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Gastrointestinal Osmolality Electrolyte and Organic Acid Composition in Five Species of East African Herbivorous Mammals

G. M. O. Maloiy and E. T. Clemens

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GASTROINTESTINAL OSMOLALITY ELECTROLYTE AND ORGANIC ACID COMPOSITION IN FIVE SPECIES OF EAST AFRICAN HERBIVOROUS MAMMALS[1]

G.M.O. Maloiy and E. T. Clemens
University of Nairobi[2], Nairobi, Kenya, East Africa

Summary

Inherent differences observed in ionic composition of gastrointestinal contents due to diet, feeding regimen and (or) site along the length of the digestive tract were controlled so that a clearer understanding of species differences could be obtained. Three species of ruminants (i.e., Zebu cattle, sheep and goat), a pseudo-ruminant (camel) and a nonruminant (donkey) were compared. Specific differences were observed in organic acid concentration, pH and electrolyte composition at various sites along the length of the tract. In general, Zebu cattle exhibited major differences in colonic volatile fatty acid, sodium and chloride concentrations when compared to other species. Donkeys, camels, sheep and goats were generally similar in their gastrointestinal ionic composition.
(Key Words: Organic Acids, Gut Electrolytes, Osmolality, Zebu Cattle, Camels, East African Herbivores.)

Introduction

Ionic composition of gastrointestinal contents varies with diet and time after feeding as well as site along the length of the tract (Boyne *et al.*, 1956; Kay and Pfeffer, 1970; Argenzio and Stevens, 1975). Obvious differences are also evident between species (Alexander, 1962, 1965). However, it is difficult to interpret which effects are due to species differences and which are due to differences in the species' dietary habits. The present study examined gastrointestinal electrolyte composition in five species of East African herbivores fed identical diets *ad libitum* and measured at similar sites along the length of the gastrointestinal tract. Since effects of diet, feeding regimen and site along the length of the tract were consistent, species differences could be more clearly investigated.

Experimental Procedures

Three animals of the following species were used: *Camelus dromedarius;* Zebu cattle, *Bos indicus;* sheep, *Ovis aires;* goats, *Capra hirars,* and donkey, *Equus asinus.* Each animal was fed lucerne hay[3] *ad libitum* for a period of 4 weeks before beginning the experiment. Drinking water was available at all times. A blood sample was taken from the jugular vein prior to sacrifice.

Each animal was rendered unconscious with a stunning gun. The abdominal cavity was then immediately opened; ligatures placed at the esophagus and rectum, and the gastrointestinal tract removed. Additional ligatures were used to separate the tract of each animal into specific segments. These consisted of the rumino-recticular area, the omasum (absent in the camel), abomasum, three equal segements of the small intestine, cecum, proximal colon, spiral colon and three segments of terminal colon (for the ruminant and pseudo-ruminant animals). The gastrointestinal tract of the donkey was separated by ligatures into the cranial and caudal halves of the stomach, three equal segments of small intestine, the cecum, right ventral colon, left ventral colon, left dorsal colon, right dorsal colon and small colon areas of the large bowel. The pH of the contents of each segment of tract was determined immediately and anaerobically by insertion of

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[2] Dept. of Vet. Physiol.

[3] Composition (as percentage of dry matter): crude fiber 26.9%; crude protein, 18.2%; ether extract, 5.3%; nitrogen-free extract, 35.6%; ash, 11.6%; calcium, 1.2%; phosphorus, .3%; magnesium, .2%; sodium, .2%; potassium, 4.1%; moisture, 8.3%.

an electrode into the axial midpoint of the tract. Total contents were removed from each segment and refrigerated immediately. The percentage of total gastrointestinal contents in each segment of tract was determined and expressed as the relative capacity of each segment. A known volume of distilled water was added to excessively dry samples and these were mixed into a slurry.

Digesta samples from each segment of tract were dried to a constant weight in a forced-air oven at 105 C for dry matter determination. Fluid volume was determined as: 1 − the fraction of dry matter × the weight of ingesta, assuming 1 g = 1 milliliter. The remaining contents were centrifuged and the supernatant collected for analysis. Volatile fatty acids (VFA) were determined on duplicate samples by steam distillation on the day of the experiment (Markham, 1942). Lactic acid was determined by the methods of Barker and Summerson (1941). Sodium and potassium concentrations were determined by flame photometry, osmolality of the fluid contents of the gastrointestinal tract by freezing-point depression and chloride with a laboratory chloridometer. Data were subjected to analysis of variance and Duncan's multiple range test was used to determine significant differences (Snedecor and Cochran, 1967).

Results

Dry matter, fluid volume and osmolality of gastrointestinal contents for each animal are shown in table 1. Dry matter consistency of ingesta was remarkably similar for all species from the stomach to the mid-colonic regions. Differences ($P<.05$) were detected only between those areas of large bowel posterior to the spiral colon of ruminants and pseudo-ruminants and in the analogous regions of the donkey's colon (i.e., dorsal and small colonic areas). All ruminants and the pseudo-ruminant (camel) had significantly drier gut contents than the donkey in the third and fourth segments of the colon. However, only the goat produced significantly drier fecal material than the donkey.

Variation in fluid volume within each segment of the tract represented differences in the size of the animals and the anatomical features of their respective gastrointestinal tracts as well as physiological differences related to absorption and secretion. Therefore, statistical analysis was not applied to these data. Data are presented for the reader's benefit and can be used for calculating quantitative values for the parameters measured.

Differences ($P<.05$) in osmolality were observed at selected sites along the intestinal tract. Osmolality of contents within the donkey's proximal small intestine was significantly lower than that for all other species, except sheep. Conversely, osmolality of the cecum and most colonic segments of Zebu cattle was significantly lower than that observed in the analogous compartments of the donkey and goat.

Concentrations of sodium, potassium and chloride observed at each site along the length of the gastrointestinal tract are presented in table 2. Differences ($P<.05$) were observed at selective points along the tract. Generally, Zebu cattle had the highest colonic concentrations of sodium and chloride while the donkey had the highest potassium concentrations.

The pH within the glandular stomach (abomasum) was highest in the camel, while the pH of colon contents was highest in sheep and goats (table 3). VFA concentrations were significantly higher at many points within the stomach and large bowel of Zebu cattle than at corresponding points in the other species investigated. Lactic acid values did not differ ($P>.05$) between species at analagous points in the gastrointestinal tract. Mean osmolality and electrolyte composition of plasma and urine for each species of East African herbivore are presented in table 4.

Discussion

The relative importance of digestion in difference compartments of the gastrointestinal tract has often been estimated by the slaughter technique (Gray, 1947; Boyne *et al.*, 1956). Various components of digesta, such as electrolytes, are observed to fluctuate from one site to another, and they represent the combined effects of absorption, secretion, diet and feeding frequency (Alexander, 1962, 1965; Kay and Pfeffer, 1970; Argenzio and Stevens, 1975). By standardizing diet and feeding patterns, one could make reasonable species comparisions pertaining to the animals' contribution to electrolyte exchange.

Although the gastrointestinal tract of ruminant, pseudo-ruminant and nonruminant animals are grossly different anatomically,

TABLE 1. MEAN (± SEM) DRY MATTER, FLUID VOLUME AND OSMOLALITY OF GASTROINTESTINAL CONTENTS MEASURED ALONG THE TRACTS OF FIVE SPECIES OF EAST AFRICAN HERBIVORES[a]

Section of tract of ruminant animal	Dry matter, %					Fluid volume, liters					Osmolality, mOsmol/kg					Section of tract of the donkey
	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	
Rumen, reticulum	13.9 (1.8)[a]	14.5 (1.9)	14.9 (.6)	13.6 (1.5)	14.0 (2.4)	38.52 (7.00)	15.92 (.52)	2.88 (.52)	2.81 (.56)	1.48 (.28)	317 (36)	349 (15)	341 (21)	371 (30)	496 (81)	Cranial stomach
Omasum		25.3 (3.2)	22.8 (2.6)	20.3 (2.3)			2.26 (.48)	.16 (.02)	.13 (.05)			307 (9)	317 (40)	334 (16)		
Abomasum	12.0 (3.6)	15.6 1.5)	11.4 (2.0)	9.6 (.4)	14.2 (2.3)	3.40 (1.30)	.43 (.07)	.11 (.04)	.17 (.04)	1.32 (.21)	269 (41)	253 (10)	260 (27)	305 (19)	373 (22)	Caudal stomach
Small intestine (1)	9.0 (1.6)	10.1 (.6)	8.7 (.8)	9.2 (1.0)	6.9 (1.4)	.91 (.10)	.33 (.08)	.06 (.01)	.05 (.01)	.31 (.06)	585^{a} (3)	564^{a} (22)	465^{ab} (48)	493^{a} (17)	425^{b} (15)	Small intestine (1)
Small intestine (2)	10.3 (.6)	11.9 (1.0)	10.4 (.6)	10.2 (.5)	6.3 (.2)	1.29 (.22)	.25 (.03)	.09 (.01)	.07 (.03)	.69 (.03)	503 (24)	518 (39)	473 (22)	497 (18)	419 (37)	Small intestine (2)
Small intestine (3)	10.4 (1.3)	10.6 (1.2)	10.4 (.5)	9.9 (.2)	6.5 (.4)	1.73 (.32)	.49 (.11)	.18 (.03)	.19 (.03)	.68 (.06)	350 (21)	356 (33)	419 (27)	439 (26)	385 (8)	Small intestine (3)
Cecum	13.0 (1.5)	15.6 (1.5)	15.9 (1.2)	15.7 (.8)	6.0 (.4)	.67 (.19)	.36 (.05)	.13 (.02)	.12 (.01)	2.87 (.29)	294^{ab} (37)	291^{b} (5)	305^{ab} (63)	369^{a} (16)	324^{ab} (22)	Cecum
Proximal colon	14.3 (1.1)	15.6 (1.6)	17.1 (.9)	18.4 (.4)	8.4 (1.4)	3.22 (.58)	.67 (.14)	.18 (.18)	.12 (.01)	3.27 (1.32)	253^{b} (30)	277^{b} (7)	270^{ab} (47)	319^{a} (10)	306^{a} (2)	Right ventral colon
Spiral colon	17.1 (1.9)	18.3 (2.6)	20.4 (1.4)	22.6 (.4)	11.5 (1.7)	2.40 (.65)	.48 (.06)	.08 (.01)	.05 (.01)	4.14 (2.44)	267 (25)	268 (13)	241 (32)	301 (37)	213 (20)	Left ventral colon
Colon (3)	25.5^{ab} (2.6)	19.4^{b} (3.2)	25.5^{ab} (3.4)	32.9^{a} (2.2)	9.0^{c} (.8)	.42 (.02)	.23 (.04)	.04 (.01)	.03 (.01)	1.33 (.14)	283^{ab} (35)	248^{b} (13)	248^{ab} (42)	316^{a} (37)	307^{a} (3)	Left dorsal colon
Colon (4)	28.2^{ab} (5.6)	21.9^{b} (4.8)	30.2^{ab} (2.5)	38.7^{a} (11.4)	12.2^{c} (1.8)	.43 (.12)	.20 (.05)	.04 (.01)	.03 (.01)	4.04 (.80)	278 (25)	260 (12)	271 (38)	348 (20)	317 (28)	Right dorsal colon
Colon (5)	35.9^{ab} (6.9)	23.8^{ab} (6.0)	37.8^{ab} (5.5)	42.2^{a} (9.8)	16.8^{b} (2.4)	.40 (.03)	.10 (.04)	.02 (.01)	.06 (.01)	1.08 (.22)	245^{b} (23)	277^{b} (9)	278^{ab} (49)	373^{a} (18)	292^{b} (7)	Small colon

[a]Values with different superscripts are different ($P<.05$).

TABLE 2. MEAN (± SEM) CONCENTRATIONS OF SODIUM, POTASSIUM AND CHLORIDE IONS MEASURED ALONG THE GASTROINTESTINAL TRACT OF FIVE SPECIES OF EAST AFRICAN HERBIVORES[a]

Section of tract of ruminant animals	Sodium, mEq/liter					Potassium, mEq/liter					Chloride, mEq/liter					Section of tract of the donkey
	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	
Rumen, reticulum	89.0^{ab} (6.8)	103.7^{a} (9.4)	74.8^{ab} (13.1)	53.7^{b} (11.5)	72.0^{ab} (8.7)	37.3^{b} (15.5)	43.7^{b} (14.2)	69.4^{ab} (16.2)	47.6^{ab} (26.5)	153.0^{a} (30.5)	12.0^{b} (2.1)	16.3^{b} (3.7)	13.8^{b} (2.0)	15.7^{b} (1.8)	81.6^{a} (7.7)	Cranial stomach
Omasum		86.7 (18.0)	60.6 (10.5)	49.7 (15.7)			56.7 (21.1)	77.6 (19.3)	95.0 (32.2)			38.7 (8.4)	39.2 (5.7)	33.7 (6.2)		
Abomasum	62.0 (11.4)	55.3 (9.8)	43.6 (7.2)	35.0 (9.5)	38.7 (5.7)	34.3 (10.4)	31.3 (10.8)	41.4 (8.0)	39.3 (14.4)	86.3 (23.4)	56.3^{b} (16.4)	100.7^{b} (•8.4)	109.4^{ab} (7.8)	113.7^{ab} (14.0)	125.7^{a} (2.3)	Caudal stomach
Small intestine (1)	101.3 (15.7)	76.0 (5.0)	77.8 (11.5)	68.3 (6.0)	83.3 (13.8)	32.7 (12.7)	46.0 (9.2)	35.0 (3.2)	32.3 (11.4)	57.3 (1.39)	71.7 (14.4)	73.0 (11.0)	90.4 (10.6)	92.3 (4.2)	84.7 (4.2)	Small intestine (1)
Small intestine (2)	116.0 (16.0)	65.7 (12.2)	106.6 (16.7)	86.3 (5.4)	114.0 (26.0)	17.3^{b} (4.4)	35.7^{a} (0.8)	31.2^{ab} (4.4)	22.7^{ab} (5.4)	54.0^{a} (12.0)	46.3 (11.8)	50.7 (2.3)	53.4 (4.5)	55.7 (9.4)	43.3 (9.3)	Small intestine (2)
Small *intestine* (3)	108.0 (25.0)	64.0 (10.0)	109.4 (15.4)	75.3 (16.8)	99.0 (8.2)	9.0^{b} (1.7)	34.7^{a} (2.7)	25.2^{ab} (4.7)	16.7^{b} (3.5)	57.3^{a} (12.9)	24.7 (6.8)	46.0 (4.9)	43.0 (2.2)	34.3 (2.4)	32.7 (9.2)	Small intestine (3)
Cecum	117.7 (37.2)	80.0 (8.1)	73.8 (8.2)	66.0 (5.1)	89.3 (8.7)	16.0^{b} (3.0)	31.3^{ab} (7.1)	30.8^{ab} (8.9)	23.3^{ab} (8.5)	55.3^{a} (10.5)	22.0 (6.6)	26.7 (1.8)	34.2 (5.5)	22.3 (4.4)	19.7 (3.4)	Cecum
Proximal	85.7^{a} (8.4)	76.7^{ab} (9.9)	66.6^{ab} (8.2)	55.3^{b} (3.8)	86.0^{a} (8.4)	17.3^{b} (2.8)	28.7^{ab} (6.8)	29.6^{ab} (8.0)	23.2^{ab} (9.8)	57.7^{a} (10.2)	20.0 (6.1)	30.0 (6.4)	29.0 (3.2)	19.0 (2.1)	19.3 (4.0)	Right ventral colon
Spiral colon	70.3^{ab} (6.4)	81.7^{a} (8.3)	69.0^{ab} (16.4)	45.3^{b} (7.4)	71.3^{ab} (7.5)	26.0^{b} (7.8)	28.0^{b} (5.7)	31.2^{ab} (8.3)	24.3^{b} (10.4)	70.0^{a} (9.2)	18.3^{ab} (5.8)	30.6^{a} (.3)	27.8^{a} (2.2)	16.3^{b} (1.7)	17.0^{b} (1.0)	Left ventral *colon*
Colon (3)	54.0^{ab} (17.0)	76.3^{a} (3.8)	43.4^{ab} (10.6)	24.7^{b} (3.8)	57.7^{a} (6.9)	43.3^{ab} (12.5)	26.3^{b} (3.3)	24.6^{b} (4.4)	22.3^{b} (9.4)	83.3^{a} (12.8)	20.0^{b} (5.8)	37.3^{a} (2.0)	23.8^{ab} (3.2)	10.0^{b} (2.1)	18.0^{b} (2.0)	Left dorsal colon
Colon (4)	48.3^{abc} (12.2)	68.3^{a} (1.2)	43.0^{abc} (9.7)	16.7^{c} (6.1)	37.0^{bc} (5.5)	41.3^{b} (12.8)	29.0^{b} (3.6)	28.6^{b} (6.6)	21.0^{b} (8.5)	109.7^{a} (15.6)	19.0^{b} (5.7)	53.0^{a} (14.0)	20.2^{b} (3.2)	6.0^{c} (1.5)	14.7^{b} (3.30	Right dorsal colon
Colon (5)	43.0^{abc} (14.0)	71.0^{a} (6.6)	40.8^{abc} (9.3)	12.0^{c} (6.1)	21.7^{bc} (1.6)	42.7^{b} (13.0)	31.0^{b} (2.6)	29.2^{b} (8.8)	17.3^{b} (7.0)	110.3^{a} (15.6)	15.3^{b} (3.7)	40.3^{a} (4.7)	19.6^{b} (1.4)	4.0^{c} (1.2)	14.3^{b} (1.4)	Small colon

[a]Values with different superscripts are different ($P<.05$).

TABLE 3. MEAN (± SEM) GASTROINTESTINAL pH, VOLATILE FATTY ACID AND LACTIC ACID CONCENTRATIONS MEASURED ALONG THE TRACT OF FIVE SPECIES OF EAST AFRICAN HERBIVORES[a]

Section of tract of ruminant animals	pH					Volatile Fatty Acids, mmoles/liter					Lactic Acid, mmoles/liter					Section of tract of the donkey
	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	Camel	Cattle	Sheep	Goat	Donkey	
Rumen, reticulum	6.67 (.08)	6.66 (.28)	6.62 (.20)	6.87 (.40)	5.69 (.09)	74.2^{b} (4.6)	173.3^{a} (22.8)	115.8^{ab} (19.3)	131.7^{a} (17.9)	106.9^{ab} (40.1)	2.06 (1.08)	3.37 (1.36)	2.72 (1.26)	.69 (.30)	10.18 (1.76)	Cranial stomach
Omasum		6.88 (.57)	6.89 (.38)	7.27 (.31)			78.2 (36.3)	85.8 (18.6)	101.9 (8.2)			3.02 (1.48)	.80 (.30)	.74 (.11)		
Abomasum	5.55^{a} (.63)	3.42^{b} (.07)	3.86^{ab} (.30)	3.97^{ab} (.44)	3.85^{ab} (.76)	35.7 (15.0)	28.2 (6.4)	18.4 (2.3)	32.7 (6.4)	44.9 (15.9)	.43 (.34)	1.95 (.53)	.61 (.21)	.68 (.18)	5.55 (2.73)	Caudal stomach
Small intestine (1)	6.39 (.16)	6.22 (.13)	5.98 (.27)	5.87 (.14)	6.42 (.20)	35.0 (15.4)	76.1 (11.4)	24.5 (7.5)	30.0 (12.1)	41.1 (13.0)	4.28 (1.70)	7.94 (3.58)	3.78 (1.09)	3.37 (1.42)	3.27 (1.47)	Small intestine (1)
Small intestine (2)	7.73 (.21)	6.90 (.03)	7.08 (.23)	7.27 (.40)	7.18 (.09)	31.5 (10.3)	94.9 (8.1)	45.2 (13.2)	32.0 (11.1)	51.1 (18.6)	4.33 (2.02)	7.82 (1.29)	7.07 (.134)	5.95 (2.70)	3.01 (.83)	Small intestine (2)
Small intestine (3)	7.73 (.02)	7.30 (.10)	7.53 (.11)	8.00 (.25)	7.40 (.12)	38.1 (25.4)	126.1 (21.8)	50.2 (8.7)	32.0 (4.6)	56.4 (18.8)	1.80 (.47)	3.47 (1.52)	4.28 (1.73)	2.61 (1.00)	1.14 (.40)	Small intestine (3)
Cecum	7.15^{a} (.08)	7.06^{a} (.07)	7.17^{a} (.07)	7.35^{a} (.15)	6.32^{b} (.11)	55.3 (26.1)	146.0 (26.8)	62.9 (11.9)	96.7 (20.3)	109.0 (25.0)	1.08 (.26)	2.72 (1.45)	4.09 (.90)	2.53 (1.01)	1.68 (.32)	Cecum
Proximal colon	7.05^{a} (.09)	7.03^{a} (.9)	7.22^{a} (.09)	7.53^{a} (.26)	6.37^{b} (.14)	43.0^{b} (15.4)	117.7^{a} (16.0)	66.0^{ab} (12.6)	88.8^{ab} (10.7)	77.9^{ab} (6.8)	1.25 (.59)	1.18 (.58)	2.76 (.85)	2.80 (.70)	1.87 (.85)	Right ventral colon
Spiral colon	7.08^{ab} (.04)	6.95^{ab} (.03)	7.47^{ab} (.18)	7.57^{a} (.13)	6.75^{b} (.22)	51.5 (19.0)	119.8 (23.9)	61.1 (8.2)	95.9 (9.5)	71.4 (11.9)	1.74 (.93)	1.52 (1.58)	2.68 (.55)	2.51 (.42)	1.23 (.40)	Left ventral colon
Colon (3)	7.03^{b} (.18)	7.00^{b} (.25)	8.14^{a} (.16)	8.10^{a} (.10)	6.83^{b} (.14)	80.7^{ab} (33.4)	111.0^{a} (13.4)	73.3^{ab} (19.0)	90.6^{ab} (15.9)	64.3^{b} (5.3)	5.61 (2.79)	2.06 (1.37)	4.53 (1.52)	3.02 (.84)	1.10 (.37)	Left dorsal colon
Colon (4)	6.99^{b} (.05)	6.83^{b} (.18)	8.10^{a} (.13)	8.07^{a} (.09)	6.77^{b} (.21)	78.2 (33.4)	108.4 (8.4)	73.9 (13.9)	98.3 (17.9)	87.3 (7.8)	7.22 (4.09)	2.48 (1.65)	4.24 (1.30)	4.02 (1.56)	1.56 (.55)	Right dorsal colon
Colon (5)	6.97^{b} (.12)	6.88^{b} (.26)	8.10^{a} (.19)	7.40^{a} (.06)	6.67^{b} (.26)	83.3^{ab} (34.9)	114.8^{a} (16.7)	60.4^{b} (7.2)	74.9^{b} (5.8)	70.4^{b} (1.8)	3.26 (1.32)	3.11 (2.38)	3.18 (1.51)	3.38 (.84)	4.37 (3.06)	Small colon

[a]Values with different superscripts are different ($P<.05$).

TABLE 4. MEAN VALUES OBSERVED FOR PLASMA AND URINE OSMOLALITY AND ELECTROLYTES IN FIVE SPECIES OF EAST AFRICAN HERBIVORES

Item		Species				
		Camel	Cattle	Sheep	Goat	Donkey
Osmolality,	Plasma	342	298	327	331	286
mOsmol/kg	Urine	1,571	958	1,066	1,346	1,311
Sodium,	Plasma	163	100	183	148	104
mEq/liter	Urine	13	22	16	28	7
Potassium,	Plasma	31	3	4	5	5
mEq/liter	Urine	464	336	744	457	486
Chloride,	Plasma	106	102	98	133	97
mEq/liter	Urine	28	27	28	68	83

physiological differences were not readily apparent. In the five species of East African herbivores, dry matter consistency of foregut contents, addition of fluids to the proximal small intestinal contents and progressive drying of ingesta from cecum to rectum were similar. Sodium concentrations increased in the small intestinal areas and diminished from cecum to rectal regions, while potassium concentrations showed an inverse relationship to sodium. In all species, chloride concentrations were highest in the glandular portion of the stomach and decreased as the ingesta moved toward the rectum. Other digestive parameters (gastrointestinal pH, osmolality, VFA and lactic acid patterns) were generally similar for the five species of herbivores.

Significant differences in some digestive measurements were observed at selective sites along the tract. Certain of these features are of particular interest. Animals that form fecal pellets (i.e., the camel, sheep and goat) produced drier fecal material than did Zebu cattle and the donkey. However, the efficiency of water conservation (i.e., the extraction ratio per gram of ingesta) for the donkey was equivalent to that for the camel, sheep and goat, while Zebu cattle were least efficient (G.M.O. Maloiy and E. T. Clemens, *unpublished data).* In addition, deprivation of water intake had no effect on this relationship (Maloiy *et al.*, 1978). It should be noted, however, that Zebu cattle demonstrate some basic differences from cattle of European origin (Quarterman *et al.*, 1957; Maloiy *et al.*, 1978).

The data further demonstrate that organic acid concentration in the cranial half of the donkey's stomach was similar to that in the rumen. This finding is in contrast to the observations of Elsden *et al.* (1946), who stated that fermentation in the stomach of the horse primarily yields lactic acid and not VFA. In any event, the volume of ingesta in the equine stomach was small relative to ruminal-recticular fill (table 5), so total amounts of VFA and (or) lactic aicd were also small. Retention time within the equine foregut is short compared with ruminal retention time (Alexander, 1963), and that is an additional feature that may limit the digestive efficiency in the equine stomach. The lower pH and high lactic acid concentration observed in the donkey's stomach contents suggest the presence of a greater lactobacillus microbial population.

Camels had a higher abomasal pH and lower chloride ion concentration than the other herbivores. By analogy with the requirements for the regulation of electrolytes and buffering of chyme, fluids within the proximal small intestine of the camel differed from those of other species, primarily in potassium and sodium concentrations. For all species, however, composition of electrolytes within the proximal small intestine represents not only components of the diet, but also a large input of electrolytes from gastric, pancreatic and biliary secretions (Alexander and Hickson, 1970). Many electrolytes are reabsorbed within the more distal regions of the small bowel. The majority of the sodium ions are reabsorbed in the mid and distal small intestine (Kay and Pfeffer, 1970). The terminal ileum is also the site of bicarbonate secretion, presumably in exchange for chloride ions (Swallow and Code, 1967; Hubel, 1969). Thus, bicarbonates become available for buffering acids produced in the cecum and colon.

TABLE 5. RELATIVE CAPACITY OF VARIOUS GASTROINTESTINAL SEGMENTS OF FIVE SPECIES OF EAST AFRICAN HERBIVORES

Gut segment	Species				
	Camel	Cattle	Sheep	Goat	Donkey
	(%)				
Stomach[a]	78.5	84.9	78.1	80.6	13.6
Small intestine	6.9	5.0	8.4	7.2	7.2
Cecum and colon	14.6	10.1	13.5	12.2	79.2

[a]Stomach represents the rumen, reticulum, omasum and abomasum of Zebu cattle, sheep and goats; rumen, reticulum and abomasum of the camels, and the cranial and caudal halves of the donkey's stomach. Each value is the mean of three animals with the following mean body weights: camels, 228 kg; cattle, 249 kg; sheep, 27 kg; goats, 24 kg; donkey, 159 kilograms.

These effects are believed to be more prominent in herbivorous than in nonherbivorous species (Van Weerden, 1961).

In the horse and pony, microbial digestion occurs principally in the cecum and colon (Alexander, 1963; Argenzio *et al.*, 1975). We observed that in the donkey, fermentation activity in the stomach and in the large bowel were comparable, as evidenced by the levels of organic acid produced. The relative capacity of the donkey's cecum and colon (approximately 79%) and stomach (approximately 14%) certainly suggests that the hindgut is the major site of activity. Organic acids are also produced in the large intestines of the camel, goat, sheep and Zebu cattle, as seen in the present study and in the study conducted by Hungate *et al.* (1959). However, in sheep and cattle, less than 20% of the fiber digestion occurs postruminally (Gray, 1947; Hale *et al.*, 1947). It should also be emphasized that microbial fermentation and organic acid production are not confined to herbivorous mammals, but may be observed in the large intestine of most nonherbivorous species, as well (Clemens, 1978; Clemens and Stevens, 1979; Banta *et al.*, 1979).

Recent studies demonstrate that the forestomach of ruminants and large intestine of nonruminants (both herbivorous and nonherbivorous species) are functionally similar (Stevens *et al.*, 1979). Not only are organic acids produced in similar concentrations within the rumen and large bowel, but colonic transport of VFA from the colon of the horse and pony (Barcroft *et al.*, 1944; Argenzio *et al.*, 1974), pig (Argenzio and Southworth, 1975), dog (Stevens, 1978) and ruminant (Argenzio *et al.*, 1975; Clemens *et al.*, 1979) is similar to rumen transport (Stevens, 1973). Such transport mechanisms may involve complex sodium, potassium, bicarbonate and VFA exchange, with the subsequent removal of water from colonic contents (Kay and Pfeffer, 1970; Argenzio *et al.*, 1977).

Membranes within the gut are permeable to particles of solute, which allows restricted as well as active movement of electrolytes, establishing a difference in electrolyte concentration between gut lumen and plasma. Plasma, however, is maintained at isoneutrality (approximately 300 mOsmol for most mammals) by the combined actions of the kidney and gastrointestinal tract. It is obvious from these data that potassium, a component which herbivores ingest in large quantities, is removed from the system by both renal and colonic mechanisms. Sodium and chloride are generally recovered by kidney and colonic tissues being recycled into the gut via gastric, pancreatic and biliary secretions.

While feeding may produce a diurnal variation in electolyte concentrations of the foregut (Boyne *et al.*, 1956), it has no effect on colonic electrolyte concentrations (Williams, 1965; Clemens, 1978). Since the diets in this study were identical for all species and the electrolyte concentrations within the large bowel are not influenced by feeding behavior, the significant differences observed in the cecum and colon of the animals under investigation can be attributed wholly to physiological differences. The most striking difference was that between Zebu cattle and camels, sheep, goats and donkeys.

Literature Cited

Alexander, F. 1962. The concentration of certain electrolytes in the digestive tract of the horse and pig. Res. Vet. Sci. 3:78.

Alexander, F. 1963. Digestion in the horse. P. 259-000. *In* D. I. Cuthbertson (Ed.) Progress in Nutritional and Allied Sciences. Oliver and Boyd, Edinburgh.

Alexander, F. 1965. The concentration of electrolytes in the alimentary tract of the rabbit. guines pig, dog and cat. Res. Vet. Sci. 6:238.

Alexander, F. and J.C.D. Hickson. 1970. The salivary and pancreatic secretion of the horse. P. 375-000. *In* A. T. Phillipson (Ed.) Physiology of Digestion and Metabolism in the Ruminants. Oriel Press, Cambridge.

Argenzio, R. A., N. Miller and W. Von Engelhardt. 1975. Effect of volatile fatty acids on water and ion absorption from the goat colon. Amer. J. Physiol. 229:997.

Argenzio, R. A. and M. Southworth. 1975. Sites of organic acid production and absorption in the gastrointestinal tract of the pig. Amer. J. Physiol. 228:454.

Argenzio, R. A., M. Southworth, J. E. Lowe and C. E. Stevens. 1977. Interrelationship of Na, HCO_3 and volatile fatty acid trasnport by equine large intestine. Amer. J. Physiol. 233:E469.

Argenzio, R. A., M. Southworth and C. E. Stevens. 1974. Sites of organic acid production and absorption in the equine gastrointestinal tract. Amer. J. Physiol. 226:1043.

Argenzio, R. A. and C. E. Stevens. 1975. Cyclic changes in ionic composition of digesta in the equine intestinal tract. Amer. J. Physiol. 228:-1224.

Banta, C. A., E. T. Clemens, M. M. Krinsky and B. E. Sheffy. 1979. Sites of organic acid production and patterns of digesta movement in the gastrointestinal tract of dogs. J. Nutr. 109:1592.

Barcroft, J., R. A. McAnally and A. T. Phillipson. 1944. Absorption of volatile fatty acids from the alimentary tract of sheep and other animals. J. Exp. Biol. 20:120.

Barker, S. B. and W. H. Summerson. 1941. The colorimetric determination of lactic acid in biological material. J. Biol. Chem. 138:535.

Boyne, A. W., R. M. Campbell, J. Davidson and D. P. Cuthbertson. 1956. Changes in composition of the digesta along the alimentary tract of sheep. Brit. J. Nutr. 10:325.

Clemens, E. T. 1978. The digestive tract: Insectivore, prosimian and advance primate. *In* K. Schmidt-Nielson (Ed.) Comparative Physiology of Primative Mammals. Cambridge University Press, Cambridge.

Clemens, E. T., G.M.O. Maloiy and E. Skadhauge. 1979. The effects of dehydration on salt and water absorption along the large intestine of the small ruminant: The Dik-dik antelope. J. Comp. Physiol. 135:165.

Clemens, E. T. and C. E. Stevens. 1979. Sites of organic acid production and patterns of digesta movement in the gastrointestinal tract of the raccoon. J. Nutr. 109:1110.

Elsden, S. R., M.W.S. Hitchcock. R. A. Marshall and A. T. Phillipson. 1946. Volatile fatty acids in the digesta of ruminants and other animals. J. Exp. Biol. 22:191.

Gray, F. V. 1947. The digestion of cellulose by sheep. J. Exp. Biol. 24:15.

Hale, E. B., C. W. Duncan and C. F. Huffman. 1947. Rumen digestion studies. II. Studies in the chemistry of rumen digestion. J. Nutr. 34:747.

Hubel, H. A. 1969. Effect of luminal chloride concentration on bicarbonate secretion in rat ileum. Amer. J. Physiol. 217:40.

Hungate, R. E., G. D. Phillips. A. McGregor, D. P. Hungate and H. K. Buechner. 1959. Microbial fermentation in certain mammals. Science 130:1192.

Kay, R.N.B. and E. Pfeffer. 1970. Movement of water and electrolytes into and from the intestine of the sheep. P. 390-000. *In* A. T. Phillipson (Ed.) Physiology of Digestion and Metabolism in the Ruminants. Oriel Press, Cambridge.

Markham. R. A. 1942. Steam distillation apparatus suitable for micro-Kjeldahl analysis. Biochem. J. 36:790.

Maloiy, G.M.O., C. R. Taylor and E. T. Clemens. 1978. A comparison of gastrointestinal water content and osmolality in East African herbivores during hydration and dehydration. J. Agr. Sci. (Camb.) 91:249.

Quarterman, J., G. D. Phillips and G. H. Lampkin. 1957. A difference in the physiology of the large intestine between European and indigenous cattle in the tropics. Nature (London) 180:552.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods (6th Ed.). The Iowa State University Press, Ames.

Stevens, C. E. 1973. Transport across rumen epithelium P. 404-000. *In* H. H. Ussing (Ed.) Transport Mechanisms in Epithelia. Munksgaard, Copenhagen.

Stevens, C. E. 1978. Physiological implications of microbial digestion in the large intestine of mammals: Relative to dietary factors. Amer. J. Clin. Nutr. 31:S161.

Stevens, C. E., R. A. Argenzio and E. T. Clemens. 1979. Microbial digestion: Rumen versus large intestine. *In* Y. Ruckebusch (Ed.) Physiology of Digestion and Metabolism in Ruminants. Beaumont, France.

Swallow, J. H. and C. F. Code. 1967. Intestinal transmucosal fluxes of bicarbonate. Amer. J. Physiol. 212:717.

Van Weerden, E. J. 1961. The osmotic pressure and the concentration of some solutes of the intestinal contents and the feces of the cow, in relation to the absorption of the minerals. J. Agr. Sci. (Camb.) 56:317.

Williams, V. J. 1965. Microbial metabolism in the forestomach and large intestine of sheep. Australian J. Agr. Res. 16:77.