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Aspects of digestion and *in vitro* fermentation in the caecum of some East African herbivores

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Caecal digestive functions were compared in 22 species of East African herbivores. Comparisons were made between ruminant pseudo-ruminant, and non-ruminant herbivores to assess the relative *in vitro* fermentation rate and composition of caecal contents from these species observed in their natural habitat. Measurements were made of caecal fermentation rate, organic acid composition, osmolality, pH and dry matter content. The data were compared by foregut structure, feed preference and body weight of the herbivores.

Contents

Introduction

East African herbivores are unique both in the diversity of species represented, and in their selective feeding habits. Their forage diet undergoes digestive fermentation, a process taking place mainly in the enlarged forestomach of ruminants and pseudo-ruminants, or in the enlarged caecum and colon of the other herbivores (Stevens, Argenzio & Clemens, 1979). More recently, Demment & Van Soest (1985) and Demment & Longhurst (1987) have presented an interesting possibility in which they offer an explanation on how the nutrition of ruminants and non-ruminant herbivores is affected by both body size as well as the constraints imposed by gut morphology. Even forestomach fermenters have quite a large caecum-colon relative to carnivores, which serves to ferment the bulky food residues passing from the small intestines (Stevens, 1988). Very few studies have hitherto been published on the role played by the caecum in digestive function of both ruminant and non-ruminant herbivores. The caecum, like the ruminant forestomach, is viewed as a major site of fermentation. The aim of the present study was to investigate caecal fermentation and composition of caecal contents as well as the digestive physiology of many of East Africa's ruminant, pseudo-ruminant and non-ruminant herbivores.

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Materials and methods

Ninety-three adult animals representing 22 species of East African herbivores were used in this study. All digesta samples obtained from non-domestic species were derived from animals destroyed by the Kenya Government during obligatory wildlife control procedures. The species were grouped according to their principal feeding habits (Hofmann, 1973; Nowak & Paradiso, 1983) as follows: BROWSERS—6 Kirk's dik-dik (*Madoqua kirki*), 8 suni (*Nesotragus moschatus*), 5 gerenuk (*Litocranius walleri*), 3 goats (*Capra hircus*), 4 sheep (*Ovis aries*), 3 bushbuck (*Tragelaphus scriptus*), 4 giraffe (*Giraffa camelopardalis*), 3 rhino (*Diceros bicornis*); INTERMEDIATE FEEDERS—7 Thomson's gazelle (*Gazella thomsoni*), 6 Grant's gazelle (*Gazella granti*), 4 impala (*Aepyceros melampus*), 5 eland (*Taurotragus oryx*), 3 African elephant (*Loxodonta africana*); and GRAZERS—3 domestic donkey (*Equus asinus*), 3 zebra (*Equus burchelli*), 4 Zebu cattle (*Bos indicus*), 4 hartebeest (*Alcephalus buselaphus*), 4 wildebeest (*Connochaetes taurinus*), 3 waterbuck (*Kobus ellipsiprymnus*), 5 oryx (*Oryx gazella*), 3 one-humped camel (*Camelus dromedarius*), and 3 African Cape buffalo (*Syncerus caffer*).

All the animals were collected from their natural habitat in conjunction with the Department of Wildlife Conservation and Management game animal control programmes. Field analysis and sample collection were begun immediately after death of the animal and generally completed within 1 hour. Body weights of the animals were obtained by weighing (small herbivores < 50 kg) with a Salter spring balance or, in the case of larger animals (> 50 kg), the weights were taken as those reported for the average species weight (Sachs, 1967; Hofmann, 1973). The giraffe and buffalo were not weighed but their weights were estimated using the body girth or shoulder height formulae (Laws, Parker & Johnstone, 1975).

The abdominal cavity of each animal was opened immediately after death. Ligatures were used to tie off the oesophagus at the cardia and the large bowel at the rectal-anal junction, after which the gastrointestinal tract was then removed. The gastrointestinal tract of each animal was further separated by ligatures into selected segments. These consisted of the reticulo-rumen, abomasum, small intestine, caecum and colon. The 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 H_2SO_4 (approx. 0·5 ml per 20 ml sample), and refrigerated for later analyses of volatile fatty acids.

Dry matter content was determined by drying a portion of each sample to a constant weight in a forced-air oven at 105 °C. Samples of whole gut contents were centrifuged and the supernatant collected for laboratory analysis. Osmolality of the supernatant fraction was determined on a wide range laboratory osmometer. Lactic acid concentration of each sample was determined by the methods of Barker & Summerson (1941). Volatile fatty acid concentrations were determined by the steam distillation method of Markham (1942). Caecal fermentation rate was studied by measurement of rate of gas production *in vitro* according to methods described for fermentation studies of rumen contents (Giesecke & Van Gylswyk, 1975; Hoppe, Qvortrup & Woodford, 1977*a*, *b*). All samples from each individual animal were analysed in duplicate.

Analysis of variance and Duncan's Multiple Range Test were used to determine significant differences (Snedecor & Cochran, 1967).

Results

The concentrations of dry matter, pH, osmolality, volatile fatty acids and *in vitro* fermentation of caecal contents observed in the 22 species of East African herbivores are given in Tables I–V. Herbivores within this study represent 17 species of ruminants (Kirk's dik-dik, suni, gerenuk, goat, sheep, bushbuck, giraffe, Thomson's gazelle, Grant's gazelle, impala, eland, Zebu cattle, hartebeest, wildebeest, waterbuck, oryx and Cape buffalo), one pseudo-ruminant (camel) and four species of non-ruminants (domestic donkey, zebra, rhino and elephant). Table I gives the composition of caecal contents obtained when these animals are grouped according to their respective foregut structure (ruminant, pseudo-ruminant and non-ruminant). With the exception of caecal osmolality, statistical differences ($P < 0·05$) were observed among all other measured ruminant and non-ruminant caecal parameters (Table I). Caecal dry matter content and pH were significantly less, and fermentation rate, volatile fatty acid (VFA) and lactic acid concentrations significantly greater in the non-ruminant when compared to ruminant species. Caecal fermentation rate of the pseudo-ruminant (camel) was significantly greater than that of the ruminant, and significantly less than that of the non-ruminant. All other parameters observed for the camel were not statistically different from either ruminant or non-ruminant species.

When herbivores were grouped according to food preference (i.e. browsers, intermediate feeders and grazers), irrespective of foregut structure, statistical differences were noted only for the osmolality of caecal contents (Table II). In this instance, the intermediate feeders had a higher value (331 mOsm/kg·H_2O) relative to browsers and grazers (300 and 305 mOsm/kg·H_2O, respectively). However, if the species were first grouped according to ruminants (Table III) and non-ruminants (Table IV) and then compared according to their respective food preference,

TABLE I

*Concentrations of dry matter, pH, osmolality, volatile fatty acids, lactic acid and in vitro fermentation of caecal contents as affected by the foregut structure in East African herbivores**

Foregut structure	Dry matter (%)	pH	Osmolality (mOsm/kg·H_2O)	Fermentation rate (μmol·gas NTPD/g·DM/h)	Volatile fatty acids (mmol/l)	Lactic acid (mmol/l)
Ruminant (N = 78, S = 17)	$15·9 \pm 0·5^{a}$	$6·95 \pm 0·08^{a}$	304 ± 5	$80·4 \pm 3·4^{a}$	$83·3 \pm 5·8^{a}$	$1·51 \pm 0·24^{a}$
Pseudo-ruminant (N = 3, S = 1)	$16·3 \pm 2·2^{ab}$	$6·99 \pm 0·38^{ab}$	299 ± 26	$108·0 \pm 16·7^{b}$	$99·3 \pm 28·5^{ab}$	$1·09 \pm 1·05^{ab}$
Non-ruminant (N = 12, S = 4)	$11·3 \pm 1·26^{b}$	$6·42 \pm 0·20^{b}$	330 ± 14	$178·6 \pm 8·8^{c}$	$126·4 \pm 15·1^{b}$	$2·82 \pm 0·61^{b}$

* Values within a column with unlike superscripts are statistically different ($P < 0·05$)
N = number of animals, S = number of species
Values are mean (±S.E.)

TABLE II

*Concentrations of dry matter, pH, osmolality, volatile fatty acids, lactic acid and in vitro fermentation of caecal contents of the major feeding groups of East African herbivores**

Food selection	Dry matter (%)	pH	Osmolality (mOsm/kg·H_2O)	Fermentation rate (μmol·gas NTPD/g·DM/h)	Volatile fatty acids (mmol/l)	Lactic acid (mmol/l)
Browsers (N = 36, S = 8)	$15·8 \pm 0·9$	$6·78 \pm 0·13$	300 ± 6^{a}	$91·0 \pm 13·2$	$90·6 \pm 9·7$	$1·88 \pm 0·40$
Intermediate (N = 25, S = 5)	$15·7 \pm 1·0$	$6·71 \pm 0·15$	331 ± 7^{b}	$103·2 \pm 15·4$	$85·0 \pm 11·8$	$2·05 \pm 0·47$
Grazers (N = 32, S = 9)	$14·0 \pm 0·8$	$7·01 \pm 0·13$	305 ± 6^{a}	$110·9 \pm 12·3$	$96·9 \pm 9·1$	$1·16 \pm 0·35$

* Values within a column with unlike superscripts are statistically different ($P < 0·05$)
N = number of animals, S = number of species
Values are mean (±S.E.)

TABLE III

The concentrations of dry matter, pH, osmolality, volatile fatty acids, lactic acid and in vitro *fermentation of caecal contents in major feeding groups of East African ruminant herbivores**

Food selection	Dry matter (%)	pH	Osmolality (mOsm/kg·H₂O)	Fermentation rate (μmol·gas NTPD/g·DM/h)	Volatile fatty acids (mmol/l)	Lactic acid (mmol/l)
Browsers (N = 33, S = 7)	15·4 ± 2·7	6·99 ± 0·21	294 ± 14	79·4 ± 15·3	79·6 ± 24·6	1·80 ± 0·69
Intermediate (N = 22, S = 4)	16·2 ± 2·0	6·97 ± 0·19	337 ± 34	87·0 ± 13·9	71·7 ± 7·6	1·89 ± 0·82
Grazers (N = 26, S = 7)	15·5 ± 1·4	6·91 ± 0·19	295 ± 13	78·2 ± 18·3	92·3 ± 31·2	1·01 ± 0·62

* Statistical differences not detected ($P > 0{\cdot}05$) between treatment groups
N = number of animals, S = number of species
Values are mean (±S.E.)

greater variability was observed, but only in the non-ruminant group. Ruminant animals demonstrated no statistical difference in composition of caecal contents when compared by food preferences (Table III). However, statistically significant differences ($P < 0{\cdot}05$) were observed between non-ruminant browsers, intermediate feeders and grazers for all of the caecal parameters measured (Table IV). Non-ruminant grazers had significantly ($P < 0{\cdot}05$) lower caecal dry matter content and VFA concentrations and higher caecal pH values than did the browsers or intermediate feeders. Non-ruminant intermediate feeders had significantly lower osmotic values and higher lactic acid concentrations than either the browsers or grazers, and significantly lower fermentation rates than browsers.

When these herbivores were compared according to their respective body weight, irrespective of foregut structure or food preference, statistical differences were observed only for VFA concentrations (Table V). The general trend suggested that herbivores with smaller body weights had lower caecal VFA concentrations than did animals of larger body size.

TABLE IV

The dry matter, pH, osmolality, volatile fatty acids, lactic acid, and in vitro *fermentation of caecal contents in major feeding groups of East African non-ruminant herbivores**

Food selection	Dry matter (%)	pH	Osmolality (mOsm/kg·H₂O)	Fermentation rate (μmol·gas NTPD/g·DM/h)	Volatile fatty acids (mmol/l)	Lactic acid (mmol/l)
Browsers (N = 3, S = 1)	15·2 ± 0·4^{a}	5·45 ± 0·71^{a}	335 ± 35^{a}	180·0 ± 2·8^{a}	145·2 ± 4·2^{a}	2·40 ± 0·59^{a}
Intermediate (N = 3, S = 1)	12·6 ± 1·2^{b}	5·67 ± 0·61^{a}	311 ± 3^{b}	164·3 ± 6·8^{b}	138·4 ± 2·2^{a}	5·50 ± 0·72^{b}
Grazers (N = 6, S = 2)	8·7 ± 1·5^{c}	7·28 ± 0·15^{b}	336 ± 12^{a}	185·0 ± 14·5^{ab}	111·1 ± 6·1^{b}	1·69 ± 0·65^{a}

* Values within a column with unlike superscripts are statistically different ($P < 0{\cdot}05$)
N = number of animals, S = number of species
Values are mean (±S.E.)

TABLE V

The effect of body weight on the dry matter, pH, osmolality, volatile fatty acids, lactic acid and in vitro *fermentation of caecal contents of East African herbivores**

Weight group	Dry matter (%)	pH	Osmolality (mOsm/kg·H₂O)	Fermentation rate (μmol·gas NTPD/g·DM/h)	Volatile fatty acids (mmol/l)	Lactic acid (mmol/l)
< 20 kg (N = 17, S = 3)	14·7 ± 1·3	7·04 ± 0·19	297 ± 13	78·5 ± 19·9	72·0 ± 11·3^{a}	2·02 ± 0·58
20–50 kg (N = 25, S = 5)	16·2 ± 1·0	6·93 ± 0·15	314 ± 10	82·5 ± 15·8	72·5 ± 9·0^{a}	2·11 ± 0·46
51–100 kg (N = 4, S = 1)	18·0 ± 2·4	7·00 ± 0·36	318 ± 24	84·5 ± 37·8	67·8 ± 21·5^{ab}	1·93 ± 1·09
101–150 kg (N = 4, S = 1)	15·0 ± 2·4	6·81 ± 0·36	291 ± 25	60·4 ± 38·7	53·6 ± 20·1^{a}	1·85 ± 0·91
151–200 kg (N = 18, S = 5)	12·8 ± 1·2	7·05 ± 0·17	311 ± 12	117·0 ± 18·2	105·1 ± 10·4^{bc}	1·14 ± 0·53
201–300 kg (N = 7, S = 2)	15·5 ± 1·9	7·00 ± 0·27	299 ± 19	107·8 ± 28·8	118·2 ± 16·4^{c}	1·67 ± 0·83
> 300 kg (N = 18, S = 5)	15·7 ± 1·2	6·41 ± 0·18	315 ± 13	119·1 ± 19·2	112·0 ± 11·0^{c}	2·12 ± 0·56

* Values within a column with unlike superscripts are statistically different ($P < 0{\cdot}05$)
N = number of observations, S = number of species
Values are mean (±S.E.)

Discussion

Hofmann (1973) has classified the East African ruminants into three major feeding groups: concentrate selectors (browsers) which have a diet of high nutritional value, low fibre, and high protein content; bulk and roughage eaters (grazers) whose diet is largely grass, often high in fibre and low protein content; and intermediate feeders whose diet consists of grasses and browse. Further, he examined the relationship between gut structure and diet in several East African herbivores. The diet of East African non-ruminant herbivores has been described by Nowak & Paradiso (1983). A re-examination of digestive tract structure and function in several East African herbivores needs to be evaluated in accordance with optimal digestion and chemical reactor theories that have recently been advanced by Sibly (1981) and Penry & Jumars (1987), respectively.

The forestomach of domestic and wild ruminants has been the subject of several investigations. It has been suggested that both diet (Bath & Rook, 1963; Hoppe *et al.*, 1977*a*) and size of the animal (Hungate *et al.*, 1959; Hoppe, 1977; Maloiy, Clemens & Kamau, 1982) influence reticulo-rumen fermentation rate. Reticulo-rumen VFA concentrations were observed to decrease with the increase in body weight and the increased consumption of grasses (Clemens & Maloiy, 1983*a*). Most studies have so far been concerned with rumen physiology (Maloiy, Taylor & Clemens, 1978; Maloiy & Clemens, 1980*a*, *b*). Furthermore, a few studies have been directed toward the study of non-ruminant herbivores (Clemens & Maloiy, 1982, 1983*b*), once again indicating that diet alters the VFA composition within the stomach and large bowel. Only a limited number of studies, on selected species, have dealt with caecal fermentation (Hungate *et al.*, 1959; Janis, 1976; Parra, 1978; van Hofen, 1980; Hoppe *et al.*, 1983; Demment & Van Soest, 1985).

The present data strongly suggest that fermentation in the ruminant forestomach sufficiently altered the ingesta so that fermentative activities within the ruminant caecum were not affected by food preference. While fermentation rates of rumen contents are clearly influenced by the selection of browse, grasses or a mixture thereof (Maloiy, 1972; Hoppe *et al.*, 1977*a*, *b*; Maloiy *et al.*, 1982; Hoppe *et al.*, 1983), caecal fermentation rates were not different. In a similar manner, caecal pH, lactic acid and VFA concentrations of ruminants were not influenced by diet selection, in this study or in previous investigations (Clemens & Maloiy, 1983*a*; Clemens, Maloiy & Sutton, 1983). However, a comparison of ruminants with non-ruminant species clearly demonstrates significant differences in caecal digestion between the two groups, and suggests that, unlike ruminants, caecal fermentation rate and digesta composition of the non-ruminants are affected by diet. Additionally, and irrespective of diet, the caecum of non-ruminant herbivores had greater fermentation rates, lactic acid and VFA concentrations and lower pH and dry matter contents than the caecum of ruminants. It is postulated that these differences are apparent mainly because readily digestible fibre will have been fermented in the forestomach of ruminants, thus not making it available as a substrate for caecal fermentation, whereas it will be so available in non-ruminants.

Caecal fermentation rate and composition of the caecal contents in the non-ruminant herbivores were influenced by diet selection, apparently the result of a less active foregut fermentation within these species. As observed with the ruminant forestomach (Maloiy, 1972; Hoppe *et al.*, 1977*a*, *b*; Maloiy *et al.*, 1982; Hoppe *et al.*, 1983), non-ruminant browsers generally had higher caecal VFA and lactic acid concentrations, and lower content pH, than grazers and/or mixed feeders. However, fermentation rates and organic acid concentrations of non-ruminant caecal contents were less than those observed within the ruminant forestomach. The significant effect of diet (browse vs. grass) on the non-ruminant caecal dry matter content is in direct contrast to the effects of similar diets on the ruminant forestomach (Maloiy *et al.*, 1982), and is at this point unexplained.

In the present study, we found no direct correlation between the body weight of the herbivore and caecal fermentation activity, which also differs from previous findings on rumen fermentation rates (Hoppe, 1977). However, an apparent relationship exists between body size and the VFA concentrations observed within the caecum, in this case VFA concentrations were generally greater in larger animals. Although this is the reverse of what has been observed within the ruminant forestomach (Clemens & Maloiy, 1983*a*; Clemens *et al.*, 1983), it is consistent with the earlier observation of enhanced caecal-colon VFA absorption with an increase in body size (Clemens & Maloiy, 1984).

Summary

(1) Caecal fermentation rate was investigated in 22 species of East African herbivores. Non-ruminant herbivores had significantly greater caecal fermentation rate (178 NTPD/g·DM/h), VFA (126 mmol/l) and lactic acid (2·8 mmol/l) concentrations than did ruminants (80 NTPD/g·DM/h; 83 mmol/l; 1·5 mmol/l, respectively).

(2) Statistical differences were not detected for ruminant browsers, intermediate feeders and grazers, non-ruminant browsers, however, had significantly higher caecal dry matter (15·3%), VFA (145 mmol/l) and lower pH (5·45) than did non-ruminant grazers (8·7%), 111 mmol/l and 7·28, respectively).

(3) While diet preference (browse, graze or mixed) did not affect caecal fermentation in ruminants, there were significant effects in non-ruminant herbivores.

(4) No effect of body size on caecal fermentation was evident except on VFA concentrations.

(5) It is suggested that removal of fermentable fibrous substrates in the rumen leads to a lesser or more uniform caecal fermentation than is seen in non-ruminants.

(6) The results obtained herein are discussed in relation to the animals' feed preference, body weight and foregut structure and function.

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Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations

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The click vocalizations of sperm whales often contain several regularly-spaced, discrete pulses of sound. Norris & Harvey (1972) hypothesized that these were caused as a single pulse of sound produced at the front of the whale's head bounced between reflective air sacs at either end of the spermaceti organ. Thus the interval between pulses will be twice the travel time for sound along the length of the spermaceti organ. It should therefore be possible to determine spermaceti organ length and thence total body length by measuring the interval between these pulses. Several workers have used an equation relating inter-pulse interval (IPI) to body length to estimate sperm whale body lengths acoustically.

In this paper, aspects of this technique are examined in some detail. In particular, variability in IPIs and trends in IPI with time and depth are investigated. Most importantly, for the first time IPIs in the vocalizations of whales of known lengths have been measured.

Variability in IPIs in the clicks of a single whale is acceptably low though there is a tendency for low and high values to occur in runs. There is no clear trend for IPI to alter significantly with the whale's depth or with the time since leaving the surface.

IPIs are positively correlated with body length though not as predicted by the equations used by previous workers. Some likely errors in these equations are discussed. A new empirically derived relationship between IPI and body length has been calculated, though more data are desirable to obtain a more accurate and reliable equation.

Contents

Introduction

Sperm whales make distinctive vocalizations, consisting of very loud wide-bandwidth clicks, for much of the time that they are diving. In an early paper, Backus & Schevill (1966) noted that, in

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