Cyclic Changes in the Osmolality and Electrolyte Composition in the Gastrointestinal Tract of the Rock Hyrax

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ABSTRACT The rock hyrax has been shown to have a very unusual and complex digestive tract. The gastrointestinal tract is comparable to that of the simple and complex stomach of mammals as well as to that of birds. Determinations of osmolality and electrolytes have been made in different sections of the gut of the hyrax. However, with the exception of the elevated potassium levels observed in the cranial stomach, the hyrax poses no unusual osmotic or electrolyte concentrations when compared to man or other mammals. The greater cation concentration and hypertonicity of the cranial stomach was largely accounted for by the elevated potassium load in this gut segment. Sodium and potassium comprised the major cations present throughout the gastrointestinal tract. Chloride was the major anion observed in the foregut; however, the electroneutrality of the mid and hindgut of the hyrax was primarily maintained by the presence of large concentrations of volatile fatty acids produced in these portions of the gut. Volatile fatty acids also accounted for the high anion concentration and hypertonicity of the cranial stomach. J. Nutr. *108*: 988–993, 1978.

INDEXING KEY WORDS rock hyrax · digestion · gastrointestinal tract · osmolality · gut electrolytes

Rock hyrax have been shown to have a very unusual and complex digestive tract (1, 2). Histologically, the foregut is similar to that of the horse, rat and mouse (1), while the midgut sacculation provides digestive functions not unlike those of the rumen (3). In addition, the duodenal loop and paired ceca are analogus to those observed in many birds (2). Although the hyrax is a strict herbivore (4) the diversity of plant material consumed is great (4–7). Preference is shown for the succulent leaves and shoots of young plants (8, 9). Such a diet has probably led to the various reports that the hyrax does not need to drink (9, 10). While a few observations indicate that the rock hyrax makes regular trips to drinking holes (8), Sale has shown that this animal may thrive in captivity for periods of 6 weeks to 6 months without drinking water (4, 9). The urine excreted by the hyrax is thick and concentrated (2, 10, 11). Maloiy and Sale (1976) reported maximum urine osmolality of 3,180 mOsm/kg H_2O in dehydrated hyraxes. Potassium was found to be the principal cation excreted by the hyrax. A reduction in urine volume and elevated urinary urea concentration accompanied dehydration in these animals (11). Thus, the rock hyrax must be equipped with an effective water conservation mechanism.

The present study addresses itself to the changes in the osmolality and electrolyte

composition along the gastrointestinal tract of the rock hyrax. It further describes these changes in relationship to the movement of the ingesta and time post-feeding.

METHODS AND MATERIALS

Twelve rock hyrax (*Procavia habessinca*) weighing an average of 1.98 ± 0.21 Kg (± SEM) were used in the study. They were fed lucerne leaves[2] and preconditioned to the diet for 3 weeks before beginning the experiment. Animals were individually caged and fed twice daily at 12 hour intervals. They were trained to consume the diet every 12 hours during a 1-hour feeding period. During the experimental period, the animals were given free access to drinking water.

Hyraxes were killed in groups of three at 2, 4, 8, and 12 hours after feeding. Each animal was anesthetized with chloroform and death was by exsanguination. Since the animals were fed at 12-hour intervals, the 12 hour post-feeding period also represents the 0 hour sample, or time just before the next meal.

After killing, the gastrointestinal tract of each animal was removed and separated by ligatures into nine segments (3). These consisted of the cranial and caudal halves of the stomach, the small intestine, proximal and distal midgut sacculation, proximal colon, ceca, and the mid and distal thirds of the remaining colon. Total contents were removed from each segment of the tract and weighed. Dry matter were determined by drying a sample of the whole contents from each segment in a forced air oven at 105° to a constant weight. The remaining contents from each segment of tract were centrifuged at 10,000 × g and the supernant collected for analysis. The osmolality of each sample was determined using a laboratory osmometer. Additional samples were analyzed for the concentration of sodium and potassium by flame photometry and chloride was determined with the aid of an automatic chloride titrator.

Analysis of Variance (12) and Duncan's New Multiple Range Test (13) were used to determine significant differences. The movement of the ingesta and the organic acid production have been reported earlier (3).
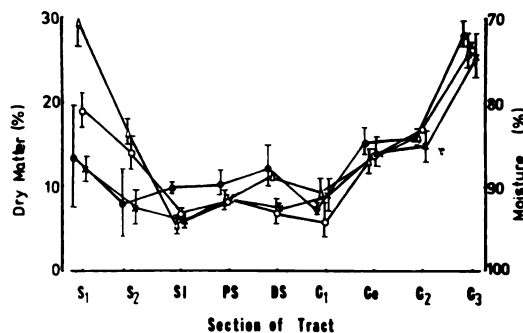

Fig. 1 Mean dry matter-moisture content (± SEM) of gastrointestinal contents of the rock hyrax. Symbols within the graph correspond to the four time periods: (●), 0 or 12 hours; (△), 2 hours; (○), 4 hours; and (X), 8 hours after feeding. Symbols along the abscissa represent the cranial stomach (S_1); caudal stomach (S_2); small intestine (SI); proximal sacculation (PS); distal sacculation (DS); proximal colon (C_1); ceca (Ce); mid colon (C_2) and distal colon (C_3).

RESULTS

Figure 1 depicts the dry matter-moisture content of the various gut segments. Significant differences were observed in the cranial and caudal stomach with the dry matter content at 2 hours post-feeding being greater than the 0 or 8 hour post-feeding periods. The dry matter content 4 hours after the meal was also greater than that at 8 hours post-feeding. The post-feeding period had no significant effect from the small intestine to distal colon. However, the dry matter content of the distal colon was significantly greater than that observed in the gut segments from the caudal stomach to the mid colon, for all post-feeding periods.

Osmolality of the cranial stomach greatly increased for the 2, 4, and 8 hour post-feeding periods over that of the pre-meal value; however, a significant difference ($P < 0.01$) was observed only for the 8 versus the 0 hour periods (fig. 2). Elsewhere in the digestive tract significant differences were observed in the small intestine with the 2 hour post-feeding period being less than the 4 hour period. The osmolality for the
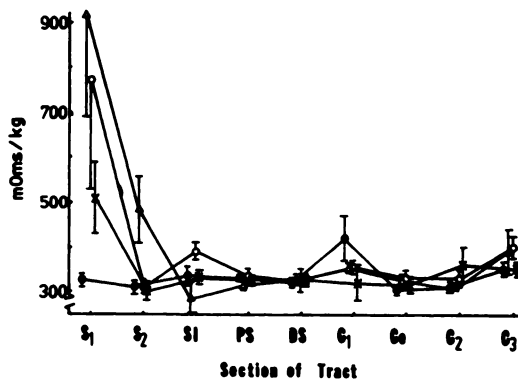
Fig. 2 Mean osmolality (± SEM) of gastrointestinal contents of the rock hyrax. Symbols within the graph correspond to the four time periods: (●), 0 or 12 hours; (△), 2 hours; (○), 4 hours; and (X), 8 hours after feeding. Symbols along the abscissa represent the sections of tract as given in Figure 1 legend (N = 3).

various gut segments indicated that while the osmolality of the cranial stomach was greater during the early post-feeding periods, significant differences were not found for the various gut segments from the stomach to distal colon.

Figures 3, 4, and 5 gives the results obtained from measurements of the gut electrolytes; sodium, potassium and chloride, respectively. Sodium concentrations in the cranial stomach were higher during the early post-feeding periods than at the 0 or 8 hour post-feeding period. Concentrations in the caudal stomach averaged approximately 40 mEq/liter with a significant increase in the proximal small intestine for all post-feeding periods. In all post-feeding periods, concentrations of sodium were maintained at higher levels from the small intestine to proximal colon. However, sodium concentrations significantly decreased from proximal to distal colon for the 0, 4, and 8 hour periods. Quantities of sodium were highest in the cranial stomach during the 2 and 4 hour periods. Quantities were also greater in the proximal sacculation and ceca than at any other gut segment for all post-feeding periods.

Similarly, during the early post-feeding periods, potassium concentrations and quantities were greatest in the cranial stomach (fig. 4). However, the concentrations and quantities were observed to decrease and be maintained at this lower level from

the caudal stomach to the colon. Concentrations of potassium tended to increase from ceca to distal colon while the quantities were observed to be maintained at the lower values.

In the cranial stomach, chloride concentrations tended to be higher before the meal and decrease with the post-feeding periods, while the quantity of chloride showed a somewhat reverse relationship with the feeding periods (fig. 5). Both the concentrations and quantity of chloride ions were observed to increase from the cranial to caudal stomach, followed by a significant decrease in the small intestine for all post-feeding periods. Concentrations and quantities of chloride ions were generally maintained at this lower level for the gut segments from the proximal sacculation to the distal colon.

DISCUSSION

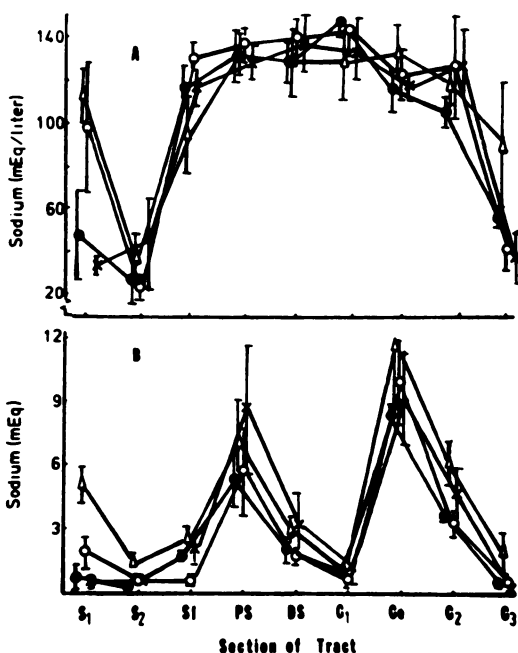The concentrations of gastrointestinal electrolytes have been measured in a num-

Fig. 3 Mean concentration (A) and quantity (B) of sodium ion (± SEM) in the gastrointestinal tract of the rock hyrax. Symbols within the graphs correspond to the four time periods: (●), 0 or 12 hours; (△), 2 hours; (○), 4 hours; and (X), 8 hours after feeding. Symbols along the abscissa represent the sections of the tract as given in Figure 1 legend (N = 3).

ber of mammals (14–16). With the exception of the greatly elevated potassium levels observed in the cranial half of the hyrax stomach, the rock hyrax posed no unusual concentration differences when the results of the present investigation are compared to these reported in earlier studies. However in the cranial stomach the potassium concentrations during the early post-feeding periods were of a magnitude 2 to 2.5 times greater than that reported in the pony (16), and some 5 to 8 times greater than that reported for the rabbit, guinea pig, dog, cat, and pig (14–15). The cation composition contributing to the hypertonicity of the digesta within the foregut of the hyrax was largely accounted for by the elevated potassium load within this digestive compartment (fig. 6). Although potassium is a major constituent of mammalian saliva (17), its presence in salivary secretions should not exceed that of sodium. Likewise,
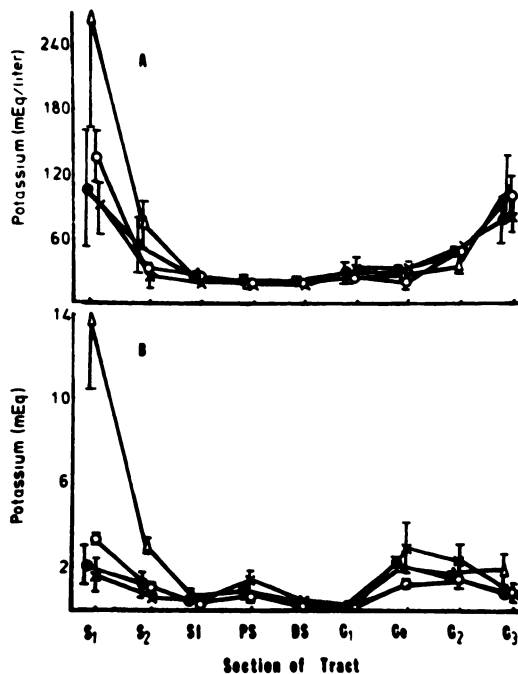

Fig. 5 Mean concentration (A) and quantity (B) of chloride ion (± SEM) in the gastrointestinal tract of the rock hyrax. Symbols within the graphs correspond to the four time periods: (●), 0 or 12 hours; (△), 2 hours; (○), 4 hours; and (X), 8 hours after feeding. Symbols along the abscissa represent the sections of the tract as given in Figure 1 legend (N = 3).

Fig. 4 Mean concentration (A) and quantity (B) of potassium ion (± SEM) in the gastrointestinal tract of the rock hyrax. Symbols within the graphs correspond to the four time periods: (●), 0 or 12 hours; (△), 2 hours; (○), 4 hours; and (X), 8 hours after feeding. Symbols along the abscissa represent the sections of the tract as given in Figure 1 legend (N = 3).
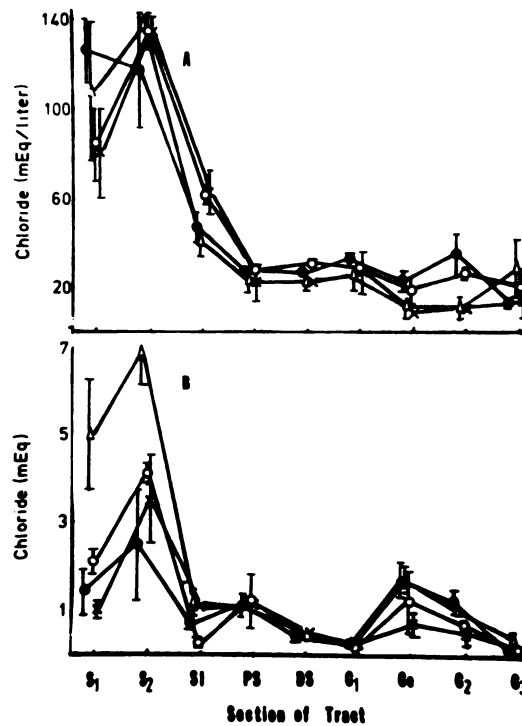
potassium is not an important component of gastric secretions, thus the origin of this potassium increase during feeding appears to be primarily due to the high levels of potassium consumed with the diet. The rapid reduction in the concentrations and quantity of potassium as the digesta moves from the cranial stomach suggests that large quantities of potassium are absorbed in the caudal stomach. Throughout the remaining segments of tract, the potassium ions followed a pattern similar to that observed in man (18) and other mammals (14–16, 19, 20). Potassium concentrations remained at a low level throughout the midgut and ceca, but increased in concentrations for the mid and distal colon, presumably entering via colonic secretion (21). Large quantities of potassium (460–800
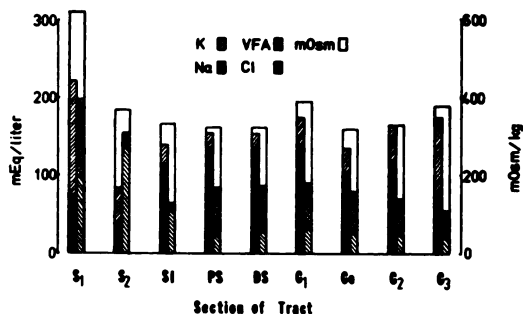
Fig. 6   Mean cation, anion and osmolality measured in the gastrointestinal tract of the rock hyrax ($N = 12$). Symbols along the abscissa denote the sections of tract as given in Figure 1.

mEq/liter) are also voided in the urine of the hyrax (11).

Numerous reports indicate that the influx of colonic potassium is associated with the simultaneous absorption of sodium (21, 22). Sodium is further linked with the movement of water from the mucosal to serosal surface (21–24). Such an interrelationship of potassium, sodium and water movement can be seen in the colon of the hyrax. This relationship is most evident in the distal colon where water and sodium fluxes demonstrate abrupt changes. Recycled sodium, which may enter the digestive tract via the saliva (17) and pancreatic-biliary secretions (25) were also evident in this study with the elevated sodium concentration in the cranial stomach during the early post-feeding periods and the levels observed in the small intestine. Since the ingesta is retained in the foregut for approximately 4 hours after a meal had been consumed (3) the lower concentrations of sodium observed in the small intestine 2 hours after the meal are consistent with these findings. With the exception of the caudal stomach, sodium and potassium comprised the major cations present throughout the entire digestive tract (fig. 6). Their combined concentrations were such that the cation deficit contributing to the osmolality was small.

Chloride ions were able to substantially contribute to the electroneutrality of the digesta only in the foregut, and primarily in the caudal stomach where they enter via gastric secretion. Considering only the chloride, a large anion deficit then existed

throughout most of the digestive tract. Recent investigators, however, have emphasized the role played by volatile fatty acids (VFA) in contributing to the osmotic balance and anion contribution of the digestive chyme (16, 26). In the present study a large portion of the anion deficit could be accounted for by considering the VFAs produced at the various sites (3). In the cranial stomach VFAs contributed greatly to the total anions present (fig. 6). Their contribution was such that only a small portion of the anions present remained unaccounted for. In the caudal stomach the chloride ion concentration was elevated such that only a small anion deficit existed, a portion of which was found to be VFA. The apparent large anion deficit in the small intestine could partly be explained by unmeasured bicarbonate ion. High levels of bicarbonate have been reported in the small intestine of man and other mammals (15, 18, 20). Chloride ion concentrations were low throughout the remaining segments of the digestive tract. On the other hand, VFA concentrations were high and thus provided the major portion of the measured anions. The anion deficit which existed for the gut segments from proximal sacculation to the distal colon can be explained by the assumed presence of bicarbonate and phosphate throughout these gut segments. Large concentrations of these ions have been reported in the large intestine of the horse, pony and pig (15, 16). The appearance of such buffers would account for the near neutral pH observed in these gut segments in the presence of the large quantities of volatile fatty acids (3).

While the data clearly show the changes in the gastrointestinal ionic compositions which contribute to the osmolality, they do not explain the hyrax's ability to conserve body water during periods of water deprivation. However, the low water exchange and an efficient kidney (11) helps to explain the ability of this small mammal to inhabit hot arid regions of East Africa and the Middle East.

ACKNOWLEDGMENTS

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