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The effect of different diets on the amount of organic acid produced in the digestive tract of *Mystromys albicaudatus*

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The white-tailed rat *Mystromys albicaudatus* (A. Smith, 1834) has a sacculated bilocular hemiglandular stomach. Its forestomach resembles a rumen, in that it has papillae and a high density of bacteria. This suggests that the forestomach of the white-tailed rat may be functionally similar to a rumen. Although the fermentation of fibre is very limited in the digestive tract of the white-tailed rat, the determination of total foregut fermentation relative to caecal fermentation was essential since ingested soluble carbohydrates may also be fermented by the forestomach bacteria. The present study investigated the effects of different diets (varying in proximate composition) on the pH, volatile fatty acid and lactic acid production for the various regions of the gut. The results indicate that *M. albicaudatus* is essentially a hindgut fermenter.

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Introduction

The white-tailed rat *Mystromys albicaudatus* (A. Smith, 1834), has a bilocular hemiglandular stomach (Maddock and Perrin 1981). The rich bacterial flora of the forestomach (corpus) is separated from the glandular stomach (antrum) by a nonglandular chamber (pregastric pouch) and a bordering fold (grenzfalte) of tissue (Maddock and Perrin 1981). The high density of corpal bacteria, stomach sacculations and simple caecum of the white-tailed rat suggest that it is the forestomach that is important in microbial fermentation processes (Maddock 1981). Superficially the forestomach resembles a rumen since it has papillae and a high density of bacteria. However, it differs from the rumen in that the papillae are not absorptive and the bacteria are associated with the epithelium while the bacteria in ruminants are mostly free-living. It appears that the forestomach of the white-tailed rat is in part functionally similar to the rumen.

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Although the fermentation of fibre is very limited in the digestive tract of the white-tailed rat (Mahida 1992), the determination of total foregut fermentation relative to caecal fermentation was essential since ingested soluble carbohydrates may also be fermented by the corpal bacteria.

The pH of various regions of the gut of *M. albicaudatus* was measured because microbial fermentation is most effective at a pH close to neutrality, and the pH of a given region of the gut reflects the suitability of that region for microbial fermentation.

In general, with acclimated animals, the higher the proportion of readily fermentable carbohydrates in the diet the greater the lactic acid concentration (Mackie 1977), while volatile fatty acids are the main end products of bacterial carbohydrate fermentation, e.g. cellulose. The present study investigated the effects of different diets (varying in proximate composition) on the pH, volatile fatty acid and lactic acid production for the various regions of the gut. The aim was to determine whether the forestomach of the white-tailed rat was to some extent functionally similar to a rumen.

Materials and methods

Thirty six adult white-tailed rats were placed in experimental cages (40 × 24 × 12 cm). They were randomly separated into four groups irrespective of age, sex or weight. The groups were maintained on different diets, either rat pellets, rabbit pellets crushed maize or lucerne for three weeks (except those on the lucerne diet which were fed lucerne for only 24 hours) before commencement of the experiment. The white-tailed rat survived poorly on lucerne.

Three rats from each group were starved for 15 hours overnight so as to monitor the sequential changes along the digestive tract in volatile fatty acid and lactic acid after feeding. The rats were then given their usual feed for two hours, after which the food was removed. Immediately after the food was removed, the first rat was killed by ether anaesthesia. Two hours later, the second rat was killed, and after a furthur two hours the third rat was sacrificed.

Immediately after killing the animal, the entire gut was dissected out. The forestomach, hind-stomach, small intestine, caecum and the proximal portion of the large intestine were separated from each other, and the weight of each part and its contents recorded. Each section was cut open and the pH of the contents was measured using a digital pH meter (Model TC pH 800). The contents were removed and the empty part was weighed.

The contents of each part of the gut was placed in a centrifuge tube; 1 ml (or a proportionate volume) of 25% metaphosphoric acid was added to 5 ml of gut content. After 5 minutes the tubes were centrifuged at 8000 rpm at 20°C using a Dupont/Sorvall RC-5 superspeed refrigerated centrifuge. The supernatant was then centrifuged at 20 000 rpm at 4°C for 20 minutes using the same centrifuge. 1 µl of the supernatant was analysed by injection into a Hewlett-Packard 5709A Series gas chromatograph with a flame ionization detector and a 2 meter glass column with an internal diameter of 2 mm. The glass column was packed with 80/120 carbopack B/ 4% carbowax 20M. The flow rate of the carrier nitrogen gas was 24 ml/min. The column temperature was 180°C and the detector temperature 200°C. The instrument was calibrated using 100 ppm of acetic, propionic, butyric, isobutyric, valeric, isovaleric acid and 200 ppm lactic acid in 0.03M oxalic acid in water. The volatile fatty acid concentration of the supernatant was determined using a Hewlett-Packard 3390A Reporting Integrator. The volume of the supernatant was also measured using a 100 µl Hamilton microsyringe to calculate the

total volatile fatty acids and lactic acid content. The above procedure was done in triplicate for each group.

Statistical analyses were not undertaken as the sample sizes were too small. Mean and standard deviation were recorded for pH, and volatile fatty acids and lactic acid content.

Complete proximate analysis (Allen *et al.* 1974) was undertaken for each feed. Moisture content was determined by drying samples in an oven at 70°C; further analyses were done on the dried samples. Energy content was determined using an adiabatic bomb calorimeter. Crude protein content was determined by the Kjeldahl (Nitrogen × 6.25) method, and crude fat content determined by ether extraction in a Soxhlet apparatus. The crude fibre content was determined by the method of Goering and Van Soest (1970), and the ash content was determined using a muffle furnace (550°C for 12 hours). The soluble carbohydrate component was calculated.

Results

The fibre content was lowest for the maize feed (1.60%) and highest in lucerne (33.08%), while the soluble carbohydrate was highest in maize (84.58%) and lowest in lucerne (45.64%) (Table 1).

Table 1. Mean proximate composition of experimental diets of rat pellets, rabbit pellets, crushed maize and lucerne.

Feed	Rat pellets	Rabbit pellets	Maize	Lucerne
Water (%)	6.45	6.75	10.68	7.00
Fat (%)	5.76	5.42	4.14	1.89
Fibre (%)	5.32	8.97	1.60	33.08
Protein (%)	20.38	16.61	8.39	10.47
Carbohydrate (%)	61.41	60.20	84.58	45.64
Energy (kj/g)	19.29	17.35	19.12	19.30

The pH values in the same parts of the gut of *M. albicaudatus*, maintained on different diets, were similar (Table 2).

The amount of volatile fatty acids (VFA) and lactic acid produced per gram of digesta by *M. albicaudatus* feeding on the different diets was very small (Table 3). In all cases the forestomach (0.8–15 μmol/g) and caecum (4–54 μmol/g) contained most of the volatile fatty acids, with the caecum at all times containing the greatest amounts. The highest lactic acid content (38.8 μmol/g) was recorded in the forestomach after two hours on a maize diet (soluble carbohydrate = 84.58%).

Discussion

Utilization of maize

Because maize feed had a very low fibre content, the total amount of VFA per gram of digesta in the forestomach of the white-tailed rat was low, but reached a maximum value within two hours of ingestion. The very high soluble carbohydrate

Table 2. Mean (± SD) pH values of various parts of the digestive tract of *M. albicaudatus* (n = 3), maintained on different feeds.

Feed	Region				
	Forestomach	Hindstomach	Small intestine	Caecum	Large intestine
			After two hours		
Rat pellets	5.72 ± 0.25	1.49 ± 0.12	7.97 ± 0.01	8.05 ± 1.34	7.15 ± 0.16
Rabbit pellets	6.67 ± 0.15	1.45 ± 0.04	7.99 ± 0.04	7.31 ± 0.25	7.25 ± 0.15
Maize	5.95 ± 1.01	1.45 ± 0.55	7.68 ± 0.23	7.27 ± 0.94	6.70 ± 0.33
Lucerne	6.27 ± 0.44	1.26 ± 0.13	7.53 ± 0.54	7.30 ± 0.96	7.11 ± 0.36
			After four hours		
Rat pellets	4.67 ± 0.17	1.28 ± 0.18	8.10 ± 0.15	6.67 ± 0.41	6.66 ± 0.15
Rabbit pellets	4.38 ± 0.38	1.08 ± 0.11	7.80 ± 0.54	7.00 ± 0.28	7.65 ± 0.39
Maize	4.08 ± 1.21	1.33 ± 0.38	7.05 ± 0.33	7.48 ± 0.19	7.08 ± 0.41
Lucerne	4.46 ± 0.36	1.15 ± 0.15	7.88 ± 0.71	7.05 ± 0.48	7.11 ± 0.28
			After six hours		
Rat pellets	4.86 ± 0.16	1.15 ± 0.10	7.71 ± 0.15	6.36 ± 0.11	7.13 ± 0.18
Rabbit pellets	4.66 ± 0.10	1.42 ± 0.21	7.14 ± 0.14	6.82 ± 0.35	7.51 ± 0.29
Maize	3.50 ± 0.18	1.60 ± 0.22	7.28 ± 0.18	7.04 ± 0.40	7.10 ± 0.32
Lucerne	4.96 ± 0.16	1.30 ± 0.28	7.15 ± 0.18	6.96 ± 0.34	7.25 ± 0.58

content of maize resulted in the high lactic acid content in the forestomach, which caused a marked decrease in corpal pH (relative to subjects fed diets with lower soluble carbohydrate content).

The pH in the glandular stomach was too low for fibre fermentation to occur. Cellulolytic bacteria require a pH close to neutrality to survive in a gut microhabitat (Mackie 1977). VFA and lactic acid cannot be absorbed through the walls of the forestomach of the white-tailed rat but pass to the glandular stomach for absorption (Maddock 1981). Therefore, the VFA and lactic acid recorded in the glandular stomach included those derived from the forestomach.

Throughout the six hour monitoring period, the pH in the small intestine was above neutrality, providing an ideal environment for bacterial fermentation. Relative to the forestomach, the VFA and lactic acid content was lower in the small intestine. Microbes cannot thrive in this region since the retention time of the digesta is shorter than the doubling time of the bacteria (Savage 1977).

The caecum is a blind ending sac and the digesta is retained for prolonged periods of time. There is frequent reference to caecal function being analogous to ruminal function (McBee 1971). Both organs have large microbial populations, but the substrates differ, since few proteins and no free amino acids or sugars are introduced into the caecum (Johnson and McBee 1967, McBee 1970). The total VFA per gram of digesta in the caecum was almost three times greater than that produced in the forestomach, indicating that *M. albicaudatus* is a hindgut fibre fermenter.

Table 3. Mean (± SD) of total volatile fatty acid (VFA) and lactic acid (μmol/g of digesta) along the digestive tract of *M. albicaudatus* (n = 3) fed different diets.

	Region				
	Forestomach	Hindstomach	Small intestine	Caecum	Large intestine
Rat pellets					
After two hours					
VFA	15 ± 13	0.2 ± 0.0	1.4 ± 1.4	12 ± 7.5	2.7 ± 1.6
Lactic	28 ± 4.0	0.8 ± 0.1	1.3 ± 0.8	1.0 ± 0.7	0.5 ± 0.0
After four hours					
VFA	11 ± 7.9	1.6 ± 1.5	1.5 ± 0.5	26 ± 9.1	1.1 ± 0.2
Lactic	17 ± 4.0	6.2 ± 5.6	1.1 ± 0.7	5.5 ± 3.4	0.5 ± 0.4
After six hours					
VFA	2.3 ± 0.3	2.7 ± 0.4	3.2 ± 0.9	54 ± 2.5	1.7 ± 0.6
Lactic	6.0 ± 2.5	22 ± 3.8	6.2 ± 3.1	5.6 ± 1.9	0.1 ± 0.0
Rabbit pellets					
After two hours					
VFA	2.1 ± 0.9	0.5 ± 0.2	1.7 ± 0.8	10 ± 4.5	0.2 ± 0.0
Lactic	2.0 ± 1.3	1.1 ± 0.2	1.2 ± 0.3	0.7 ± 0.4	0.2 ± 0.0
After four hours					
VFA	1.6 ± 0.1	0.1 ± 0.0	0.4 ± 0.1	17 ± 6.4	1.0 ± 0.1
Lactic	1.2 ± 0.2	0.8 ± 0.1	0.7 ± 0.1	1.4 ± 0.7	0.2 ± 0.1
After six hours					
VFA	1.0 ± 0.0	0.1 ± 0.0	1.5 ± 0.3	33 ± 3.6	3.4 ± 0.5
Lactic	1.6 ± 0.2	1.0 ± 0.2	4.3 ± 0.0	1.5 ± 0.6	0.8 ± 0.2
Maize					
After two hours					
VFA	15 ± 5.9	0.1 ± 0.0	1.9 ± 0.9	9.2 ± 1.8	0.8 ± 0.6
Lactic	39 ± 9.6	0.5 ± 0.2	2.5 ± 1.7	2.0 ± 1.6	0.2 ± 0.1
After four hours					
VFA	1.0 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	4.0 ± 0.1	1.5 ± 0.3
Lactic	4.6 ± 0.2	18 ± 7.4	0.5 ± 0.0	2.6 ± 0.3	0.2 ± 0.0
After six hours					
VFA	0.8 ± 0.1	0.2 ± 0.0	1.8 ± 0.0	34 ± 6.5	4.9 ± 1.0
Lactic	9.9 ± 3.5	14 ± 3.4	5.5 ± 0.2	3.1 ± 0.0	0.8 ± 0.1
Lucerne					
After two hours					
VFA	3.2 ± 0.5	–	0.9 ± 0.2	5.7 ± 0.2	0.4 ± 0.0
Lactic	6.5 ± 0.8	0.1 ± 0.0	1.5 ± 0.3	0.2 ± 0.0	0.2 ± 0.0
After four hours					
VFA	1.1 ± 0.1	–	0.8 ± 0.0	5.7 ± 0.5	1.6 ± 0.2
Lactic	1.0 ± 0.0	–	0.8 ± 0.1	0.5 ± 0.1	0.5 ± 0.2
After six hours					
VFA	1.8 ± 0.2	0.5 ± 0.2	1.6 ± 0.6	15 ± 1.2	1.7 ± 0.9
Lactic	1.5 ± 0.0	0.2 ± 0.1	1.0 ± 0.3	2.0 ± 0.2	0.1 ± 0.0

Since soluble carbohydrates were at very low concentrations when the digesta reached the caecum, the lactic acid content was very low relative to its activity in the forestomach. Although the pH in the proximal colon was close to neutrality very few VFA and lactic acid were produced, probably due to the low fibre content of the maize feed, and the low soluble carbohydrate concentration of the digesta in the large intestine.

Utilization of rat pellets

The higher fibre content of rat pellets than maize resulted in the production of more VFA in the forestomach. Lactic acid was also produced in large amounts because of the high soluble carbohydrate content of the diet. Interestingly, although a higher VFA and lactic acid content was recorded the forestomach of the white-tailed rat fed rat pellets, the pH was higher (4 and 6 hours after ingestion) than those obtained with the maize feed. This is probably due to the buffering capacity of the bacterial amylase and host salivary amylase.

Conditions in the glandular stomach were similar to those reported for the subjects fed maize. The small and large intestine contained few VFA. The total VFA per gram of digesta in the caecum were three times greater than in the forestomach, indicating that the caecum is more important in fibre fermentation.

Utilization of rabbit pellets

The overall results obtained with rabbit pellets are similar to that obtained with the maize and rat pellet diets. The caecum, however, contained fifteen times more VFA than the forestomach (fibre content of diet = 9%), corroborating that the white-tailed rat is a hindgut fibre fermenter.

Utilization of lucerne

M. albicaudatus lost weight rapidly and died within a few days when maintained on lucerne (Mahida 1992). Only a small quantity of the feed was ingested, probably due to the high fibre content and a possible antibiotic effect of the lucerne. The reduction in bacterial density (Mahida 1992) and the small quantity of food ingested limited fermentation activity. The VFA content of the caecum was still, however, greater than in the forestomach.

In conclusion, *M. albicaudatus* is essentially a hindgut fermenter and the forestomach has not evolved as a functional rumen. This does not support the theory proposed by Vorontsov (1962) that the complex stomach of rodents suggests ruminant-like pregastric fermentation.

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