THE DIGESTION IN THE HYRAX *PROCAVIA CAPENSIS* (PALLAS, 1766)

by

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ABSTRACT

The results of a field and laboratory digestion study on the monogastric hyrax, *Procavia capensis*, have been compared with the results reported for ruminants and non-ruminants. In the hindgut of hyrax two sites of digesta retention and fermentation were found. The sac was of larger mass than the caeca and also produced more VFA energy per day than the caeca. The caeca played a more important role during the dry seasons when food quality was lowest and caeca sizewere greatest. Seasonal differences in VFA production rates were found and was the result of diet differences. High fibre / low protein rations fed to hyrax had lower VFA production rates and apparent digestibilities than the low fibre / high protein rations. The highly efficient digestion of low quality food in the hindgut of hyrax was essential in the evolution of the species to ensure successful inhabitance of arid rocky hills.

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C O N T E N T S

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

VFA	Volatile fatty acids
G.E.	Gross energy
F.E.	Faecal energy
D.E.	Digestible energy
U.E.	Urine energy
G.P.D.	Gas production
BMR	Basal metabolic requirements
ME	Metabolisable energy
RMR	Resting metabolic rate
NDF	Neutral detergent fibre
ADF	Acid detergent fibre
ADL	Acid detergent lignin

CHAPTER 1 INTRODUCTION

The Hyracoidea are the most primitive living ungulates and based on fossil evidence they are phylogenetically linked with the orders Proboscidea and Sirenia. Living Hyracoidea have been in existence for over 10 million years in restricted areas of Africa and the Middle East (Winge, 1942). Research done by Winge (1942) and Simpson (1945) indicated that the following features of the present day Hyracoidea are related to the Sirenia and Proboscidea:

1. Several digits with poorly developed hoofs.
2. Anterior upper incisors modified as 'tusks'.
3. Reduced canines and molariform molars developed for mastication.
4. The testes fail to descend into the scrotum.
5. No gallbladder is present.
6. No sweatglands are found.

It was found by Kurten (1971) that the 'Giant Hyraces' of the Oligocene period were browsers as their dentition was found to be similar to the living species of today. Hyrax feed (browse and graze) on a diversity of vegetation (Coe, 1962; Turner and Watson, 1965; Sale, 1966a ; Hoeck, 1975) and have the ability to feed on plant species unpalatable and poisonous to domestic animals (Sale, 1965b). They have a seasonal food preference (Meltzer, 1967 ; Hoeck, 1975), selecting young plant material in summer, but do eat coarser, low quality food and even select bark in winter (Hoeck, 1975). Hyrax feed in groups and like ungulates, a territorial male guards the group (Sale, 1966b). They feed in short foraging periods of up to two hours during sunrise and sunset (Sale, 1965a, 1965b).

Sale (1966b) described the upper incisors as well developed, with a diastema between them and the molars. The long cutting edge of the molars enables a large amount of food to be taken at a rapid rate. The tongue was described by Elias (1945) as having no visible taste-buds on the dorsal surface but foliate papillae were found on the margins while fungiforme papillae appear on the appex, similar to the tongues of the Rodentia and Ungulata. The abdominal viscera is lined with thick epithelium up to where the stomach bends upon itself (Owen, 1868). The cardiac

stomach is lined with stratified squamous epithelium, as is also found in the mouse and horse, and possesses no glands in contrast to the pyloric stomach which is lined with tubular glands (Elias, 1945). The gallbladder is absent and the bile-duct drains the two-lobed liver into the upper small intestine (Grasse, 1955). Two conical caeca are found as in birds and a few species of Edentate mammals (Owen, 1832).

Clemens (1977) reported three major sites of digesta retention and microbial fermentation. According to him the cranial stomach produced up to 6,25 mM / 100 ml / h of volatile fatty acids. While the mid-gut sacculation and caeca each produced 4,08 mM / 100 ml / h of volatile fatty acids. Von Engelhardt, Wolter, Lawrenz and Hemsley (1978) found that *Procavia habissinica* produced 2,4 - 8,4 ml methane / kg body mass / hour. Leon (1980) described aspects of ruminant-like metabolism in *P. capensis* and found high concentrations of volatile fatty acids in the stomach and promixal caeca, and appreciable amounts in the proximal colon, distal caecum and appendices.

In South Africa the hyrax, *Procavia capensis*, is of special interest because this species has become an agricultural pest in certain areas where their predators have been eliminated (Hanse, 1962). The feeding habits of *P. capensis* were studied in detail by Lensing (1979). No detailed information about the digestion of the *P. capensis* was however available and therefore a study examining the digestive tract and in particular the unique hindgut was proposed.

The following key questions were asked:

1. What amount of metabolizable energy is produced from the hyrax's food?
2. Which are the major areas of VFA production?
3. How much VFA is produced in these major areas?
4. What percentage of the maintenance energy requirements is available to the hyrax as VFA?
5. How much potential energy from the plant or food material is lost as methane?
6. Are any particular digestive adaptations found in the anatomy, digestive economy or behaviour of the hyrax?

CHAPTER II METHODS

STUDY AREA

The fieldwork was carried out on the farm Wolwekraal near Brits, Transvaal, South Africa : 25°35' S, 27°44'E. The area of 12-15 acres is part of the geological system called the 'Bushveld coagulation complex'.

From a field laboratory, 1110 meters above sea level, the habitat is mountainous and ranges in elevation from 1140 meters to 1310 meters above sea level. The mountains consist of rocky cliffs and outcrops of boulders which provide ideal cavities where five hyrax colony sites were located. At every site hyrax groups of about 40 animals were found. Adult to juvenile ratios were estimated as 5 : 1.

The vegetation could be described as sour bushveld (Acocks, 1975) and is characterized by the following plants:

Acacia tortilis, Lannea discolor, Croton gratissimus, Combretum molle, Ficus soldanella, Melhania acuminata, Maytenus tenuispina, Maytenus undata, Cyphostemma sulcatum, Ziziphus zeyeriana, Peltophorum africanum, Dombeya rotundifolia, Pouzolzia hypoleuca, Solanum coccineum, Pappea capensis, Iboza riparia, Grewia bicolor, Grewia monticola, Grewia occidentalis, Urea tenax, Hibiscus subreniformis, Cynodon dactylon, Panicum maximum, Themeda triandra and *Chrysopogon motanus*.

The total rainfall during the study year 1979 was 874,3 mm with most rain falling during the summer and early autumn (Fig. 1a). The means of maximum and minimum temperatures measured 0,45 meter above soil level varied between 26,7°C in January to 13,6°C in July (Fig. 1b).

ANIMALS

Field animals

Thirty-five hyrax were collected over a period of 12 months, starting in March 1979. Nineteen hyrax were taken during the cool wet autumn, seven during the cold dry winter, six during the cool dry spring and three in the hot wet summer.

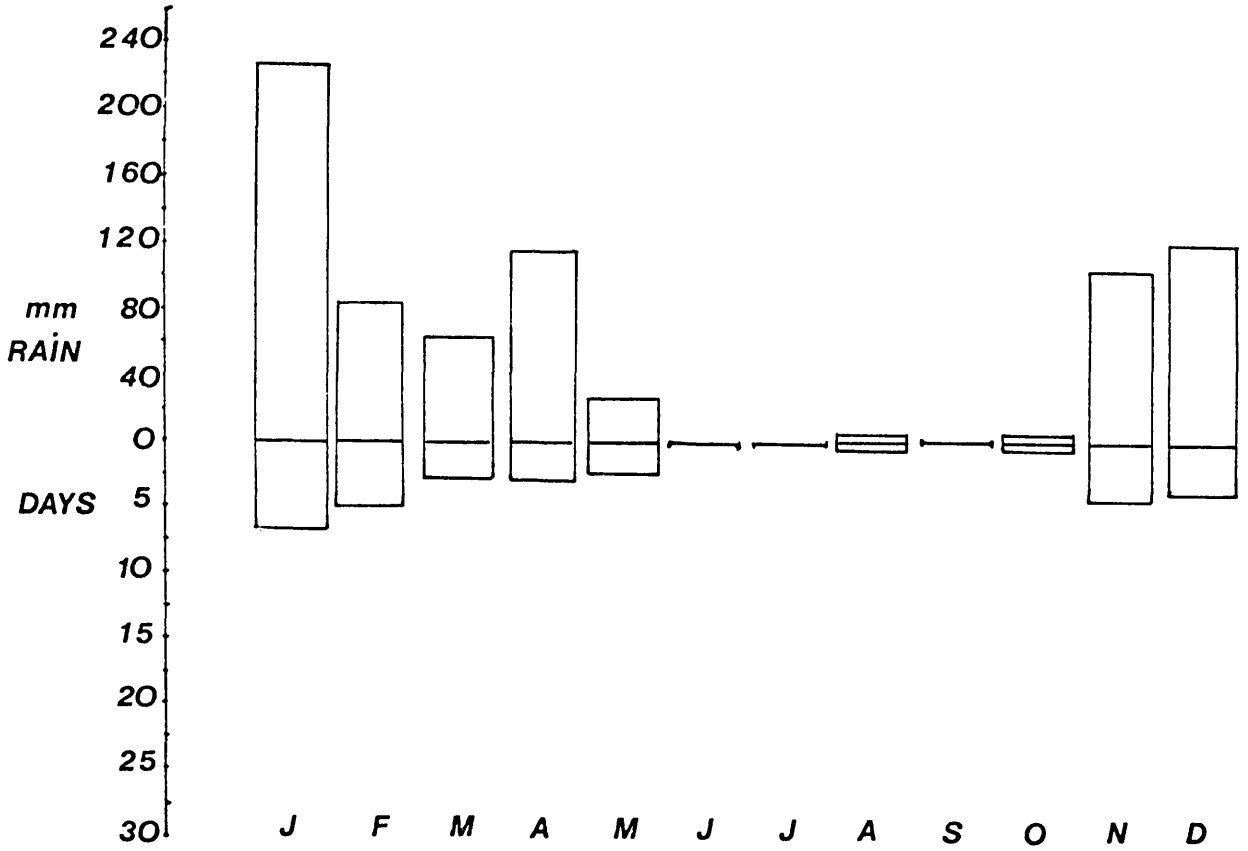

Fig. 1a Rainfall pattern for Wolwekraal.

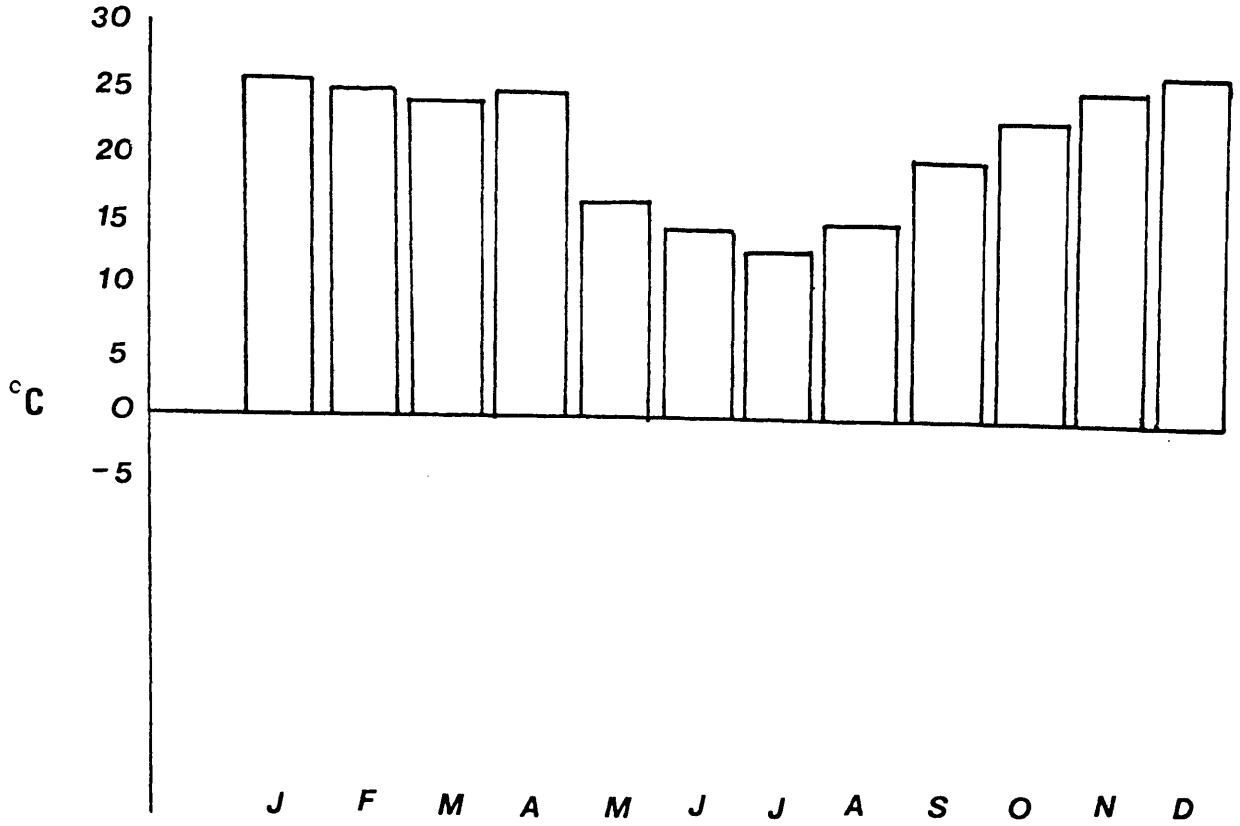

Fig. 1b Mean monthly temperatures at Wolwekraal.

Laboratory animals

The laboratory study was conducted on sixteen captive hyrax of approximately similar age and mass from a captive colony kept at the animal facility of the Mammal Research Institute of Pretoria University. These animals were housed in individual cages and fed six different pelleted rations with varying combinations of protein and fibre (Table 1).

Table 1a. Protein and fibre analyses of the rations fed to laboratory hyrax

Ration	% Protein	% NDF	% Cellulose	% ADL	Crude fibre
1.	19,83	22,55	9,5	7,5	17,0
2.	14,64	49,50	11,5	5,0	19,5
3.	15,21	24,00	2,5	7,5	10,0
4.	14,54	23,00	8,0	8,5	16,5
5.	19,20	15,50	5,5	6,0	11,5
6.	7,83	49,50	17,5	14,0	31,5

Feeding trials took place in stainless steel metabolic cages at room temperature (26°C) with *ad libitum* water available. All the rations were given for an adaptation period of four weeks before a seven day collection period. Faeces and urine collected, were analysed for digestibility and the four animals fed on rations 1-3 were then released back into the colony, while the hyrax fed on rations 4-6 were sacrificed for further study. These hyrax were caged in three groups, each group being fed on one of the remaining rations 4, 5 and 6 and digestibility determined. One animal in group two was removed from the experiment when it refused to eat due to stress and a male in group three died during the adaptation period. In both cases the study was therefore conducted on three animals.

SAMPLING

Field animals

Animals from the study area were brought to the field laboratory within 20 minutes of being shot. After weighing the hyrax,the digestive tract was removed, tied at both ends and put in a waterbath at 39°C. Throughout the study the digestive tracts were divided into seven parts as schematically shown in Fig. 2.

Before any incisions were made, gas samples were taken from each segment with a hypodermic syringe and stored in 5 ml evacuated tubes (vacutainer). The pH of each segment was measured with a portable pH-meter by inserting the electrode directly into the digesta.

Fermentation rates were measured by determining the gas production of the contents in the two fermenting chambers: the sacculation and the caeca, following the method of El-shazly and Hungate (1965).

The zero-time rate method of Caroll and Hungate (1954) was used to determine volatile fatty acid (VFA) production. Twenty milliliter quantities of digesta from the sacculation (sac) and caeca were incubated in a waterbath (39°C) for three or four hours depending on the sample size. From these 20 ml samples, zero-time samples of 4 ml were immediately taken. Additional sub-samples of 4 ml each were obtained at hourly intervals from zero-time. To ensure that fermentation ceased, in the 4 ml sub-samples, 2 ml of mecuric chloride was added to each sample, which was then placed in ice.

Additional samples were taken and preserved with mecuric chloride to determine qualitative VFA, dry matter percentage and protozoa counts from each tract part. The residual digesta was removed and mass of empty tissues were recorded.

Laboratory animals

The rate of was measured by incorporating coloured plastic pieces into the pelleted rations. Pellets were fed and faeces samples collected every hour for two days to calculate first and last appearances of the plastic particles.

Each group of hyrax were starved 24 hours before being fed pellets with plastic particles at 03h00 of the morning of the first killing which commenced at 07h00. The following three animals were then sacrificed on set intervals of six hours ie. 13h00, 19h00 and 01h00. The same sampling procedures were followed after each killing as described under field animals and all samples were placed in a freezer until analysed.

ANALYTICAL METHODS

Fermentation gas

The composition of the fermentation gas was determined using a 'Pye Unicam' gas chromatograph with a thermal conductivity detector. A 5 A molecular sieve 90 / 100 mesh column packing was used with argon as carrier gas.

Qualitative analysis of VFA

The total VFA in the zero- and sub-samples treated with mecuric chloride were extracted by steam distillation as described by Fenner and Elliot (1963) and estimated by titration with 0,1N NaOH using phenolfthalein as indicator.

Qualitative analysis of the VFA composition

Samples of 4 ml were centrifuged for 20 minutes at 2000 r.p.m., 0,6 µl as the supernatant was used for separation. The molar ratios of the individual VFA's were then determined using a gas chromatograph with a flame-ionization detector (F.I.D.). Chromosorb WAW 80/100 mesh coated with 10% SP 1000 / 1% H_3PO_4 column packing was used.

Energy analysis

All faeces and urine samples collected during the experimental weeks, dry matter samples taken from all seven tract parts of field and laboratory hyrax, and samples from the six pelleted rations were dried in an oven at 75^{o}C for five days or until the mass of the samples were constant. These samples were then ground and from each of these ground samples three 0,5 gram samples were combusted in a 'Gallenkamp' ballistic bomb calorimeter, to determine the gross energy values, using the mean of these three determinations.

Protein analysis

Two 0,5 gram samples of the dried and ground samples were used to analyse protein content by the Kjeldahl method (Horwitz, 1970).

Fibre analysis

Two 0,5 gram samples of the dried and ground samples were used to analyse the fibre content by the method of Van Soest (1964) using a 'Fibre-tec 1020' hot extraction apparatus. The general formula of Van Soest and Moore (1965) was used to calculate the digestible organic matter.

Protozoa

Protozoa were prepared and identified according to Eadie (1967). Numbers were determined in each digestive tract segment using a McMaster counting chamber (Boyne, Eadie and Raitt, 1957).

Calculation of energy requirements

The total VFA production and its contribution to the BMR (basal metabolic rate) of field hyrax and the ME (metabolisable energy) of hyrax fed on rations 4, 5 and 6 were calculated, using the method of Allo, Oh, Longhurst and Connolly (1973).

The estimated rates of VFA production of the sac and caeca were separately multiplied with 24, to determine the daily VFA production. These values were then multiplied with the amount of grams that the dry matter weighed per milliliter and thereafter these values were corrected for 100 grams. The amount of mmoles VFA per 100 gram dry matter in the sac and caeca were then corrected for the dry matter mass in each organ. The total daily VFA production in the organ in turn was multiplied by the estimated net kilojoule energy value of total VFA (Table 5) to determine the amount of VFA energy produced daily. The total daily VFA energy produced in each group of animals was calculated by adding the VFA energy values of the sac and caeca. These totals were then converted to a percentage of the BMR and ME produced per day, to compare data with results in the literature (Table 14).

Statistics

Differences between animals of the field and laboratory study and between their two important fermentation chambers, the sac and caeca were calculated for every digestive parameter measured, using a one-way or two-way analysis of variance (ANOVA) available as a SPSS package (Nie, Hadla, Hull, Jenkins, Steinbrenner and Bent, 1975) on the IBM computer at the University of Pretoria. Pearson's correlation coefficient was used (Brown and Hollander, 1977). In all statistical analyses carried out on the data, significance was tested to the 95% level ($P<0,05$). Where means were calculated they are presented with standard deviations (SD).

CHAPTER III RESULTS AND CALCULATIONS

DIGESTIVE SYSTEM

The digestive system of the hyrax is schematically shown in Fig. 2. The oesophagus is a muscular tube 10 cm long. The stomach is 12 cm long and 9 cm wide and is divided by a 'constriction' very similar to the margo plicatus of the horse.

The small intestine is 1,0 - 1,5 cm in diameter and 1,5 meters long and passes into a sacculation (sac), 13 cm wide and 11 cm long. The sac has a 'rumen-like' appearance as it is formed out of four or five sacs or haustra and narrows to become the sigmoid proximal colon, which is 2 cm in diameter and 25 cm long. The proximal colon terminates between the paired caeca. Each of these caeca is 4 cm in diameter at the base and gradually narrows until it terminates in a veriform appendage about 1,5 cm long and 0,5 cm in diameter. No haustra were found as in the elephant caecum. The distal colon stretches from the caeca as a 3 cm wide tube which narrows after 1,0 to 1,5 cm. The colon terminates in a flexure which leads into the rectum. The length of the distal colon is 55 - 60 cm, making the length of the whole intestinal tract about 3 meters, approximately six times the length of the animal (50 cm).

For the purpose of this study the digestive system was separated into seven segments as illustrated in Fig. 2. No definite division of the sacculation and the colon were made as digesta of the mid and distal parts of the organs were in direct contact.

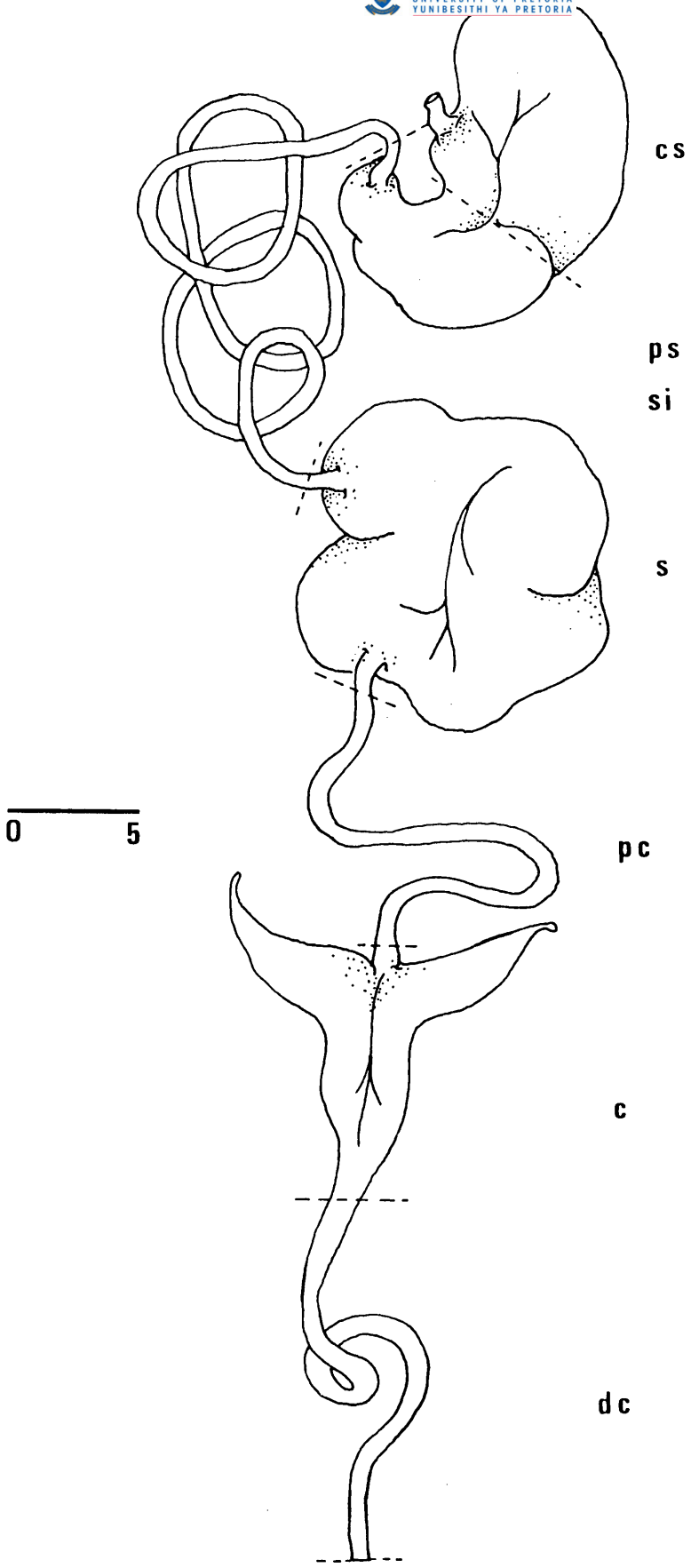

Fig. 2 Gastrointestinal tract of the hyrax: Procavia capensis. Symbols represent the cardiac stomach (cs); pyloric stomach (ps); small intestine (si); sacculation (s); proximal colon (pc); caeca (c); distal colon (dc).

TRANSIT TIME

No significant differences in transit time of digesta were found for rations 1, 3, 4 and 5 (Table 2a). In hyrax fed on rations 2 and 6 a significantly slower transit time of digesta was found, than in hyrax fed on rations 1, 3, 4 and 5. Measurements of retention times in the different tract parts were made for rations 4, 5 and 6; these are listed in Table 2b. Plastic material was visible in the sac four hours after feeding, for animals fed on all three rations. After 10 hours of feeding, plastic particles were detected in the caeca of animals fed on rations 4 and 5 but only after 16 hours could particles be found in the caeca of animals fed on ration 6.

Significant negative correlations were found between transit time and NDF content of the rations ($r = -0,97$) and cellulose content ($r = -0,87$). No other measured parameters correlated with the transit time.

Table 2a. Transit time of digesta through the laboratory hyrax fed on six different rations (hours).

Ration*	First appearance	Last appearance
1	35 ± 0,5	47 ± 6,0
2	[a]43 ± 2,0	57 ± 8,0
3	36 ± 0,5	48 ± 4,0
4	38 ± 1,0	56 ± 2,0
5	34 ± 2,0	48 ± 3,0
6	[a]44 ± 1,0	59 ± 9,0

* See Table 1.

Values bearing superscript [a] were significantly different from all others but not from each other.

Table 2b. Ingesta movement in the alimentary tract of laboratory hyrax.

Ration	Animal no.	Time between feeding and killing* (hours)	Furthest gut part containing plastic particles
4	13	4	Sac
	14	10	Caeca
	15	16	Caeca
	16	22	Caeca
5	17	4	Sac
	18	10	Caeca
	19	16	Caeca
6	20	4	Sac
	21	10	Sac
	22	16	Caeca

* All animals were fed at 03h00.

pH

In both the field and laboratory studies of pH of the alimentary canal parts, the stomach was found to be significantly more acidic than the rest of the tract.

In the field animals significant seasonal differences in pH were only found in the stomach (Fig. 3). The cardiac pH differed significantly from that of the pyloric region, except in the cool wet season. No correlations between the components of stomach content of the field hyrax sacrificed during the seasons and pH were found.

The pH values between the cardiac and pyloric stomachs of laboratory hyrax did not differ significantly from each other as was found for the field hyrax. The pH values of the stomachs as a whole of animals fed on ration 6 differed significantly from the pH values measured in animals fed on rations 4 and 5 (Fig. 4). A correlation of r = -0,94 was found between the NDF values of the three rations and the pH of the cardiac stomach contents of hyrax fed on rations 4, 5 and 6. No other correlations were found.

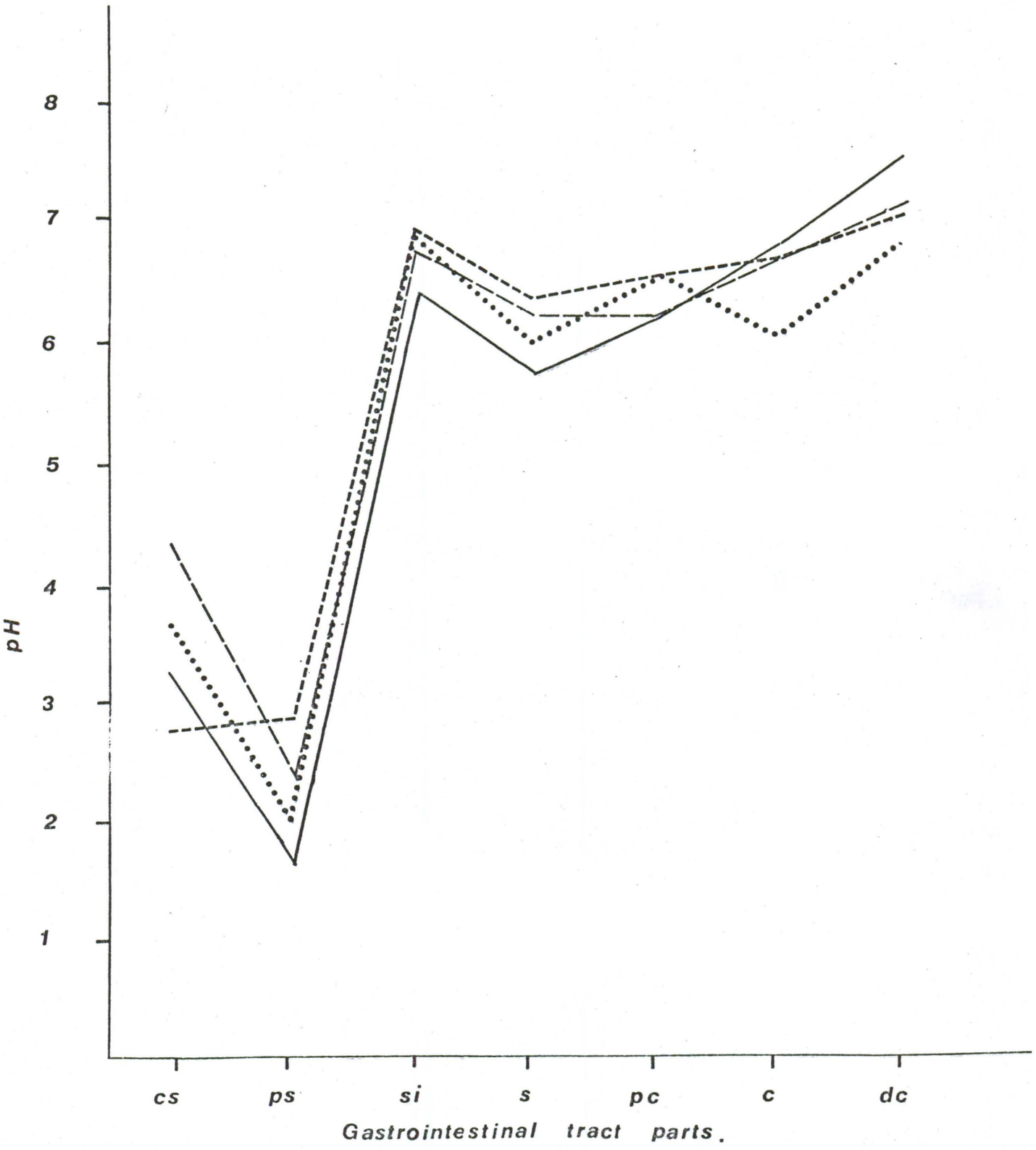

Fig 3. Mean pH values of the seven gastrointestinal tract parts of the 34 field animals. Symbolic lines correspond to the seasons:

Cool wet ---------
Cold dry ———————
Cool dry .....

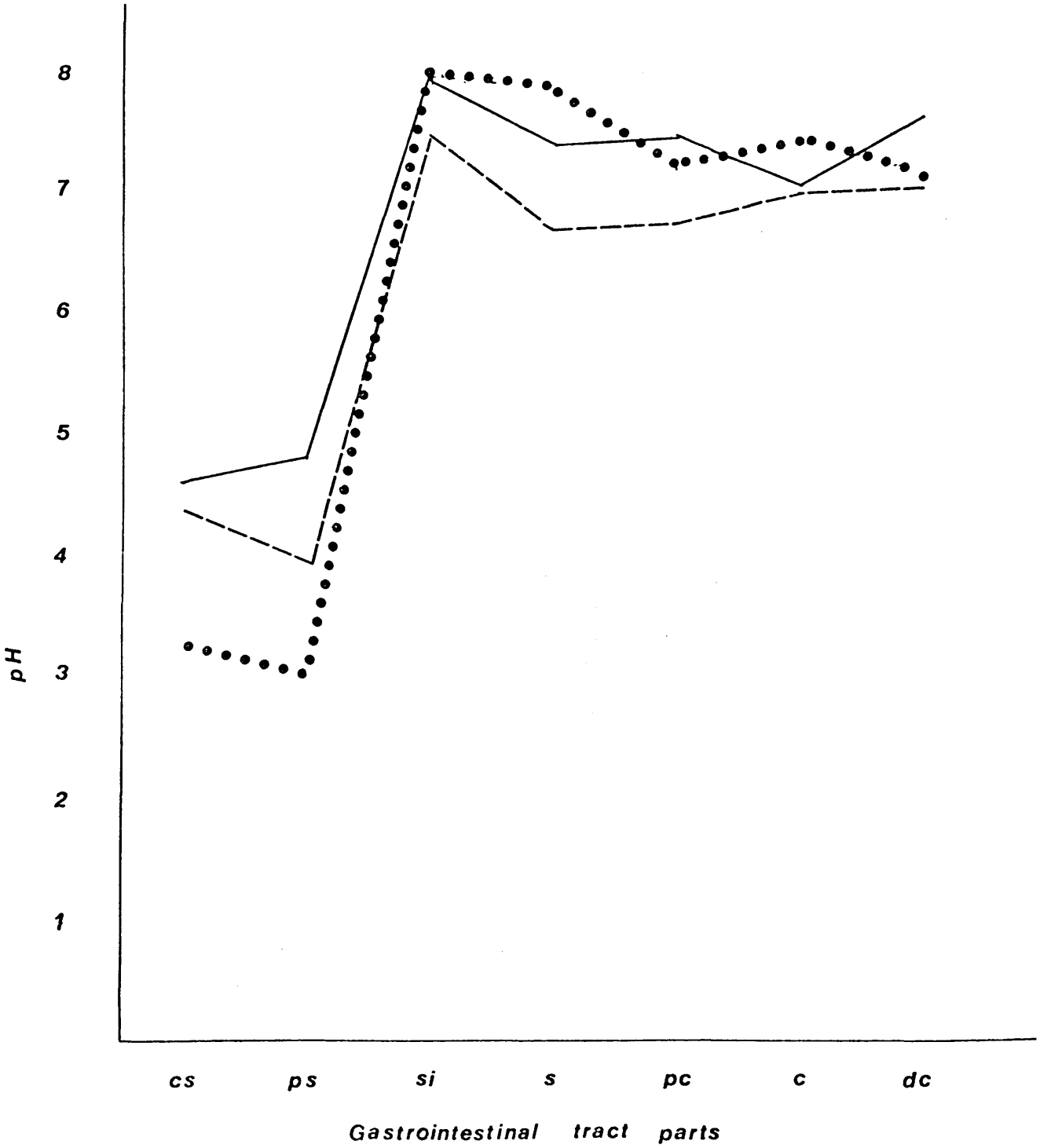

Fig 4. Mean pH values of the seven gastrointestinal tract parts of 10 laboratory Hyrax. Symbolic lines correspond to the ration

Ration 4 ————
5 — — —

DIGESTIVE TRACT CONTENT MASS AND VOLUME

From Table 3 it was found for both field and laboratory hyrax that the stomach, sac and caeca content masses and volumes were significantly different from each other. In both the field and laboratory hyrax the content masses and volumes of the sacs were higher than the other gut parts. The caeca content masses and volumes were higher than those of the stomach, except for hyrax fed rations 5 and 6.

In field hyrax the only significant differences found between seasons were those of the sac volumes, with hyrax sacrificed in the cool dry season having the largest volume. However, the stomach volumes, sac and caeca content masses and volumes of laboratory hyrax differed significantly when adapted to each of the three rations. The sac and caeca masses and volumes of hyrax fed on ration 5 were the lowest of all hyrax studied.

Comparing the stomach, sac and caeca content masses and volumes of field and laboratory hyrax the only significant difference found was the low caeca content mass of hyrax fed on ration 5.

For field hyrax the mean content masses as a percentage of body mass were found as follows; stomach: 3,2%, sac: 6,0% and caeca: 4,3%. However for laboratory hyrax a higher mean stomach to body mass percentage of 3,4%, but lower sac (4,9%) and caeca (2,8%) values were found.

The NDF, ADL and cellulose content of rations and the rate of passage of digesta in laboratory hyrax correlated to the sac content masses ($r = 0,97$) and volumes ($r = 0,89$).

TABLE 3 Mean body mass, digestive tract content mass and volume of field hyrax and laboratory hyrax fed on rations 4, 5 and 6.

Seasons or rations	Animal mass (kg)	Stomach content mass (g)	Stomach content mass as % of body mass	Stomach volume (ml)	Sac content mass (g)	Sac content mass as % of body mass	Sac volume (ml)	Caeca content mass (g)	Ceaca content mass as % of body mass	Caeca volume (ml)
Cool wet	2,3 ± 0,9	96,9 ± 17,9	4,2	139,5 ± 23,8	139,0 ± 20,5	6,0	^{a}220,0 ± 33,4	93,3 ± 17,7	4,1	168,0 ± 2,0
Cold dry	20 ± 1,3	100,6 ± 16,6	5,0	169,7 ± 18,1	150,0 ± 15,0	7,5	^{a}269,0 ± 15,4	101,0 ± 22,0	5,1	183,6 ± 1,0
Cool dry	2,8 ± 0,2	95,0 ± 20,1	3,3	184,0 ± 20,5	158,0 ± 20,0	5,6	^{a}240,7 ± 19,9	99,2 ± 23,7	3,6	193,0 ± 1,0
Hot wet	2,2 ± 0,2	90,8 ± 35,6	4,1	155,0 ± 19,2	103,0 ± 32,3	4,7	^{a}200,0 ± 23,1	98,0 ± 18,0	4,5	165,0 ± 6,0
4	3,6 ± 0,4	108,0 ± 8,1	3,0	^{b}165,0 ± 9,0	^{b}150,0 ± 7,0	4,1	^{b}250,0 ± 20,0	^{b}112,0 ± 20,6	3,1	^{b}193,0 ± 8,0
5	3,3 ± 0,6	94,3 ± 11,9	2,9	^{b}145,0 ± 14,0	^{b}105,0 ± 14,0	3,2	^{b}220,0 ± 11,0	^{b}66,0 ± 5,3	2,0	^{b}177,0 ± 3,0
6	2,6 ± 0,5	110,2 ± 25,6	4,2	^{b}120,0 ± 22,0	^{b}193,3 ± 7,7	7,4	^{b}290,0 ± 26,0	^{b}89,6 ± 42,7	3,5	^{b}200,0 ± 7,0

Values with common superscrips a or b in columns, were significantly different from each other.

QUALITATIVE ANALYSIS OF VFA COMPOSITION

Acetic, propionic, iso-butyric, butyric, iso-valeric and valeric acids were identified from the sac and caeca of field and laboratory hyrax. From Table 4 it is clear that acetic acid was the most abundant, propionic acid second and butyric acid third.

In field hyrax no significant differences in the VFA ratios were found between the sac and caeca,but between seasons iso-valeric and valeric acid percentages significantly increased for hyrax sacrificed during the hot wet season.

In the laboratory hyrax no significant differences were found between the VFA's in the sac and caeca but the concentration of acetic acid in the sac differed significantly with each of the rations eaten. Propionic acid concentrations in the sac of hyrax fed on ration 6 also differed significantly from the concentrations measured in the sacs of animals fed on the other two rations (4 and 5). Butyric acid concentrations in the sac of hyrax fed on ration 5 differed significantly from the concentrations measured in the sacs of the animals fed on the other two rations (4 and 6). Iso-butyric and valeric acid concentrations were significantly higher in the sacs of hyrax fed on ration 4 but iso-valeric acid concentrations were higher in the sacs of hyrax fed on ration 5. While iso-butyric acid concentrations were high in the caeca of hyrax fed rations 4 and 5, but iso-valeric and valeric acid concentrations were the highest in hyrax fed ration 4. In the caeca the acetic, propionic and butyric acid concentrations of hyrax fed ration 6 differed significantly from rations 4 and 5.

Comparing the different VFA compositions of the laboratory and field hyrax, acetic and butyric acid concentrations in both the sac and caeca of animals fed ration 5 differed significantly from those measured in all the field hyrax. Acetic acid concentrations of the sac and caeca of hyrax fed on ration 5 were significantly lower than acetic acid concentrations measured in the same gut parts of all the field hyrax. On the other hand, butyric acid concentrations of the sac and caeca of hyrax fed on ration 5 were significantly higher than the butyric acid concentrations measured in the sac and caeca of all field hyrax.

Positive correlations were found between the acetic acid percentages in the sac and caeca of laboratory hyrax and the NDF content (r = 0,98) and ADL content (r = 0,97) of the rations. Positive correlations were also found between butyric acid and the protein content of the rations in both the sac (r = 0,92) and caeca (r = 0,97).

VFA ENERGY VALUES

To determine the total amount of VFA energy produced every day in the hyrax, the individual kJ / mole values of the VFA's in the sac and caeca were summed (Table 5).

In the field hyrax only one significantly higher total VFA energy value was found, that being for the sac in the hot wet season. Otherwise, the sac and caeca showed no significant differences in total VFA energy for the different seasons. The higher total VFA energy values of the sacs of hyrax shot in the hot wet season, and those fed on ration 5 as well as the caeca of hyrax fed on ration 4 and 5, differed significantly from the rest but not from each other.

TABLE 4 Percentage composition of VFA in the sac and caeca of field and laboratory hyrax.

FIELD ANIMALS

Sac	**VFA conentrations : %**					
SEASON	Acetic	Propionic	I-Butyric	Butyric	I-Valeric	Valeric
Cool wet	68,2 ± 7,0	20,5 ± 5,0	1,5 ± 0,9	7,6 ± 2,6	1,1 ± 0,2	1,4 ± 0,6
Cold dry	65,8 ± 5,0	22,0 ± 3,2	0,2 ± 0,1	8,4 ± 3,4	0,3 ± 0,1	2,9 ± 0,6
Cool dry	63,5 ± 5,0	20,6 ± 0,6	2,9 ± 0,3	8,2 ± 2,6	1,6 ± 0,3	2,2 ± 0,6
Hot wet	58,2 ± 0,9	19,3 ± 2,0	2,0 ± 0,2	10,9 ± 4,3	4,0 ± 2,3	5,6 ± 3,1
Caeca						
Cool wet	67,8 ± 9,0	16,8 ± 6,7	3,5 ± 0,3	6,8 ± 0,4	3,7 ± 0,8	1,4 ± 0,2
Cold dry	67,2 ± 8,0	18,3 ± 5,1	4,1 ± 0,3	4,8 ± 0,6	3,5 ± 5,0	2,3 ± 0,9
Cool dry	64,6 ± 7,8	18,8 ± 2,2	4,2 ± 0,8	6,3 ± 2,3	3,3 ± 0,9	2,9 ± 0,1
Hot wet	62,5 ± 0,4	18,9 ± 1,3	4,5 ± 1,2	5,7 ± 0,4	4,1 ± 0,5	4,3 ± 2,4

LABORATORY ANIMALS

Sac	**VFA concentrations : %**					
RATION	Acetic	Propionic	I-Butyric	Butyric	I-Valeric	Valeric
4	$59,9^{bc} \pm 6,4$	$23,4^{b} \pm 1,6$	$5,1^{b} \pm 4,9$	$6,8^{b} \pm 1,6$	$1,0^{c} \pm 0,6$	$2,8^{bc} \pm 0,9$
5	$49,3^{bc} \pm 1,7$	$22,4^{c} \pm 9,4$	$0,5^{c} \pm 0,2$	$15,4^{bc} \pm 4,8$	$10,6^{bc} \pm 6,0$	$1,1^{c} \pm 0,3$
6	$76,1^{bc} \pm 5,1$	$14,3^{bc} \pm 6,0$	$1,1^{b} \pm 0,4$	$4,9^{c} \pm 4,0$	$0,2^{b} \pm 0,0$	$0,3^{b} \pm 0,0$
Caeca						
4	$54,5^{b} \pm 4,2$	$20,1^{b} \pm 1,0$	$6,5^{b} \pm 4,5$	$9,1^{b} \pm 3,1$	$5,4^{bc} \pm 1,3$	$4,6^{bc} \pm 1,6$
5	$48,8^{c} \pm 1,4$	$21,9^{c} \pm 4,0$	$8,7^{c} \pm 5,5$	$15,5^{c} \pm 6,0$	$2,7^{c} \pm 0,6$	$2,4^{b} \pm 0,6$
6	$77,1^{bc} \pm 6,1$	$16,1^{bc} \pm 6,2$	$1,5^{cb} \pm 0,6$	$5,0^{cb} \pm 0,5$	$0,1^{b} \pm 0,0$	$1,7^{c} \pm 0,2$

Values in the same vertical column bearing no superscript were not significantly different. Values in the same column bearing different superscripts : b or c are not significantly different from each other, but combined superscripts bc are significantly different from the rest.

Table 5*. Total energy values (kJ) of VFA in the sac and caeca of field and laboratory hyrax.

FIELD ANIMALS

Seasons	Sac		Caeca	
	$\bar{X}$	SD	$\bar{X}$	SD
Cool wet	1172,0	± 25,5	1246,8	± 30,2
Cold dry	1198,9	± 44,0	1205,9	± 30,0
Cool dry	1241,4	± 45,8	1257,0	± 56,0
Hot wet	[a]1457,3	± 35,6	1268,2	± 42,0

LABORATORY ANIMALS

Rations	Sac		Caeca	
	$\bar{X}$	SD	$\bar{X}$	SD
4	1256,4	± 13,2	[a]1404,1	± 18,9
5	[a]1473,3	± 31,0	[a]1434,3	± 36,0
6	1115,7	± 22,0	1100,9	± 17,7

* kJ/mole/ of: Acetic:874,4; Propionic:1527,3; I-Butyric:2183,5; Butyric:2183,8; I-Valeric:2837,8; Valeric:2837,8 (Weast, 1978)

[a] Values in vertical columns bearing superscript a were significantly different from other values but not from each other.

FERMENTATION RATES, PROTOZOA COUNTS, VFA PRODUCTION RATES AND GAS COMPOSITION OF FIELD AND LABORATORY HYRAX

The results of fermentation rates, protozoa counts, VFA production rates and gas compositions in the fermentative digestion compartments of hyrax are shown in Table 6.

Fermentation rates in the sacs of field hyrax were significantly higher than in the caecas. No seasonal differences were recorded in either compartment. In spite of the differences in fermentation rate, VFA production rates in the sac and caeca were of a similar magnitude and here too, no seasonal differences were apparent.

Hyrax fed on rations low in fibre content (rations 4 and 5) had high fermentation rates in the sac and when fed on the high fibre ration 6, a significantly lower fermentation rate was measured. Hyrax fed on rations 4 and 5 had higher fermentation rates in the sac than found in the field hyrax. In contrast, the fermentation rates in the caeca of laboratory hyrax were on the whole equivalent to that in the field hyrax. Negative correlations were found between the fermentation rates of the sac in laboratory hyrax and the NDF ($r = -0,98$) and the cellulose content of the rations ($r = -0,95$).

VFA production rates in the sac of hyrax fed on rations 4 and 5 followed the fermentation rate pattern mentioned above and were higher than in the field hyrax, while hyrax fed on ration 6 produced VFA in the sac at a similar rate to the field animals. In the caeca of laboratory hyrax VFA production was very much the same as in the field hyrax. The rate of VFA production in the sac of laboratory hyrax was negatively correlated with the NDF content of the rations ($r = -0,97$). No other measured parameters correlated with the rate of VFA production.

No correlations were found between protozoa counts and all other measured parameters in field hyrax. However for the laboratory hyrax a positive correlation was found between the protein content of the rations and the protozoa numbers of the sac ($r = 0,99$) and caeca ($r = 0,98$). Only two species of protozoa were found, both from the class Ciliophora. *Blepharosphaera intestinalis* and *Paraisotricha beckeri* have also been recorded in the horse (Hsiung, 1930) and the elephant (Eloff and Van Hoven, 1980) and the counts were relatively low in the hyrax. Chatton and

Perard (1919) described the genera *Nicollela* and *Colinella* in the hyrax. These protozoa were not found. Material corresponding to their description when investigated by scanning electronmicroscopy indicated that these workers might have mistaken *Acacia* leaves for these protozoa.

Gas composition was variable in both fermentation chambers and differed between the field and laboratory animals. No methane was measured in the sac of field hyrax with resulting higher values of carbon dioxide. Caecal values for methane on the other hand were similar in the field and laboratory animals. Although variable, the percentage of methane produced in hyrax fed on ration 6 was higher in both sac and caeca corresponding to the lower fermentation rate measured.

TABLE 6 Fermentation rates, protozoa counts, VFA production rates and gas composition of field and laboratory hyrax.

FIELD ANIMALS

Season	Fermentation rate [a.]	Protozoa counts	VFA production rate [b.]	Gas composition % CH_4	CO_2	H_2	N_2
			Sac				
Cool wet	241,9 ± 21	4,8 ± 0,37 x 10^3	3,23 ± 0,96	0,0	63	0,2	36,8
Cold dry	232,3 ± 21	4,4 ± 0,12 x 10^3	2,73 ± 0,72	0,0	70	0,3	29,7
Cool	254,9 ± 13	5,9 ± 0,06 x 10^3	3,45 ± 0,31	0,0	68	0,3	31,7
Hot wet	226,5 ± 11	5,3 ± 0,26 x 10^3	3,13 ± 0,15	0,0	71	0,3	28,7
			Caeca				
Cool wet	150,3 ± 21	6,3 ± 0,34 x 10^3	3,30 ± 0,25	25	34	0,2	40,8
Cold dry	146,3 ± 30	4,7 ± 0,17 x 10^3	2,58 ± 0,22	*33	30	0,4	36,6
Cool dry	151,9 ± 17	6,0 ± 0,17 x 10^3	2,35 ± 0,16	20	39	0,3	40,7
Hot wet	173,2 ± 21	6,9 ± 0,65 x 10^3	3,03 ± 0,10	18	43	0,4	38,6

LABORATORY ANIMALS

Ration	Fermentation rate [a.]	Protozoa counts	VFA production rate [b.]	Gas composition % CH_4	CO_2	H_2	N_2
			Sac				
4	367,5 ± 24	5,8 ± 0,19 x 10^3	4,01 ± 0,19	18	56	1,4	24,6
5	389,4 ± 23	6,7 ± 0,28 x 10^3	4,20 ± 0,44	13	57	1,7	28,3
6	*289,8 ± 11	4,8 ± 0,14 x 10^3	3,30 ± 0,14	*24	46	0,4	29,6
			Caeca				
4	158,7 ± 13	5,6 ± 0,25 x 10^3	2,80 ± 0,14	21	50	1,2	27,8
5	185,6 ± 18	5,9 ± 0,03 x 10^3	2,66 ± 0,31	18	58	2,2	21,8
6	*164,9 ± 15	4,6 ± 0,10 x 10^3	2,90 ± 0,21	*32	39	0,3	28,7

a. μmol gas/ g DM / hour

b. mmoles VFA / 100 ml digesta / hour

* Means in columns bearing a superscript were significantly different.

METHANE PRODUCTION

In Table 7 methane production in the sac and caeca of field and laboratory hyrax is listed in terms of the energy loss from the diet. These values were then expressed as a percentage of the daily digestible energy (DE).

In the field hyrax methane was only found in the caeca. Methane produced during the cool wet season was significantly higher than the other seasons. A positive correlation was found between the methane production and cellulose content of the food in the stomach (r = 0,97).

In laboratory hyrax methane was produced in both the sac and caeca. Methane production in the sac did not differ significantly between the rations, however in the caeca a significantly higher production was found when fed ration 6. A positive correlation between methane production (r = 0,98) of the caeca and the NDF content of the rations was also found. This connection between dietary fibre and methane production is also seen in the field animals where significantly higher methane production was found in the cool wet and cold dry seasons.

The mean total methane production of the field hyrax was 0,55 liter per day, while a higher amount of 1,19 liter / day was produced in the laboratory hyrax fed on rations 4, 5 and 6.

TABLE 7 Methane production, in field and laboratory hyrax.

Season or ration	A Organ	B Total gas production in l/24h	C Methane produced in l/24h	D Body mass kg	E [a]Methane	F [b]Energy content of C	G F as a % of D.E.c.
	Sac	2,83 ± 0,05					
Cool wet	Cacca	2,53 ± 0,05	*0,64	2,25 ± 0,9	11,81 ± 4,4	25,31	-
Cold dry	Sac	2,64 ± 0,07					
	Caeca	1,90 ± 0,07	*0,63	2,03 ± 1,4	12,93 ± 2,9	24,90	-
Cool dry	Sac	2,95 ± 0,03					
	Caeca	2,41 ± 0,03	0,48	2,78 ± 0,2	7,19 ± 0,5	18,97	-
Hot wet	Sac	2,78 ± 0,05					
	Caeca	2,39 ± 0,03	0,43	2,20 ± 0,2	8,14 ± 0,1	17,01	-
4	Sac	3,83 ± 0,11	0,69		8,00 ± 0,1	27,26	2,9
	Caeca	2,28 ± 0,07	0,48	3,60 ± 0,4	5,56 ± 0,1	18,93	1,9
	Total						4,8
5	Sac	5,17 ± 0,28	0,67		8,46 ± 2,2	26,57	2,9
	Caeca	1,74 ± 0,01	0,35	3,30 ± 0,6	4,42 ± 0,7	13,76	1,5
	Total						4,4
6	Sac	2,89 ± 0,06	0,52		8,24 ± 1,7	20,56	2,9
	Caeca	2,65 ± 0,04	*0,85	2,63 ± 0,5	*13,47 ± 2,2	33,61	4,5
	Total						7,4

a. Methane = ml/ kg body mass / hour.

b. One liter CH_4 = 39,54 kJ (Brower, 1965).

c. Digestible energy values from Table 10.

* Values bearing a superscript differ significantly from the rest.

METABOLIC ENERGY REQUIREMENTS

Metabolizable energy (ME) is defined as the heat of combustion of the food consumed less the heat of combustion of the faeces, gas and urine produced in the animal (Blaxter and Clapperton, 1965). Energy loss in faeces and urine of laboratory hyrax were measured for all animals fed rations 1 - 6, while the loss through methane was only measured in hyrax fed rations 4 - 6 and all field hyrax (Table 6 and Table 7).

In Tables 8a - 10 the contribution of VFA towards the basal metabolic needs (BMR) and the ME was calculated. The metabolic rates of field hyrax could not be determined and therefore BMR was calculated using Kleiber's formula (1961). ME of the laboratory hyrax was determined from the digestion trials (Table 9). The mean of VFA production and mean mass of digesta in the sac and caeca over a four hour period was assumed to be representative of a 24 hour period. It was also assumed that all VFA produced was absorbed, since none was found in the faeces of laboratory hyrax.

In the field hyrax (Table 8a and Table 8b), total VFA produced in the sac and caeca accounted for nearly 72 percent of the basal energy requirement except during the cool wet season when it supplied more than 80 percent. The picture for hyrax fed laboratory rations (Table 10) was very different with the high and low fibre rations (6 and 5) supplying close to 60 percent of the basal energy requirements. While the intermediate fibre ration 4 had the lowest VFA energy contribution value of about 50 percent corresponding to the low apparent digestibility (Table 13).

TABLE 8a Basal metabolic energy requirements and daily VFA production expressed as a percentage of basal metabolic energy for hyrax sacrificed during the cool wet and cold dry seasons.

	COOL WET		COLD DRY	
	Sac	Caeca	Sac	Caeca
Rate of VFA production (mmole/100 ml/hr)[a]	3,2 ± 0,96	3,3 ± 0,25	2,7 ± 0,72	2,6 ± 0,22
[b] 1 ml =	0,65 g	0,43 g	0,67 g	0,52 g
VFA production/ 24 h (mmole/100 g DM digesta).	118,1 ± 19,7	184,7 ± 28,4	97,0 ± 13,0	121 ± 17,0
Total digesta (g/DM)	139,0 ± 20,0	93,3 ± 17,7	150,0 ± 15,0	101,0 ± 22,0
Total VFA production/ 24 h / organ (mmole)	164,1 ± 33,8	172,3 ± 27,7	145,0 ± 20,5	122,0 ± 12,3
Total kJ value of VFA[c]	1172,0 ± 25,5	1246,8 ± 30,2	1198,8 ± 44,0	1205 ± 30,0
VFA energy / 24 h	192,3 ± 9,9	214,8 ± 14,4	173,8 ± 21,0	147,4 ± 8,7
Average body mass/kg	2,25 ± 0,87		2,03 ± 1,39	
Metabolic mass/kg^{0,75}	1,84 ± 0,87		1,701 ± 0,91	
BMR (kJ/day)[d].	538,0 ± 254,0		498 ± 263,6	
	Sac	Caeca	Sac	Caeca
VFA as a % of BMR	38,8	43,4	37,6	31,6
Total VFA as a % of BMR :	82,2		69,2	

a. From Table 6.

b. 1 ml digesta = x gram DM digesta

c. From Table 5.

d. From Kleiber's formula : 292,88 kJ / kg^{0,75} / 24 hours (1961).

TABLE 8b Basal metabolic energy requirements and daily VFA production expressed as a percentage of basal metabolic energy for hyrax sacrificed during the cool dry and hot wet seasons.

	COOL DRY		HOT WET	
	Sac	Caeca	Sac	Caeca
Rate of VFA production (mmole/100ml/hr)[a.]	3,5 ± 0,31	2,4 ± 0,16	3,1 ± 0,31	3,0 ± 0,10
1 ml = [b.]	0,66 g	0,47 g	0,72 g	0,52 g
VFA production/ 24 h (mmole/100 g DM digesta)	128,0 ± 18,9	123,3 ± 24,0	103,0 ± 15,5	139,9 ± 24,0
Total digesta (g/DM)	158,0 ± 20,0	99,2 ± 23,7	103,0 ± 32,3	98,0 ± 18,0
Total VFA production 24 h/ organ (mmole)	202,0 ± 12,3	122,3 ± 21,3	107,1 ± 10,5	137,2 ± 25,6
Total KJ value of VFA [c.]	1241,4 ± 45,8	1257,0 ± 56,0	1457,8 ± 35,6	1268,2 ± 42,0
VFA energy / 24 h	250,8 ± 14,5	153,7 ± 12,6	156,1 ± 19,6	173,9 ± 11,0
Average body mass/kg	2,80 ± 0,20		2,20 ± 0,20	
Metabolic mass / kg ^{0,75}	2,16 ± 0,49		1,81 ± 0,20	
BMR (kJ/day)[d.]	633,9 ± 95,8		529,1 ± 43,9	
	Sac	Caeca	Sac	Caeca
VFA as a % of BMR	44,1	27,0	32,2	36,0
Total VFA as a % of BMR :	71,1		68,2	

a. From Table 6.

b. 1 ml digesta = x gram DM digesta

c. From table 5.

d. From Kleiber's formula : 292,88 kJ /kg ^{0,75} / 24 hours (1961).

TABLE 9 Calculation of the metabolic rates per 24 hours of four laboratory hyrax fed on rations 1, 2 and 3.

	RATION 1		RATION 2		RATION 3	
Body massa (kg)	4,0	± 0,82	3,75	± 1,16	3,68	± 0,94
Intake/g/ 24 h	102,13	± 8,5	115,00	± 13,3	99,92	± 5,6
Food energy kJ/g	17,82		19,39		18,51	
G.E. (kJ)	1819,9	± 48,7	2229,6	± 275,3	1849,0	± 121,9
F.E. (kJ)	620,7	± 151,2	590,4	± 179,6	523,0	± 75,9
D.E. (kJ)	1199,2	± 125,7	1639,2	± 110,9	1326,5	± 36,0
U.E.	30,6	± 2,3	26,8	± 2,5	32,1	± 2,0
*G.P.D. (kJ)	66,1	± 15,1	67,2	± 15,4	65,0	± 10,2
M.E. (kJ)	1101,5	± 124,3	1545	± 114,5	1228,7	± 204,0
kJ/g/24h	0,2729	± 0,05	0,4080	± 0,08	0,3340	± 0,09
BMR (kJ/day)	828,38		789,25		778,17	

* No gas end-products were measured as no animals were sacrificed. The mean CH_4 value of the three following rations (4, 5 and 6) in Table 10 was used to calculate the M.E.

TABLE 10 Daily metabolic energy values (kJ) and daily VFA production expressed as a percentage of metabolic energy for hyrax fed on rations 4, 5 and 6.

	RATION 4		RATION 5		RATION 6	
	Sac	Caeca	SAC	Caeca	Sac	Caeca
Rate of VFA production (mmole/100 ml/hr)[a.]	40 ± 0,18	2,8 ± 0,14	4,3 ± 0,44	2,7 ± 0,31	3,3 ± 0,14	2,9 ± 0,21
1 ml[b] =	0,77	0,62	0,65	0,38	0,84	0,46
VFA production/ 24 h (mmole/100 g DM)	125,9 ± 19,1	108 ± 12,2	158,1 ± 23,2	170,3 ± 7,1	93,9 ± 5,2	151,4 ± 55,4
Total digesta (g)	150,0 ± 7,0	112,0 ± 20,6	105,7 ± 14,0	66,0 ± 5,3	193,3 ± 7,7	89,6 ± 42,7
Total VFA production/ 24 h / digestive organ/	188,9 ± 17,1	121,6 ± 38,6	167,0 ± 28,0	112,3 ± 11,4	181,2 ± 8,5	135,7 ± 28,8
Total kJ value of VFA[c.]	1256,4 ± 13,2	1404,1 ± 18,9	1473,3 ± 31,0	1434,3 ± 36,0	1115,7 ± 22,0	1100,9 ± 17,7
VFA energy / 24 h	237,4 ± 20,9	170,9 ± 40,1	246,1 ± 41,8	161,4 ± 22,6	202,1 ± 15,6	149,4 ± 13,6
Average body mass (kg)	3,6 ± 0,4		3,3 ± 0,61		2,6 ± 0,4	
Intake per gram / 24 h	76,2 ± 8,3		52,7 ± 3,6		55,0 ± 6,4	
Food energy content (kJ)	18,10		19,14		18,30	
G.E. intake (kJ)	1380,9 ± 115,9		1009,1 ± 69,8		1000,4 ± 31,8	
F.E. (kJ)	429,5 ± 36,7		106,2 ± 20,1		244,4 ± 11,0	
D.E. (kJ)	951,4 ± 102,9		902,9 ± 53,2		756,0 ± 18,4	
U.E. (kJ)	30,2 ± 2,5		22,6 ± 7,1		6,3 ± 1,8	
G.P.D. (kJ)	46,2 ± 1,7		40,3 ± 4,5		61,1 ± 5,7	
Metabolic energy (kJ)	875,0 ± 103,6		840,0 ± 59,0		688,6 ± 23,9	
Metabolic rate : kJ/g/24 h	0,2440 ± 0,08		0,2619 ± 0,07		0,2644 ± 0,04	
VFA in the sac and Caeca as a % of ME :	26,8	19,9	29,3	19,2	29,4	21,7
Total VFA as, a % of ME :	46,7		48,5		51,1	
BMR (kJ/day)[d]	765,45 ± 91,7		717,09 ± 131,2		599,68 ± 101,5	
VFA in ths sac and caeca as a % of BMR :	31,0	22,3	34,3	22,5	33,7	24,9
Total VFA as a % of BMR :	53,3		56,8		58,6	

a. From Table 6

b. 1 ml digesta = x gram DM digesta

c. From Table 5

d. Kleiber's formula (1961)

CHEMICAL COMPOSITION OF THE NATURAL FOOD AND THE LABORATORY RATIONS

The chemical composition of seasonal stomach content, rations and faeces is listed in Tables 11, 12 and 13.

A negative correlation was found between protein and ADL content of the stomachs of field hyrax shot during the seasons (r = -0,94). The mean NDF value of seasonal stomach contents was 46,8% and was higher than the mean NDF value of 30,7% found for the rations. The ADL value of 29,4% of the seasonal stomachs was also higher than the 7,5% ADL content of the rations (Tables 11 and 12). The NDF content of the stomach content of field hyrax was correlated (r = 0,96) with the NDF content of the faeces. No other significant correlations between stomach content and faeces components were found.

For laboratory hyrax (Table 12), the highest NDF content was found in rations 2 and 6, while the lowest NDF and ADL contents were found in rations 1 and 5. The highest protein content was also found in rations 1 and 5. The only significant correlation found was between the NDF content of the rations and the faeces (r = 0,82).

The digestibilities of dietary components of the rations were calculated using the quantitative collections of daily intake and faeces output of the experimental weeks (Lloyd, McDonald andCrampton, 1978). Cellulose digestion was the most efficient in rations 1 and 6, and the least efficient in rations 3 and 4. Protein digestibilities (Table 13) correlated negatively with the ADL content (r = -0,90) in the different rations.

TABLE 11. Chemical composition of seasonal stomach contents and faeces of field hyrax, in percentage.

Chemical components	Cool wet		Cold dry		Cool dry		Hot wet	
	Stomach	Faeces	Stomach	Faeces	Stomach	Faeces	Stomach	Faeces
Protein	19,3	40,2	13,9	26,5	24,1	38,7	21,0	33,4
NDF_a	42,0	48,0	41,5	51,0	54,5	62,0	49,5	55,0
ADF_b	40,0	32,0	37,0	41,0	43,0	49,0	40,5	45,0
$Hemicellulose_c$	2,0	16,0	4,5	10,0	11,5	13,0	6,0	10,0
Cellulose	21,0	26,0	28,9	20,4	19,4	13,0	3,0	10,0
ADL_d	28,0	4,6	37,0	12,0	26,2	46,5	26,5	47,0
Ash	0,05	0,30	0,94	1,60	1,20	4,50	1,90	1,80
Silica	0,80	1,00	2,40	0,50	0,50	1,30	0,30	0,20

a. Neutral detergent fibre.

b. Acid detergent fibre.

c. NDF – ADF = Hemicellulose.

d. Acid detergent lignin.

TABLE 12 Chemical composition of the rations and faeces of laboratory hyrax. (% concentration)

Chemical components	Ration 1	Faeces	Ration 2	Faeces	Ration 3	Faeces	Ration 4	Faeces	Ration 5	Faeces	Ration 6	Faeces
Protein	19,8	43,2	14,6	25,3	15,2	43,1	14,5	17,8	19,2	32,1	7,8	13,3
*NDF	22,5	35,0	49,5	42,0	24,0	37,5	23,0	23,5	15,5	28,5	49,5	62,5
ADF	7,5	24,5	31,5	31,0	9,0	21,5	11,5	33,1	6,5	0,5	32,5	51,0
Hemicel-lulose	15,0	10,5	18,0	11,0	5,0	16,0	11,5	10,4	9,0	28,0	17,0	11,5
Cellulose	19,5	11,8	14,5	26,0	2,5	17,0	8,0	7,0	5,5	6,1	17,5	1,5
ADL	3,5	7,2	5,0	8,2	7,5	15,5	10,5	11,0	4,0	15,4	14,0	19,3
Ash	0,5	0,6	0,2	0,2	0,5	0,0	0,7	0,2	0,5	0,2	0,1	1,0
Silica	0,7	1,9	0,7	1,0	0,3	1,0	0,3	1,0	0,3	1,1	0,3	0,6

* Cell content is the NDF value – 100

TABLE 13 Mean digestibilities of the chemical compounds of the rations %

Ration	1	2	3	4	5	6
Intake (g)	102,13	115,42	100,03	76,29	52,82	55,00
Faeces (g)	17,20	15,83	11,97	31,04	8,33	18,17
Digestibility %	83,16	86,28	88,03	59,31	84,22	66,96
% Protein dig.	64,33	76,22	66,08	50,19	73,99	44,29
% NDF	73,80	88,36	81,30	59,31	71,00	58,29
% Hemi dig.	88,21	86,50	87,26	63,21	50,94	77,65
% Cellu dig.	89,80	75,41	66,51	64,39	82,51	97,17
*DOM dig. %	83,90	82,52	87,72	58,83	90,38	65,23

*Digestible organic matter as calculated by the Van Soest three - fold formula (Van Soest and Moore, 1965).

CHAPTER IV DISCUSSION

The hyrax, *Procavia capensis*, feed for very short periods in the early morning and late afternoon, totalling less than two hours per day. They consume large volumes of food in these short periods, chewing it with their molars, and spend the rest of the day basking in the sun with little or no activity (Sale, 1966b; Hoeck, 1975). This limited feeding period and large food intake suggests that the hyrax has a digestive tract adapted to retain digesta over long periods to ensure efficient digestion.

The 'optimal foraging' theory of Tinbergen (1960) and MacArthur and Pianka (1966) postulated that natural selection acts to maximize the rate of intake of nutrients (energy). This can be interpreted as maximizing total intake or minimizing the time spent foraging. Hyrax appears to practise both concepts. In short periods of time it consumes large quantities of food and to maximize energy processing the food is passed through the gut from 34 - 44 hours depending on the ration. It has a slower rate of passage than the 23 hours of the horse (Alexander, 1946) and 17 hours of the pig (Castle and Castle, 1956).

The transit time of foodstuffs through the digestive system is affected by the physical nature of the food : particle size and maturity of plant cells; chemical composition : fibre and lignin content; and the amount of food consumed (Balch, 1950; Castle, 1956; Shellenberger and Kestler, 1961).

All the pelleted rations given to the laboratory hyrax were physically the same but differed chemically. The food transit time was negatively correlated with NDF and cellulose content of the rations. Hyrax fed on high fibre rations 2 and 6 had significantly slower food transit times than those fed on low fibre rations 1, 3, 4, and 5. Ration 4 had a transit time intermediate to the above mentioned extremes. The highest fibre ration 6 had a NDF value of 49,5% and when fed to hyrax, it was found to have a six hour slower transit time than found for the other rations, probably to ensure efficient fibre digestion.

The food transit time of field hyrax could not be measured, but one can assume that the high NDF and ADL values of their stomach contents must have caused an even longer retention of digesta than measured for laboratory hyrax fed on ground pelleted rations.

In the ruminant, rumen-size is related to body mass (Church, 1979). However this general relationship varies greatly as the physiologically effective volume differs between animals of the same mass and in the same animal from time to time because of differences in the diet (McBee, 1970). Yang, Manoharan and Mickelsen (1970) and Schneeman and Gallaher (1980) found that the rat did not increase food intake but increased caecal mass and volume when dietary fibre was high. The same was noted for rabbits (Hoover and Heitmann, 1972) and pigs (Farrell and Johnson, 1970). It seems therefore that monogastric animals tend to increase caecal or colon volumes and masses when feeding on high fibre diets by delayed transit to utilize structural carbohydrates effectively (Table 3).

In the field hyrax, sac masses and volumes were higher than the other gut parts. Although no correlations were found between the sac or caeca masses and volumes of field hyrax and the dietary fibre components of food eaten, the stomach, sac and caeca volumes and sac masses were the highest for hyrax sacrificed during the cold dry season and may be due to the low protein and high ADL and cellulose levels of the natural food. The lowest sac masses were found in the hot wet season when high protein, low cellulose and ADL values were found in the stomach contents of sacrificed hyrax (Table 11).

Hyrax fed the high fibre ration 6 had the highest mean sac mass and volume of 193,3 g and 290,0 ml respectively and also had the largest caeca content mass of all the laboratory hyrax studied. These higher masses were due to the slow transit rate of 44 hours of digesta as no increase of voluntary intake took place (Tables 9 and 10). The lowest caeca content mass was found in hyrax fed ration 5 and can be attributed to the high protein, low NDF and ADL contents which caused an increase in passage rate of digesta. However,with increase in fibre it was found that the caeca's role as a retention chamber increased slightly as illustrated by the small increase of caeca mass in animals fed ration 6.

Similarly, in the field hyrax a larger caeca mass was found during the cold dry season when the food was high in fibre (cellulose and ADL values were high). The results indicated that the caeca of field hyrax might play a more important digestive role than the caeca of laboratory hyrax, probably because of higher fibre levels in the natural foods.

In the gut, pH varies depending on the quality of the diet (Church, 1979). Field hyrax were found to have a more acidic tract (although not significant) than the laboratory hyrax. No correlations between pH and chemical properties of stomach contents of field hyrax could be found, but it may be the coarse physical (unground) state of field plant material which caused an abrasive action on the pyloric stomach wall, consequently releasing hydrochloric acid. The pH of the pyloric region of the laboratory hyrax was not significantly lower than the cardiac region and can be the result of the ground pelleted rations. The low pH values found in the cardiac and pyloric stomachs of hyrax when fed on ration 6 may be the result of the high NDF content which was a physical stimulus for hydrochloric acid release.

The mean pH of the small intestine of the field and laboratory animals were 6,7 $\pm$ 0,14 and 6,8 $\pm$ 0,57 respectively and suggests that pancreatic juice (bicarbonate-rich) and enzymes were secreted. In the sac and caeca of the field and laboratory animals, the pH decreased as VFA production increased and it can be assumed that cyclic variations of pH changed with VFA concentrations.

The presence of organic acids along the digestive tract of non-ruminants have been demonstrated repeatedly *in vivo*. Their concentrations are high and reach a maximum in the caeca and colon and decrease in the rectum (Elsden, Hitchcock, Marshall and Phillipson, 1946). These compounds represent the end-products from microbial digestion of food, and consist regardless of the type of food of four major acids: acetic acid, propionic acid, butyric acid and lesser amounts of valeric acid (Czerkawski, 1969; Eadie, Hylgaard-Jensen, Mann, Reid and Whitelaw, 1976). These end-products of fermentation were also found in the hindgut of hyrax.

In Table 14 the findings of the present study were compared to published data for various non-ruminants and a few ruminants. Leon (1980) found acetic, propionic and butyric acids in the sac of *P. capensis* comprising of 69%, 22% and 8% respectively. These results were higher than found in the present study and were probably due to the free volatile fatty acids present in the lucerne diet Leon (*pers. comm.*) fed them.

In the present study only trace amounts of VFA were found in the stomach with acetic acid concentrations similar to that recorded by Leon (1980), but it must be stressed that no VFA production were found in both the cardiac and pyloric stomachs. This was also noted by Von Engelhardt *et. al.* (1978) for hyrax. Although Leon (1980) and Clemens (1977) measured high concentrations of lactic and acetic acid in the cardiac stomach, they did not measure the amounts of VFA produced. In contrast with their higher pH measurements, low pH values were found in both the stomach compartments which made fermentation almost impossible, only bacteria ingested with the food eaten could cause the presence of acetic acid concentrations.

A number of studies have shown that VFA concentrations were influenced by the diet and site of production. In the large intestine of the pig a high cellulose diet caused a rise in the acetic acid content and a decrease in propionic acid (Friend, Cunningham and Nicholson, 1963; Rèrat, 1978). In the hyrax sac and caeca the same was found when the high fibre ration 6 was fed, as soluble carbohydrates were most likely too low to support propionic acid production (Hungate, 1966).

TABLE 14 Molar percentages of VFA in various avian, marsupial and mamalian caeca.

Species	Organ	C_2	C_3	i-C_4	C_4	i-C_5	C_5	VFA as % of maintenance	Author
Ptarmigan	Caeca	70,4	21,3		8,0			18,0	Gasaway, 1976 a,
Grey kangeroo	Caecum	82,0	13,0	0,5	4,0	0,3	0,4		Kempton, Murray and Leng, 1976
Rat	Caecum	65,9	8,4		25,7			4,7	Yang et al, 1970.
Rabbit	Caecum	67,0	11,0		22,0			12,0	Hoover and Heitmann, 1972
Eritizon	Caecum	74,0	12,0		14,0			33,0	Johnson and McBee, 1967
Beaver	Caecum	66,0	12,0		20,0			33,0	Currier, Kitts and Cowan, 1960
Dog	Large intestine	46,8	37,8		15,8		2,0	28,0	Phillipson, 1947
Procavia capensis	Stomach	87,0	9,0		3,0				
	Sac	69,0	22,0		8,0				
	Caeca	75,0	17,0		2,0				Leon, 1980
P. capensis	Sac	63,9	20,0	1,7	8,5	2,0	4,8	35,5	
	Caeca	66,0	18,2	3,8	5,7	3,7	2,7	29,1	Present study
Swart wildebeest	Rumen	70,3	12,3	1,4	12,9	1,7	1,2	66,7	
	Caecum	73,9	12,2	2,6	5,5	1,1	1,8	5,5	Van Hoven and Boomker, 1981
Hippopotamus	Caecum	65,8	23,7	0,5	8,1	1,0	1,3		Van Hoven, 1978
Horse	Caecum	72,0	22,5		5,5				
	Colon	67,0	19,5	13,5					Elsden et al, 1946
Pig	Caecum	60,0	32,0		7,5				Friend et al, 1963
Sheep	Rumen							80,0	
	Caecum	79,0	14,0	0,4	5,0	0,6	0,9	8,0	Kempton et al, 1976
Cattle	Rumen	68,0	21,0		11,0			72,0	Caroll and Hungate, 1954

A rise in the production of butyric acid is caused by a decreased fibre content in the diet of pigs (Rèrat, 1978) and rats (Hoover and Heitmann, 1972). Glucose, fructose and sucrose are fermented most rapidly in the rumen which lead to increased formation of propionic and/or butyric acid (Sutton, 1969). Selective culturing of micro-organisms to ferment protein in the rumen was also found (Youssef and Allen, 1969). In hyrax fed ration 5, butyric acid concentrations were significantly higher and acetic acid concentrations significantly lower as the direct result of decreased fibre (NDF) and increased protein contents as well as higher protozoa numbers which hydrolyze proteins.

The carbon skeletons for amino-acid synthesis and cellolytic and methanogenic bacterial growth have tc be formed from fermentation end-products : carbon dioxide, acetic, n-butyric, iso-butyric, n-valeric and iso-valeric acids. Branched-chain fatty acids are required for the growth of cellulolytic bacteria, produced from amino-acids by non-cellulytic and non-methanogenic bacteria, while methanogenic bacteria needs n-valeric acid for growth formed from carbohydrates, also by non-cellulytic and non-methanogenic bacteria (Hungate, 1966).

Although little iso-butyric, iso-valeric and n-valeric acids were present in the guts of field and laboratory hyrax, they were found to be present in significantly higher percentages in the caeca than in the sac. Iso-valeric and valeric acids were the highest in the sac of the hot wet season, indicating that amino-acid synthesis from fermentation end-products might mainly take place in the caeca. The high valeric acid concentrations in both the sac and caeca of hyrax fed ration 4 (valeric acid being the only growth factor of bacteria formed from carbohydrates) might be the result of high soluble carbohydrate content of the ration (Table 12). In hyrax fed ration 5, high iso-valeric acid concentrations in the sac and high iso-butyric acid concentrations in the caeca were a result of the high protein content of the diet and indicated a contribution towards bacteria growth.

In the sac and caeca of field hyrax VFA were produced in a constant pattern and were not comparable with the concentration values found for hyrax fed on rations 4, 5 and 6 as these rations were compiled with definite varying combinations of protein and fibre content.

It was evident that dietary quality affected not only the composition and production of VFA, but also the energy values of VFA (Table 5). In the sac and caeca of laboratory animals where significant differences in VFA concentrations for rations 4, 5 and 6 (Table 4) were found, VFA energy values showed a similar pattern. Valeric and butyric acid energy values are the highest per mole and where these two acids were found abundantly (hot wet season and ration 5) the total VFA energy values were highest (Table 5). When the total VFA energy values of the field and laboratory hyrax were compared, the hot wet season and ration 5 produced similar and the highest values which can be related to their low cellulose and high protein contents.

Elsden *et al.* (1946) found that in the hindgut of non-ruminants such as the rabbit, pig and horse, large amounts of VFA were produced, reaching a maximum in the caecum and colon and decreasing in the rectum. VFA production rates of up to 7,5 mmoles / 100 ml / h, were measured in the caecum and colon of the horse, pig, rabbit, rat and guinea-pig (Alexander and Davies, 1963). In the rumen of cattle a VFA production rate of 6,2 mmoles / 100 ml / h was found (Whitelaw, Hylgaard-Jensen, Reid and Kay, 1970) and in the rumen of sheep Faichney (1969) obtained a value of 5,5 mmoles / 100 ml / h.

In the sac and caeca of field hyrax no significant differences in the rate of VFA production were found, but generally the rate was higher in the sac than in the caeca (Table 6). The VFA production rates of the sac reached a maximum value of 3,45 mmoles / 100 ml / h in the cool dry season, which may be due to the high protein and low ADL contents of food available, but in the caeca a lower value of 2,35 mmoles / 100 ml / h was recorded (Table 6). However in the cool wet season the picture was reversed, the caeca produced 3,3 mmoles / 100 ml / h of VFA, while the sac only produced 3,2 mmoles / 100 ml / h of VFA.

In the sacs of laboratory hyrax fed ration 5, a high mean VFA production value of 4,2 mmoles / 100 ml / h was recorded and in the caeca a significantly lower 2,66 mmoles / 100 ml / h was found. The greater qualitative diet differences of rations 4, 5 and 6 resulted in significantly higher VFA production in the sac than in the caeca. In this study the highest

VFA production rates of 4,0 and 4,2 mmoles / 100 ml / h were measured in the sacs of hyrax fed on rations 4 and 5 respectively, and were due to the low NDF contents of the rations. When cellulose levels in the food of pigs were increased, VFA production rates decreased in the large intestine (Friend *et al.*, 1963). A lower VFA production rate of 3,3 mmoles / 100 ml / h was found in the sacs of hyrax fed ration 6 as a result of high NDF and cellulose levels.

The absence of VFA production in the small intestine, proximal and distal colon of hyrax, resembles that observed at similar sites in the rabbit (Pickard and Stevens, 1972) and goose (Clemens, Stevens and Southworth, 1975). These organs probably lack digestive enzymes, and no protozoa were found. It was assumed that volatile fatty acids were absorbed at the site of their formation; that is through the walls of the sac and caeca. Since the proximal colon is a connecting chamber between the sac and caeca it is probably also a site of VFA absorption. The distal colon stores faeces for water absorption and controlled expulsion of faeces.

Comparing the VFA production rates of field and laboratory hyrax, no significant differences between the sacs and caecas of these groups were found; however laboratory hyrax generally produced more VFA. This was probably due to the pelleted rations, as Sutton (1980) reported that pelleting increased surface area available for microbial attack and increased VFA production rates in ruminants. These results indicated that VFA production rates were associated with the quality of food, fermentation rates (Table 6), microbial numbers (Table 6) and substrate availability. It must be stressed that high VFA production rates do not indicate that more VFA energy will be produced. The total VFA produced was affected by total mass and transit time of the digesta as well as VFA composition, VFA absorption, VFA interconversion and usage by bacteria.

All gases found in the alimentary tracts of animals are known products of bacterial metabolism, except nitrogen and oxygen which are swallowed. Carbon dioxide is always present in higher concentrations than in the atmosphere. Hoppe, Qvortrup and Woodford (1977) have shown high fermentation rates in wild grazers due to selection of green sheaths and leaves, for example blue wildebeest produced an average of 210 µmol / gas / g DM / h in the rumen. In browsing field hyrax an average fermentation rate of 239 µmol / gas / g DM / h was produced in the sac and 155 µmol / gas / g DM / h in the caeca, while in laboratory hyrax 348 µmol / gas / g DM / h was produced in the sac and 159 µmol / gas / g DM / h in the caeca.

More gas was produced in the sac than in the caeca of field and laboratory hyrax, emphasizing the sac as the major microbial fermentation site.

The higher fermentation rates produced in the sacs of laboratory hyrax, may be due to the lower ADL contents of the rations which caused increased microbial fermentation of cell contents. Fermentation rates in the sac and caeca of laboratory hyrax were the highest for hyrax fed ration 5. High protein content in the food and resultant higher microbe numbers, might have caused the increased fermentation rate. A significantly lower fermentation rate was found in the sac and caeca when fed ration 6 as a result of the high NDF and cellulose values of the food.

On the whole, fermentation rates produced in the sac and caeca of field and laboratory hyrax were high. Hyrax seemed to select green plant material high in protein content as the stomach analysis of field hyrax reflected high protein values (Table 11) and their efficiency to utilize protein was underlined by the high protein digestibilities found when hyrax were fed high protein rations (Table 13).

Czerkawski (1969) showed that methane production increased with fibre content and decreased with an increase of crude protein in the food. Methane production is associated with a slow steady process and not with an explosive type of fermentation. The major precursors of rumen methane are hydrogen, carbon dioxide, formate and acetic acid, and usually

constitutes from 15% to 30% of the total amount of gas produced in herbivores such as cattle, sheep, horses and rabbits (Church, 1979). Its production is influenced by the physical and chemical nature of the food and amount consumed (Hungate, 1966; Sutton, 1980).

No methane was found in the sacs of field hyrax and was probably due to the absence of methanogenic bacteria. However methane was produced in high quantities in the caeca of field hyrax. The amount of food consumed by field hyrax could not be measured, but it was found that hyrax sacrificed during the hot wet season had the lowest stomach, sac and caeca masses and could be the result of rapid fermentation of more digestible food. This coupled with the low cellulose content of the season's food of only 3% caused a slightly lower acetic acid value (62,5%) in the caeca and a lower methane production of 0,43 / l / 24 h. During the cool wet and cold dry seasons, methane production averaged 25 and 33 percent respectively of the total gas composition and means of 0,64 and 0,63 / l / 24 h methane were produced (Table 7). These results were higher than the methane production of the hyrax sacrificed in the cool dry (0,48 / l / 24 h) and hot wet (0,43 / l / 24 h) seasons and was probably due to the higher cellulose and ADL contents of the natural food (Table 11). The amount of food consumed by laboratory hyrax was measured and when the high protein ration 5 was fed to them, a lower intake of food caused a lower methane production, amounting to only 4,4% of the digestible energy produced (Table 7). Methane production was highest in hyrax fed ration 6. In the caeca of hyrax fed this ration methane averaged 32% of the total gas composition, with a production of 0,85 / l / 24 h which was significantly higher than the production found in the sac and caeca of hyrax fed on rations 4 and 5 of all hyrax sacrificed in the field (Table 7).

The means of carbon dioxide and hydrogen gas percentages in the sacs of laboratory hyrax were higher than those of the field hyrax, indicating a high methane production. No methane was found in the sacs of field hyrax and it was assumed that the higher total production of methane in laboratory hyrax is probably a result of the pelleted rations and was a loss of energy. Bergen and Yokoyama (1977) found that an inhibition of methane production can enhance rumen fermentation efficiency. It might be that the caeca of field hyrax played an equally important part in the fermentation process as the sac. This was indicated by the

VFA production rate and fermentation rate values (Table 6), and could be the reason for the absence of methane in the sac.

The mean methane production in *P. capensis* sacrificed in the field varied between 7,19 - 12,93 ml / kg body mass / h and for laboratory hyrax total values of up to 21,71 ml / kg body mass / h was measured. These values were higher than the 2,4 - 8,4 ml methane / kg body mass / h measured for *P. habessinica* by Von Engelhardt *et al.* (1978).

It was found that 40 to 80 percent of the basal metabolic needs (BMR) of ruminants are derived from ruminal VFA (Table 14). It is accepted that the remaining requirements are met by soluble carbohydrates absorbed in the small intestine, microbial formation of lactic and succinic acids in the rumen and that the fermentative contribution of the hindgut is negligible (Caroll and Hungate, 1954). In non-ruminants, several studies on pigs (Farrell and Johnson, 1970), rabbits (Hoover and Heitmann, 1972), rats (Yang *et al.* 1970) and ptarmigans (Gasaway, 1976a and 1976b) have indicated that there is little contribution from caecal fermentation to the overall energy budget. However studies by Johnson and McBee (1967) on porcupines and Hoover and Clarke (1972) on beavers, suggested that production of VFA in the caecum, if absorbed, could account for up to 33% of the maintenance energy requirement (Table 14).

The nutritional contribution of end-products in the hindgut of hyrax are very important. Digestion in the sac and caeca of field hyrax seemed to contribute equally towards the total VFA energy produced each day. A trend was found towards higher VFA production in the caeca of hyrax sacrificed during the hot wet and cool wet seasons. The total VFA produced in the sac of field hyrax measured during the cool dry season comprised up to 44% of the BMR and was higher than the results obtained from any of the rations (Table 10).

The lower VFA contribution in the sacs of laboratory hyrax (a maximum of 33,8% when fed ration 5) can be due to the ground state of the pelleted rations and presence of higher amounts of soluble carbohydrates (Table 12).

Field hyrax stomach samples had higher NDF values than the rations fed to laboratory hyrax and therefore less soluble carbohydrates were available for enzymatic breakdown and more VFA had to be produced to compensate and to provide enough energy. The same trend was found in the caeca of field hyrax, where the VFA energy produced in the cool wet season comprised up to 43,4% of the BMR, while laboratory hyrax fed ration 6 produced only a maximum percentage of 25,5% of the BMR as VFA energy (Tables 8a, 8b and 10).

No significant differences were found between the six different metabolisable energy values determined for laboratory hyrax (Tables 9 and 10). Values calculated for rations 1, 2 and 3 were higher than those of the rations 4, 5 and 6. This could be due to the higher food intake of hyrax with a higher body mass and to the fact that hyrax fed rations 1, 2 and 3 were not sacrificed and no methane energy could be measured. The mean methane values of rations 4, 5 and 6 were used and could underestimate the actual values.

The highest ME value of 0,4050 $\pm$ 0,08 kJ / g / 24 h and lowest ME value of 0,2440 $\pm$ 0,03 kJ / g / 24 h were calculated for rations 2 and 4 respectively (Tables 9 and 10). McNairn (*pers. comm.*) determined the RMR (with a mean mass of 3,2 kg) at 26^{o}C and found that hyrax required 0,2408 $\pm$ 0,06 kJ / g / 24 h. Oxygen consumption is a more accurate estimate of metabolic demands, but this result corresponds with all the ME measurements made in digestibility trials, which emphasizes the usefulness and accuracy of these trials for measuring metabolic needs.

The digestibility of protein is mainly influenced by the amount of food consumed, the transit time of digesta, presence of inhibitors and the amount of indigestible fibre (Sauer, Eggum and Jacobsen, 1979). A negative relationship between dietary crude fibre and protein digestibility was found in pigs (Schneider, 1934; Gargallo and Zimmerman, 1980) and rats (Meyer, 1956; Schneeman and Gallaher, 1980). Different levels of protein should be compared in diets with the same type and level of fibre. In this study the type and amounts of fibre differed for every season and ration (Tables 11 and 12).

Apparent protein digestibility could be calculated for laboratory hyrax and a decreased protein digestibility was found in hyrax fed on rations 4 and 6. This was due to the increased ADL content of rations (Tables 12 and 13). In ration 2, where the NDF was higher, no decrease in protein digestibility was found due to a low ADL content (Tables 12 and 13). This emphasizes the major influence ADL had on protein digestibility.

Protein digestibility could not be calculated for field hyrax as no intake and output values were available. However, from the results and interpretation of protein digestibilities calculated for laboratory hyrax, certain assumptions could be made. ADL values were much higher than even ration 6 and therefore it can be expected that protein availability in the field is much lower than the amounts determined from stomach analysis. Also the fact that hyrax could maintain themselves on a low protein diet, like ration 6, for limited periods of time, shows that *P. capensis* can digest low quality food. Although high NDF values of 54,5% and 49,5% for the cool dry and hot wet seasons respectively were measured, the ADL values of 26,2% and 26,5% respectively were lower than those of the cold dry (37%) and the cool wet (28%) seasons. Higher protein digestibilities could be expected during the cool dry and hot wet seasons with lower protein digestibilities during the cold dry and cool wet seasons.

The abrasive action, water holding capacity, lignification and silification of fibre affects its availability to animals. When cellulose is completely freed from lignin, cutin and silica, it is more or less completely digestible by micro-organisms in the digestive tract (Van Soest, 1973). Micro-organisms in the intestines of animals are responsible for the degradation of cellulose and contribute by producing volatile fatty acids, B-complex vitamins, and by synthesizing and absorbing amino-acids.

The 'proximate' method of analysis is a 'crude' estimate of the true content of fibrous cell wall constituents since it includes most of the relatively digestible hemicelluloses, but omits the highly indigestible lignin. The method of Van Soest (1964) showed that digestibility is related to the total cell wall content, proportion of lignin in the cell walls and the silica content.

Cell wall components were considered to be chemically inactive when fed to monogastric animals. Research in the last decade has indicated that structural carbohydrates are fermented in the hindgut by micro-organisms, similar to that in the rumen and that non-ruminants do not digest cellulose as effectively as ruminants. Cellulose and hemi-cellulose digestion in the sheep were estimated to be 67% and 77% respectively (Keys, Van Soest and Young, 1969). However, in non-ruminants like rats (Yang *et al.*, 1969), beavers (Currier *et al.*, 1972), rabbits (Hoover and Heitmann, 1972) and pigs (Keys, Van Soest and Young, 1970) cellulose digestibility was found to be only 43, 30, 34 and 44% respectively. These results give an indication of the ability of monogastric animals to digest fibre, but a factor that can influence results is the amount of fibre in the experimental diets fed to these different species.

The mean capacity of the hyrax to digest cellulose was 80% and for hemi-cellulose 76%, measured during the experimental weeks feeding hyrax six different rations. The effect of pelleted rations might have influenced the digestibility, but there is no doubt that the hyrax can digest fibre equally well as ruminants. Like ration 4 (23,0%) and ration 6 (49,5%), ration 2 had a high NDF value (49,5%), but in contrast a high apparent digestibility of 86,3%. This could be due to the low ADL content of 5,0% in comparison with the high lignin content of ration 4 (10,5%) and ration 6 (14,0%) (Table 12). This high lignin content caused a lower protein and NDF digestibility. The cellulose in ration 6 was digested very effectively. It could be accomplished through an increase in mass and volume of the sac (Table 3) and a lower transit time of digesta (Table 2a) and not necessarily through an increase in fermentation rate. This was also found for rabbits (Hoover and Heitmann, 1972) and beavers (Hoover and Clarke, 1972). Ration 5 had a high protein, low NDF content and highest apparent digestibility when fed to hyrax. Fermentation rates, VFA production rates and protozoa numbers were also higher in the digestive tract of hyrax fed ration 5, than of hyrax fed rations 4 and 6.

In the cool wet and cold dry seasons food had a low protein, high cellulose and lignin content. In the caeca of hyrax sacrificed during these seasons, the rate of fermentation, VFA production and protozoa numbers decreased, but the caeca mass and volume increased to ensure maximum digestion and absorption (Table 3).

On the whole digestibility of cellulose in the hyrax can be related to the degree of cellulose lignification and types of cellulolytic bacteria. Although digestibility of food in field hyrax could not be calculated, the VFA production per day, when compared with VFA production rates of laboratory hyrax, indicated similar abilities to digest fibre efficiently.

Erasmus, Penzhorn and Fairall (1978) found that the chemical composition (ADL, NDF, ADF fractions and ether extract) of springbok and mountain zebra faeces reflected veld quality. In the present study only the NDF content of food and faeces could be correlated with each other and it can be concluded that total cell wall content (NDF) of hyrax faeces was the only reliable component that showed seasonal variations of the quality of food available to hyrax in the field.

Gradual evolution of higher plants and the resultant change of the nutritional environment, must have set the framework within which mammals developed and evolved (Kurtén, 1971). Up to the Eocene the landscape had been dominated by forest and it was not until the Miocene that large areas of herb and grass developed, favoured by the cooler and drier climates of the time (Pearson, 1964). During the Miocene and Pliocene a rapid radiation of bovids and macropods occurred, concurrently with the development of widespread grasslands (Janis, 1976). Kurtén (1971) suggested that hyrax was at that time an established browser. The microbial populations which arose long before mammals evolved, have been in association with vertebrates for more than two million years, and had the ability to adapt to food regimes not previously encountered (Moir, 1968).

In nearly all herbivores one or more parts of the digestive tract expanded to form an organ which accommodates a microbial population which commensally aids in the fermentation of food material. The exploitation and colonization of new and more restricted trophic environments necessitated the development of increasingly complex digestion systems. These were the caecum and colon of mono-gastric mammals and the rumen of digastric herbivores. The range of respective functions, enzymatic degradation, fermentation, rumination and coprophagy, developed to ensure

the mechanical breakdown of fibre. Janis (1976) described caecal digestion in the non-ruminants as a superior adaptation for dealing with food high in fibre content. Parra (1978, from Hume and Warner, 1980), suggested that body size is important in determining an animal's tolerance of high fibre. Larger animals can tolerate poorer quality diets as they need less energy and protein per unit body mass. This assumption is not necessarily true, McNairn and Fairall (1979) found that the hyrax has a lower rate of energy expenditure than predicted by Kleiber's formula. Therefore poor quality food can be used, as digestion and absorption is facilitated by a slow transit time through the gut. The development of a peculiar hindgut with fermentation as its main function aids the survival of hyrax in a predominantly semi-arid environment.

The contents of the digestion tract parts as a percentage of body mass in non-ruminants and ruminant herbivores and non-ruminant omnivores is given in Table 15. The relatively larger caecums and colons in the non-ruminant herbivores such as the ptarmigan, *Cryptomys*, *Otomys*, the rabbit, beaver, hyrax and horse, should be emphasized. It was found that the hyrax hindgut represented 11,5% of body mass in comparison to the mean of 1,9% for ruminant herbivores and 3,8% for non-ruminant omnivores and is only equalled by *Otomys*, a non-ruminant roughage feeder.

Digestion and absorption of soluble and readily available substrates probably occurs in the small intestine of hyrax. The development of the enlarged sac as major fermentation chamber must have been influenced by the coarse nature of the food and the great bulk of food ingested in short feeding periods. The sac seems to be a 'rumen-like' organ and probably developed together with the 'bird-like' caeca to increase volume and surface area for successful digestion, storage and absorption of end-products.

Hyrax successfully colonized arid rocky hills with small home ranges. They are exposed to harsh environmental conditions such as intense solar radiation, absence of water and limited food resources and have adapted by lowering the rate of energy expenditure with regard to body size, feeding with intense speed on food sometimes low in nutritional value and developing the ability to digest fibre effectively.

TABLE 15 The contents of digetion tract parts as a percentage of the body mass in various animals. Standard deviation where available are included.

Species	*Feeder	Organ	Contents as a % of body mass	Reference
Willow ptarmigan	H	Caecum	5,9	Gasaway, 1976 a.
Red-necked wallaby	H	Stomach	9,5 ± 1,3	
		Hind-gut	0,5 ± 0,1	Hume, 1977
Pademelon	H	Stomach	9,5 ± 0,2	
		Hind-gut	1,3 ± 0,2	Hume, 1977
Cryptomys	H	Stomach	0,5	
		Caecum	10,5 ± 1,2	Perrin and Curtis, 1980
Saccostomus	O	Stomach	0,7	
		Caecum	4,0 ± 0,8	Perrin and Curtis, 1980
Otomys	H	Stomach	1,0 ± 0,2	
		Caecum	11,1 ± 5,9	Perrin and Curtis, 1980
Rat		Caecum	3,9	Scheeman and Gallaher, 1980
Rabbit	H	Stomach	8,2	
		Caecum	7,8	
		Colon	0,9	Elsden et al, 1946
Vole	O	Caecum	6,2 ± 1,4	McBee, 1970
Eritizon	O	Stomach	4,1	
		Caecum	6,0	Johnson and McBee, 1967
Hystrix	O	Stomach	9,9	
		Caecum	2,3	Authors own data.
Beaver	H	Caecum	6, 12	
		Upper colon	1,57	Hoover and Clarke, 1972
Hyrax	H	Stomach	3,9 ± 1,1	
		Sac	6,9 ± 2,2	
		Caeca	4,6 ± 1,3	Present study.
Horse	H	Stomach	2,9	
		Caecum	2,4	
		Upper colon	5,8	Elsden et al, 1946
Pig	O	Caecum	0,4	Farell and Johnson, 1970
Sheep	H	Rumen	14,2 ± 1,9	
		Hind-gut	4,9 ± 0,9	Hume, 1977
Ox	H	Rumen	15,0	
		Caecum	0,7	
		Rectum	0,3	Elsden et al, 1946
Buffalo	H	Rumen	16,0	
		Caecum	0,1	Van Gylswyk and Giesecke, 1973
Black Wildebeest	H	Rumen	11,8	Van Hoven and Boomker, 1981
		Caecum	0,9	

*H = herbivore
O = omnivore

CONCLUSIONS

In conclusion an attempt can now be made to answer the questions posed for this study.

1. The hyrax was found to be efficient in assimilating energy from its food. A mean value of 68,6% ME was obtained from a variety of rations, while a mean of 52,8% of the gross energy intake was necessary for basal maintenance.

2. The sac was the largest organ of the digestive tract and was not only a major site of digesta retention, but also provided the most important site of fermentation. The caeca were the second largest organ of the digestive tract and also the next most important area of digesta retention and fermentation. Together these two compartments are by far the most important digestive areas in the whole tract.

3. In the sac VFA levels of 2,7 - 4,3 mmoles / 100 ml / h were produced (comparable with that of the rumen), depending on the season or ration. This amounted to 193,3 and 228,5 kJ VFA energy per day in field and laboratory hyrax respectively.

   In the caeca VFA concentrations of between 2,6 - 3,3 mmoles / 100 ml / h were produced depending on the season and rations fed. In this case 172,5 and 160,5 kJ / day were produced. Although the sac was the most important fermenting chamber when high quality digestible rations were fed to hyrax, the caeca were more effective in attaining maximum digestion on lower quality high fibre rations.

4. An average of 72,7% of the BMR of field hyrax comprised of VFA. The sac and caeca produced 38,2% and 34,5% of the VFA respectively. However in the laboratory hyrax a mean of 55,9% of the BMR was produced as VFA. The sac and caeca produced 32,8% and 23,1% of the VFA respectively.

5. A mean of 4,3% of the basal metabolic energy requirements of field hyrax were lost as methane produced in the caeca only.
   In the laboratory hyrax a mean of 5,8% of the basal energy requirement or a mean of 5,5% of the digestible energy was lost as methane produced both in the sac and in the caeca.

6. An enlarged hindgut with two fermenting chambers developed in the hyrax to ensure efficient storage, digestion and absorption of digestive end-products. The sac has a peculiar rumen-like appearance while the two-horned caeca played almost an equivalent part in energy production.

CHAPTER V SUMMARY

The hyrax, *Procavia capensis*, smallest of the present day Paenungulata, has a mono-gastric digestive tract. It consists of a simple enzymatic stomach and complex hindgut. Terminal to the small intestine there is a sac, rumen-like in appearance, connected to a two-horned caeca via the proximal colon. The distal colon connects the caeca to the rectum from which faeces are excreted.

The digestive tract of hyrax has adapted to retain digesta for up to 44 hours by increasing the sac and caecal mass and volume, when food of a lower quality is utilized.

Acetic acid concentration increased in the sac and caeca when high fibre rations were fed, conversely butyric acid concentrations increased on a high protein ration.

In the sac of hyrax, mean VFA production rates of 3,8 mmoles / 100 ml / h were higher than the caeca 2,5 mmoles / 100 ml / h. When the NDF content of food was increased, lower VFA production rates were found in both the sac and caeca.

The fermentation rates of hyrax were high, up to 389,4 µmol gas / g DM / h and 185,6 µmol gas / g DM / h being produced in the sac and caeca respectively, when fed on a high protein, low fibre ration. Highest fermentation rates in field hyrax were found during the cool dry season when the protein of stomach content were high.

More VFA energy was produced per day in the field hyrax as more structural carbohydrates were available for fermentation. Means of 72,7% and 55,9% of the basal metabolic energy requirements of field and laboratory hyrax respectively, consisted of VFA, while an equivalent of 5,1% of the basal metabolic energy requirement of hyrax was lost as methane.

Protein digestibilities of food fed to laboratory hyrax was negatively correlated with lignin content in the diet.

Hyrax evolved as browsers to inhabit arid rocky environments and could even adapt to low quality food by enlarging their hindguts to ensure efficien storage, digestion and absorption of fermentation end-products.

OPSOMMING

Die dassie is die kleinste lid van die teenswoordige Paenungulata en is mono-gastries. Die kleinintestinum gaan oor in 'n rumen-agtige sak wat via die proksimale kolon met gepaarde seka verbind is. Die seka is verbind met die distale kolon en laastens die rektum vanwaar ekskresie van faeces geskied.

Die spysverteringskanaal van die dassie is aangepas om die deurgang van voedsel met 'n lae kwaliteit tot 44 uur te vertraag deurdat die sak en seka se massa toeneem en volume vergroot word.

Met 'n hoë veselinhoud in die dieet neem die asynsuur konsentrasie in die sak en seka toe, terwyl die bottersuur konsentrasie toeneem as dassies 'n proteinryke dieet gebruik.

Die gemiddelde produksietempo van vlugtige vetsure (VVS) in die sak van die dassie (3,8 mmol / 100 ml / uur) was hoër as in die seka (2,5 mmol / 100 ml / uur). Met 'n hoër suiwer neutrale veselinhoud, verlaag die VVS-produksie in beide die sak en seka.

Die fermentasietempo in die sak en seka van die dassie was so hoog as 398,4 µmol gas / g DM / uur en 185,6 µmol gas / g DM / uur onderskeidelik wanneer die diere 'n hoë protein - lae veseldieet gevoer is. By velddassies was die fermentasietempo die hoogste tydens die koel droë seisoen waar proteinanalise van die maaginhoud hoë waardes opgelewer het.

Velddassies het meer VVS-energie per dag geproduseer as laboratorium-dassies omdat meer strukturele koolhidrate in die velddieet teenwoordig was. VVS voorsien in gemiddeld 72,7% en 55,9% van die basale metaboliese energiebehoeftes van veld-en laboratoriumdassies onderskeidelik. 'n Hoeveelheid gelykstaande aan 5,1% van die BME geproduseer deur dassies gaan as metaan verlore.

Die proteinverteerbaarheid van voedsel gevoer aan laboratoriumdassies het negatief met die lignieninhoud daarvan gekorreleer.

Die dassie het as blaarvreter en bewoner van klipkoppies in droë omgewings ontwikkel, en kan selfs 'n lae kwaliteit voedsel benut deur die agterderm te vergroot en sodoende doeltreffend fermentasie-eindprodukte berg, verteer en absorbeer.

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