



Fibre utilization by Kalahari dwelling subterranean Damara mole-rats (*Cryptomys damarensis*) when fed their natural diet of gemsbok cucumber tubers (*Acanthosicyos naudinianus*)

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Kalahari dwelling Damara mole-rats (*Cryptomys damarensis*) naturally feed on a high fibre diet of underground gemsbok cucumber tubers, *Acanthosicyos naudinianus*. We investigated the degree of fibre utilization and fermentation on this diet by measuring caecal characteristics (namely temperature, pH and weight) and *in vitro* rates of gas and short chain fatty acid (SCFA) production in these underground dwelling hind-gut fermentors. Rectal temperatures ($33.8 \pm 0.6^\circ\text{C}$) were consistently higher than caecal temperatures ($33.3 \pm 0.6^\circ\text{C}$). Furthermore, a 0.8°C gradient of temperatures existed within the caecum, with the lowest temperature occurring in the *corpus caeci*. Both rates of gas production (4.74 ± 0.6 ml/g dry matter/hr) and SCFA production (266.80 ± 9.251 $\mu\text{mol}/\text{caecum per hr}$) were high, with proportionately more acetic acid produced than any other SCFA. Nevertheless, the initial concentrations of SCFAs present in the caecum were low (52 ± 17 mM) implying a rapid rate of absorption of these SCFAs. The high rates of fermentation provide a considerable amount of energy that would otherwise be trapped in fibre and thus unavailable to the animal. This highly efficient caecal fermentation enables the Damara mole-rat to maximally exploit the underground food resources in the arid-zone ecotope.

Key words: Mole-rats; Bathyergidae; *Cryptomys damarensis*; Higher fibre; Fibre fermentation; Caecal fermentation; Caecal temperature; Short chain fatty acids.

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Introduction

The Damara mole-rat (*Cryptomys damarensis*) inhabits the semi-arid and arid zones of south western Africa (De Graaff, 1981). These subterranean dwelling mam-

mals feed exclusively on the underground portions of plants (Jarvis and Bennett, 1991). Resource characteristics in the arid habitat of *C. damarensis* are such that there is a marked predominance of one geophyte species in any particular area (Lovegrove and Knight-Eloff, 1988). The Damara mole-rat is abundant in areas where the dominant geophyte is the gemsbok cucumber (*Acanthosicyos naudinianus*). Despite

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Table 1. Nutrient composition of *Acanthosicyos naidinianus* tubers

Water content (% wet weight)	80.00
Energy content (kJ/g dry weight)	17.73 \pm 0.05
Neutral detergent fibre content (% dry mass)	60.4
Protein content (% dry mass)	7.0

the fact that this tuber has low density random distribution (Lovegrove and Knight-Eloff, 1988), where present Damara mole-rats feed exclusively on it. The gemsbok cucumber is considered a poor quality diet, with both a low protein and high fibre content (Table 1), similar to that of poor quality grasses (Yahav and Choshniak, 1990) and that usually consumed by specialized ruminants (van Soest, 1982). Utilization of poor quality diets requires specific digestive processes depending primarily on the presence of micro-organisms in specialized gastrointestinal compartments. Most of the energy produced by plants is stored in structural polymers comprising plant cell walls and plant fibres, yet herbivorous mammals lack the necessary enzymes to tap this energy source. In most rodents, fermentation occurs in the caecum (McBee, 1977). Here, short chain fatty acids (SCFAs, namely acetic, propionic and butyric acids) are produced, which serve as important energy sources to the host animal (McBee, 1977; Rechkemmer *et al.*, 1988). The remaining by-products of fermentation include gaseous waste products (e.g. CO₂, H₂ and CH₄). The quantity and proportions of both SCFAs and gaseous waste products are useful indicators of fermentation function and efficiency (El-Din and El-Shazley, 1969).

In ruminants, fermentation is an exergonic process that results in a fermentation chamber 2–4°C warmer than the abdominal surrounds (van Soest, 1982). Little is known about the microclimatic conditions within the fermentation chamber of hindgut fermenters. In the only study to date in which caecal temperatures have been measured, these were found to be lower than rectal or core temperature (Yahav and Buffenstein, 1992a). We speculate that Damara mole-rats, feeding exclusively on gemsbok cucumbers, must also employ fermentative digestive processes if they are to exploit this scarce food resource. In this

study we examine fermentation function, efficiency and caecal microclimatic conditions in freshly caught Damara mole-rats feeding on their preferred natural diet.

Materials and Methods

Animals

Seven mature animals of both sexes, average mass 93.1 \pm 13.5 g, were collected in the Kalahari desert (Hotazel, North W. Cape). After capture, animals were euthanized with Euthenase (200 mg sodium pentobarbitone; 0.01 ml/g body mass; Centaur Laboratory, South Africa) and immediately thereafter were assessed for fermentation capacity and caecal characteristics.

Dietary measurements

The gemsbok cucumber tubers were analysed for their moisture, energy, neutral detergent fibre and protein content following methods described by Davies (1988).

Caecal measurements

Rectal temperature (T_r) and caecal temperature (T_c) were measured simultaneously using calibrated (within 0.1°C) copper constantan thermocouples and an electronic digital thermometer (Bailey). Caecal thermocouples were placed in hypodermic needles (21 gauge) and inserted through a small abdominal incision 10–15 mm into the caecum.

Temperature measurements were also made in the anatomically distinct regions of the caecum after the abdominal cavity was opened and the caecum exposed. All caecal measurements were compared with simultaneous rectal recordings.

The pH was measured in the caecum. The caecum was then separated from the rest of the gastrointestinal tract and weighed (to 0.001 g). Thereafter, the caecal contents were mixed to obtain uniform aliquots. These were then used to assess fermentative efficiency.

The percentage dry mass of caecal content was determined from weighed aliquots of caecal contents which were dried at 100°C to constant mass.

Table 2. Caecal characteristics of the Damara mole-rat ($N = 9$)

Caecum wet weight (% body weight)	6.34 ± 2.16
Caecum weight (g DM)	1.02 ± 0.15
Dry matter (%)	32.06 ± 1.93
pH	6.65 ± 0.12
Rectal temperature ($^{\circ}\text{C}$)	33.8 ± 0.6
Caecal temperature ($^{\circ}\text{C}$)	33.3 ± 0.6
Gas production (ml/g/hr @ STP)	4.7 ± 0.7

Data are expressed as mean \pm SE.

Fermentation capacity

Uniform aliquots of approximately 0.3 g were used in fermentation studies. Fermentative capacity was determined by measuring rates of gas production and SCFA production following the methods described by Carrol and Hungate (1954). Weighed caecal samples were placed in a 25 ml Warburg flask and the air therein was rapidly displaced with CO_2 . The manometric apparatus was kept open for 5 min, allowing the displacement of CO_2 by the gases produced during fermentation. Thereafter, the flasks were sealed and incubated at 33°C , the caecal temperature of the animals (Yahav and Buffenstein, 1992b). The volume of gas produced in the flasks was monitored every 5 min for 1 hr, using standard manometric techniques. The rate of gas production at the time the caecum was excised was extrapolated from the exponential relationship between gas production and time, in compliance with the methods of Carrol and Hungate (1954).

The rate of SCFA production was determined from the difference in SCFA concentration in caecal samples taken before and after the completion of gas production measurements (McBee, 1970). Known amounts of sodium hydroxide were added to each sample. Samples were then stored at -20°C for later analysis. The concentration of SCFAs was determined using gas-liquid chromatography (Carlo Erba Strumentazione 4200, Searle Instruments, Johannesburg) using pivalic acid as the internal standard (Davies, 1988).

Statistical analyses

All results are expressed as means \pm standard deviations. Statistical analyses included analysis of variance and linear regression analysis, in accordance with the methods described by Zar (1974).

Results

Caecal characteristics

Gemsbok cucumber tubers were analysed for their moisture, energy, NDF and protein content (Table 1).

The full caecum weighed more than any other gastro-intestinal compartment. It was comparatively large and contributed $6.3 \pm 2.2\%$ to total body weight. Dry matter content was high and the pH within the caecum was suitable for microbial fermentation (Table 2).

Caecal temperature was consistently ($P < 0.05$) lower than that of rectal temperature (Table 2). A temperature gradient of 0.8°C existed within the caecum. Given the considerable variability, there was no significant difference in the temperatures of the three caecal regions measured (Table 3).

Fermentation efficiency

Acetic, propionic and *n*-butyric acids were present in measurable amounts in caecal liquor. Acetic acid was the predominant SCFA contributing 59% to the total SCFA concentration (Fig. 1). The rate of total SCFA production was high $267 \pm 93 \mu\text{mol}/\text{caecum per hr}$ with rates of acetic acid production exceeding those of propionic and *n*-butyric acids (Fig. 2).

High rates of both SCFA production and gas production (Table 2) indicate that fermentation did occur in the caecum and that it was an efficient process.

Discussion

The Damara mole-rat feeds exclusively on a plant with poor nutritional quality (Table 1). Stomach content studies by Bennett and Jarvis (in preparation) confirm the exclusiveness of the diet, yet show that the digestive efficiency is comparatively high

Table 3. The range of temperatures in three anatomically distinct regions of the caecum in the Damara mole-rat ($N = 5$; $\bar{X} \pm \text{SE}$)

Caecal region ($^{\circ}\text{C}$)	Temperature ($^{\circ}\text{C}$)
Ampulla caeci	30.4 ± 0.6
Corpus caeci	30.1 ± 0.8
Apex caeci	30.5 ± 0.8
Gradient with caecum	0.8 ± 0.1
Δ Corpus caeci–Apex caeci	0.5 ± 0.3

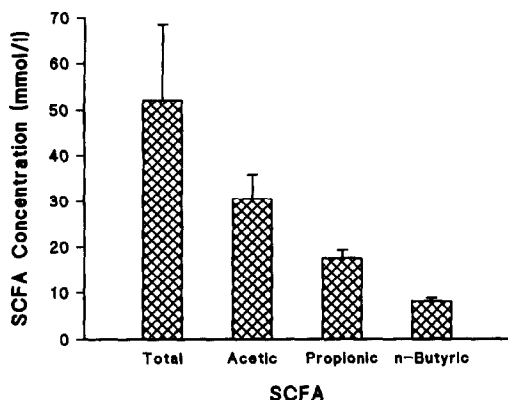


Fig. 1. Initial short-chain fatty acid (SCFA) concentration in the caecum of the Damara mole-rat (*Cryptomys damarensis*) when fed its natural diet of gembok cucumbers (*Acanthosicyos naudinianus*).

(52.5%), if one takes into account the fibre content (van Soest, 1982). The relatively high digestive efficiency on this diet enables maximal exploitation of the available food and may be facilitated by fermentative processes in the hindgut.

Damara mole-rats have a relatively large caecum compared with other rodents (Perrin and Curtis, 1980). This finding, together with the high % dry matter of the caecal liquor, conforms with the prediction of Silby (1981) that animals eating poorer quality diets have larger digestive chambers, facilitating extended food retention and effective fibre degradation.

Damara mole-rats show similar caecal/body mass ratios, pH and temperature profiles (Table 2) to the naked mole-rat (*Heterocephalus glaber*) another Bathyergid mole-rat species (Buffenstein and Yahav, 1991). This might indicate a genetic component to digestion of fibre or alternately may reflect their very similar habits and habitat.

Temperatures in the caecum of both the Damara and naked mole-rat species (Yahav and Buffenstein, 1992a) are lower than those reported for foregut fermenters (Clark, 1977). Both mole-rat species show a temperature gradient within the caecum, although the gradient in the Damara mole-rat is not as pronounced. The regions of lowest temperatures within the caecum in the two species are, however, different: the lowest caecal temperature in the naked mole-rat is located in the apex caeci, whereas in the Damara mole-rat, the tem-

peratures within the three anatomically distinct regions are similar (Table 3). In all cases, caecal temperatures of Damara mole-rats, like that of naked mole-rats (Yahav and Buffenstein, 1992a) were lower than rectal temperatures (Table 2). We do not know whether all hindgut fermenters have lower temperatures within the caecum compared to the core or whether this feature is unique to arid-adapted subterranean dwelling mammals. In mole-rats, the caecum may act as a heat sink. This would be most advantageous in an underground milieu, where heat dissipation via convection, evaporation and radiation is impeded (McNab, 1979) and where heat production by animals during burrow excavations and foraging is already high (Lovegrove, 1989).

Like all other herbivorous rodents, the Damara mole-rat has a capacious vat maintained at a favourable pH (Table 2) for microbial fermentation of fibre (McBee, 1977; Parra, 1978). Fibre fermentation in the caecum was evident as both gases and SCFAs were produced in the caecal liquor (Table 2; Figs 1 and 2). Gas production was comparatively high, being 2.6 times greater than that in the caecum of naked mole-rats fed a moderately high (NDF 15.6%) fibre diet (Buffenstein and Yahav, 1991), and also more than twice that of both fat jirds and levant voles (Yahav and Choshniak, 1990). High rates of gas production may indicate superior efficiency of fermentation by the Damara mole-rat when fed its natural diet.

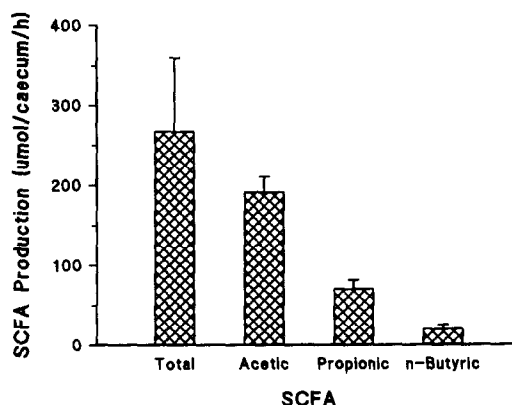


Fig. 2. Rates of short-chain fatty acid (SCFA) production in the caecum of the Damara mole-rat (*Cryptomys damarensis*) when fed its natural diet of gembok cucumbers (*Acanthosicyos naudinianus*).

The SCFAs produced during microbial fibre fermentation are an important source of energy to the host, for these are rapidly absorbed into the bloodstream and used in the citric acid cycle to supply energy to the herbivore (Parra, 1978). Like all other herbivorous mammals, proportionately more acetic acid was present than other volatile fatty acids (van Soest, 1982; Engelhardt *et al.*, 1983). The molar proportion of acetic:propionic:butyric acids in this *in vitro* study (57:27:15) differed from that commonly occurring in hindgut fermenters (70:20:10). These differences may be attributed to differences in dietary carbohydrate content (van Soest, 1982; Foley *et al.*, 1989).

Most mammals maintain hindgut concentrations of SCFAs at approximately 100 mM, irrespective of the diet or digestive system (Engelhardt and Rechkemmer, 1983). The SCFA concentration in the caecum of the Damara mole-rat (55 ± 17 mM) was almost half this, but similar to that shown in arboreal marsupials (Foley *et al.*, 1989), naked mole-rats (Buffenstein and Yahav, 1991), rabbits (Hoover and Heitman, 1972), fat jirds and levant voles (Yahav and Choshniak, 1990). Foley *et al.* (1989) suggested that the SCFA concentration at any one time reflects the balance between rates of production and absorption. Given the high rates of gas (Table 2) and SCFA production (Fig. 2) the comparatively low SCFA concentrations, when compared to most other mammals, suggest that these SCFAs, upon production, are rapidly absorbed from the hindgut. The SCFAs absorbed during passage through the caecum and large intestine, serve as an important energy source (Rechkemmer *et al.*, 1988). Rates of SCFA production in the Damara mole-rat are more than twice that produced by the naked mole-rat when fed a diet moderately high in fibre, but are similar to the very rapid fermentation rates in the caecum of the howler monkey (*Alouatta palliata*) when fed a high sugar diet of fruit pulp (Milton and McBee, 1983). These high rates of production and absorption would liberate a considerable amount of energy otherwise trapped in fibre and thus unavailable.

In conclusion, it appears that Damara mole-rats, rather than compete for limited

higher quality diets, have modified gut function to thrive on a less popular, more readily available poor quality food source. Highly efficient caecal fermentation facilitates adequate energy and nutrient intake and therefore enables the Damara mole-rat to maximally exploit the underground food resources in the arid-zone ecotope.

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References

- Buffenstein R. and Yahav S. (1991) The effect of diet on microfaunal population and function in the caecum of a subterranean naked mole-rat, *Heterocephalus glaber*. *Brit. J. Nutr.* **65**, 249–258.
- Carroll E. J. and Hungate R. E. (1954) The magnitude of microbial fermentation in bovine rumen. *Appl. Microbiol.* **2**, 205–214.
- Clark R. T. J. (1977) Gut micro-organisms. In *Microbial Ecology of the Gut* (Edited by Clark R. T. J. and Bauchop T.), pp. 36–71. Academic Press, New York.
- Davies J. (1988) *Laboratory Methods*. Irene, Transvaal: Animal Nutrition Subdirectorate Animal and Dairy Science Research Institute.
- De Graaff G. (1981) *The Rodents of Southern Africa*, pp. 267. Butterworths, Durban S.A.
- El-Din M. Z. and El-Shazly K. (1969) Evaluation of a method of measuring fermentation rates and net growth of rumen micro-organisms. *Appl. Microbiol.* **17**, 801–804.
- Engelhardt W. V. and Rechkemmer G. (1983) The physiological effects of short-chain fatty acids in the hindgut. In *Fibre in Human and Animal Nutrition* (Edited by Wallace G. and Bell L.), pp. 149–155. R. Soc. N.Z. Bull. **20**.
- Foley W. J., Hume I. D. and Cork S. J. (1989) Fermentation in the hindgut of the Greater glider (*Petauroides volans*) and the Brushtail possum (*Trichosurus vulpecula*)—two arboreal folivores. *Physiol. Zool.* **62**, 1126–1143.
- Hoover W. H. and Heitmann R. N. (1972) Effects of dietary fibre levels on weight gain, caecal volume and volatile fatty acid production in rabbits. *J. Nutr.* **102**, 375–380.
- Jarvis J. U. M. and Bennett N. C. (1991) Ecology and behaviour of the family Bathyergidae. In *Biology of the Naked Mole-rat* (Edited by Sherman P. W.,

- Jarvis J. U. M. and Alexander R. D.), pp. 66–96. Princeton University Press, Princeton, NJ.
- Lovegrove B. G. (1989) The cost of burrowing by the social mole-rat (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. *Physiol. Zool.* **62**, 449–469.
- Lovegrove B. G. and Knight-Eloff A. (1988) Soil and burrow temperatures, and the resource characteristics of the social mole-rat *Cryptomys damarensis* (Bathyergidae) in the Kalahari Desert. *J. Zool. Lond.* **216**, 403–416.
- McBee R. H. (1970) Metabolic contributions of the caecal flora. *Am. J. clin. Nutr.* **23**, 1514–1518.
- McBee R. H. (1977) Fermentation in the hindgut. In *Microbial Ecology of the Gut* (Edited by Clarke R. T. J. and Bauchop T.), pp. 185–222. Academic Press, New York.
- McNab B. K. (1979) The influence of body size on the energetics and distribution of fossorial and burrowing animals. *Ecology* **60**, 1010–1021.
- Milton K. and McBee R. H. (1983) Rates of fermentative digestion in the howler monkey, *Alouatta palliata* (Primates: Cebioidea). *Comp. Biochem. Physiol.* **74A**, 29–32.
- Parra R. (1978) Comparison of foregut and hindgut fermentation in herbivores. In *The Ecology of Arboreal Folivores* (Edited by Montgomery G. G.), pp. 205–229. Smithsonian Institution Press, Washington DC.
- Perrin M. R. and Curtis B. A. (1980) Comparative morphology of the digestive system of 19 species of South African myomorph rodents in relation to diet evolution. *S. Afr. J. Zool.* **15**, 22–33.
- Rechkemmer G., Ronnau K. and Engelhardt W. V. (1988) Fermentation of polysaccharides and absorption of short chain fatty acids in the mammalian hindgut. *Comp. Biochem. Physiol.* **90A**, 563–568.
- Silby R. M. (1981) Strategies in digestion and defecation. In *Physiological Ecology, an Evolutionary Approach to Resource Use* (Edited by Townsend C. R. and Calow P.), pp. 109–139. Sinauer Associates, Sunderland, MA.
- Van Soest P. J. (1982) Gastrointestinal fermentation. In *Nutritional Ecology of the Ruminant* (Edited by Van Soest P. J.), pp. 152–229. O. and B. Books, Corvallis, OR.
- Yahav S. and Buffenstein R. (1992a) Caecal function provides the energy of fermentation without liberating heat in the poikilothermic mammal *Heterocephalus glaber*. *J. comp. Physiol. B* **162**, 216–218.
- Yahav S. and Buffenstein R. (1992b) The effect of temperature on caecal fermentation processes in ectothermic mammal, *Heterocephalus glaber*. *J. thermal Biol.* **16**, 345–349.
- Yahav S. and Choshniak I. (1990) Response of the digestive tract to low quality dry food in the fat jird (*Meriones crassus*) and in the levant vole (*Microtus guentheri*). *J. Arid Envir.* **19**, 209–215.
- Zar J. H. (1974) *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.