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Daily Intake, Digestibility, and Rate of Digesta Passage in the Dik-Dik (<u>Madoqua kirki</u>) Fed Alfalfa Leaf and a Complete Pelleted Feed

presented by

David Jonathan Baer

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DAILY INTAKE, DIGESTIBILITY, AND RATE OF DIGESTA PASSAGE IN THE DIK-DIK (MADOQUA KIRKI) FED ALFALFA LEAF AND A COMPLETE PELLETED FEED

Ву

David Jonathan Baer

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ABSTRACT

DAILY INTAKE, DIGESTIBILITY, AND RATE OF DIGESTA PASSAGE IN THE DIK-DIK (MADDQUA KIRKI) FED ALFALFA LEAF AND A COMPLEX PELLETE FELL

Вv

David Jonathan Baer

Dik-dik (Madoqua kirki) are small concentrate selectors. While metabolic body size is related to body mass. 75, gut capacity is related to body mass 1.0. To cope with this difference, small ruminants may rely on higher rates of digesta flow and selection of lower fiber feeds. The dik-dik's ability to digest forage fiber may be limited. Four captive dik-dik were fed alfalfa leaf (AL), a 1:1 ratio of AL:pelleted feed (PF) and PF to assess body weight (BW) changes, daily dry matter intake (DMI), digestibility of dry matter (DM), organic matter (OM), gross energy (GE), neutral detergent fiber (NDF), acid detergent fiber (ADF), hemicellulose and cellulose, and the rate of digesta passage fitted by a two-pool model using a single dose of chromiummordanted fiber. BW, DMI, DM digestibility and OM digestibility were similar across all treatments (P>0.10). GE digestibility was lower on AL than PF (P<0.025). NDF. ADF, hemicellulose and cellulose digestibilities were higher on AL than PF (P<0.001). Total mean retention time of digesta was longer on AL than PF, but there were no differences in transit time.

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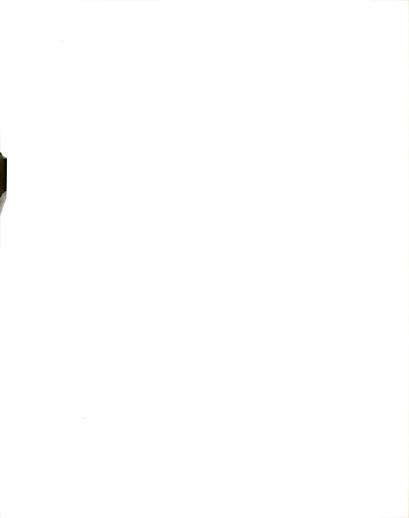
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I. DAILY INTAKE AND DIGESTIBILITY

Introduction

Herbivorous animals have evolved in a nutritional niche involving diets high in plant fiber but relatively low in digestible energy. The body size of animals, such as ruminants, that are primary consumers influences their metabolic rate (Kleiber, 1975), total energy requirement, feed intake and digestive efficiency (Demment & Van Soest, 1983; Van Soest, 1982). Dik-dik (Madoqua kirki) are among the smallest of true ruminants. The dik-dik's feeding behavior, digestive physiology and morphology are consistent with their classification as concentrate selectors (Hofmann, 1973). As small concentrate selectors, the dik-dik's ability to digest plant fiber may be limited.

Metabolic rate is related nonlinearly to body size but linearly to metabolic body size $(BW_{kg}^{O.75})$. Since metabolic rate influences total nutrient and energy requirements (metabolic requirement (MR)), smaller animals have higher requirements per unit of body mass. However, herbivore gut capacity (GC) is related linearly to body weight $(BW_{kg}^{1.0})$ (log(wet weight gut contents (kg))=1.032log(body weight (kg))-0.936, r=.99, n=59, weight range=0.015-5177.6 kg) (Demment & Van Soest, 1983; Demment, 1982; Parra, 1978).

Therefore, smaller herbivores have a higher MR/GC ratio (Demment & Van Soest. 1983).

To cope with this constraint, smaller ruminants may adapt in several ways. Since ruminants have evolved to use the end-products of fiber digestion as their major energy source, the extent of fiber digestion is an important factor in determining energy balance. Fiber digestion in ruminants is controlled, at least in part, by the time of contact between the substrate and the microbial population of the rumen. Therefore, factors that influence rate of digesta flow will influence digestion. These factors include morphology of the gut (e.g., ruminal pillars or restricted ostia), and physical characteristics of the feed (e.g., particle size). Dense papillation of the ruminoreticulum aids in quick absorption of volatile fatty acids (VFAs, the end-products of anaerobic microbial fermentation) (Hofmann. 1973). Behaviorally, selection of feeds that are relatively high in digestible energy (e.g., low in dietary fiber and high in nonstructural carbohydrates) will help maximize energy utilization.

There are limited data on the diet of free-ranging dik-dik. Behavioral observations and stomach sample analyses indicate that the majority of their diet consists of leaves and stems, flowers, shoot tips and twigs. Consumption of fallen plant material (fresh litter) has also been observed. Some grasses, particularly leaf tips or seeds, are also consumed (Tinley, 1969; Simonetta, 1966; Hofmann, 1973; Hoppe et al., 1983). Unfortunately, there are no data on

time spent foraging on different plant species or parts.

There are also limited data available on the nutrient composition of these natural feeds.

There are few species in the niche occupied by small ruminants (BW < 10 kg). The constraints of body size on feed intake, feed digestion and energy balance may have influenced exploitation of this niche by ruminants. Dry matter intake and digestibility by dik-dik have been investigated for only one diet, alfalfa leaves (Hoppe, 1977). Data on intake and digestibility for other small ruminants are also scarce (Nordin, 1978a,b; Cowan et al., 1976; Hoppe, 1977). Poor survival of dik-dik in captivity has been a problem in some zoos and may be related to nutritional management. The possibility that dik-dik can digest forage fiber to only a limited extent may be relevant to the problems of maintaining dik-dik in captivity.

Feeding trials were conducted to quantitate dry matter intake by dik-dik and to assess their ability to utilize formulated diets that varied in the amount of alfalfa leaf. a relatively good quality forage fiber, and a complete pelleted feed. Nutritionally, this increase in the high quality forage:pelleted feed ratio increased the fiber levels of the diet and decreased the digestible energy density.

Materials and Methods

Four dik-diks were used for this study in a randomized complete block design (RCBD) with each animal as a block. Animals were reproductively mature (three males and one female) and captive born in zoos. All animals were injected with 1-2 mg Ivormec (MSD Agvet, Merck and Co., Inc., Rahway, NJ) subcutaneously for control of internal and external parasites prior to use in this study. Based on records of previous physical examinations, there were no discernible health problems in these animals.

The animals were individually housed in indoor 2.44 m² pens at the National Zoological Park, Washington, DC. The pens were constructed of 0.64 cm plywood, and the walls were 1.22 m high. Concrete floors were covered with rubber matting to prevent animal slipping. Temperature and humidity were continuously recorded with a hygro-thermograph (Belfort Instrument Co., Baltimore, MD). Some natural lighting was available, but overhead fluorescent lights were set on a 12:12 L:D cycle. on at 0700 hr.

Animals were sequentially fed three diets. Amounts of feed offered were based on individual ad libitum intakes of similar feeds during a 42-d preliminary period (a second female was also involved in the preliminary period). The diet for trial I consisted of a 1:1 ratio of alfalfa leaf (AL) from hay and a pelleted feed (PF) (Ziegler Bros., Gardners, PA) (Tables 1 and 2). The AL was manually removed from the stem and shaken through a 1.3 x 1.3 cm screen mesh

to remove pieces of stem. During trial I, the animals were offered 90% of their ad libitum intake to insure that a 1:1 AL:PF ratio was actually consumed. The diets for trials II and III were 100% AL and 100% PF, respectively. The animals were gradually switched from one diet to the next over a 3-to 7-d period. There was a 14-d adaptation period to the new diet prior to any collections for digestibility estimates. Following the adaptation period, total fecal collections were conducted for 7 days. Daily fecal samples collected were not pooled.

Table 1. Ingredient composition of the pelleted feed (PF).

Ingredient	% of diet		
Corn grain	33.9		
Alfalfa meal, sun-cured	22.0		
Soybean meal (44% CP)	13.0		
Alfalfa meal, dehy (17% CP)	10.0		
Wheat middlings	10.0		
Cane molasses	7.5		
Soybean oil	1.5		
Mono-dical phos (18% Ca, 21% P)	0.9		
Salt	0.5		
Vitamin premix	0.5		
Mineral premix ^D	0.5		
Calcium propionate	0.2		

 $^{^{\}rm a}$ Formulated to provide per kg of diet: 6000 IU vitamin A, 500 IU vitamin D $_{\rm 3}$, 130 IU vitamin E, 2 mg menadione, 5 mg thiamin, 4 mg riboflavin, 40 mg niacin, 6 mg pyridoxine, 0.2 mg blotin, 25 mg D-Ca-pantothenate, 3 mg folic acid, 30 mcg vitamin B $_{\rm 1,0}$, 770 mg choline.

bFormulated to provide per kg of diet: 100 mg Fe, 7 mg Cu, 80 mg Zn, 40 mg Mn, 700 mcg I, 0.2 mg Se, 0.1 mg Co, 400 mg Mg.

Table 2. Nutrient composition of alfalfa leaf (AL) and pelleted feed (PF) (% of dry matter) (Mean+SEM).

Nutrient	AL (N=10)	PF (N=3)
Dry matter	92.7+0.5	92.5+0.7
Organic matter	83.3+0.5	85.5+0.7
Gross energy	4.52+0.11	4.46+0.13
Crude protein	24.7 <u>+</u> 0.2	17.6±0.3
Ash	9.3+0.4	7.0 <u>+</u> 0.2
Neutral detergent fiber	35.7 <u>+</u> 0.4	21.6+0.4
Acid detergent fiber	22.7+0.5	16.2+0.3
Acid lignin	5.9+0.3	5.4+0.2
Hemicellulose	12.9+0.5	5.4+0.4
Cellulose	16.8+0.4	10.8+0.2

aKcal/g dry matter.

Water was provided ad libitum in ceramic crocks. The crocks were washed, and the water was changed, daily. PF and AL were fed in separate containers to accurately quantify consumption of each feed item.

Feed intake was monitored daily. Animals were fed daily at approximately 0900 hr, and uneaten feed was removed after approximately 24 hr and re-weighed. All offered and residual feed was weighed with an electronic balance to the nearest 0.1 g. Feces were collected daily using a small brush and a dustpan. Feces were weighed in pre-tared aluminum pans (25.4 cm diameter) lined with aluminum foil. During fecal collection periods, feces were dried in a forced air oven at 55 C for 24 hr. The dried feces were then re-weighed, stored in heavy duty plastic freezer bags and frozen (0 C) for subsequent analyses.

Animals were weighed at the beginning of the study and

at the end of each trial. Individual animals were moved into plastic kennels (Model #200P, Doskocil Mfg. Co. Inc., Arlington, TX) and weighed with a mechanical beam balance. The sides and door of the kennels were covered with towels to darken the inside and to minimize agitation and excitement of the animals. Weights were not recorded until the animals were completely still in the kennel.

Feed samples and the partially dried feces were ground in a Wiley mill fitted with a 2 mm screen. Feed and feces were analyzed for dry matter (DM), ash, gross energy (GE), neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid lignin (ALIG). An electronic balance was used for all analytical weighing to the nearest 0.001 g. Dry matter was determined on approximately 0.500 g of subsample in an aluminum weighing dish by overnight drying in a forced air oven at 105 C. Ash was determined by igniting approximately 0.800 g of subsample in a muffle furnace (650 C) for 'four hr. GE was determined by complete combustion in a Parr adiabatic oxygen bomb calorimeter (Parr Instrument Co., Moline, IL). Approximately 0.800 g of subsample was combusted for GE, and the remaining residue was titrated with 0.0725 N sodium carbonate to correct for the heat of formation of nitric acid. NDF and ADF were determined by the procedures of Goering and Van Soest (1970) as modified by Robertson (1978). Approximately 0.500 g and 1.000 g subsamples were used for the NDF and ADF procedures, respectively. Alpha-amylase (Catalog No. A1278, Sigma Chemical Co., St. Louis, MO.) was used in the NDF analysis

(Robertson & Van Soest, 1977). ALIG was determined on the ADF using 72% sulfuric acid (Goering & Van Soest, 1970).

Organic matter (OM) was calculated as DM-ash, cellulose (CELL) was calculated as ADF-ALIG, and hemicellulose (HEMI) was calculated as NDF-ADF. Crude protein (CP) was determined on feed samples with the Semiautomated Method (7.025) with approximately 0.100 g of subsample (Williams, 1984). All analyses were performed in duplicate. Total fecal collections permitted the use of the direct method to calculate apparent digestibility coefficients for DM, OM, GE, NDF, ADF, HEMI, CELL and ALIG (Schneider & Flatt, 1975).

Hotelling's multivariate T^2 test was used to test for self-selection of different quality AL for two randomly selected times during the 42-d preliminary period. AL was fed to the five dik-dik. Following approximately 24 hr, the residual AL was collected. These residual AL samples, and subsamples of the offered AL, were ground and assayed for CP, NDF and ADF. A T^2 statistic was calculated and compared with the critical value $T^2_{0.10.3.4} = 54.97$ (Gill, 1978).

Analyses of variance for RCBD and orthogonal polynomials (linear and quadratic effects) (Gill, 1978) were performed on a microcomputer using LOTUS 1-2-3 software and the MS-DOS operating system. Mean dry matter intake and digestibility coefficients of 7-d collections were used in the statistical analyses.

Results

Mean ambient temperature (+SE) was 24+0.3 C and mean relative humidity (+SE) was 49+0.7% (N=18). The relatively consistent and controlled environmental conditions (light cycle, temperature, and relative humidity) permitted the sequential dietary treatments fed to all animals simultaneously. Any residual diet effects were confounded with animal and treatment. However, the controlled environment and use of standard feeding trial methodology (Schneider & Flatt, 1975), including adaptation periods to new diets. should have minimized or eliminated any residual effects. Offered and residual AL in the preliminary trial were similar in nutrient composition (P>0.1). Thus, animals were not selecting different fractions of the offered AL, at least not on the basis of CP, NDF and ADF concentration. Therefore, in subsequent trials, residual AL was not analyzed for nutrient composition.

Mean daily dry matter intake and mean body weights did not differ across treatments (Table 3). Mean daily dry matter intake per metabolic body size was 40.6, 34.6, and $36.1~g/BW_{kg}^{0.75}$ for the AL, AL:PF, and PF trials, respectively. These values were not statistically different.

Mean dry matter and organic matter digestibilities were similar across all treatments (Table 4). There was a slight (P<0.10) linear trend for organic matter digestibility to decrease as the proportion of AL increased.

Table 3. Daily dry matter intake (DMI) and body weight (BW) relationships (N=4).

Factor	Treatment mean			SEM	F value
	AL	AL:PF	PF		value
BW (kg)	4.23	4.26	4.48	0.08	1.06
DMI (g)	117.5	102.2	110.5	3.9	1.31 ^a
DMI (% of BW)	2.85	2.42	2.48	0.08	2.81 ^a
DMI/Metabolic BW (/BW ^{0.} /) 40.6	34.6	36.1	1.1	2.51

aNot significant (P>0.10).

Table 4. Mean apparent digestibility (%) of alfalfa leaf (AL) and pelleted feed (PF) from 7-d total fecal collections (N=4).

Factor	Treatment mean			SEM	F value
	AL	AL:PF	PF		
Dry matter	65.0	66.5	68.6	0.9	1.5 ^a
Organic matter	69.5	70.0	72.9	0.7	2.3 ^a
Gross energy	65.6	68.0	71.9	0.8	5.7 ^b
Neutral detergent fiber	66.5	48.3	36.5	0.7	143.2°
Acid detergent fiber	56.6	46.6	37.9	1.0	27.6
Hemicellulose	80.8	53.1	32.7	1.0	200.7°
Cellulose	66.6	55.9	41.5	1.0	57.8 ^C

aNot significant (P>0.10). P<0.05.

Whereas energy digestibility decreased as the proportion of AL increased, NDF, ADF, hemicellulose and cellulose digestibilities increased (Table 4). Gross energy digestibility (P<0.025) and fiber fraction digestibilities (P<0.001) showed very strong linear components. NDF

P<0.001.

digestibility showed a very slight curvilinear component (P<0.10). No other changes in energy or fiber fraction digestibility had a curvilinear component.

Discussion

The daily dry matter intake for dik-dik in this study was slightly lower than previously reported. Hoppe (1977) found the average intake for adult dik-dik fed alfalfa leaf with similar gross energy density (4.50 kcal GE/g DM) to be 117 g of DM, and this DM intake corresponded to 3.76% of body weight. Hoppe (1977) suggested that this level of intake was high even though the GE density of the alfalfa leaf was high. Dry matter intakes of other small ruminants are presented in Table 5.

Table 5. Body weight (BW) and daily dry matter intake (DMI) of small adult ruminants.

Species	N	BW (kg)	DMI (g) (%	DMI of BW)	Diet
Tragulus javanicus a (Lesser mousedeer)	8	1.4	33.4	2.4	Mixed (hay & produce)
Nesotragus mochatus b	5	3.21	111	3.5	Alfalfa leaf
Cephalus monticola C (Blue duiker)	3	4	81	2.0	Alfalfa leaf (fresh)

a Nordin, 1978. Hoppe, 1977.

Cowan et al., 1976.

Evidence from larger, domesticated ruminants supports the hypothesis that dry matter intake is controlled by gut fill and digestible energy (DE) density (kcal/g) of the diet. Gut fill is determined by volume, not weight, of the feed. Therefore, bulkiness of a diet is an important component in regulating dry matter intake. The mechanisms by which DE density regulates dry matter intake are not understood. It is possible DE density influences intake through several interrelated mechanisms in ruminants with signals from different metabolic paths (Baile and Forbes, 1974; NRC, 1987). Regardless of the mechanism, at low DE densities, dry matter intake is probably limited by gut fill (distention) and factors influencing palatability. As DE density increases, dry matter intake will increase but is still limited by gut fill and distention of the GIT. As DE density increases further, dry matter intake decreases but DE intake (kcal/d) remains constant owing to the higher DE density of the diet (Montgomery and Baumgardt, 1965; Ammann et al., 1973). Differences in DE are related to the level of NDF, a constituent of forage that is fermented slower than the cell soluble fraction. As the NDF level of a diet increases, DE and dry matter intake should decrease (Mertens, 1973).

No statistical differences were found in dry matter intake across treatments for the dik-dik in this study. The current model for dry matter intake would predict that as the proportion of AL increases, and hence bulkiness and NDF level, dry matter intake would decrease. Although GE

densities (kcal/g) of the diets were similar, DE intake (kcal/d) was lower as the proportion of AL increased. The GE of AL in this study was similar in digestibility to that reported for comparable diets in other studies (65.6% in the current study versus 69.1% for similar quality alfalfa leaf) (Hoppe, 1977).

All diets contained sufficient amounts of DE to at least meet maintenance energy requirements, as indicated by maintenance of body weight. However, dry matter intake was expected to decrease as the ratio of AL to PF increased. At steady state conditions, influx and efflux are equivalent. The amount of dry matter consumed would then be equivalent to the amount of dry matter leaving the rumen through one of two processes, passage to the lower GIT or digestion (Van Soest, 1982). The PF should have higher rates of passage than AL, related to the physical form of the PF and higher rates of digestion due to its composition and ground physical form. Why dry matter intake did not conform to current dogma is not clear.

Small ruminants seem to select feeds that are readily fermented. High rates of fermentation have been reported from in vitro studies of rumen contents from free-ranging dik-dik. Production of between 395 and 526 umoles of fermentation gases/hr/g dry matter by dik-dik rumen contents is higher than for other East African wild ruminants studied (Clemens et al., 1983; Hoppe et al., 1983). These high fermentation rates are consistent with the relatively large

salivary glands of dik-dik (Hofmann, 1973; Kay et al., 1980) that produce buffers essential for the rumen ecosystem.

Dry matter and energy digestibilities were similar to previously published data. Hoppe (1977) suggested that dry matter digestibility (67.5%) of alfalfa leaf fed to dik-dik was moderate considering the high nutritional quality of the alfalfa leaf. Organic matter digestibility has been estimated (by regression of percentage of nitrogen in the organic matter of the feces) for free-ranging dik-dik and found to be relatively high (78% and 85% for two animals) (Hofmann & Musangi, 1973). However, the regression equation used to estimate dry matter digestibility in these free-ranging animals was developed for sheep and may be invalid (Hoppe, 1977).

Previously reported fiber digestibility coefficients for similar diets fed to dik-dik were lower than those in the current study (54.2% for crude fiber and 39.7% for cellulose) (Hoppe, 1977). There could be several explanations for these differences. Animals in the current study were all captive born and raised whereas animals in the previous study were in captivity for only three months prior to the start of those studies. Therefore, animals in the current study may have been better adapted to alfalfa leaf than the wild caught animals. While it is difficult to make direct comparisons of the crude fiber and the detergent systems for forage fiber analysis, crude fiber best represents the ADF fraction of the detergent system (Van Soest, 1982). The crude fiber concentration in the dry

matter of the alfalfa leaf fed dik-dik by Hoppe (1977) was 20.9%, similar to the ADF level of 22.7% in the dry matter of the alfalfa leaf used in the current study. Lignin is refractory to microbial fermentation and reduces fiber digestibility. The lignin content was not reported for the alfalfa fed to Hoppe's dik-dik and was 5.9% in the current study. Methodological differences in cellulose determination may explain the large differences in cellulose digestibility. Age differences can probably be ruled out since animals were adults or reproductively mature in both studies.

Fiber fraction digestibilities in this study increased in a linear fashion as the proportion of AL increased. Conversely, since dry matter digestibility was similar across treatments, the cell soluble fraction digestibility decreased as the AL increased. The cell soluble fraction was higher in the PF and was digested (either fermented in the rumen or passed to the lower tract) more readily than the NDF fraction. Thus, as the ratio of AL to PF and consequently the ratio of NDF to cell solubles increased, the animal (presumably through changes in the microbial population of the rumen) became more efficient at digesting fiber. The relative fraction of energy derived from fiber appeared to increase with the increasing AL. Similar changes in fiber fraction digestibilities have been reported in dairy cows (Uden, 1984) and horses (Thompson et al.. 1984) fed increasing ratios of hay to concentrate.

While digestion models suggest that small ruminants may be limited in their ability to digest forage fiber, the dikdik in this study were able to extract enough energy from AL to maintain body weight. Unpublished necropsy reports from the National Zoo Department of Pathology indicated that body fat of necropsied dik-dik was low, especially during the winter months and early spring. Hoppe (1984) reported in published conference proceedings that the most fat found on one dik-dik was only 2.3% of bodyweight. Unfortunately, the methods used to measure body fat were not reported in the proceedings. These observations on body composition and energy stores suggest that dik-dik may be limited in their ability to survive prolonged cold stress.

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II. RATE OF DIGESTA PASSAGE

Introduction

Herbivorous animals are adapted to use the end products of anaerobic fermentation, the volatile fatty acids, as a source of energy and as a substrate for the synthesis of glucose, amino acids, and proteins. The extent of fermentation in ruminants is a function of the amount of time that feeds are in contact with the symbiotic microbial populations of the host and the composition of the diet.

Many factors have been identified that influence digesta flow through the ruminant gastrointestinal tract (GIT). Some factors are related to the physical and chemical properties of the consumed diet. These properties include particle size (Ellis et al., 1979), density (Ehle et al., 1984), and the rate of digestion of the feed (Mertens, 1977). Body size, the morphology of the GIT of the animal (Mertens, 1973; Demment & Van Soest, 1983; Hofmann, 1973), and the level of dry matter intake, an interaction between the diet and the animal, also influence digesta flow.

The terminology associated with digesta flow includes rate of digesta flow, transit time, mean retention time, turnover rate and turnover time. The rate of digesta flow is the weight or proportion of digesta that moves a specified distance in a given unit of time. The rate of

digesta flow is difficult to measure directly. However, by marking the beginning of a meal, it is possible to measure the time required for a given meal to pass through the gastrointestinal tract, which is defined as the transit time (TT). It is also possible to calculate the total mean retention time (TMRT) which is the sum of the transit time and the turnover times of the individual compartments of the gastrointestinal tract (Kotb and Luckey, 1972).

Digesta flow through the ruminant digesta tract is a complex process. The relatively capacious fermentation vat allows for digesta mixing. The process has been mathematically modelled as a two-pool, nonreturnable system by the relationship:

$$Y = A e^{-k} (T-TT) - Ae^{-k} (T-TT)$$
 for $T \ge TT$;

Y = O for T < TT

where Y is the marker concentration in the fecal dry matter at time T (hr) post-dosing. The A is biologically undefined. TT (hr) is the calculated time for first appearance of the marker in the feces. The rate constants, k_1 and k_2 , have been suggested to represent two pools of the GIT (Grovum and Williams, 1973). The biological significance of some of the parameters of this model have been investigated and established for domesticated sheep and cattle. One assumption of the model is complete mixing of the marker with the digesta (Brandt & Thacker, 1958). The model can not be used if k_1 = k_2 because the predicted marker concentration would be equal to zero for all sampling times. This model has been used to describe the fecal excretion of

markers in domesticated animals (Grovum and Williams, 1973; Hartnell and Satter, 1979). The fact that the appearance of a marker in the feces can be described by this model does not imply that two pools physically exist in the animal. Fitting of this model to small ruminants such as dik-dik has not been reported previously.

Materials and Methods

Five dik-dik were used to model rates of digesta flow using a two pool, nonreturnable model developed and tested for sheep (Grovum and Williams, 1973). Housing conditions and feeding regimes were as previously described. Chromiummordanted fiber (Uden et al., 1980) was used as the marker and was prepared by adding a 10% sodium dichromate solution to an oven-dried (100 C), neutral detergent fiber (NDF) fraction of the alfalfa leaf (AL) and the pelleted feed (PF). This mixture was washed in tap water for 30 min. A 1% solution (approximate) of ascorbic acid (Catalog #4640, Eastman Kodak Company, Rochester, NY) was then added to the NDF fraction and allowed to react for at least two hours. The ascorbic acid reduced the Cr from the +4 valence state to the +3 valence state to facilitate tighter binding to the NDF. The mordanted AL and PF were then thoroughly washed under running tap water and refluxed in NDF solution to remove unbound Cr and NDF. The mordanted AL and PF were dried overnight at 60 C (Uden et al., 1980).

Following a 3-week adaptation to the three dietary treatments (100% AL, 50% AL:50% PF, and 100% PF), the animals were fed approximately 0.5 g of the mordanted fiber. Following adaptation to the AL:PF diet the animals were first fed the mordanted AL and following that 72 hr collection period plus an additional 24 hr, the animals were fed the mordanted PF. For all trials, the animals were fed the marker at approximately 0900 hr and then fed their usual amounts of diet dry matter. Fresh water was provided ad libitum. The animal enclosures were visually checked for fecal excretion, and the time was recorded every hour for 36 hr, followed by a visual check every 3 hr for 36 hr. If feces were present, they were collected, weighed, bagged and frozen for subsequent dry matter (DM) and Cr analyses.

For Cr analysis, the samples were dried in a forced air convection oven for at least 12 hr at 105 C. After drying, the samples were ground in a small Wiley mill to pass through a screen with 2 mm openings. The samples were prepared for atomic emission spectrophotometry by digestion in approximately 6 ml of concentrated nitric acid and approximately 2 ml of 70% perchloric acid (Fenton & Fenton, 1979). Following digestion, the samples were diluted with distilled, deionized water. Standards in the range of 1 to 5 ppm of chromium were prepared from a 1000 mcg Cr/ml (at 20 C) solution of chromium (Alfa Products, Danvers, MA). An atomic absorption/emission spectrophotometer (Model 951, Instrumentation Laboratory Inc., Wilmington, MA) was used with the emission wavelength set at 425.4 nm. All analyses

were performed in duplicate.

The data were fitted to the two pool, nonreturnable model to estimate digesta flow rates by the iterative method of Hartnell (1979). To fit the data to this model, the natural logs of Cr concentration in the fecal dry matter versus hours post-dosing were plotted to visually determine the peak Cr concentration. The k_1 rate constant was calculated based on the linear regression of the natural log of Cr concentration in the declining phase of Cr excretion. To estimate the best linear fit, the first linear regression was calculated from the peak of the curve to the tail. Subsequently, linear regressions were calculated by removing data points from each end of the curve. Linear regression analyses were performed using LOTUS 1-2-3 version 2 on a MS-DOS operated microcomputer. The three sets of data points that provided the three highest r² values for k, were used in subsequent modelling to calculate the second rate constant, k_2 , and the transit time (hr). Transit time (TT) and k_2 were estimated using a FORTRAN computer program (Appendix A) that held k_1 and k_2 constant, incremented k_2 from $0.03+k_1$ to $3.03+k_1$ by 0.001 1/hr units and TT from 5 to 12 by 0.25 hr units (Hartnell, 1979). The value for A was calculated as equal to $A_1e^{-k_1TT}$ (Grovum & Williams, 1973). For each data set, a chi-square value was calculated. $\mathbf{k_1}$, $\mathbf{k_2}$ and TT from the fit that produced the lowest chisquare value was used for subsequent calculations of digesta flow.

A set of sample calculations are presented in Appendix B. Chromium concentration in fecal dry matter from an individual animal is presented in Table 9. The three sets of data points that produce the three highest \mathbf{r}^2 for the linear regression for \mathbf{k}_1 and the \mathbf{A}_1 are presented in Table 10. The resultant \mathbf{k}_2 and TT from the iterative calculations providing the lowest chi-square value for each set of data points are presented in Table 11. The overall lowest chi-square value for the fit of the actual data with the expected fit is provided if points 7-16 are used to estimate \mathbf{k}_1 and \mathbf{A}_1 (Table 11). Model parameters for individual animals are presented in Appendix C. Plots of observed and predicted Cr excretion are presented in Appendix D.

TMRT was calculated as $TT+1/k_1+1/k_2$. The half times were calculated as 0.693 divided by the rate constant. Daily turnovers of the pools were calculated as 24 divided by the turnover time of the pool (1/rate constant).

Analyses of variance were computed for the randomized complete block design with each animal as a block. SAS least squares procedures (SAS, 1982) were used to minimize the standard errors. Orthogonal contrast between 1) AL and PF, and 2) AL and PF during the mixed dietary treatment (AL:PF) were also calculated with SAS on the Michigan State University IBM 4381 computer.

Results

The ANOVA revealed statistically significant treatment differences in the rate constant k_1 (1/hr) (P<0.04), the number of turnovers/day for pool 1 (P<0.04), and the total mean retention time (hr) (P<0.09). ANOVA for other variables of the model did not reveal statistical differences (Table 6). The specific orthogonal contrasts revealed additional statistical differences.

The rate constant k_1 (1/hr) was statistically lower on the AL treatment than the PF treatment (P<0.01). There was no statistical difference for k_1 between the AL and PF during the mixed dietary treatment (AL:PF). Orthogonal contrasts indicated that turnover rate (hr) was higher and half-life (hr) was longer on the AL treatment than on the PF treatment (P<0.06). No statistical differences were detected for the turnover rate and half-life of the marker between the AL and PF during the mixed AL:PF dietary treatment. The number of turnovers/day was lower on the AL diet than the PF diet (P<0.01) but was not statistically different between the AL and PF diets during the AL:PF mixed dietary treatment (Table 6).



Table 6. Marker kinetics in the dik-dik gastrointestinal tract fed three diets: alfalfa leaf (AL), pelleted feed (PF):AL, and PF.

Variable	;					
	AL	AL:PF	AL:PF		value	
	(N=4)	AL Marked (N=3)	PF Marke (N=5)	(N=4)		
Rate constant	3			•	h	
k ₁ (1/hr)	.05 <u>+</u> .01	.05 <u>+</u> .02	.05 <u>+</u> .01	.11 <u>+</u> .01	4.56 ^b	
Rate constant k ₂ (1/hr)	1.10+.60	.15 <u>+</u> 0.69	1.93 <u>+</u> .54	. 48 <u>+</u> . 60	1.78 ^c	
2 Turnover	-	_	_	_		
time	27.07 <u>+</u> 5.49	27.41 <u>+</u> 6.34	23.86 <u>+</u> 4.91	9.92 <u>+</u> 5.49	2.07 ^c	
Turnover time					C	
k ₂ (hr)	2.61 <u>+</u> 1.04	3.57 <u>+</u> 1.20	1.70 <u>+</u> .93	3.05 <u>+</u> 1.04	.58 ^c	
T _{1/2} k ₁ (hr)	18.76 <u>+</u> 3.80	18.99 <u>+</u> 4.39	16.53 <u>+</u> 3.40	6.87 <u>+</u> 3.80	2.07c	
T _{1/2} k ₂ (hr)	1.81 <u>+</u> .72	2.48 <u>+</u> .83	1.17 <u>+</u> .65	2.11 <u>+</u> .72	.58c	
Turnovers, pool 1	/day 1.12 <u>+</u> .32	1.15 <u>+</u> .37	1.20 <u>+</u> .29	2.57 <u>+</u> .32	4.60 ^b	
Turnovers, pool 2		3.6 <u>+</u> 16.6	47.1 <u>+</u> 12.9	11.4 <u>+</u> 14.4	1.78 ^c	
Transit to		9.89 <u>+</u> .93	11.10 <u>+</u> .72	9.16 <u>+</u> .80	1.14 ^c	
Total mean	n					
	39.39 <u>+</u> 4.64	40.88 <u>+</u> 5.36	36.65 <u>+</u> 4.15	22.12 <u>+</u> 4.64	3.09 ^d	

aMean<u>+</u>SEM.
bP<0.04 within row.
cP>0.1 within row.
dP<0.09 within row.

The rate constant k_2 (1/hr) was statistically lower for AL than PF during the AL:PF mixed dietary treatment (P<0.08). However, no statistical difference was detected for AL and PF when they were fed individually. No statistical differences were revealed between AL and PF during the mixed AL:PF treatment or AL and PF when fed separately for the turnover rate (hr) or for the half-life (hr) of k_2 . The number of turnovers/day was lower for the AL than the PF during the mixed treatment (P<0.08) but was not statistically different for the AL and PF when fed individually (Table 6).

Statistical differences were not found for either of the two contrasts for the transit time (hr). AL and PF during the mixed dietary treatment had statistically similar total mean retention times (hr). However, when fed separately, AL had a statistically longer total mean retention time than PF (P<0.03) (Table 6).

Discussion

The major sites of fermentation are the ruminoreticulum and the cecum and colon. The development of anatomical features that delay digesta in these organs varies phylogenetically. In the rumen, some species lack morphological features such as blind sacs that trap feed, and pillars that impair feed movement. Digesta in these species should flow unimpeded. Other species which have these morphological features should have the ability to

retain feeds for more extensive fermentation. Concentrate selectors have the morphological characteristics commensurate with quick, unimpeded digesta flow, whereas roughage selectors have morphological characteristics that would slow the rate of digesta flow and allow fermentation of more refractory fiber fractions. Dik-dik lack the morphological features in the gastrointestinal tract (GIT) that assist in decreasing rate of digesta flow (Hofmann, 1973). The dik-dik's ruminoreticulum is simple and S-shaped with few, poorly developed ruminal pillars. Digesta flow within the foregut is unimpeded by a wide ostium intraruminale and ostium reticulo-omasicum (Hofmann, 1973).

To be effective in measuring the flow of digesta, a particulate phase marker must meet several criteria (Kotb and Luckey, 1972). Chromium-mordanted fiber fulfills many of these criteria. The Cr in Cr-mordanted fiber is tightly bound to the NDF and is inert and non-toxic to the animal. Tight binding insures that the marker will not migrate to other digesta fractions. In vitro and at physiological pH, the Cr is 98% recoverable from the NDF (Uden et al., 1980). The Cr-mordanted fiber can also be fed as a small proportion of the total dry matter consumed (Uden et al., 1980), and the Cr is easily measured using atomic emission spectroscopy. The Cr is not metabolized nor absorbed from the GIT (Uden et al., 1980).

Two criteria of Cr-mordanted fiber as a marker that remain untested are the effect of Cr-mordanted fiber on the

normal microflora of the GIT and the effect of Cr-mordanted fiber on the normal digestive processes. Since the Cr is tightly bound to the fiber, it is unlikely that the mordanted fiber will adversely affect the normal flora or the normal digestive processes. Another criterion for an adequate marker is that it be uniformly mixed and distributed with the digesta throughout the GIT. In an animal with rapid turnover rates, the extent to which the marker can mix with the digesta may be limited.

One advantage of Cr-mordanted fiber as a marker is its likeness to the physico-chemical properties of normally consumed dietary fiber. Therefore, the Cr-mordanted fiber will flow with a digesta fraction that is biologically related to the animal, unlike some other particulate markers previously used, such as beads or chromic oxide, which flow independent of either the fluid or particulate fractions (Van Soest, 1982). Mordanting allows marking of a fraction of the actual diet.

Unfortunately, the mordanting process can increase the density of the NDF. Denser particles tend to have turnover rates that are slightly higher than less dense particles (Ehle et al., 1984). While the density of the Cr-mordanted AL and PF were not measured in this study, different densities may be a possible source of error and variation, as the Cr concentrations of the marked NDF were certainly different.

The patterns of fecal Cr excretion of the dik-dik in this study seem to fit the model. However, the

identification and interpretation of what the two pools represent is debated. All organs of the GIT can represent at least one pool (Stevens, 1978). Grovum and Williams (1973) suggested that the two pools represent the turnover of digesta in the pregastric (ruminoreticulum) and postgastric (cecum and or colon) compartments. Hungate (1966) and Ellis et al. (1979) suggested that the two rate constants represent two pools of different sized particles in the ruminoreticulum. In any case, the declining phase represents the pool with the slowest turnover rate. The other pool has the faster turnover rate and is usually smaller. However, if turnover rates of different pools are nearly equal, it is impossible to mathematically separate the pools.

There are at least three fates for a feed particle upon entering the ruminoreticulum. The feed particle can undergo digestion in the ruminoreticulum, the feed particle can be passed out of the ruminoreticulum or the feed particle can be ruminated. Mastication during the rumination process physically reduces the particle size which may increase the rate of digestion by increasing the ratio of surface area to volume of the particle as well as to increase the rate of passage. Smaller particles have higher rates of passage than larger particles.

Rate of passage refers to the passage of undigested digesta. On the other hand, rumen turnover is the sum of two competing processes, the rate of digestion and the rate

of passage (Van Soest, 1982). Rate of digestion depends on the microbial populations and the nutrient density of the feed particle, especially the fiber and lignin content. Anything that reduces microbial growth (e.g., nitrogen deficiency, inappropriate pH) may reduce fermentation (Hungate, 1966). Rate of passage depends on the size and density of the particle, the level of dry matter intake and the morphology and body size of the host.

Mean retention time of some ruminants is reported in Table 7. The two methods typically used to calculate mean retention time (Hartnell, 1977; Castle, 1956) provide similar results (Hartnell, 1977). The dik-dik in this study had overall rates of digesta retention that were slightly longer than those of other small ruminants such as suni (Table 7). While it was expected that the lesser mousedeer may have the shortest mean retention time due to its small body size, the mean retention time is actually quite long (52 hr). One explanation for this long mean retention time in the lesser mousedeer is the use of stained sorghum grain, a very novel and unusual feed item in the normal lesser mousedeer diet. Mean retention time in lesser mousedeer measured with chromium sesquioxide yielded mean retention times of 26.5 hr (Morat & Nordin, 1978). Red deer may be expected to have longer mean retention times than that reported in Table 7 because of their large size. However, the red deer used in that study were only 1 year old (Milne et al., 1978).

Table 7. Mean retention time of digesta in ruminants.

Species		retent me (hr)	ion Source
Suni	Alfalfa leaves	16.8	Hoppe & Gwynnwe, 1978
Suni	Alfalfa stems	20.5	Hoppe & Gwynnwe, 1978
Red deer	Dried grass, pellets	21.9	Milne <u>et al</u> ., 1978
Dik-dik	Pelleted diet	22.1	This study
White tailed-deer	Natural diet	22.5	Mautz & Petrides, 1971
White tailed-deer	Hay, concentrates	22.7	Mautz & Petrides, 1971
Lesser mousedeer (using Cr)	Peanuts, <u>Ipomea</u>	26.5	Morat & Nordin, 1978
Sheep	Dried grass, pellets	31.4	Milne <u>et al</u> ., 1978
Dik-dik	Alfalfa leaf, pelleted diet	36.7	This study
Goat	Hay, concentrate	38.0	Castle, 1956
Dik-dik	Alfalfa leaves	39.4	This study
Dik-dik	Alfalfa leaf, pelleted diet	40.9	This study
Lesser mousedeer (using sorghum)	Peanuts, <u>Ipomea</u>	52.8	Morat & Nordin, 1978
Yak	Mixed alfalfa- brome	78	Schaefer, 1978
Bison	Mixed alfalfa- brome	79	Schaefer, 1978

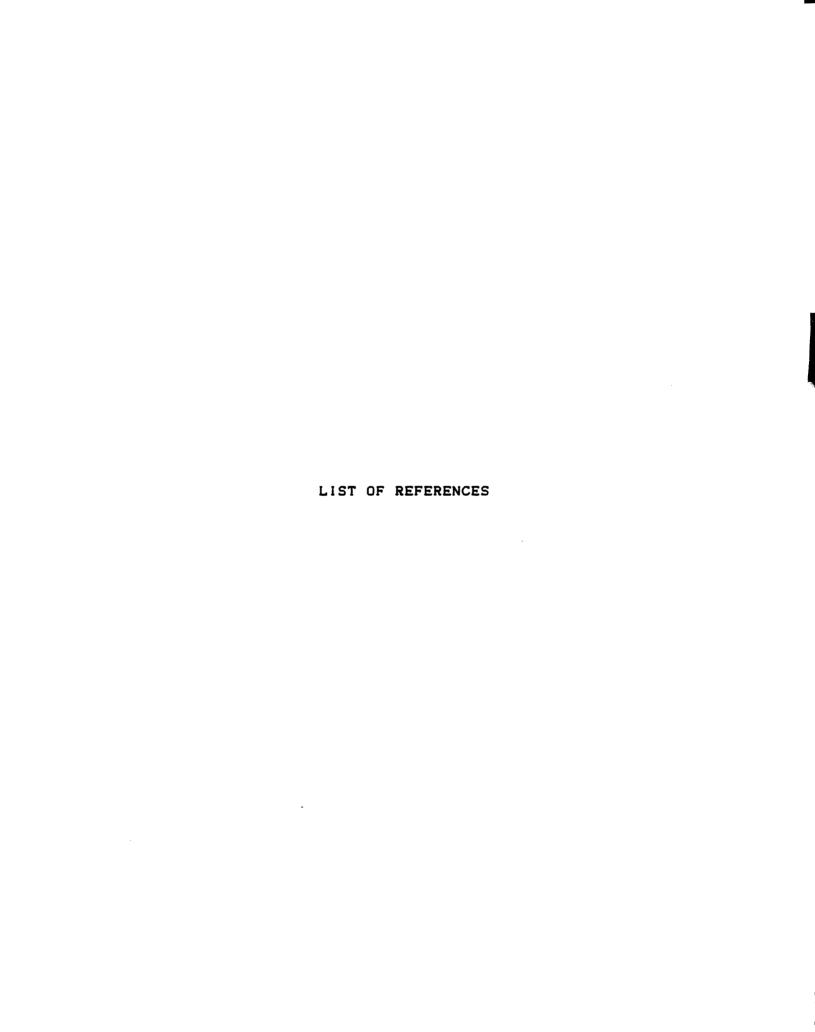
From an energetic and morphological point of view, the retention of AL for a longer time than the PF seems contradictory. However, the physical grinding and pelleting of the PF certainly plays a part in the shorter retention time for PF than for AL. The physical form of the diet may account for some differences in rate of passage. Diets that are ground tend to have faster rates of passage. Pelleted feeds may disintegrate in the rumen and have flow



characteristics and rates similar to the liquid phase (Regelin, 1981).

While there were no statistically significant treatment effects for the transit time, there were statistical differences in the rate constant for \mathbf{k}_1 . The overall result was a statistical difference in the TMRT (hr). Contrasts between the AL and PF when fed separately indicated statistical differences in \mathbf{k}_1 while contrasts between the AL and PF when fed together revealed statistical differences in \mathbf{k}_2 . These known differences limit extrapolation of information regarding rate constants of pools and digesta flow from the effects of one diet to another. Individual animals have also been identified as a major source of variation in transit time (Castle, 1956).

A possible digestion strategy for dik-dik may include the selection of feeds low in fiber and relatively high in digestible energy, and an intake and rumination pattern that is constant throughout the day and rapid passage of digesta to the lower tract. Another possible adaptation to compensate for a large difference between the energy required for the metabolic body size and the energy provided for a given gut capacity may include an adaptively lower metabolic rate. Although experimental evidence of lower metabolic rates in dik-dik is limited, the data collected to date support this hypothesis (Kamau & Maloiy, 1981).





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III. Appendix A

Table 8. Computer program to calculate the best transit time (TT), A, and rate constant k₂ with k₁ and A₁ held constant.

```
Metacommands for MS FORTRAN
$STORAGE:2
$NOFLOATCALLS
$NODEBUG
        INTERFACE TO SUBROUTINE TIME (N.STR)
        CHARACTER*10 STR [NEAR, REFERENCE]
        INTEGER*2 N [VALUE]
        END
        INTERFACE TO SUBROUTINE DATE (N.STR)
        CHARACTER*10 STR [NEAR, REFERENCE]
        INTEGER*2 N [VALUE]
C
        Program for determining the best TT and R2 for the
C
        rate of passage curves fitting the data to a double
С
        exponential curve of Grovums' method modified by
С
        Gary F. Hartnell and by David J. Baer, November,
С
        1986 to run under MS-DOS MS-FORTRAN with an 8087
С
        chip
C
        rectal grab samples
      DIMENSION T(30), P(30), A(30), PR(30)
      REAL*8 LIMIT, A1, STARTIME, T, A, P, PR, TT, D, R1, R2, C2,
     CE, B1, SS, B, G, H
      INTEGER NUMTIME, AA, NUM
      CHARACTER FNAME*12, FNAME2*12, TSTR*10, DSTR*10
      OPEN (5.FILE='TEMP.DAT')
      REWIND 5
   50 READ (5,47) FNAME, FNAME2
      READ (5,6) R1, C2, E, B1, NUM
      LIMIT = 3.0
      NUMTIME = 300
      STARTIME = 5.
      OPEN (6, FILE=FNAME, STATUS='NEW')
      OPEN (7.FILE=FNAME2.STATUS='NEW')
      WRITE (6,*) 'FILE: ', FNAME
      WRITE (*,*) 'FILE: ',FNAME
      CALL TIME (10, TSTR)
      WRITE (6,*) 'TIME: ',TSTR
      WRITE (*,*) 'TIME: ',TSTR
      CALL DATE (10, DSTR)
      WRITE (6,*) 'DATE: ',DSTR
C
      R1=K1, C2=approx. K2, E=the last time of excretion,
      B1=A1
      D0 55, AA = 1,30
        T(AA) = 0.0
        A(AA)=0.0
      DO 56 I=1.NUM
        READ (5,8) T(1),A(1)
   56
        CONTINUE
```

Table 8 (con't.).

```
47 FORMAT (T1, A12, 1X, A12)
    6 FORMAT (2(F7.5,1X), F6.2,1X, F7.1,1X, I3)
    8 FORMAT (F6.2,1X,F6.3)
      IF (R1-99.998) 51,52,52
   51 TT=STARTIME
   45 R2=C2-LIMIT
      DO 40, NZ = 1.NUMTIME
        R2=R2+(LIMIT/NUMTIME)
        SS=0.
        I = 0
        A1 = EXP(DLOG(B1) - R1 * TT)
    9
        I = I + 1
        K = I
        IF (T(I)-TT) 10,10,11
   10
        P(I)=0.
        GOTO 60
        P(I) = DLOG(A1 * EXP(-R1 * (T(I) - TT)) - (A1 * EXP(-R2 * (T(I) - TT)))
   11
        -TT))))
С
        CHI SQUARE = (OBSERVED-EXPECTED) **2/EXPECTED
        B=SS
        SS=((A(I)-P(I))**2)/ABS(P(I))+B
   60
        IF (T(I)-E) 9,12,12
   12
        IF (NZ-1) 80,80,78
   78
        IF (SS-D) 80,80,82
   80
        D=SS
        G=R2
        H = TT
        DO 81, I=1,K
   81
           PR(I) = P(I)
   82
         IF (NZ-NUMTIME) 40,13,13
   40
        CONTINUE
   13 WRITE (6.29)
      WRITE (6,30) D,H,R1,G,T(1),PR(1),A(1)
      WRITE (6,31) (T(I), PR(I), A(I), I=2,K)
      WRITE(7,32) D,H,R1,G
   29 FORMAT (3X,'ChiSqr',5x,'TT',6X,'K1',8X,'K2',6X,'T(I)',
     c2X,'PR(I)',3X,'A(I)')
   30 FORMAT (' ',F8.6,3X,F5.2,3X,F6.5,3X,F7.5,2X,F6.2,
     c2X, F5.3, 2X, F5.3
   31 FORMAT (37(38X, F6.2, 2X, F5.3, 2X, F5.3/))
   32 FORMAT (' ',F8.6,1X,F5.2,1X,F6.5,1X,F7.5)
      TT=TT+.25
      If (TT-12.) 45,45,50
   52 END
```

IV. Appendix B

Table 9. Concentration of chromium (Cr) in fecal dry matter of animal #5 fed pelleted feed (PF).

Sample number	Sampling time (hr)	Cr in fecal DM			
number		(ppm)	(ln(ppm))		
1	6.13	1.00	0.000		
2	7.13	1.00	0.000		
3	10.13	365.40	5.901		
4	12.13	894.26	6.796		
5	16.13	948.61	6.855		
6	18.13	970.68	6.878		
7	19.13	813.22	6.701		
8	21.63	707.69	6.562		
9	28.63	684.71	6.529		
10	32.13	434.41	6.074		
11	35.63	443.63	6.095		
12	36.13	348.97 ·	5.855		
13	42.63	280.34	5.636		
14	45.63	195.59	5.276		
15	48.13	134.56	4.902		
16	53.63	102.41	4.629		

Table 10. Determination of k_1 values using linear regression with the three sets of data points that provide the three highest r^2 .

Set #	Set of samples used	r ²	ln(A ₁) (ln(ppm))	A ₁ (ppm)	k ₁ (1/ħr)
1	6-16	0.95	8.016	3027.8	0.0604
2	7-16	0.94	8.044	3115.1	0.0610
3	6-14	0.94	7.787	2409.5	0.0518

Table 11. Calculated best fit model parameters $(k_2, TT, and A)$ with k_1 and A_1 held constant.

Set #	k ₁ (1/ħr)	k ₂ (1/ħr)	TT (hr)	A (ppm)	Chi-square
1	0.0604	0.3504	9.25	1731.8	0.0439_
2	0.0610	0.3410	9.25	1771.2	0.0429 ^a
3	0.0518	0.5118	9.50	1473.0	0.0795

aOverall lowest chi-square.

V. Appendix C

Table 12. Model parameters for individual animals.

Diet	Anima #	l TT ^e (hr)	A (ppm)	k ₁ f (17hr)	r ² of k ₁	k ₂ f (1/hr)	x ^{2g}
AL AL AL AL: (PF AL: (PF AL: (PF (AL): PI (AL): PI (AL): PI (AL): PI	1 2 4 5 5 3) c 1 F F	11.00 7.00 11.75 10.25 7.50 11.75 11.25 11.00 11.75 11.25	1903.7 1826.1 1245.7 834.2 1816.3 1165.1 2006.8 186.8 1863.6 1558.1	0.049 0.069 0.033 0.020 0.040 0.023 0.052 0.057 0.089 0.031	0.94 0.96 0.92 0.89 0.95 0.90 0.78 0.96 0.98 0.83	0.339 0.319 0.233 2.880 0.230 0.803 0.192 2.897 0.557 3.119 3.061	0.4184 0.0547 0.2206 0.0488 0.0948 0.0752 0.1459 0.1053 0.0530 0.0465 0.0385
(AL):PI PF PF PF PF		10.25 11.00 5.75 11.75 9.25	2168.4 1354.2 4517.0 1841.5 1771.2	0.046 0.139 0.155 0.058 0.061	0.94 0.90 0.99 0.93 0.94	0.176 0.329 0.315 0.298 0.341	0.0254 0.1558 0.8756 0.1202 0.0429

a Alfalfa leaf. b Marked alfalfa leaf - mixed diet. c Marked pelleted feed - mixed diet. d Pelleted feed. e TT = transit time. f k and k 2 = rate constants.

 g_{χ}^2 = calculated chi-square value.

VI. Appendix D

