - \frac{\frac{k_1}{k_2}\,\gamma_2\, Z}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right]$$

$$= (\gamma_2) Z \left[1 - \frac{\frac{k_2}{k_2}\,\gamma_2}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right]$$

$$\frac{dZ_2}{dt} = (\gamma_2) Z \left[\frac{\gamma_1 + \gamma_0}{\gamma_2 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right] \qquad (10)$$

From equation 9 and 10, intake of the insoluble fraction may now be calculated.

$$\frac{dZ_2}{dt} + \frac{dZ_1}{dt} = \left[\frac{\gamma_1 + \gamma_0}{\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right] \gamma_2\, Z$$

$$+ \left[\frac{\frac{k_1}{k_2}\,(\gamma_1 + \gamma_0)\,\gamma_2 Z}{(\gamma_1 + \gamma_0 + \frac{k_1}{k_2}\,\gamma_2}\right]$$

$$\frac{dZ}{dt}\ \text{insoluble} = \frac{(\gamma_1 + \gamma_0)\,\gamma_2\, Z}{(\gamma_1 + \gamma_0)\, k_2 + k_1\,\gamma_2}$$

because $k_2 + k_1 = 1$

To include solubility this may be written as follows:

$$\frac{dZ}{dt}\ \text{insoluble + soluble} =$$

$$\frac{(\gamma_1 + \gamma_0)\,\gamma_2\, Z}{(\gamma_1 + \gamma_0)\, k_2 + k_1 \gamma_2} \times \frac{100}{100\text{-solubility}} \qquad (11)$$

$$= \text{Intake}$$

Because the soluble fraction is supposed to dissolve immediately (c 30 min.) in the rumen liquor it is not calculated with the fractions which cause rumen fill.

Table 3

Design matrix for multiple regression analysis

Mass of insoluble fermentable O.M. in rumen (g)					
Young Cenchrus	Lucerne	Mature Cenchrus	Maize cob leaves	Wheaten straw	Mass of insoluble O.M. fermented in rumen (g)
X_1	X_2	X_3	X_4	X_5	Y
386	0	0	0	0	483
401	0	0	0	0	481
0	192	0	0	0	396
0	171	0	0	0	340
0	0	280	0	0	228
0	0	337	0	0	249
0	0	0	535	0	416
0	0	0	511	0	631
0	0	0	438	0	494
0	0	0	0	375	175
0	0	0	0	309	228

Table 9

Percentage soluble organic matter in the diets

	Young cenchrus	Lucerne	Mature cenchrus	Maize cob leaves	Wheat straw
Organic matter solubility (%)	11,85	17,12	10,4	5,1	8,5

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