

## NUTRIENT DIGESTIBILITY AND GASTROINTESTINAL ELECTROLYTE FLUX IN THE ELEPHANT AND RHINOCEROS

E. T. CLEMENS and G. M. O. MALOY

Department of Veterinary Physiology, University of Nairobi, P.O. Box 30197,  
Nairobi, Kenya and  
Department of Veterinary Science, Institute of Agriculture and Natural Resources,  
The University of Nebraska-Lincoln, Lincoln, NB 68583-0905, U.S.A.

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**Abstract**—1. Nutrient digestibility and absorption-secretion were studied in elephants and rhinoceros.  
2. Prehension and diet selection are discussed.  
3. Rhinoceros select less fiber, which may account for their greater digestive efficiency.  
4. Foregut digestion and fermentation were most evident in rhinoceros, while elephants possessed greater caecal-colonic digestion.  
5. Relative to rhinoceros, elephants demonstrated greater intestinal VFA absorption and less sodium-potassium flux.

### INTRODUCTION

Feeding behaviour of the elephant and rhinoceros has been the subject of several publications (Ritchie, 1963; Dougall, 1964; Goddard, 1970; Douglas-Hamilton, 1973; Alexander, 1978). Digestibility of nutrients by these large ungulates has been less frequently investigated (Benedict, 1936; McCullagh, 1969), and most recently by Foose (1982). However, digestive processes occurring within the gastrointestinal tracts of the elephant and rhinoceros have not been previously reported. The present investigation reports on nutrient digestibility of free-ranging elephants and rhinoceros observed in their natural habitat. Furthermore, nutrient digestibility, gastrointestinal water and electrolyte flux were determined at several sites along the gastrointestinal tract of the elephant and rhinoceros.

### METHODS AND MATERIALS

Three adult elephants (*Loxodonta africana*) and three black rhinoceros (*Diceros bicornis*) were used in the study. All animals were collected from their natural habitat during obligatory control programs. Field analyses and sample collections were begun immediately after sacrifice and generally were completed within two hours after death of the animal. Details of sample collection, analytical procedures and the composition of gastrointestinal contents were reported earlier (Clemens & Maloy, 1982).

The gastrointestinal tract of each animal was separated by ligatures into eleven segments (Fig. 1). These consisted of the cranial and caudal halves of the stomach, three equal segments of small intestine, the caecum and five segments of the colon. The nutrient composition of the cranial half of the stomach of each animal was regarded as the composition of ingesta. Nutrient digestibility was determined at each site along the gastrointestinal tract by the lignin ratio technique (Kobt & Luckey, 1972). Apparent absorption and secretion of fluids, organic acids and electrolytes at each site along the tract was determined by the methods of Staaland (1975). However, the assumption made by Staa-

land concerning dry matter disappearance was corrected in the present study, thus improving the accuracy of the technique.

Analysis of variance was used to determine significant species differences (Steel & Torrie, 1960).

### RESULTS

Tables 1, 2 and 3 give results obtained for apparent nutrient digestibility at each site along the gastrointestinal tract of the elephant and rhinoceros. Dry matter digestibility was greater in the rhinoceros than in the elephant at all sites along the tract. However, significant differences ( $P < 0.05$ ) were noted only within the caudal stomach and proximal colon (Table 1). Digestible energy values were more variable than dry matter, and significant differences were not observed between species at any site along the gastrointestinal tract. However, like dry matter digestibility, digestible energy values tended to favor the rhinoceros. Conversely, when consideration is given for the one elephant with the unusual values, the percent ash digested was generally greater in the elephant, than rhinoceros.

Apparent digestibility of crude protein was greater in the elephant than rhinoceros stomach, yet less in the small and large intestine (Table 2). Statistically significant differences ( $P < 0.05$ ) were observed in the proximal colon. Crude fiber values were extremely variable for subsequent gastrointestinal sites within a given species. Species differences in crude fiber, nitrogen-free extract and ether extract digestibility were not detected at any site along the gastrointestinal tract. Digestibility of nitrogen-free extract was greatest of all nutrients measured. As with most other parameters (i.e. dry matter, energy, crude protein and ether extract values), nitrogen-free extract digestibility increased most dramatically when comparing small intestine to caudal stomach of each species. Ether extract values were variable between gut segments for

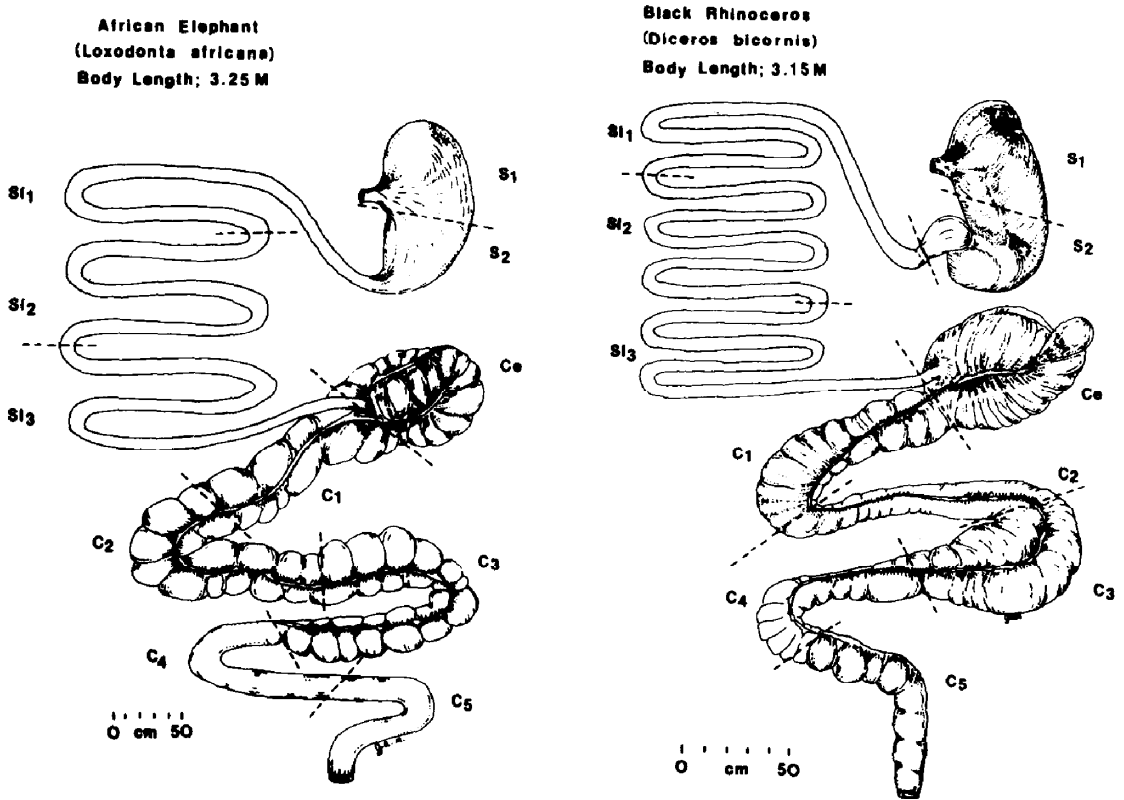


Fig. 1. Scale drawings of the elephant and rhinoceros gastrointestinal tracts. Body length represents the linear distance from mouth to anus in the intact animal. Symbols within the drawings represent the sections of tract: cranial ( $S_1$ ) and caudal ( $S_2$ ) halves of the stomach; proximal ( $SI_1$ ), mid ( $SI_2$ ) and distal ( $SI_3$ ) thirds of the small intestine; caecum (Ce) and five segments of colon ( $C_1$ – $C_5$ ), for the elephant and rhinoceros. Figure modified from Clemens & Maloij (1982) *J. Zool. Lond.* **198**, 141–156.

Table 1. Apparent digestibility ( $\pm$ SEM) of dry matter, energy and ash observed at various sites along the gastrointestinal tract of the elephant and rhinoceros

Section of tract	Dry matter (%)		Energy (%)		Ash (%)	
	Elephant	Rhino	Elephant	Rhino	Elephant	Rhino
Cranial stomach	7.4 (2.7)	20.3 (12.7)	5.9 (0.2)	4.3 (0.5)	41.0 (12.5)	26.4 (2.6)
Caudal stomach	10.9 (2.0)	26.2 (8.4)	9.2 (0.2)	11.6	31.1 (16.6)	13.3
Small intestine	22.1 (0.9)	47.9 (20.2)	28.4 (2.6)	33.6 (6.8)	10.5 (1.9)	22.2 (3.9)
Caecum	27.8 (5.1)	30.4 (18.8)	43.9 (2.2)	21.6 (4.1)	–73.8* (85.7)	33.5 (14.5)
Colon (1)	28.2 (1.7)	55.2 (14.7)	28.1 (0.5)	34.0 (5.0)	–90.0 (97.1)	20.3 (7.2)
Colon (2)	25.8 (12.2)	57.4 (14.0)	29.0 (3.5)	37.7 (5.3)	–95.1 (128.1)	8.7 (7.9)
Colon (3)	20.5 (8.1)	42.4 (15.1)	19.7 (1.6)	33.5 (5.0)	–228.8 (218.8)	4.4 (12.1)
Colon (4)	15.8 (6.2)	36.1 (15.8)	28.9 (1.8)	32.2 (5.1)	–119.9 (146.9)	1.0 (11.6)
Colon (5)	31.6 (6.2)	39.1 (9.1)	28.7 (1.7)	32.8 (3.0)	11.8 (23.8)	15.5 (2.5)

\* The negative values for ash are largely the result of one animal. Mean values for the remaining two elephants for caecum to colon (5) were: 12.9, 6.9, 18.6, 12.2, 20.0 and 21.0 respectively.

Table 2. Apparent digestibility ( $\pm$ SEM) of major nutrients as determined by the lignin ratio technique for various sites along the gastrointestinal tract of the elephant and rhinoceros

Section of tract	Crude protein (%)		Crude fiber (%)		NFE (%)		Ether extract (%)	
	Elephant	Rhino	Elephant	Rhino	Elephant	Rhino	Elephant	Rhino
Cranial stomach	30.1 (6.0)	27.1 (4.5)	15.0 (7.3)	16.0 (5.7)	26.2 (7.7)	18.7 (7.8)	31.1 (7.5)	18.9 (5.6)
Caudal stomach	29.0 (10.6)	16.0* (9.0)	6.9 (3.0)	6.1 (1.7)	15.6 (1.7)	30.7 (4.1)	36.0 (5.4)	25.4 (5.1)
Small intestine	34.4 (12.8)	54.3 (9.0)	17.1 (4.8)	23.0 (7.1)	54.0 (12.0)	64.7 (4.1)	40.2 (12.6)	46.6 (5.1)
Caecum	37.8 (11.2)	36.0 (7.9)	24.4 (4.8)	5.3 (4.8)	62.1 (11.1)	51.2 (9.0)	47.0 (11.7)	37.3 (4.1)
Colon (1)	29.2 (10.9)	51.7 (4.2)	9.8 (6.2)	19.0 (6.7)	45.7 (11.7)	64.4 (6.5)	32.7 (13.1)	43.8 (3.1)
Colon (2)	32.2 (13.0)	58.3 (4.8)	10.7 (4.9)	23.5 (8.1)	52.5 (10.3)	65.3 (5.7)	52.4 (7.3)	54.9 (6.7)
Colon (3)	33.0 (15.0)	57.3 (5.7)	23.0 (9.4)	19.7 (6.4)	50.3 (12.6)	61.4 (2.7)	37.6 (10.5)	45.4 (12.5)
Colon (4)	43.8 (11.2)	51.5 (6.4)	9.8 (3.4)	20.2 (7.9)	62.3 (11.7)	63.1 (7.4)	34.0 (13.5)	35.8 (10.6)
Colon (5)	36.9 (15.0)	49.3 (8.3)	12.6 (7.7)	14.5 (7.1)	58.6 (5.4)	52.5 (1.7)	23.0 (10.9)	23.2 (8.9)

\* Insufficient sample could be obtained from the small intestine of each rhinoceros for complete analysis, therefore all three samples were composited for a single analysis of all components.

Table 3. Apparent digestibility of the cell wall, cellulose and hemicellulose observed at various sites along the gastrointestinal tract of the elephant and rhinoceros

Section of tract	Cell wall (%)		Cellulose (%)		Hemicellulose (%)	
	Elephant	Rhino	Elephant	Rhino	Elephant	Rhino
Cranial stomach	16.2	10.5	15.4	20.2	7.2	30.3
Caudal stomach	3.2	1.5	10.8	3.2	9.8	26.6
Small intestine	21.9	16.8	25.6	19.8	-4.1	33.7
Caecum	27.2	4.6	39.8	4.8	3.9	21.5
Colon (1)	14.7	12.0	13.6	21.3	15.6	23.3
Colon (2)	15.1	14.3	16.3	18.4	1.2	32.6
Colon (3)	8.6	15.6	24.0	34.4	-6.0	38.4
Colon (4)	23.1	19.6	24.1	16.5	25.1	32.8
Colon (5)	15.1	26.9	26.2	31.1	15.6	45.3

both species. The elephant appeared more effective at digesting fats within the stomach, while the rhinoceros relied to a greater extent upon the small intestine for fat digestion.

The fat digestibility of fibrous components was further broken down into the apparent digestibility of cell wall, cellulose and hemicellulose fraction (Table 3). The rhinoceros demonstrated greater digestibility of hemicellulose at all sites, and greater cellulose digestibility at most sites along the entire gastrointestinal tract. The digestibility of cell wall components was variable for both species.

Net water, organic acid and electrolyte flux are presented in Figs 2, 3 and 4. Fluids were observed to enter the small intestine of the elephant and rhinoceros (Fig. 2). The greater net water flux was observed in the rhinoceros' small intestine. Small intestine fluids were rapidly absorbed in the caecum and colon of both the elephant and rhinoceros, such that 40–50% of the water present in the cranial stomach was absorbed along the tract. Significant difference ( $P > 0.05$ ) in fluid recovery was not detected between the elephant and rhinoceros.

Net appearance of volatile fatty acids (VFA) was most evident in the caecum and proximal colon of the elephant (Fig. 2). Conversely, net VFA flux in the rhinoceros was such that VFA's accumulated in the small intestine, reaching peak values in the caecum. Net VFA flux was significantly greater in the caecum of the elephant, than in the rhinoceros. The loss of VFA's (i.e. absorption and/or utilization) occurred within the mid to distal colon of both species. Lactic acid concentrations demonstrated little change within successive sites along the tract (Fig. 2). However, net disappearance was consistently greater in the rhinoceros than in the elephant.

The flux of the major VFA components (i.e. acetate, propionate and butyrate) is presented in Fig. 3. Net appearance and disappearance of acetate in the elephant and rhinoceros followed a pattern similar to that of total VFA movement. Acetate was the primary acid present in the volatile fraction. Net flux of propionate and butyrate were considerably less than that of acetate. Maximum increase in acetate was observed in the caecum of both species. Concentrations reached 120 mmol/l for the elephant and 75 mmol/l in the rhi-

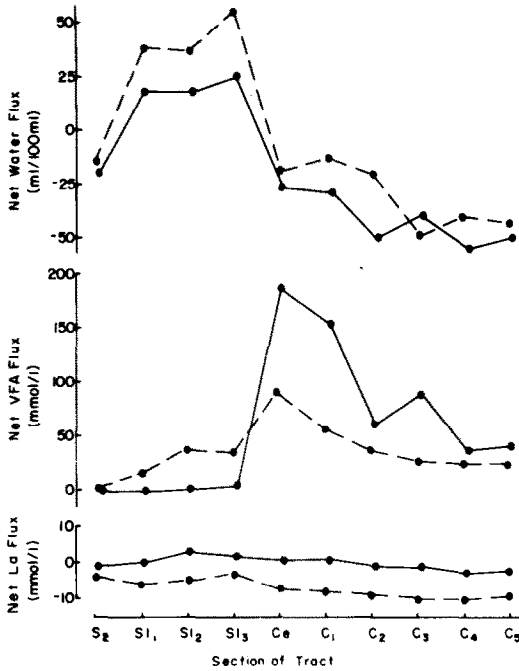


Fig. 2. Mean water, volatile fatty acid (VFA) and lactic acid (LA) flux as measured at each site along the gastrointestinal tract of the elephant (solid line) and rhinoceros (broken line). Absorption (or disappearance) indicated by negative values and secretion (or appearance) by positive values. Values are expressed as the change relative to the quantity observed in the cranial stomach. Symbols along the abscissa represent the sections of tract as given in Fig. 1.

noceros. However, only 15–25 mmol of acetate per liter of fluids were present in the distal colon of both species, demonstrating significant absorption and/or utilization of acetate throughout the mid and distal colonic areas.

Net flux observed for sodium, potassium and chloride ions at each site along the gastrointestinal tract of the elephant and rhinoceros is given in Fig. 4. Sodium ion flux was minimal throughout the elephant's gastrointestinal tract. A net sodium secretion was evident in the rhinoceros small intestine. However, sodium ions were adsorbed within the caecum and proximal colon such that the final gastrointestinal flux was minimal. Potassium ions were absorbed in the elephant's proximal small intestine, and with the exception of colon (3), remained at the lower values for segments of the lower bowel. Potassium ion flux was more variable in the rhinoceros and showed net secretion in the proximal colon. Chloride ions were absorbed throughout the gastrointestinal tract of the rhinoceros and elephant. Net chloride flux was consistently greater in the elephant than in the rhinoceros.

#### DISCUSSION

The African elephant and black rhinoceros are herbivores with distinctly different feeding habits. The black rhinoceros is a strict browser, selecting only the leaves of herds, shrubs and small trees (Ritchie, 1963; Mukinya, 1977). The rhinoceros is a continuous feeder and shows little dependence upon the need

for available drinking water (Ritchie, 1963; Mukinya, 1977). Conversely, the African elephant is a mixed feeder, preferring grasses yet consuming leaves, branches and bark of trees (Anderson & Walker, 1974; Alexander, 1978). Water is an important part of their diet. Elephants frequent the drinking holes during most of the night and mid-day (Benedict, 1936; Douglas-Hamilton, 1973), with the peak feeding periods being the early morning and late afternoon (Guy, 1976).

The gross anatomical features of elephant and rhinoceros digestive tracts, as well as the composition of their gastrointestinal contents, are quite different (Clemens & Maloiy, 1982). In addition, the present study demonstrates marked differences in digestive processes between the elephant and rhinoceros. The prehensile advantage which the rhinoceros has over the elephant allows for selection of less fibrous plant material (Clemens & Maloiy, 1982). Subsequently, digestive processes within the rhinoceros gastrointestinal tract appear more efficient. The higher values obtained for dry matter, energy, crude protein, nitrogen-free extract, cellulose and hemicellulose digestibility observed for the rhinoceros, relative to the elephant, are probably the result of selection. The rhinoceros consumed a smaller proportion of the less digestible components (i.e. cellulose, hemicellulose, ash) and a greater proportion of protein (Clemens & Maloiy, 1982). Thus, values expressed as percent of intake digested favor the readily digestible constituents. On the other hand, geophagia and the consumption of greater quantities of plant fiber (i.e. branches,

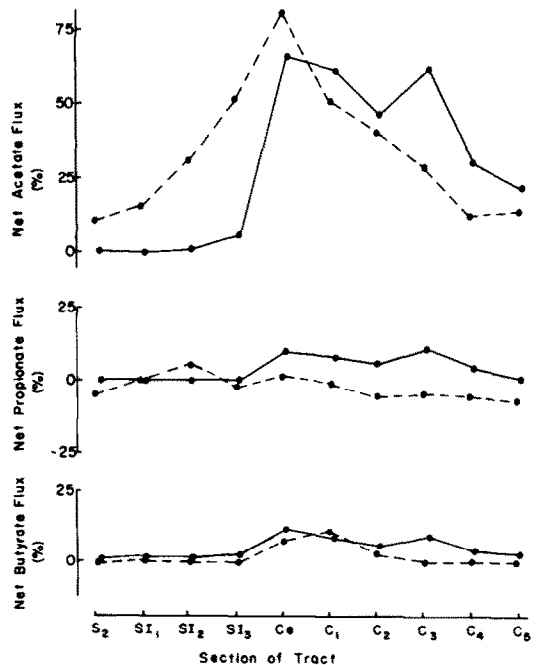


Fig. 3. Mean acetate, propionate and butyrate flux as measured at each site along the gastrointestinal tract of the elephant (solid line) and rhinoceros (broken line). Absorption (or disappearance) indicated by negative values and secretion (or appearance) by positive values. Values are expressed as the change relative to the quantity observed in the cranial stomach. Symbols along the abscissa represent the sections of tract as given in Fig. 1.

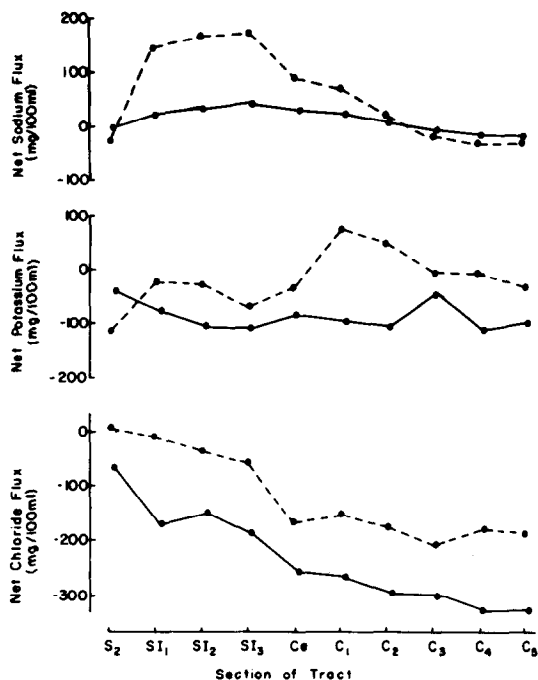


Fig. 4. Mean sodium, potassium and chloride ion flux as measured at each site along the gastrointestinal tract of the elephant (solid line) and rhinoceros (broken line). Absorption indicated by negative values and secretion of positive values. Values are expressed as the change relative to the quality observed in the cranial stomach. Symbols along the abscissa represent the sections of tract as given in Fig. 1.

bark) as seen in the elephant, reduce the overall digestibility. The extent of geophagia incurred by the elephant was most evident in one animal, which was observed to contain large quantities of earth and gravel within its caecum and colon. The accumulation of such material leads to the negative digestibility values for these sites.

Consumption of quantities of fibrous material suggests greater dependence upon enteric fermentation processes. Estimates of fermentation processes are generally derived from measurements of organic acids (Elsden *et al.*, 1946; Hungate, 1968; Stevens *et al.*, 1980). However, since these organic acids can be produced and utilized within the gastrointestinal tract, as well as absorbed and secreted, net flux can only be described as appearance and disappearance.

Caecal and colonic fermentation processes within the elephant are most evident in the net appearance of VFA's within these gut segments. These data further indicate greater accumulation of VFA within the rhinoceros small intestine and less VFA in the caecum-colon than was observed for the elephant. Earlier reports attribute the species differences to consumption of the more readily digestible substances by the rhinoceros, and the rhinoceros' ability to ferment these substances within the stomach (Clemens & Maloiy, 1982). Subsequently, less substrate is available for fermenting within the lower tract (Phillips, 1961; Hoppe, 1977). Several recent studies have shown the importance of VFA in colonic transport systems (Dawson *et al.*, 1964; Argenzio *et al.*, 1977;

Ruppin *et al.*, 1978). Their value in maintaining osmotic balance within the foregut and hindgut has also been indicated (Maloiy & Clemens, 1980a). Absorption of VFA's by the colon of the elephant and rhinoceros would be expected, since these organic acids are readily absorbed by colonic mucosa of numerous mammalian species, including man (Ruppin *et al.*, 1978), sub-human primates (Clemens & Maloiy, 1981), dogs (Stevens *et al.*, 1980), swine (Argenzio & Southworth, 1975) and several species of herbivores (Stevens *et al.*, 1980; Maloiy & Clemens, 1980b).

Maintenance of gastrointestinal osmotic balance relies upon the flux of electrolytes. The major cations, sodium and potassium, generally respond in opposition to one another (Maloiy & Clemens, 1980b). The elephant demonstrated little net flux of either sodium or potassium ions. However, the rhinoceros showed greater net sodium secretion within the small bowel and re-absorption within the large bowel. The pattern was generally reversed for potassium ions. Such data on electrolyte flux fit well with the isotonic and hypertonic values obtained for gastrointestinal contents within the elephant and rhinoceros, respectively (Clemens & Maloiy, 1982).

For the anions, chloride ion flux was greater within the proximal segments of tract and VFA's in the distal segments, for both species. The other major gastrointestinal anion, bicarbonate, was not measured in the present study.

It is most likely that physiological digestive processes differ very little between animal species (Schmidt-Nielsen *et al.*, 1980). The observed differences in overall nutrient digestibility, or digestion at any one particular site along the tract, are principally the result of differences in food consumed. Diet selection in free ranging animals is largely the result of the animals' ability for, or limitations in, stripping food from the environment. Comparing elephant and rhinoceros, the rhinoceros possesses the prehensile advantage in utilization of the lips to select more desirable plant parts (Ritchie, 1963; Mukinya, 1977). Thus, digestive efficiency is apparent. The clumsy feeding habits of the elephant are also apparent in the digestive results. However, confinement of these animals to the "zoo" environment and controlled feeding programs removes natural physiological differences. Therefore, feeding the elephant and rhinoceros identical controlled diets results in little or no difference in digestibility values (Foose, 1982).

Anatomical features of the gastrointestinal tract undoubtedly play a major role in digesta movement (Stevens, 1977; Clemens, 1980). However, complexity or simplicity of the tract may be either advantageous or disadvantageous, depending upon the parameter under investigation. The rhinoceros possesses the more complex foregut and hindgut, when compared to the elephant (Clemens & Maloiy, 1982).

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