

The digestive physiology of three East African herbivores: the elephant, rhinoceros and hippopotamus

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(Accepted 8 December 1981)

(With 2 figures in the text)

Studies were conducted to compare structural and physiological differences in the digestive functions of three species of large ungulates; the elephant (*Loxodonta africana*), the Black rhinoceros (*Diceros bicornis*) and the Hippopotamus (*Hippopotamus amphibius*). Major differences were noted in the composition of ingesta and the sites of bacterial fermentative activity. Comparisons are also made as to the influence of feeding behaviour on digestive functions, and as to the similarities of their digestive systems to that of domestic animals.

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Introduction

The large ungulates, the elephant, hippopotamus and rhinoceros, are favourite subjects of ecological and behavioural science. However, due to their immense size and limited availability these animals are much less accessible for physiological studies. Data on their digestive physiology is, with the exception of the hippopotamus, almost non-existent. During a three-year period from 1975 to 1978 we were able to conduct studies on the digestive physiology of animals destroyed by the Kenya Government during obligatory wildlife control procedures.

Methods and materials

Three adult elephants (*Loxodonta africana*), three Black rhinoceros (*Diceros bicornis*) and one Hippopotamus (*Hippopotamus amphibius*) were collected from their natural habitat during obligatory wildlife control procedures. Field analysis and sample collection were begun immediately after killing and generally completed within 2 h after the death of the animal. An estimate of body weight of each animal was obtained by selected body measurements (Langman, pers. comm.).

The abdominal cavity of each animal was opened immediately after death. Urine and blood samples were collected and refrigerated. Ligatures were used to tie off the oesophagus at the cardia and the

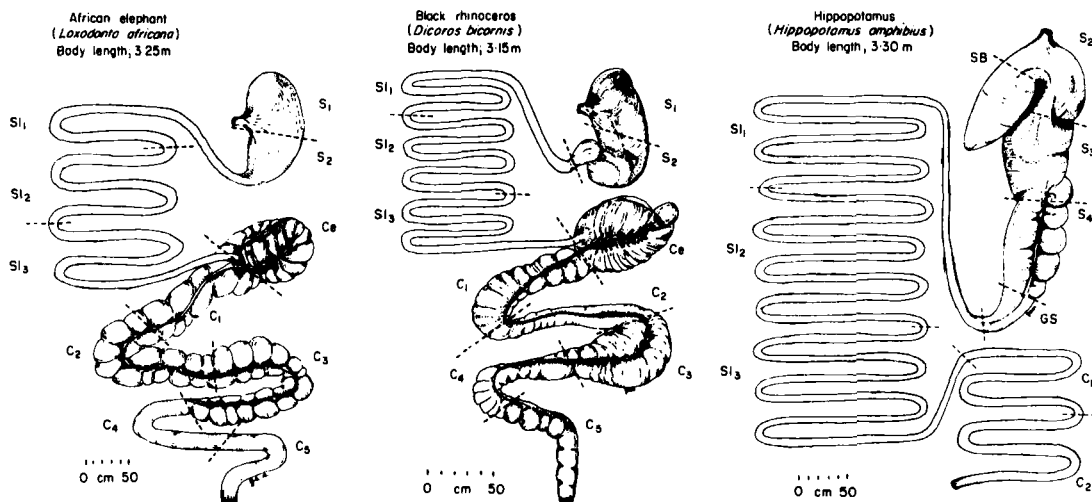


FIG. 1. Scale drawings of the elephant, rhinoceros and hippopotamus gastrointestinal tracts. Body length represents the linear distance from mouth to anus in the intact animal. Symbols within the drawings represent the sections of tract: cranial (S₁) and caudal (S₂) halves of the stomach; proximal (SI₁), mid (SI₂) and distal (SI₃) thirds of the small intestine; caecum (Ce) and five segments of colon (C₁-C₅), for the elephant and rhinoceros. For the hippopotamus symbols represent the parietal (stomach) blind sac (SB), three segments of the connecting chamber (S₂-S₄), glandular stomach (GS), three equal segments of small intestine (SI₁-SI₃) and two equal segments of colon (C₁ and C₂).

large bowel at the rectal-anal junction, and the gastrointestinal tract removed. The tract of one animal of each species was photographed for use in developing the scaled drawings presented in Fig. 1. After removal from the abdominal cavity, the gastrointestinal tract of each animal was separated by ligatures into selected segments. For the elephant and rhinoceros these consisted of the cranial and caudal halves of the stomach, three equal segments of the small intestine, the caecum and five segments of the colon. The gastrointestinal tract of the hippopotamus was separated by ligatures into the visceral blindsac, three segments of the connecting chambers*, the glandular portion of the stomach, three equal segments of the small intestine and two equal segments of colon.

The pH of each segment was measured immediately and anaerobically by insertion of an electrode into the axial midpoint of each segment of tract. Total contents were removed from each segment, weighed and a representative sample refrigerated for later analysis. Additional samples were strained through cheese cloth, the supernatant acidified with concentrated H₂SO₄ (approx. 0.5 ml/20 ml sample) and refrigerated for later analysis of volatile fatty acids and ammonia-nitrogen determination. An additional large aliquot of particulate material was collected from each segment of tract and from a recent faecal dropping for the analysis of the cellular components of ingesta.

The dry matter content of each sample was determined by drying a portion of each sample to a constant weight in a forced-air oven at 105°C. The samples of whole gut contents were centrifuged and the supernatant collected for laboratory analysis. The osmolality of the supernatant fraction was determined on a laboratory osmometer, sodium and potassium concentrations by flame photometry

*Accurate demarcation between the parietal blindsac, vestibulum and connecting chamber was not possible, therefore stomach (2) consists predominantly of contents from the parietal blindsac and stomach (3) primarily the proximal half of the connecting chamber. Vestibulum contents were part of both stomach (2) and stomach (3) segments. Designation of foregut segments according to Van Hoven (1978).

and the chloride concentration was determined with the use of a chloridometer. The lactic acid concentration of each sample was determined by the methods of Barker & Summerson (1941). Volatile fatty acids were determined by the steam distillation methods of Markham (1942), and by partition chromatography of the short chain fatty acids.

Approximately 1 kg of particulate material collected from each segment of tract and fresh faecal samples collected in the field were dried at 98°C in a forced-air oven for 48 h and finely ground for proximate analysis (AOAC, 1965). Gross components of analysis included the ash, ether extract, crude protein and crude fibre. The nitrogen-free extract was determined by difference. Additional fibre analyses were conducted to determine the cell wall content, cellulose, hemicellulose and lignin within each sample (Goering & Van Soest, 1970). The energy content of each sample was determined by bomb calorimetry.

Results

Table I gives the total weight of contents within each segment of tract and the relative proportions, by weight, of each segment as a percentage of the total gastrointestinal contents. The nutrient composition of gastrointestinal contents removed from the elephant, rhinoceros and hippopotamus are presented in Table II to Table X.

Despite the aquatic habitat and the presumed similarity of the hippopotamus stomach to that of the ruminant forestomach, the mean dry matter within the non-glandular portions of the hippopotamus stomach was not different from that observed within the elephant's stomach (Table II). However, the cranial (non-glandular) portion of the rhinoceros' stomach was eight to ten percentage units drier than that for comparable segments of the elephant and hippopotamus tract. The dry matter consistency of each segment of hippopotamus tract from glandular stomach to rectum was such that the fluid content was 90% or greater.

TABLE I
Mean weight of contents and relative capacity observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| Sections of tract for the elephant and rhinoceros | Weight of contents (kg) | | | Relative capacity (% of total wt) | | | Sections of tract for the hippopotamus |
|---|-------------------------|-------|-------|-----------------------------------|-------|-------|--|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | |
| | | | | | | | |
| | | | 29 | | | 15.5 | Stomach blind sac |
| | | | 38 | | | 20.3 | Stomach (2) |
| Cranial stomach | 22 | 19 | 50 | 5.3 | 11.0 | 26.7 | Stomach (3) |
| | | | 21 | | | 11.2 | Stomach (4) |
| Caudal stomach | 36 | 18 | 3 | 8.7 | 10.4 | 1.6 | Glandular stomach |
| Small intestine (1) | 6 | 2 | 6 | 1.4 | 1.2 | 3.2 | Small intestine (1) |
| Small intestine (2) | 10 | 3 | 11 | 2.4 | 1.7 | 5.9 | Small intestine (2) |
| Small intestine (3) | 12 | 4 | 10 | 2.9 | 2.3 | 5.4 | Small intestine (3) |
| Caecum | 75 | 40 | | 18.1 | 23.1 | | |
| Colon (1) | 76 | 33 | | 18.3 | 19.1 | | |
| Colon (2) | 44 | 9 | 9 | 10.6 | 5.2 | 4.8 | Colon (1) |
| Colon (3) | 84 | 31 | | 20.2 | 17.9 | | |
| Colon (4) | 31 | 8 | 10 | 7.5 | 4.6 | 5.4 | Colon (2) |
| Colon (5) | 19 | 6 | | 4.6 | 3.5 | | |

TABLE II

Mean (\pm S.E.M.) dry matter, fluid volume and osmolality observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | Dry matter (%) | | | Fluid volume (l) | | | Osmolality (mOsm/kg) | | | |
|--|----------------|-------|-------|------------------|-------|-------|----------------------|-------|-------|------------------------|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | |
| | | | | | | | | | | |
| | | | 15.0 | | | 24.6 | | | 390 | Stomach, blind sac |
| | | | 15.8 | | | 32.0 | | | 384 | Stomach (2) |
| | | | 16.4 | 19.0 | 14.2 | 41.8 | 286 | 386 | 347 | Stomach (3) |
| | | | (3.5) | (0.7) | (9.5) | (2.7) | (35) | (51) | | |
| | | | 13.0 | | | 18.3 | | | 278 | Stomach (4) |
| | | | 8.6 | 29.5 | 14.5 | 2.7 | 219 | 303 | 236 | Glandular stomach |
| | | | (3.5) | (13.5) | (1.5) | | (51) | (52) | | |
| | | | 10.1 | 5.4 | 2.0 | 5.4 | 246 | 439 | 578 | Small intestine (1) |
| | | | (1.3) | (1.8) | (2.4) | (0.4) | (22) | (65) | | |
| | | | 7.7 | 8.3 | 2.4 | 10.3 | 247 | 478 | 429 | Small intestine (2) |
| | | | (4.0) | (1.9) | (3.7) | (0.3) | (25) | (74) | | |
| | | | 6.8 | 10.6 | 3.5 | 8.8 | 240 | 425 | 351 | Small intestine (3) |
| | | | (2.5) | (1.4) | (4.5) | (0.4) | (35) | (54) | | |
| | | | 14.8 | 65.8 | 34.2 | | 311 | 455 | | |
| | | | (2.5) | (3.0) | (2.6) | | (29) | (54) | | |
| | | | 13.3 | 66.1 | 28.7 | | 301 | 404 | | |
| | | | (2.4) | (18.8) | (3.4) | | (28) | (38) | | |
| | | | 9.8 | 38.4 | 8.0 | 8.1 | 291 | 490 | 205 | Colon (1) |
| | | | (1.3) | (4.8) | (0.2) | | (20) | (15) | | |
| | | | 18.7 | 70.2 | 25.5 | | 331 | 330 | | |
| | | | (1.6) | (18.5) | (2.5) | | (13) | (28) | | |
| | | | 10.7 | 22.4 | 6.0 | 8.5 | 254 | 380 | 185 | Colon (2) |
| | | | (1.8) | (7.8) | (1.0) | | (28) | (45) | | |
| | | | 26.9 | 15.2 | 4.5 | | 204 | 268 | | |
| | | | (7.0) | (4.5) | (1.1) | | (36) | (5) | | |
| | | | (4.2) | | | | | | | |

Colonic contents of the hippopotamus suggested limited drying of faecal material as the ingesta moved aborally. Drying of faecal contents within the distal colon of the elephant and rhinoceros were most evident.

The volume of fluid observed at each site along the gastrointestinal tract is also presented in Table II. Total gut contents and the relative proportion of contents within each segment of tract are presented in Table I. Foregut contents of the hippopotamus comprised 75.3% of total gut weight compared to 14.0% and 21.4% for the elephant and rhinoceros, respectively. Conversely, the large intestinal area of the hippopotamus contained 10.2% of the total contents while that of the elephant and rhinoceros were 79.3% and 73.4%, respectively. The proportions were not appreciably changed when only the fluid volumes were considered (i.e. foregut, 74.4, 13.8, 20.0%; and hindgut, 10.3, 79.2, 74.5% for the hippopotamus, elephant and rhinoceros, respectively). Thus, the fluid to dry matter ratios were not greatly altered from foregut to hindgut for any species investigated. There were, however, variations in fluid to dry matter ratio at various sites within each gut section.

Osmolality of the elephant's gastrointestinal contents was generally hypotonic to plasma, while that of the rhinoceros was hypertonic (Table II). The hippopotamus' gastrointestinal contents demonstrated an alternating, two-cycle pattern of hyper- and hypotonicity as the ingesta moved from blind sac to rectum. Plasma osmolality values were 278 for the elephant, 294 for the rhinoceros and 291 for the hippopotamus. The osmolality of gut contents reflects the gross ionic concentrations within the tract. The major electrolytes of mammalian gut contents consisted predominantly of the cation sodium and potassium and the anions, chloride, bicarbonate and organic acids.

For the elephant and rhinoceros, concentrations of sodium and potassium within the gastrointestinal tract were inversely related to one another (Table III). Highest concentrations of potassium ions were observed in the stomach and distal colon while sodium concentrations were observed at their highest levels within the small intestine and caecum. Unlike its counterparts, the hippopotamus demonstrated elevated foregut sodium concentrations and an increase in potassium concentrations within the small intestine to nearly two times greater in the hippopotamus than in the elephant and rhinoceros.

TABLE III

Mean (\pm S.E.M.) sodium, potassium and chloride concentrations observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | Sodium (mEq/l) | | | Potassium (mEq/l) | | | Chloride (mEq/l) | | | | |
|--|---------------------|----------------|---------------|-------------------|----------------|----------------|------------------|----------------|----------------|--------------------|---------------------|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | | |
| | | | 94.0 | | | 36.0 | | | 5.0 | Stomach, blind sac | |
| | | | 86.0 | | | 48.0 | | | 8.0 | Stomach (2) | |
| | | | 72.0 | | | 62.0 | | | 18.0 | Stomach (3) | |
| Section of tract for the elephant and rhinoceros | Cranial stomach | 31.7 (15.3) | 34.2 (8.1) | 59.3 (9.3) | 68.5 (19.0) | 62.0 | 101.8 (11.1) | 95.9 (15.5) | | | |
| | | | 44.0 | | | 50.0 | | | 77.0 | Stomach (4) | |
| | Caudal stomach | 31.3 (15.5) | 23.9 (2.5) | 40.0 | 52.7 (8.2) | 47.3 (16.3) | 44.0 | 90.5 (15.9) | 95.0 (14.9) | 89.0 | Glandular stomach |
| | Small intestine (1) | 59.3 (19.5) | 75.7 (0.4) | 55.0 | 44.3 (9.8) | 49.3 (10.3) | 58.0 | 79.6 (10.8) | 69.1 (3.6) | 49.0 | Small intestine (1) |
| | Small intestine (2) | 60.0 (11.4) | 83.7 (3.2) | 51.0 | 36.7 (6.7) | 48.7 (10.7) | 66.0 | 74.5 (10.8) | 61.7 (3.0) | 27.0 | Small intestine (2) |
| | Small intestine (3) | 65.7 (13.6) | 85.3 (1.3) | 50.0 | 35.3 (5.3) | 35.3 (3.5) | 63.0 | 66.8 (16.4) | 54.5 (4.8) | 25.0 | Small intestine (3) |
| | Caecum | 66.0 (11.1) | 83.3 (4.8) | | 48.0 (8.0) | 61.3 (0.7) | | 40.3 (8.6) | 33.5 (3.3) | | |
| | Colon (1) | 64.0 (6.8) | 60.9 (4.5) | | 49.0 (9.0) | 79.5 (8.0) | | 41.3 (7.3) | 32.4 (0.7) | | |
| | Colon (2) | 67.0 (7.8) | 50.3 (6.3) | 20.0 | 60.0 (5.8) | 92.7 (6.4) | 66.0 | 32.8 (3.9) | 33.1 (2.6) | 18.0 | Colon (1) |
| | Colon (3) | 38.0 (14.0) | 38.2 (2.8) | | 72.7 (8.2) | 93.6 (11.8) | | 24.4 (5.4) | 29.0 (1.0) | | |
| | Colon (4) | 27.7 (15.7) | 31.2 (4.8) | 10.0 | 64.3 (10.1) | 99.0 (9.3) | 56.0 | 20.8 (5.1) | 34.0 (1.2) | 17.0 | Colon (2) |
| | Colon (5) | 15.7 (11.2) | 17.3 (1.9) | | 63.3 (8.8) | 90.2 (6.6) | | 18.2 (7.0) | 39.8 (3.3) | | |

Section of tract for the hippopotamus

Chloride ions were the major anion within the elephant and rhinoceros stomach and within the glandular portion of the hippopotamus stomach (Table III). The concentrations (89 to 95 mEq/l) were similar in all three species at these sites. Chloride concentrations decreased as the ingesta moved in an aboral direction. However, chloride concentrations within the distal colon of the rhinoceros were twice those of the elephant and hippopotamus.

The mean electrolyte concentrations (mEq/l) of plasma were: chloride 69, 72, 51; sodium 102, 122, 127; and potassium 18, 36, 14, for the elephant, rhinoceros and hippopotamus, respectively.

Gastrointestinal pH values appeared to parallel chloride concentrations in each species investigated (Table IV). The pH of contents was lowest in those areas of tract where chloride ion concentrations were highest. The reverse was also true. Associated with the elevated chloride concentrations within the distal colon of the rhinoceros was a lower pH relative to similar gut segments in the elephant and hippopotamus. The stomach pH was significantly

TABLE IV
Mean (\pm S.E.M.) pH, lactic acid and volatile fatty acid concentrations observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | pH | | | Lactic acid (mmoles/l) | | | Volatile fatty acids (mmoles/l) | | | |
|---------------------|----------|--------|-------|------------------------|--------|-------|---------------------------------|--------|-------|---------------------|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | |
| | | | | | | | | | | |
| | | | 5.58 | | | 0.46 | | | 150.4 | Stomach, blind sac |
| | | | 5.60 | | | 1.45 | | | 153.3 | Stomach (2) |
| | 3.13 | 4.48 | 5.71 | 2.90 | 9.53 | 0.81 | 10.3 | 34.9 | 140.0 | Stomach (3) |
| | (0.42) | (0.04) | | (0.39) | (1.83) | | (2.3) | (8.4) | | |
| | | | 4.56 | | | 0.66 | | | 60.0 | Stomach (4) |
| Cranial stomach | 3.36 | 2.01 | 3.98 | 1.74 | 6.26 | 1.35 | 9.7 | 42.6 | 30.1 | Glandular stomach |
| | (0.37) | (0.25) | | (0.32) | (0.37) | | (2.1) | (17.6) | | |
| Small intestine (1) | 4.63 | 5.84 | 6.28 | 3.45 | 2.30 | 6.60 | 10.1 | 37.3 | 37.7 | Small intestine (1) |
| | (0.09) | (0.12) | | (1.17) | (1.32) | | (2.3) | (16.1) | | |
| Small intestine (2) | 4.93 | 6.01 | 6.88 | 5.55 | 3.23 | 4.11 | 12.8 | 39.6 | 28.3 | Small intestine (2) |
| | (0.50) | (0.16) | | (2.92) | (1.92) | | (4.6) | (21.3) | | |
| Small intestine (3) | 5.64 | 6.08 | 6.89 | 4.76 | 4.97 | 3.46 | 17.1 | 51.7 | 48.5 | Small intestine (3) |
| | (0.71) | (0.29) | | (2.47) | (1.39) | | (10.3) | (24.8) | | |
| Caecum | 5.65 | 5.23 | | 5.48 | 2.53 | | 137.6 | 144.4 | | |
| | (0.14) | (0.16) | | (1.65) | (1.45) | | (26.4) | (45.8) | | |
| Colon (1) | 5.75 | 5.51 | | 5.10 | 0.96 | | 121.9 | 79.5 | | |
| | (0.14) | (0.16) | | (2.31) | (0.32) | | (21.2) | (32.4) | | |
| Colon (2) | 5.93 | 5.78 | 6.99 | 3.74 | 0.98 | 0.68 | 128.7 | 80.7 | 28.0 | Colon (1) |
| | (0.15) | (0.09) | | (1.61) | (0.25) | | (22.4) | (47.3) | | |
| Colon (3) | 6.23 | 5.74 | | 3.26 | 0.86 | | 148.3 | 78.6 | | |
| | (0.44) | (0.13) | | (1.83) | (0.27) | | (18.2) | (41.6) | | |
| Colon (4) | 6.55 | 5.99 | 7.00 | 1.85 | 0.80 | 0.36 | 114.2 | 72.0 | 34.9 | Colon (2) |
| | (0.41) | (0.10) | | (1.38) | (0.39) | | (24.0) | (35.4) | | |
| Colon (5) | 7.01 | 5.86 | | 0.38 | 0.86 | | 64.6 | 53.3 | | |
| | (0.51) | (0.28) | | (0.28) | (0.51) | | (25.9) | (19.5) | | |

different between the cranial and caudal halves of the rhinoceros stomach, but not the elephant.

Lactic acids were considerably lower in concentration than volatile fatty acids (VFA) throughout the entire gastrointestinal tract of these animals (Table V). Concentrations never exceeded 10 mEq/l and were observed in their highest concentrations within the stomach of the rhinoceros, small intestine of the hippopotamus, and the small intestine and caecum of the elephant.

Volatile fatty acids (VFA) were generally found in higher concentrations within those areas of the gastrointestinal tract where chloride ions were reduced in concentration (Table IV), the exception being the hippopotamus colon where concentrations of VFA and chloride were noticeably low. VFA's were most prevalent within the complex forestomach of the hippopotamus, caecum of the rhinoceros and caecum and colon of the elephant. VFA concentrations were also greater in the stomach and small intestine, yet lower in the colon of the rhinoceros than in comparable segments of the elephant's tract.

TABLE V
Mean (\pm s.e.m.) acetic, propionic and butyric acid composition (%) of fatty acids observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | Elephant | | | Rhinoceros | | | Hippopotamus | | | | |
|--|---------------------|----------------|----------------|----------------|----------------|----------------|---------------|------------|---------|--------------------|---------------------|
| | Acetic | Pro-pionic | Butyric | Acetic | Pro-pionic | Butyric | Acetic | Pro-pionic | Butyric | | |
| | | | | | | | 70.6 | 19.6 | 8.3 | Stomach, blind sac | |
| | | | | | | | 72.5 | 17.8 | 8.1 | Stomach (2) | |
| | | | | | | | 71.8 | 18.9 | 7.2 | Stomach (3) | |
| Section of tract for the elephant and rhinoceros | Cranial stomach | 39.4 (5.7) | 43.4 (8.2) | 7.9 (1.4) | 49.5 (12.9) | 41.3 (13.2) | 6.9 (0.7) | | | | Stomach (4) |
| | Caudal stomach | 43.1 (15.4) | 43.2 (11.9) | 8.1 (2.5) | 62.6 (11.7) | 30.9 (11.3) | 4.2 (0.8) | 79.1 | 16.8 | 4.1 | Glandular stomach |
| | Small intestine (1) | 35.0 (6.2) | 48.3 (6.3) | 13.2 (2.2) | 57.9 (14.7) | 36.7 (12.5) | 4.6 (2.3) | 78.1 | 9.5 | 2.2 | Small intestine (1) |
| | Small intestine (2) | 39.8 (3.5) | 45.9 (5.6) | 10.2 (3.3) | 71.7 (2.4) | 23.0 (3.8) | 4.5 (3.5) | 84.3 | 10.0 | 4.9 | Small intestine (2) |
| | Small intestine (3) | 53.3 (17.0) | 24.0 (7.5) | 21.3 (10.3) | 80.4 (0.8) | 15.0 (2.3) | 3.7 (2.5) | 66.0 | 20.7 | 5.8 | Small intestine (3) |
| | Caecum | 62.8 (11.8) | 20.2 (6.7) | 15.1 (4.9) | 78.8 (4.0) | 14.0 (1.4) | 6.0 (3.1) | | | | |
| | Colon (1) | 73.1 (3.4) | 14.5 (1.6) | 10.0 (1.0) | 71.0 (0.7) | 15.0 (0.6) | 12.4 (1.5) | | | | |
| | Colon (2) | 70.9 (5.7) | 17.4 (2.0) | 8.5 (1.5) | 71.9 (2.4) | 13.8 (3.4) | 12.6 (2.6) | 73.9 | 16.2 | 5.3 | Colon (1) |
| | Colon (3) | 70.6 (3.5) | 15.5 (2.8) | 8.9 (0.5) | 74.2 (0.8) | 14.5 (1.0) | 7.4 (0.3) | | | | |
| | Colon (4) | 70.4 (0.6) | 17.8 (0.7) | 7.8 (0.3) | 65.2 (10.6) | 14.7 (1.5) | 13.7 (7.3) | 75.8 | 16.6 | 4.3 | Colon (2) |
| | Colon (5) | 73.7 (3.1) | 13.3 (3.0) | 7.9 (0.1) | 69.3 (6.1) | 20.2 (5.2) | 7.6 (1.4) | | | | |

Section of tract for the hippopotamus

TABLE VI

Mean (\pm S.E.M.) isobutyric, valeric and isovaleric acid composition (%) of fatty acids observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | Elephant | | | Rhinoceros | | | Hippopotamus | | | |
|---------------------|-------------|---------|-------------|-------------|---------|-------------|--------------|---------|-------------|---------------------|
| | Iso-butyric | Valeric | Iso-valeric | Iso-butyric | Valeric | Iso-valeric | Iso-butyric | Valeric | Iso-valeric | |
| | | | | | | | 0.4 | 0.8 | 0.3 | Stomach, blind sac |
| | | | | | | | 0.4 | 0.7 | 0.5 | Stomach (2) |
| | | | | | | | 0.6 | 0.7 | 0.9 | Stomach (3) |
| | | | | | | | 0.5 | 0.8 | 1.1 | Stomach (4) |
| Cranial stomach | 0.0 | 2.7 | 6.2 | 0.6 | 0.2 | 0.4 | 0.6 | 0.7 | 0.9 | Glandular stomach |
| | | (1.8) | (0.8) | (0.2) | (0.1) | (0.3) | | | | |
| | | | | | | | 0.0 | 0.0 | 0.0 | Stomach (4) |
| Caudal stomach | 0.6 | 2.7 | 2.2 | 1.3 | 0.6 | 0.3 | 0.0 | 0.0 | 0.0 | Glandular stomach |
| | (0.5) | (0.9) | (1.9) | (0.3) | (0.4) | (0.3) | | | | |
| | | | | | | | 0.4 | 3.0 | 6.8 | Small intestine (1) |
| Small intestine (1) | 0.0 | 0.9 | 3.3 | 0.3 | 0.5 | 0.0 | | | | |
| | | (0.5) | (1.7) | (0.1) | (0.2) | | | | | |
| | | | | | | | 0.1 | 0.4 | 0.3 | Small intestine (2) |
| Small intestine (2) | 3.4 | 0.1 | 2.3 | 0.2 | 0.1 | 0.5 | | | | |
| | (1.8) | (0.1) | (2.3) | (0.1) | (0.1) | (0.2) | | | | |
| | | | | | | | 3.3 | 0.0 | 4.2 | Small intestine (3) |
| Small intestine (3) | 1.6 | 0.1 | 0.0 | 0.2 | 0.7 | 0.3 | | | | |
| | (0.7) | (0.1) | | (0.1) | (0.2) | (0.3) | | | | |
| | | | | | | | | | | |
| Caecum | 0.5 | 0.4 | 0.9 | 0.4 | 0.5 | 0.3 | | | | |
| | (0.2) | (0.1) | (0.3) | (0.2) | (0.1) | (0.2) | | | | |
| | | | | | | | | | | |
| Colon (1) | 1.6 | 0.5 | 1.1 | 0.3 | 0.3 | 0.4 | | | | |
| | (0.8) | (0.1) | (0.4) | (0.1) | (0.1) | (0.2) | | | | |
| | | | | | | | 1.3 | 2.0 | 1.3 | Colon (1) |
| Colon (2) | 1.1 | 0.8 | 1.3 | 0.6 | 0.5 | 0.7 | | | | |
| | (0.8) | (0.3) | (1.2) | (0.3) | (0.3) | (0.3) | | | | |
| | | | | | | | | | | |
| Colon (3) | 1.6 | 1.2 | 2.2 | 1.4 | 0.8 | 1.8 | | | | |
| | (0.3) | (0.1) | (0.2) | (0.1) | (0.1) | (0.1) | | | | |
| | | | | | | | | | | |
| Colon (4) | 1.4 | 0.9 | 1.7 | 2.7 | 1.3 | 2.3 | 1.5 | 0.4 | 1.5 | Colon (2) |
| | (0.2) | (0.2) | (0.1) | (1.3) | (0.4) | (0.6) | | | | |
| | | | | | | | | | | |
| Colon (5) | 1.8 | 0.4 | 2.1 | 1.9 | 0.9 | 1.7 | | | | |
| | (0.1) | (0.1) | (0.2) | (0.5) | (0.3) | (0.5) | | | | |

The composition of fatty acids making up the VFA fraction at each site along the gastrointestinal tract were further assessed by partition chromatography. The relative proportion of acetate, propionate, butyrate, isobutyrate, valerate and isovalerate for each species is given in Tables V and VI. The acetate to propionate ratio for each site and species is given in Table VII. With the exception of the cranial stomach and mid-small intestinal segments of the elephant's gastrointestinal tract, the three major fatty acids (i.e. acetate, propionate and butyrate) comprised more than 95% of the fatty acids present. Butyric acid values were observed at their highest levels within the elephant's small intestine and caecum, and within the colon of the rhinoceros. The acetate to propionate ratio was generally low (less than 3 : 1) in the stomach and small intestine of the elephant and rhinoceros. Acetate to propionate ratios exceeded 3 : 1 at each site throughout the colon of these species and throughout the entire tract of the hippopotamus.

The gross composition of the major nutrients observed at each site along the gastrointestinal tract is presented in Tables VIII and IX. Ingesta within the gut segment proximal to the

TABLE VII
Mean (\pm S.E.M.) acetate to propionate ratio observed at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| | Acetate : Propionate ratio | | | |
|---------------------|----------------------------|-----------------|-------|---------------------|
| | Elephant | Rhino | Hippo | |
| Cranial stomach | 1.05 (0.38) | 1.81 (1.02) | 3.60 | Stomach, blind sac |
| | | | 4.07 | Stomach (2) |
| | | | 3.80 | Stomach (3) |
| Caudal stomach | 1.54 (1.02) | 2.78 (1.07) | 3.86 | Stomach (4) |
| | | | 4.71 | Glandular stomach |
| Small intestine (1) | 0.79 (0.26) | 2.92 (2.02) | 8.22 | Small intestine (1) |
| Small intestine (2) | 0.91 (0.30) | 3.29 (1.09) | 8.43 | Small intestine (2) |
| Small intestine (3) | 2.97 (1.23) | 5.65 (0.93) | 3.19 | Small intestine (3) |
| Caecum | 2.26 (1.37) | 5.79* (0.91) | | |
| Colon (1) | 5.22 (0.84) | 4.74 (0.13) | | |
| Colon (2) | 4.26 (0.81) | 6.11 (1.96) | 4.56 | Colon (1) |
| Colon (3) | 4.99 (1.22) | 5.16 (0.42) | | |
| Colon (4) | 3.96 (0.18) | 4.65 (1.11) | 4.57 | Colon (2) |
| Colon (5) | 6.29 (1.72) | 3.95 (1.03) | | |

*Values significantly different at the $P < 0.05$ level.

oesophagus would, presumably, closely represent the composition of the diet of each animal (i.e. the composition of ingesta within the cranial half of the elephant's and rhinoceros' stomach and in the blind sac of the hippopotamus stomach). All species were similar in the percent fat and nitrogen-free extract at this site. The elephant had the lowest crude protein value, while the hippopotamus had the lowest crude fibre and highest ash value.

Quantitative measurement of the ingesta within the stomach of each species indicated that the elephant, although two to three times heavier in body weight than the rhinoceros, had less than 1 kg more dry matter (9.42 and 8.51 kg dry matter, respectively). The hippopotamus with its complex foregut retained more than 44 kg of dry matter within its stomach.

The components of the fibre fraction at each site along the tract of the elephant and rhinoceros were further analysed for cell wall content, cellulose, hemicellulose and lignin components (Table X). Prominent differences between these species were most evident for the lignin fraction.

TABLE VIII

Mean values observed for the crude protein, crude fibre and fat analysis at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| Sections of tract of the elephant and rhinoceros | Crude protein (%) | | | Crude fibre (%) | | | Fat (%) | | | Sections of tract of the hippopotamus |
|--|-------------------|-------|-------|-----------------|-------|-------|----------|-------|-------|---------------------------------------|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | |
| | | | | | | | | | | |
| | | | 13.7 | | | 36.8 | | | 3.8 | Stomach, blind sac |
| | | | 14.5 | | | 31.3 | | | 4.4 | Stomach (2) |
| Cranial stomach | 12.3 | 15.1 | 15.9 | 43.9 | 44.4 | 28.5 | 4.2 | 3.2 | 5.8 | Stomach (3) |
| | | | 15.1 | | | 29.8 | | | 8.9 | Stomach (4) |
| Caudal stomach | 9.9 | 11.6 | 14.4 | 41.6 | 46.2 | 27.0 | 3.3 | 3.7 | 9.3 | Glandular stomach |
| Small intestine | 10.3 | 14.7 | 11.7 | 40.6 | 44.0 | 27.0 | 3.2 | 3.5 | 6.7 | Small intestine |
| Caecum | 9.2 | 11.0 | | 43.3 | 58.1 | | 3.3 | 3.0 | | |
| Colon (1) | 10.0 | 12.3 | | 44.1 | 57.9 | | 3.2 | 3.0 | | |
| Colon (2) | 9.2 | 11.2 | 9.1 | 45.5 | 58.7 | 28.5 | 3.3 | 3.2 | 5.7 | Colon (1) |
| Colon (3) | 9.4 | 10.1 | | 45.8 | 58.0 | | 2.6 | 2.7 | | |
| Colon (4) | 6.8 | 9.6 | 9.1 | 47.7 | 57.0 | 29.2 | 2.8 | 3.8 | 5.9 | Colon (2) |
| Colon (5) | 7.9 | 11.3 | | 43.3 | 55.7 | | 3.8 | 3.7 | | |

TABLE IX

Mean values observed for the nitrogen free extract, ash and energy analysis at various sites along the gastrointestinal tract of the elephant, rhinoceros and hippopotamus

| Sections of tract for the elephant and rhinoceros | Nitrogen free extract (%) | | | Ash (%) | | | Energy (kcal/g) | | | Sections of tract for the hippopotamus |
|---|---------------------------|-------|-------|----------|-------|-------|-----------------|-------|-------|--|
| | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | Elephant | Rhino | Hippo | |
| | | | | | | | | | | |
| | | | 30.1 | | | 15.7 | | | 4.24 | Stomach, blind sac |
| | | | 30.2 | | | 19.6 | | | 4.23 | Stomach (2) |
| Cranial stomach | 33.4 | 30.0 | 27.0 | 11.0 | 6.8 | 22.2 | 4.33 | 4.34 | 4.35 | Stomach (3) |
| | | | 21.0 | | | 25.2 | | | 3.99 | Stomach (4) |
| Caudal stomach | 38.1 | 32.8 | 25.4 | 7.1 | 5.7 | 23.9 | 4.30 | 4.34 | 4.07 | Glandular stomach |
| Small intestine | 35.5 | 30.3 | 26.1 | 8.2 | 5.7 | 23.9 | 4.15 | 4.31 | 3.84 | Small intestine |
| Caecum | 27.6 | 18.9 | | 13.3 | 9.1 | | 3.95 | 4.55 | | |
| Colon (1) | 25.1 | 20.6 | | 15.0 | 6.1 | | 3.48 | 4.37 | | |
| Colon (2) | 27.9 | 18.1 | 24.7 | 12.6 | 8.8 | 32.1 | 3.52 | 4.33 | 3.58 | Colon (1) |
| Colon (3) | 27.6 | 18.5 | | 7.9 | 10.8 | | 3.75 | 4.30 | | |
| Colon (4) | 29.5 | 19.3 | | 10.5 | 10.3 | 30.4 | 3.56 | 4.37 | 3.60 | Colon (2) |
| Colon (5) | 27.4 | 15.8 | | 12.0 | 10.7 | | 3.65 | 4.32 | | |

TABLE X

Mean values observed for the cell wall, cellulose, hemicellulose and lignin analysis at various sites along the gastrointestinal tract of the elephant and rhinoceros

| Section of tract | Cell wall (mg/g) | | Cellulose (mg/g) | | Hemicellulose (mg/g) | | Lignin (mg/g) | |
|------------------|---------------------|-------|---------------------|-------|-------------------------|-------|------------------|-------|
| | Elephant | Rhino | Elephant | Rhino | Elephant | Rhino | Elephant | Rhino |
| Cranial stomach | 65.7 | 66.4 | 28.5 | 25.8 | 13.8 | 8.2 | 9.4 | 9.0 |
| Caudal stomach | 61.2 | 62.0 | 28.1 | 27.4 | 10.2 | 7.7 | 9.1 | 9.4 |
| Small intestine | 73.4 | 66.6 | 29.2 | 30.5 | 12.0 | 8.7 | 9.7 | 10.1 |
| Caecum | 64.8 | 78.3 | 28.8 | 36.1 | 12.4 | 11.2 | 11.7 | 13.2 |
| Colon (1) | 64.8 | 77.4 | 25.7 | 35.3 | 9.6 | 11.0 | 13.2 | 11.4 |
| Colon (2) | 69.9 | 78.4 | 29.5 | 33.8 | 12.7 | 10.7 | 10.4 | 13.6 |
| Colon (3) | 67.3 | 81.3 | 31.6 | 37.0 | 14.4 | 11.2 | 11.2 | 14.3 |
| Colon (4) | 57.0 | 76.2 | 23.6 | 32.4 | 8.1 | 9.8 | 9.3 | 13.7 |
| Colon (5) | 61.8 | 76.4 | 26.1 | 34.1 | 12.0 | 9.8 | 10.9 | 12.3 |

Discussion

Figure 2 depicts the three large East African herbivores in this study. Morphological differences are readily apparent in their body conformation and size. What is not apparent are the major differences in their food selection and methods of prehension. The Black rhinoceros is a strict browser rarely, if ever, consuming grasses (Mukinga, 1977). The leaves of herbs, shrubs, and small trees comprise more than 95% of its diet. Each leaf is individually selected with the prehensile, narrow lips (Ritchie, 1963). The absence of incisors (and canines) make grazing difficult. The Black rhinoceros is a daytime, open-range browser. Surface water is not an important part of its diet; it visits drinking holes as infrequently as every other day (Ritchie, 1963; Mukinga, 1977).

The African elephant, although preferring grasses, is a mixed feeder consuming grasses as well as the stems, bark and leaves of trees and shrubs (Anderson & Walker, 1974). The prehensile trunk (and club-like movements of the foot) limits the selective nature of grazing such that only tall grasses can be obtained (Buss, 1961). Whole branches rather than just the leaves are taken with the browse (Field, 1976). Water is an important part of its diet. Elephants frequent the drinking holes during most of the night and mid-day (Benedict, 1936; Douglas-Hamilton, 1973), peak feeding periods being the early morning and late afternoon (Guy, 1976).

The hippopotamus is a strict grazer, selecting only the short grasses. Its blunt teeth, flat snout and wide, straight lips enables it to graze close to the soil surface (Laws, 1968; Scotcher, Stewart & Breen, 1978). This unselective feeding behaviour results in the consumption of considerable amounts of soil with the short grasses. Browse is not a significant part of its diet (Scotcher, Stewart & Breen, 1978). Unlike the rhinoceros and elephant, the hippopotamus is a nocturnal feeder, intensely grazing the area within a few hundred metres of its aquatic environment (Lock, 1972; Mackie, 1976). Surface water is a vital part of the hippopotamus' habitat.

The gastrointestinal tracts of the hippopotamus, rhinoceros and elephant are markedly

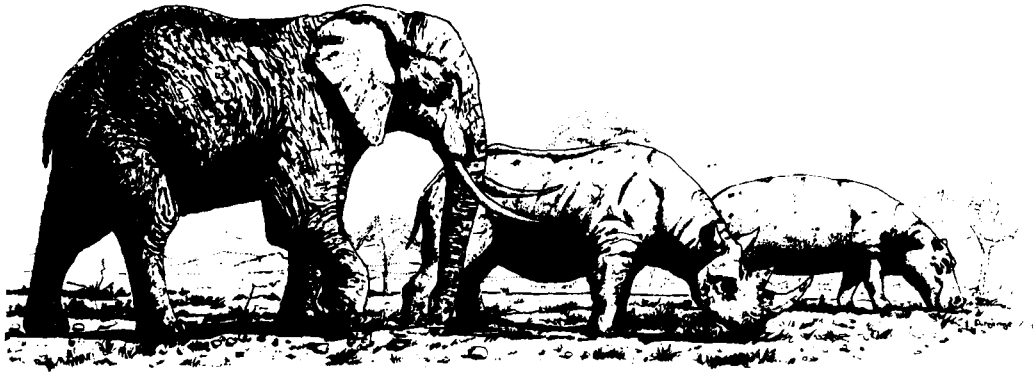


FIG. 2. Comparative morphology of the elephant, rhinoceros and hippopotamus.

different (Fig. 1). Structurally the stomach of the hippopotamus is most complex. Previous investigators describe this segment of tract as being comprised of two blindsacs close to the gastroesophageal junction, a vestibulum, connecting chamber and a glandular region of the stomach (Van Hoven, 1978). In the present study, the visceral blindsac could be clearly defined giving the appearance of a true caecum with a generally small orifice. The parietal blind sac described by Van Hoven (1978) was not clearly defined, appearing more as an ill-defined diverticulum having a single large, continuous opening into the vestibulum. The small intestine (39.1 m long) and the large intestine (8.2 m long) were smooth cylindrical organs. The demarcation between the small and large bowel could be accurately identified only by palpating a muscular mass (physiological or anatomical sphincter) at this junction. No caecum is present at the junction and the external diameter of the large bowel was not appreciably greater than that of the small intestine.

The stomach of the rhinoceros is considerably less complex than that of the hippopotamus. It is generally non-compartmentalized with the cranial one-half to two-thirds comprised of stratified squamous tissue and the caudal portion glandular epithelium (Cave & Aumonier, 1963). The apparent pyloric stomach (between the large stomach and small intestine) had not been described by other investigators. The contents of the pyloric stomach were examined separately but were similar in composition to those of the caudal, glandular contents and were thus included with the data on the caudal stomach area. The large intestine of the rhinoceros is considerably more complex than that of the hippopotamus and structurally resembles that of other *Perissodactyla* (i.e. the horse and donkey) (Stevens, 1977). The caecum of the rhinoceros is large, voluminous and sacculated. The colon is sacculated, compartmentalized and shows areas of small and large volumes of ingesta. Taenia and haustra were evident throughout the large bowel, except for the most distal regions of the bowel.

The gastrointestinal tract of the elephant has not been described before. The elephant's stomach is balloon shaped. Like the rhinoceros, the cranial region is comprised of non-glandular epithelium and the caudal region glandular epithelium. The elephant's caecum is less voluminous than that of the rhinoceros, relative to the other segments of tract. The elephant's colon appears non-compartmentalized with the bulk of the ingesta within the proximal two-thirds of the large bowel. The distal third of the large intestine lacks taenia and haustra, and is relatively non-voluminous.

From the data obtained in the present investigation, it appears that the rhinoceros, with

its prehensile advantage, selects a diet rich in protein. Fibrous material is, however, a major component of all three species. The lower crude fibre value observed in the stomach of the hippopotamus is probably due to the high proportion of minerals (ash) within these segments of tract. This is, most likely, the end-result of the hippopotamus' inability to be more selective in grazing, and the increased incidence of geophagia (Laws, 1968; Scotcher, Stewart & Breen, 1978). The mineral content of the elephant's diet, although not as great as that of the hippopotamus, is considerably more than that of the rhinoceros. This is again due to the inability of the elephant to select leaves from the stem and bark, as the rhinoceros is able to do.

Fibrous components, and the more readily fermentable materials (NFE), constitute 60 to 75% of the ingesta. It is well accepted that herbivorous species such as the elephant, hippopotamus and rhinoceros rely upon the enteric microbes to degrade this material. Traditional methods for determining the site and extent of bacterial action within the gut involve measurements of the organic acids produced (i.e. VFA's and lactic acid) (Elsden *et al.*, 1946). Lactic acid concentrations within the digestive tract have been used as an indication of rapid fermentation rates, when associated with a fall in intestinal pH. *Lactobacillus* microorganisms are known to proliferate in the slightly acid environment producing lactic acid as an end-product of metabolism (Hungate, 1968). However, lactic acid may also enter the gut via tissue metabolism and thus, cannot be construed as an accurate measure of *Lactobacillus* activity. VFA's on the other hand originate only from the bacterial actions on the ingesta. VFA concentrations are frequently used as an index of bacterial fermentative processes (Elsden *et al.*, 1946; Hungate, 1968; Stevens, Argenzio & Clemens, 1980).

Volatile fatty acid concentrations within the gastrointestinal tracts indicate that the stomach of the hippopotamus, caecum of the rhinoceros, and caecum and colon of the elephant are the principal sites of fermentation. The VFA concentrations observed at these sites are comparable to those concentrations observed in the reticulorumen of domestic cattle, animals to which we attribute the advantage of intensive fibre digesting abilities. The concentrations of VFA within the rhinoceros colon (53 to 80 mmoles/l) suggest that fermentation may be occurring within the large intestine of these animals, although not to the extent observed in the colon of the elephant.

Components of VFA (i.e. acetate, propionate and to a lesser extent butyrate) give some indications as to the rate of fermentation at each site (Church, 1969). An increased proportion of propionate (and lactic acid) are suggestive of an increased rate of fermentation. The elevated levels of VFA and the low acetate to propionate ratio within the caecum of the elephant imply a more rapid fermentation of ingesta at this site, relative to the remaining segments of the large bowel. Compared to the elephant, similar sites within the rhinoceros tract suggest that caecal fermentation activities are at a somewhat slower rate (higher acetate to propionate ratio), and that the rate and extent of colonic fermentation within the rhinoceros is less than that of the elephant.

For the rhinoceros, however, the stomach appears to be a more important site of bacterial activity than that of the elephant stomach. This is evident by the higher VFA concentrations. The data further suggest that although the extent of fermentation is low relative to the large bowel, fermentation is occurring at a faster rate (as indicated by the low acetate to propionate ratio, and the elevated lactic acid concentration). The organic acid and electrolyte concentrations observed within the tract of the rhinoceros are not unlike values obtained for the pony and donkey (Argenzio & Stevens, 1975; Maloiy & Clemens, 1980).

The forestomach of the hippopotamus is obviously the major site of bacterial activity in this animal (Thurston, Noirot-Timothee & Arman, 1968; Arman & Field, 1973; Van Hoven, 1978). Protozoa may also play a significant role in the fermentation process (Thurston, Noirot-Timothee & Arman, 1968; Thurston & Grain, 1971; Arman & Field, 1973; Van Hoven, 1974). The acetate to propionate ratio and low lactic acid concentrations indicate a moderate rate of fermentation. Similar organic acid ratios were observed by Van Hoven (1978). The rapid decline in VFA concentrations within the distal stomach imply an effective absorption of these acids.

The low pH of the rhinoceros and elephant stomach contents and that within the glandular portion of the hippopotamus stomach are generally considered prohibitive for extensive bacterial activities. The pH, sodium, potassium and osmolality differences between the cranial and caudal contents of the rhinoceros stomach suggest less mixing of ingesta and possibly greater compartmentalization of the stomach than is structurally apparent. Such differences are not readily apparent for the elephants' stomach.

An unusual feature of the elephant's gastrointestinal tract is the observed lower pH of contents within the small intestine. Most mammals are capable of neutralizing the chyme within the proximal regions of the small intestine (Clemens, 1978; Maloiy & Clemens, 1980), as are the hippopotamus and rhinoceros. The process is thought necessary for effective activation of pancreatic and intestinal digestive enzymes (Davenport, 1977). How the elephant accomplishes this at the lower pH is a question of interest. The low sodium ion concentration observed within the elephant's proximal small intestine is also suggestive of a reduction in pancreatic and biliary secretions. The concentrations of sodium ions within the elephant's small intestine were less than that observed in the rhinoceros, and within the small intestine of other ruminant and non-ruminant herbivores (Maloiy & Clemens, 1980).

Summary

The prehensile feeding of the rhinoceros enables this animal to selectively obtain a diet which is higher in protein and lower in minerals than the elephant or hippopotamus. Structurally and physiologically the digestive tracts of these three ungulates are different. Each of the herbivorous animals rely on the enteric microbes for fermentative activities and degradation of fibrous materials. The hippopotamus ferments the ingesta predominately within the complex forestomach, while the caecum and colon are major fermentation sites for the elephant and rhinoceros. The elephant appears capable of a more rapid rate of caecal fermentation and continued colonic fermentation than is the rhinoceros. The rhinoceros, on the other hand, demonstrates considerably more bacterial activities within its stomach than do elephants. An apparent inability of the elephant to buffer small intestinal contents and the lower pH of this chyme leaves questions as to the elephant's effectiveness in pancreatic and biliary secretions.

Structural characteristics and physiological properties of the rhinoceros gastrointestinal tract are not unlike that of the pony and donkey (Argenzio & Stevens, 1975; Maloiy & Clemens, 1980). Digestive processes of the hippopotamus have been likened to that of the ruminant (Arman & Field, 1973). However, while both ferment ingesta anterior to the glandular stomach, few other similarities can be readily drawn. With the exception of the elephant's small intestine, the organic acid and electrolyte composition of this animal is not unlike that of herbivorous, sub-human primates, and perhaps swine (Clemens, Stevens & Southworth, 1975; Clemens & Maloiy, 1981).

We are most grateful to Mr D. Sindiyo, Director, Department of Wildlife Conservation and Management, for Permits and assistance in obtaining research specimens, and Dr J. Sutton, National Institute for Research in Dairying, Reading, England, for VFA analysis. Professors J. Robertson, and P. Van Soest, Cornell University, and Mr S. Nganga of the Nutrition Laboratory, University of Nairobi carried out the proximate analysis for which we are most grateful. The competent technical assistance in the field and in the laboratory from Dr R. Njau, Mr J. Nturibi and J. Gatihi and our Medical Illustrator Ms Ginger Mills is greatly appreciated.

This study was supported by research grants from the University of Nairobi Dean's Committee Research Funds, and from the Leverhulme Trust, London, England.

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